SEASONAL PATTERNS IN THE GROWTH OF THE GIANT KELP, *MACROCYSTIS PYRIFERA*

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To all these people and many others I am grateful. Thank you all very much.

ABSTRACT

Field surveys revealed seasonal growth changes in the Giant Kelp, Macrocystis pyrifera. Frond counts were used to measure average sporophyte size in the study bed and to follow vegetative growth of a typical plant for about sixteen months. Storm induced wave motions and sea urchin grazing were primary causes of whole plant losses.

The importance of fish grazing on kelp was estimated during field surveys. Average damage varied from light to moderate during the study period.

Kelp consumption rates by Opaleye Perch, Girella nigricans, were measured in aquarium experiments. Preference for specific kelp tissues was established.

Mathematical relationships between kelp growth and environmental conditions were established by multiple linear regression analysis. Regression equations modeled growth patterns observed in field surveys. Average frond number was expressed as a function of sunlight, water temperature, fish grazing, and upwelling index.

A regression model was used to hindcast kelp growth fluctuations for conditions at Point Loma, San Diego County, from 1950 to 1969.

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CHAPTER 1

INTRODUCTION

A. Scope and Objectives

Macrocystis pyrifera lives in a fluid environment. Its natural history is characterized by a flexibility needed to cope with environmental variation. Living conditions change continually and rapidly both in time and space. Water temperature where kelp is attached to the sea floor may differ widely from surface temperatures where kelp canopies float. Light intensity varies as the sun passes across the sky and as changing atmospheric conditions absorb and reflect incoming energy. Shear stresses from waves build and relax repeatedly. Each of these changing environmental conditions affects life processes of *Macrocystis*. Some effects are momentary, others may span several years.

Most quantitative research on kelp development has focused on separate environmental variables. However, relationships between the alga and a single parameter dominate for only short periods of time in nature. The need to understand isolated functions is unquestioned. Nevertheless, we must also relate parameters one to another and to the long term patterns observed in nature.

My research and analysis deal with longer term variations. Presumably, health of a Macrocystis population can be quantitatively related to the overall complex of changing environmental conditions. All factors influencing kelp health cannot be identified nor can we hope to analyze finer details regarding interactions of these plants and their surroundings. My approach involved monitoring growth and health of a kelp population for more than a year. Data were then quantitatively related to a set of corresponding environmental factors assumed to be most influential.

A kelp bed at Abalone Cove, Palos Verdes, in Los Angeles County had been successfully restored in recent years. This provided a convenient site for my sixteen month study. I studied water temperature, light, upwelling, wave motion, and grazing as likely major parameters determining natural patterns of kelp growth. Kelp condition was quantitatively related to environmental parameters by multiple linear regression techniques.

Chapter II describes the sixteen month field study in Abalone Cove. Kelp growth data gathered during this phase were the dependent variable for the regression analyses discussed later. Individual plant survivability is also discussed in the second chapter. Field studies included

investigation of fish grazing evidenced by kelp tissue losses.

Chapter III discusses laboratory experiments on fish grazing. Daily damage by each grazing fish to Macrocystis was measured. Experiments also showed grazer preferences for different portions of kelp plants.

Regression analyses are developed in the fourth chapter. Kelp growth statistics collected in the field were expressed as a simultaneous function of four environmental variables: light, temperature, upwelling, and grazing.

The final chapter gives a summary and conclusions.

B. Macrocystis physiology and ecology

The dominant seaweed in coastal waters of southern California is Macrocystis pyrifera (Linneaus) C. A. Agardh. Known as Giant Kelp, this alga normally forms dense canopies within beds along many shores.

Root-like holdfasts anchor Macrocystis plants to the rocky bottom (Figure 1). Above the holdfast the primary stipe or stem branches into numerous fronds extending up to the water surface. Each frond consists of a stipe and numerous leaf-like blades. Three types of blades are found on most healthy fronds. At the distal tip is a specialized growing blade or apical meristem from which each succeeding

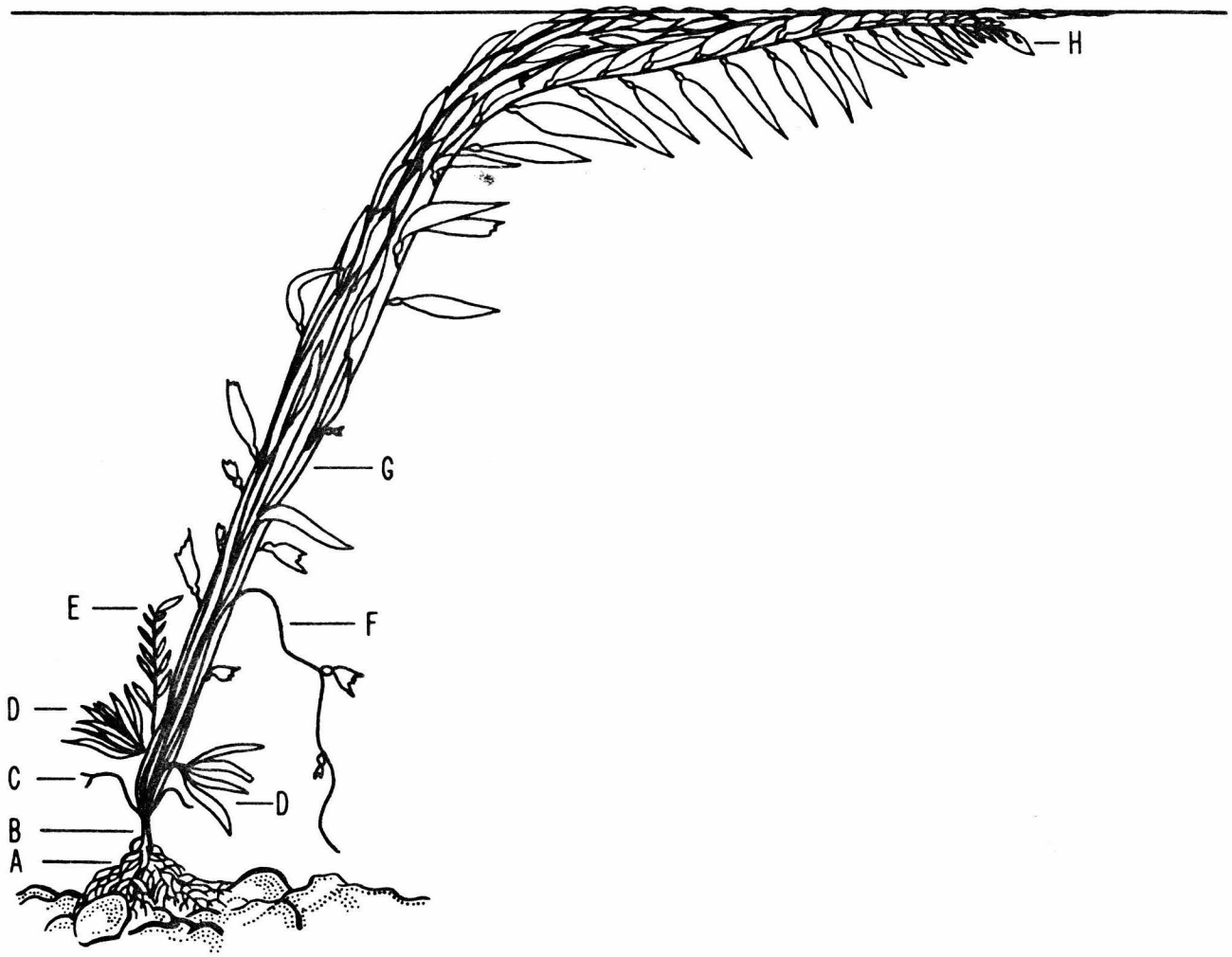


Figure 1. Typical Macrocystis pyrifera sporophyte standing in 10 meters depth. A, holdfast; B, primary stipe; C, broken stipe; D, sporophylls; E, young frond with growing tip; F, senile frond; G, frond bundle; H, growing tip in canopy.

blade separates. Below the growing tip, separated blades are joined to the stipe by gas-filled bladders called pneumatocysts. These gas sacs buoy fronds toward the surface where light intensity is greatest. The third blade type, the sporophyll, is located at the frond base. Sporophylls generally have no pneumatocysts but contain reproductive structures where spores are developed.

Vegetative growth, as distinct from reproductive growth, occurs throughout plant tissues. Certain areas, however, grow more rapidly than others. New fronds emerge from basal meristems near the primary stipe. Developing fronds elongate principally at the tip. Growth in these two areas depends on the distribution of photosynthetic capacity along the frond. Figure 2 (from North, 1971) shows that most of the photosynthetic capacity is concentrated near the front tip. Towle and Pearse (1973) reported that >98% of production occurred in the kelp canopy.

Some photosynthetic products are used in metabolism. The rest contribute to plant growth. Production of new cells in most algae occurs near the photosynthesizing cells. In Macrocystis, however, photosynthate may be transported considerable distances from the formative sites. Translocation of these products (Schmitz and Lobban, 1976) allows new frond production to depend on the photosynthetic activity of the entire plant. Mature blades grow slowly or not

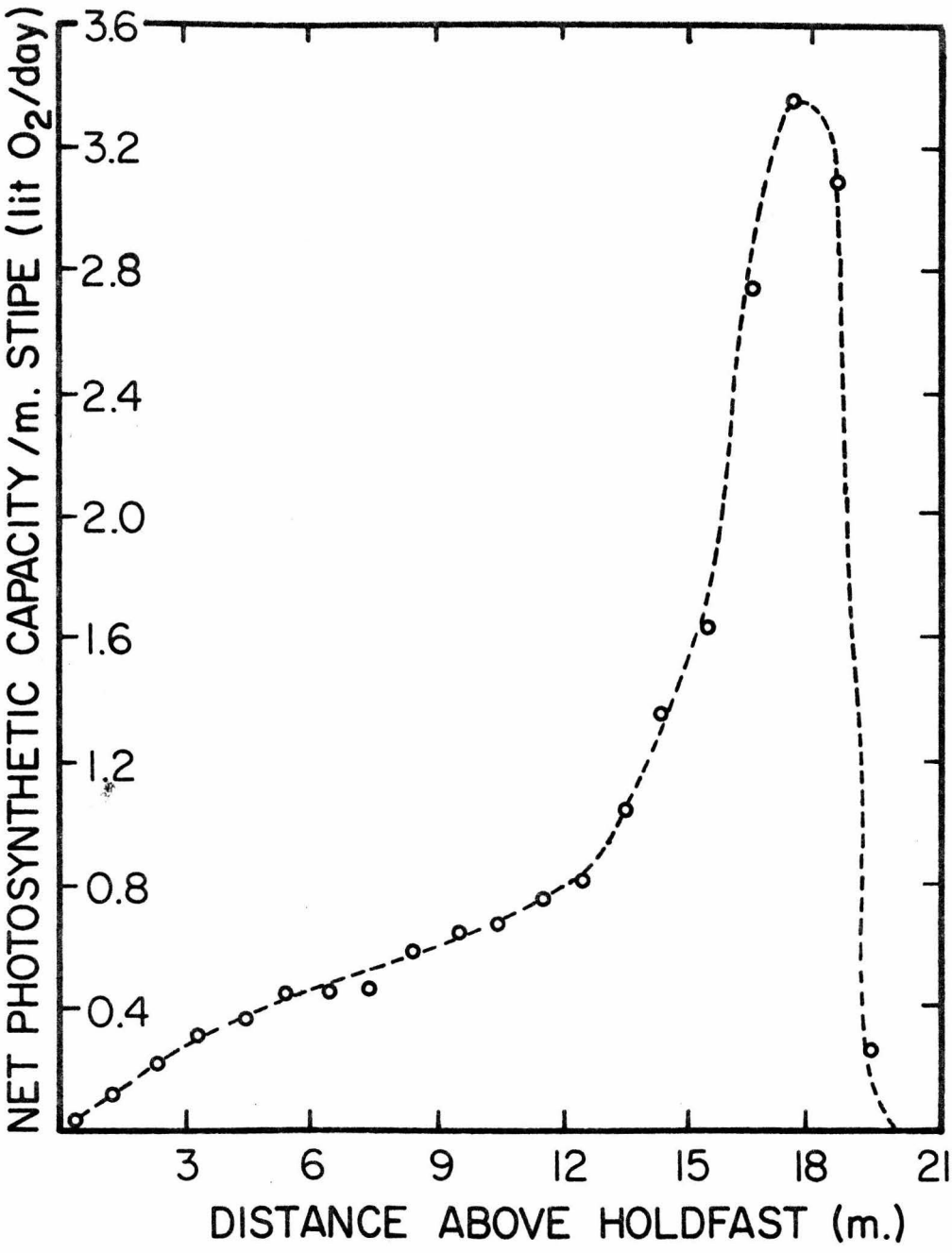


Figure 2. Distribution of net photosynthetic capacity along a Macrocystis frond (from North, 1971).

at all. Their photosynthesis produces a surplus which can be translocated to juvenile tissues. Juvenile regions grow rapidly even though they have little surface area and are shaded by older fronds. Frond development thus gives an indication of the recent photosynthetic activity or health of the plant as a whole.

The life span of individual fronds is about six months (Cribb, 1954; North, 1961; Miller and Geibel, 1973; Barrales and Lobban, 1975; Gerard, 1976). Whether this is a predetermined genetic limit or a limit imposed by environmental factors is not known. The best information suggests that senility of individual fronds is an internal limitation occurring at about six months. I will use this presumption in the following discussions and analyses.

Photosynthesis depends primarily on light intensity and nutrient availability. Light varies with the sun's cycles and with local weather. Nutrient availability depends on currents, particularly upwelling which brings nutrient-rich waters up from the depths. Water temperature can influence photosynthetic and metabolic rates. These three physical factors, light, upwelling, and temperature, play important roles in kelp ecology. A fourth physical factor, stress associated with wave motion, can control kelp losses.

ZoBell (1971) monitored types and amounts of drift seaweeds on more than fifty miles of beaches near La Jolla

for over twenty years. He observed that:

> Among the many factors affecting the appearance of seaweeds in the surf are (a) the age, size, nature, and buoyancy of the plants, (b) weakening of plants by predators, parasites, or infectious agents, (c) the character of the bottom substrate where the seaweeds grow, (d) direction and force of water movements, (e) abnormally high water temperatures in the kelp beds, (f) nutrient and oxygen content of the water, and (g) activities of man.

ZoBell noted that his observations were biased because he saw only material drifted ashore. While he regularly found large amounts on the beaches, he estimated that 10 to 100 times more drifted out to sea or sunk to the bottom as detritus. Mitchell and Hunter (1970) reported that large floating kelp rafts were commonly found drifting in deep water far from shore. They described a somewhat complex community of organisms normally associated with these kelp paddies. Follett et al. (1960) speculated that drifting kelp rafts might expand geographical distributions of closely associated species.

Recently Rosenthal et al. (1974) studied a sample of tagged plants in a bed near Del Mar, San Diego County. They stated that "Three factors probably accounted for most of the plant mortality in this location: 1) storms and strong surge, 2) entanglement of drifting plants with attached Macrocystis, and 3) kelp harvesting."

ZoBell was sure that harvesting did not cause significant contributions to beach drift. Rosenthal et al., on

the other hand, listed harvesting as a significant factor. My study did not contribute to the question because kelp has not been harvested around Palos Verdes for many years.

Macrocystis generations alternate between large, asexual sporophytes and microscropic, sexual gametophytes. Plants observed in kelp canopies are all the asexual phase. Gametophytes, while integral to the life cycle, are inconspicuous. Recruitment of sporophytes thus depends on spore production, gametophyte development, and availability of substrate within the spore and gamete dispersal area. Anderson and North (1966) showed that spores are produced throughout the year. Little is known about the microscopic stages in nature except by inference. Juvenile sporophytes have been observed 80 to 100 meters from the nearest adults (North, 1969). Juveniles have been observed 32 days after substrate has been cleared in February (McPeak, 1974), after 80 days in summer and 120 days in fall (North, 1965). Foster (1975) found that the greatest numbers of sporophytes were recruited during spring months. His observations validate qualitative impressions of others (North, 1974; McPeak, 1973).

Kelp interacts with environmental biological elements in four ways. As a primary producer it provides food for grazers, influences dissolved oxygen levels, and contributes material to detritus food chains. Kelp plants provide

shelter and substrate for a variety of animals and other algae. Kelp canopies shade the water column and bottom below, altering the environment for other organisms. Finally, kelp plants must compete for space to produce offspring.

Fish grazing is recognized as a normal ecological element in healthy kelp beds. Occasionally local grazer densities become high and serious damage occurs. Normally grazers then move to new areas where food is more abundant, perhaps dispersing in the process. Thus stress is relieved in the damaged area and it may recover.

Grazing damage to Macrocystis from fishes was an acute problem in Abalone Cove in 1971 (McPeak, Stephan, and North, 1972). Transplanted kelp was consumed so rapidly that restoration efforts were overwhelmed. The initial stock of kelp as food was small. Apparently no alternative diet was available. The grazing pressure was relentless and required artificial control.

Opaleye Perch, the principal grazing fish in Abalone Cove, attack only the leaf-like blades of the kelp plant. The attack can be so concentrated that often only barren stipe bundles supported by defoliated air bladders remain. Most photosynthesis occurs in the blades. Thus concentrated grazing can outstrip plant productivity leaving so little viable tissue that recovery cannot occur. Damage to a few

plants in a healthy bed might not matter but can become critical in isolated or developing beds.

Quantitative information necessary to understand the nature and magnitude of fish grazing has not been available. The questions were pertinent to my studies and were investigated as part of my research.

C. Literature review

A number of descriptive ecological studies list floral and faunal associations common in kelp beds (McLean, 1962; Turner, Ebert, and Given, 1964 and 1965; North, 1971; Aleem, 1973; Barrales and Lobban, 1975). These often contain qualitative descriptions of the interactions of kelp plants with their environment. Some investigators have focused on animal life in kelp beds (Andrews, 1945; Pequegnat, 1964; Mitchell and Hunter, 1970; Ghelardi, 1971; Jones, 1971; Quast, 1971; Wing and Clendenning, 1971; Woolacott and North, 1971; Feder, Turner, and Limbaugh, 1974). Others have concentrated on the other seaweeds found commonly in kelp beds (Dawson, Neushul, and Wildman, 1960; Devinny and Kirkwood, 1974).

Three quantitative studies of Macrocystis ecology have been reported recently. Miller and Geibel (1973) studied the effects of commercial harvesting of kelp canopies on kelp bed ecology near Monterey, California. They measured frond elongation rates in cut and uncut areas for about a

year. They also investigated changes in animal populations affected by harvesting. Rosenthal, Clarke, and Dayton (1974) surveyed a kelp bed in San Diego County for more than five years. They investigated long term population fluxes. They identified causes of plant mortality and the seasonal nature of kelp recruitment. They also measured distribution patterns of some conspicuous invertebrates in the bed. Gerard (1976) studied energy flow in the ecosystem in which Macrocystis provides most of the primary productivity. She measured standing crop, production, and losses as functions of time. She related kelp losses to water motion but did not establish relationships with light, temperature, grazing, or upwelling.

Several researchers have quantified Macrocystis dependence on fundamental environmental parameters individually. ZoBell (1971), for example, monitored the appearance of kelp plants washed ashore after storms. Neushul and Haxo (1963) and Clendenning (1971) showed the effects of varying light intensity on kelp growth. North (1971) measured kelp growth as a function of water temperature. Jackson (1975) investigated the dynamics of nutrient chemistry in the kelp bed.

Each of these studies has demonstrated the importance of one facet of the marine environment on some aspect of kelp development. I contend, however, that one must be

aware of every change in the environment in order to understand kelp growth variability over a long time period. Because of limited resources I have studied one aspect of Macrocystis growth, the number of fronds per plant. I related this to the environmental variables most likely to have major roles affecting frond number.

An important part of Macrocystis ecology has not been adequately treated in the literature. Fish grazing is known to be an important factor. Principal grazers have been identified by direct observation (Feder, Turner, and Limbaugh, 1974) and by gut contents analysis (Williams and Williams, 1955; Follett, Gotshall, and Smith, 1960; Quast, 1971). McPeak, Stephan, and North (1972) estimated the magnitude of grazing pressure on a transplanted population, but their analysis was inconclusive. To date no one has adequately quantified the impact of fish grazing on Macrocystis.

To fill this void I monitored grazing as a part of my field studies and I measured grazing rates in a laboratory study.

D. The Study Site

Abalone Cove in Los Angeles County lies about a mile east of Point Vicente and a little more than three miles west of White's Point on the Palos Verdes Peninsula (Figure 3). The site is sheltered from most large waves except

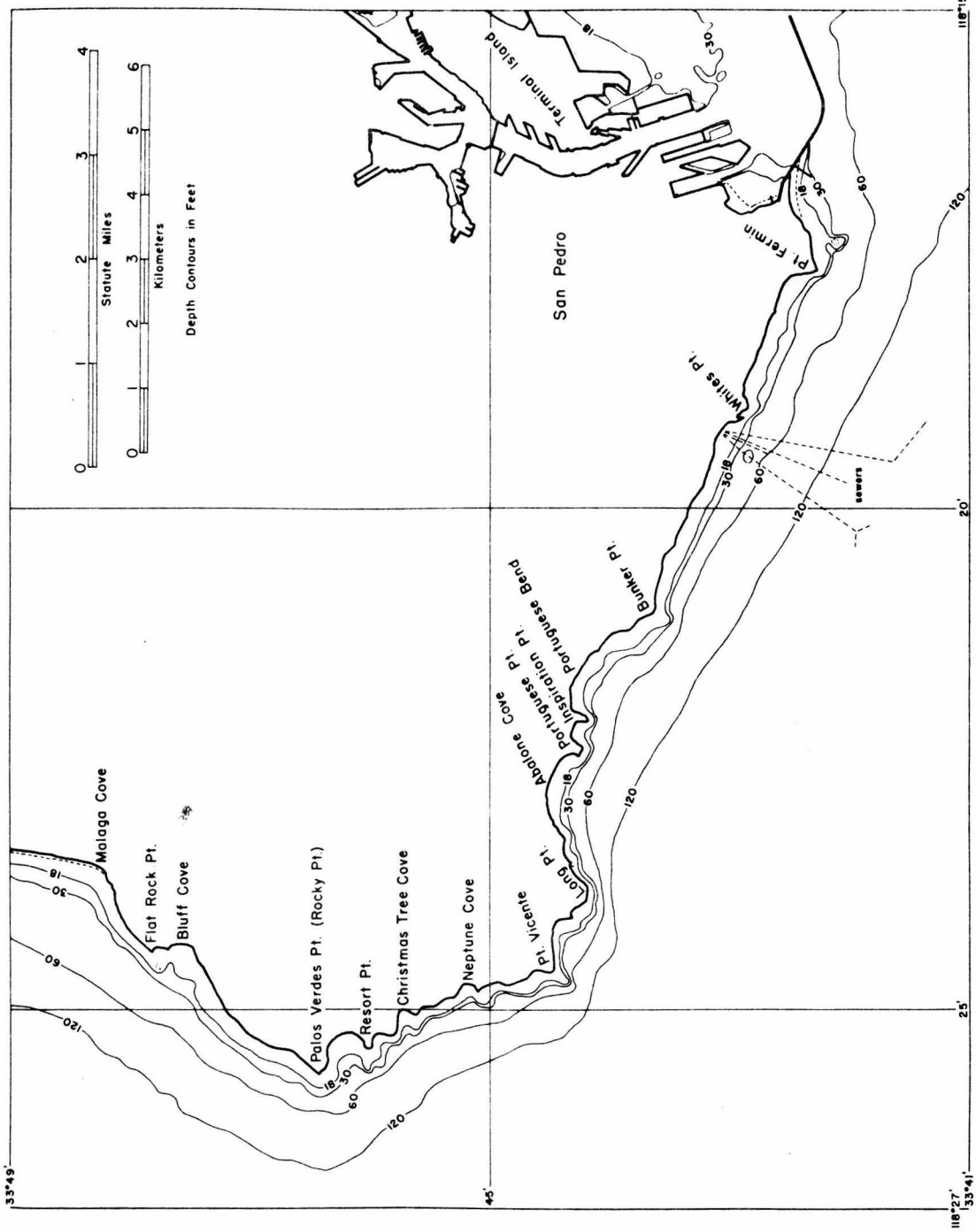


Figure 3. Palos Verdes peninsula, Los Angeles County. Field study conducted in Abalone Cove. (Prepared by L. G. Jones)

those associated with local winter storms and occasionally south swell in summer months. Upwelling often brings cold water into the cove from offshore depths. Water temperatures consequently can be several degrees lower than those north of nearby Rocky Point.

Rich beds of Macrocystis formerly lined the Palos Verdes peninsula. The population declined steadily. Finally by 1960 only a small patch remained in Abalone Cove (Figure 4). These plants deteriorated until 1967 when they too were lost to storms and grazing. In that year restoration activities were begun by a Caltech group. They were joined by California Department of Fish and Game biologists in 1972. When my study began in 1974, a stable, naturally reproducing kelp bed had been successfully reestablished. The canopy area was measured at that time by Department of Fish and Game aerial survey and totaled 3.1 acres. Development continued and by April 1976 the bed covered 25.4 acres (Figure 5).

A naturally recruited bed was discovered in Bluff Cove northeast of Rocky Point early in 1975. Restoration efforts have continued so that Macrocystis now occurs in many places along the Palos Verdes coast. Expansion by these populations will probably continue.

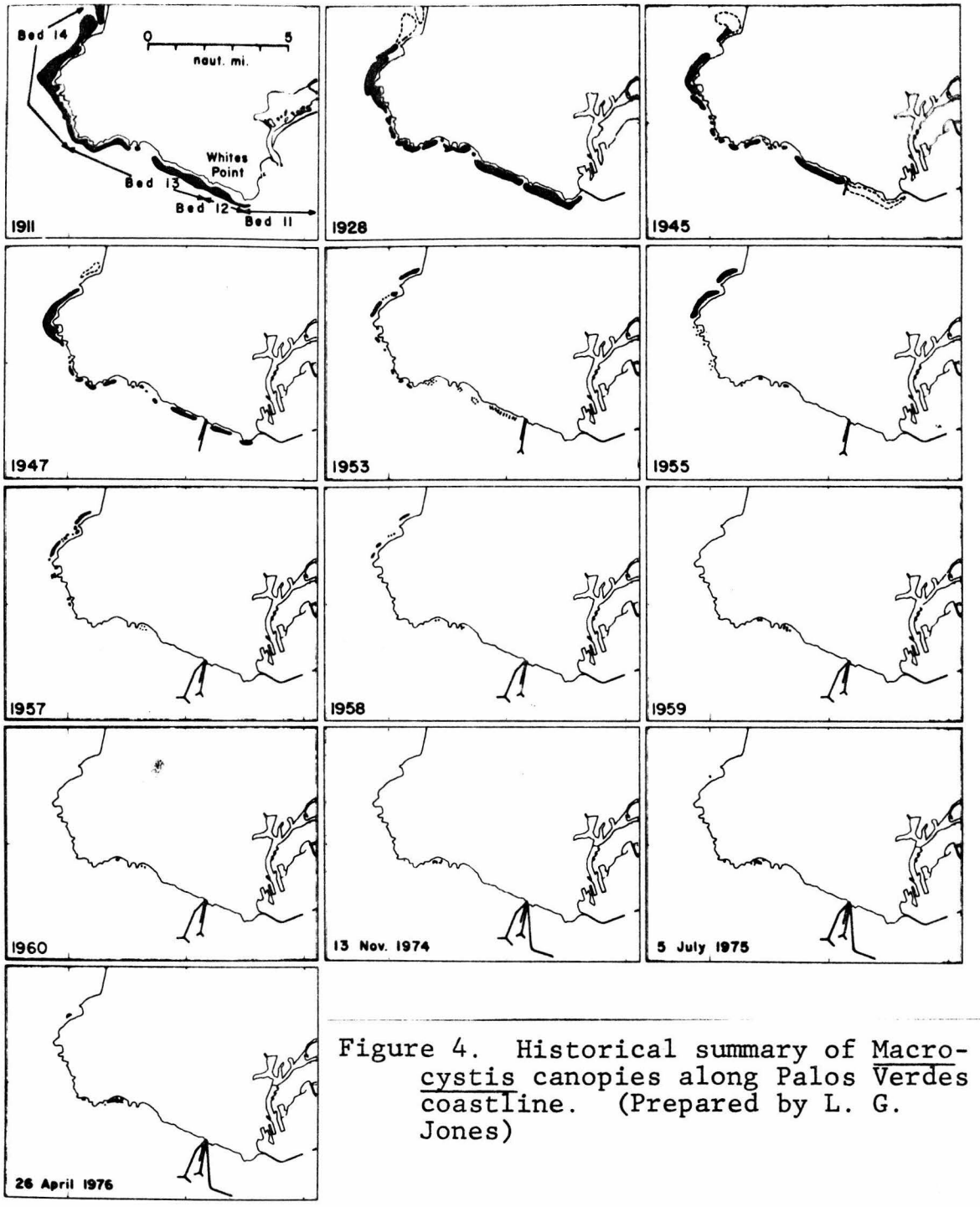


Figure 4. Historical summary of Macrocystis canopies along Palos Verdes coastline. (Prepared by L. G. Jones)

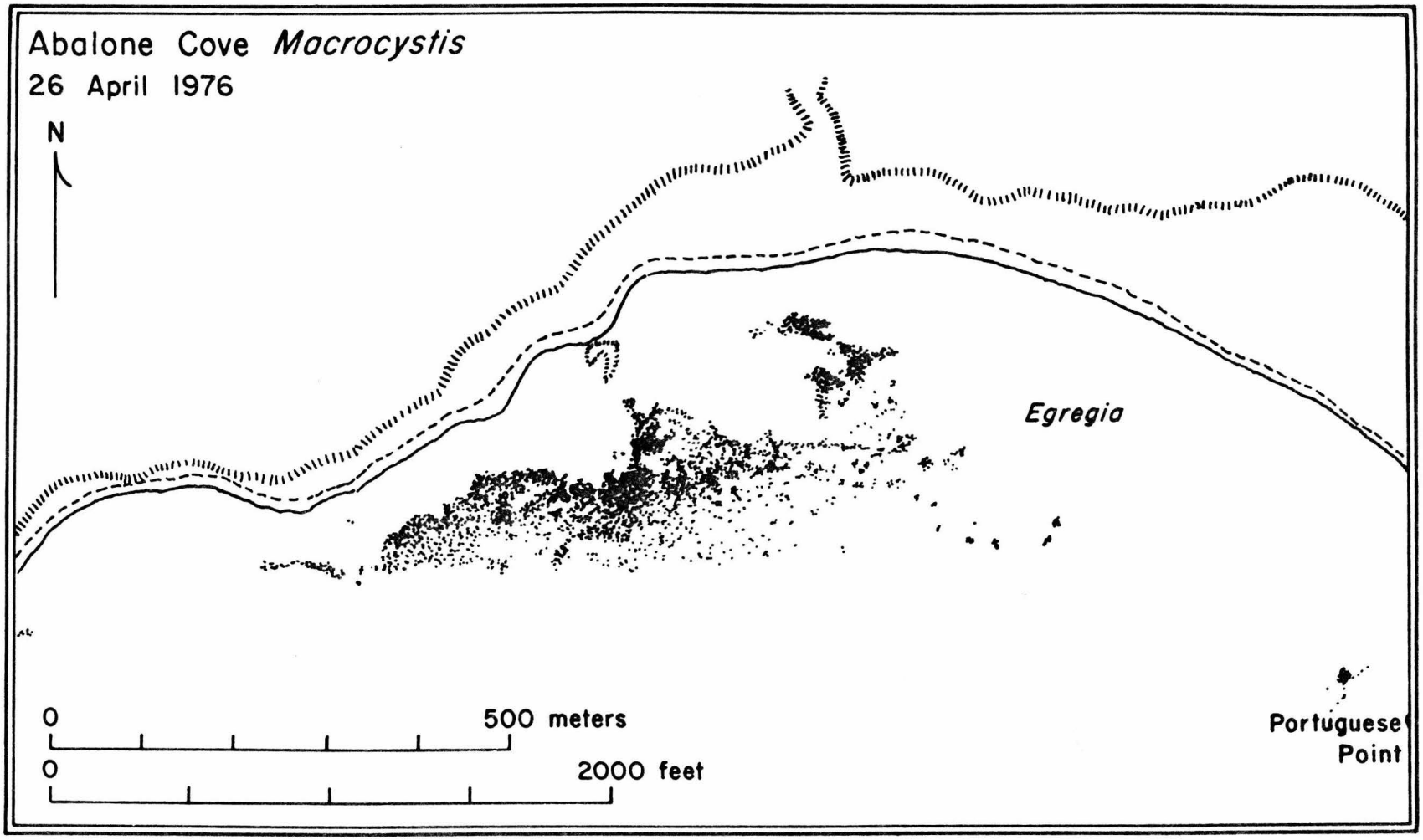


Figure 5. Macrocystis canopy in Abalone Cove from an aerial survey 26 April 1976. Area equals 25.6 acres. (Prepared by L. G. Jones)

Macrocystis populations nearest to Palos Verdes lie approximately 30 miles northwest near Malibu, Los Angeles County, and about 30 miles southeast near Corona del Mar, Orange County.

CHAPTER II

FIELD STUDIES

A. Scope and objectives

Data discussed in this chapter were gathered during a sixteen month study in Abalone Cove. I observed a sample population of kelp plants along a fixed transect line. Resultant data indicate seasonal patterns of kelp growth, some important causes of plant mortality, and the variable level of fish grazing. Discussion and analysis in this chapter derive exclusively from field observations. Development of a mathematical relationship between the observed growth patterns and environmental parameters is presented in Chapter IV.

B. Macrocystis growth and mortality

1. Methods

In October 1974, using SCUBA, I installed a one hundred meter transect line perpendicular to shore through the healthiest appearing portion of the Abalone Cove kelp bed (Figure 6). I marked one plant every two meters within a strip two meters wide along the transect. Plants were chosen without regard to size or condition. Thin strings laced through the holdfasts tethered small buoys about 75 cm above the bases (Figure 1). These floats supported

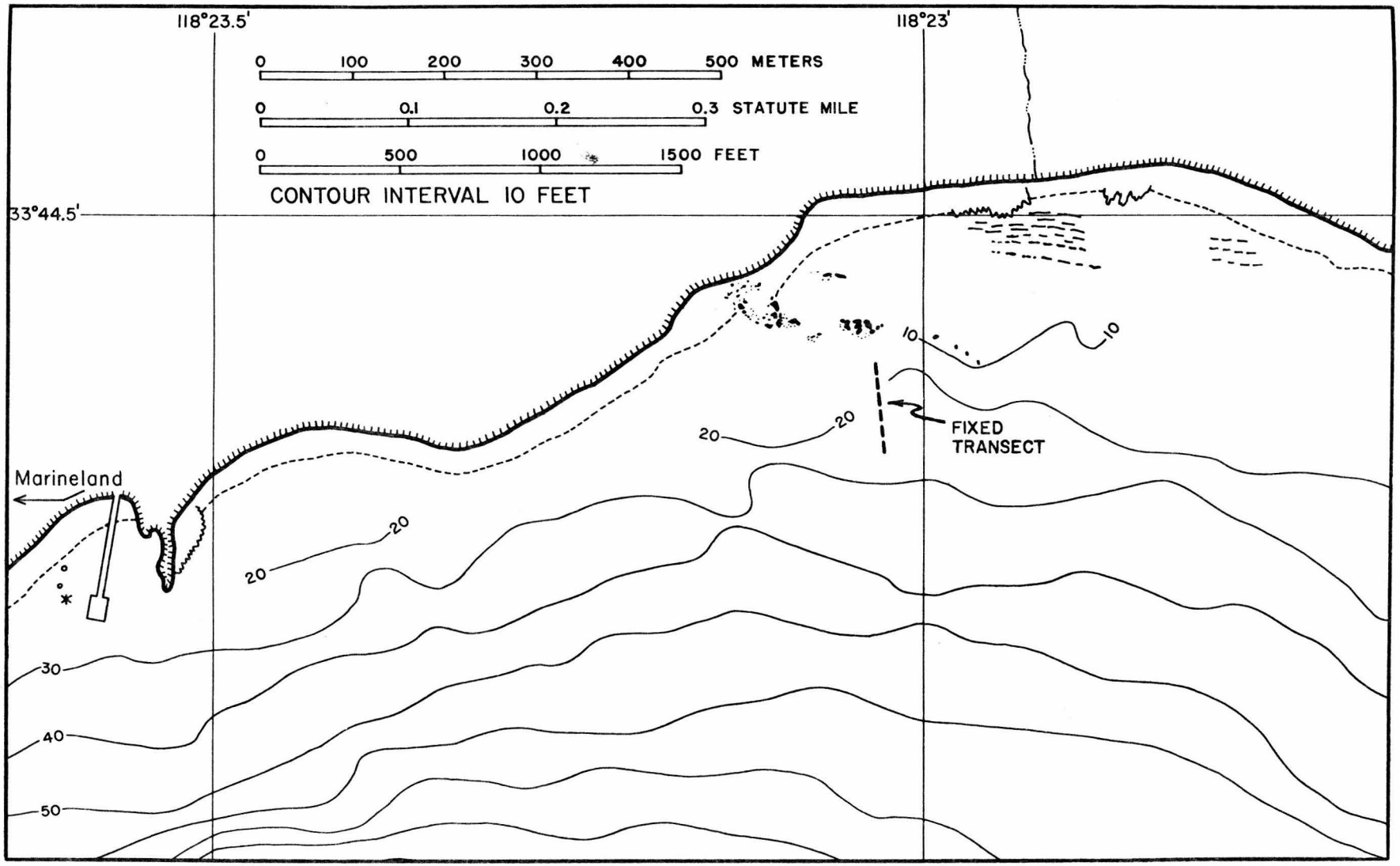


Figure 6. Location of 100 meter transect line in Abalone Cove. (Prepared by L. G. Jones)

numbered, white plastic tags which were usually easy to find even when encrusted with algae and invertebrates.

As a prelude to the principal study, I tagged plants in a separate section of the Abalone Cove kelp bed. Many of these tags were lost because of insecure attachment. Subsequently I improved the marking technique. Tagging reliability was enhanced as I grew familiar with the location and spacing of the tags along the transect. I could then confidently conclude that a missing tag indicated a missing plant. Confidence in ability to relocate samples was especially important when underwater visibility was less than five feet and strong surge was a factor.

I visited the transect site 24 times from October 17, 1974 to March 13, 1976 at approximately three week intervals. Time between visits varied from six to forty-nine days because of circumstances such as weather. Average time between visits was twenty-one days.

Fifty plants were tagged to start the study. Additional sets of plants were tagged to replace lost plants. Replacements were located as close as possible to the space once occupied by the missing plant. Newly tagged individuals were chosen without regard to size. Plants tagged late in the study might not have existed when the original samples were selected. Replacements were added in groups on five occasions 3, 7, 8½, 11 and 11½ months after the study began.

(See Appendix A for individual plant data.) Eighty-four plants total were tagged. Because lost samples were not replaced immediately, an average of forty tags were present at any time during the study.

Numbers of fronds per plant were counted. For consistency I counted all stipes that reached to or above the small marking buoy. Shorter stipes were not included in the count. These shorter stipes included some broken off mechanically or stubs remaining from senile deterioration as well as young fronds not yet grown sufficiently long to qualify for counting. After each plant's fronds were counted, I noted the general condition. I recorded whether the plant was under attack by urchins, if anchoring was insecure, or any entanglement with other plants. Certain plants near rocky outcrops showed abrasion due to rubbing against rocks during wave-induced motion. A lace-like appearance of blades indicated grazing by amphipods or other tiny invertebrates (Jones, 1971).

2. Results and discussion

Mean values of frond numbers for the Abalone Cove surveys are plotted against time with days reckoned from January 1, 1974 (Figure 7). The study actually began on October 17, 1974, so the first data point occurred at day 290.

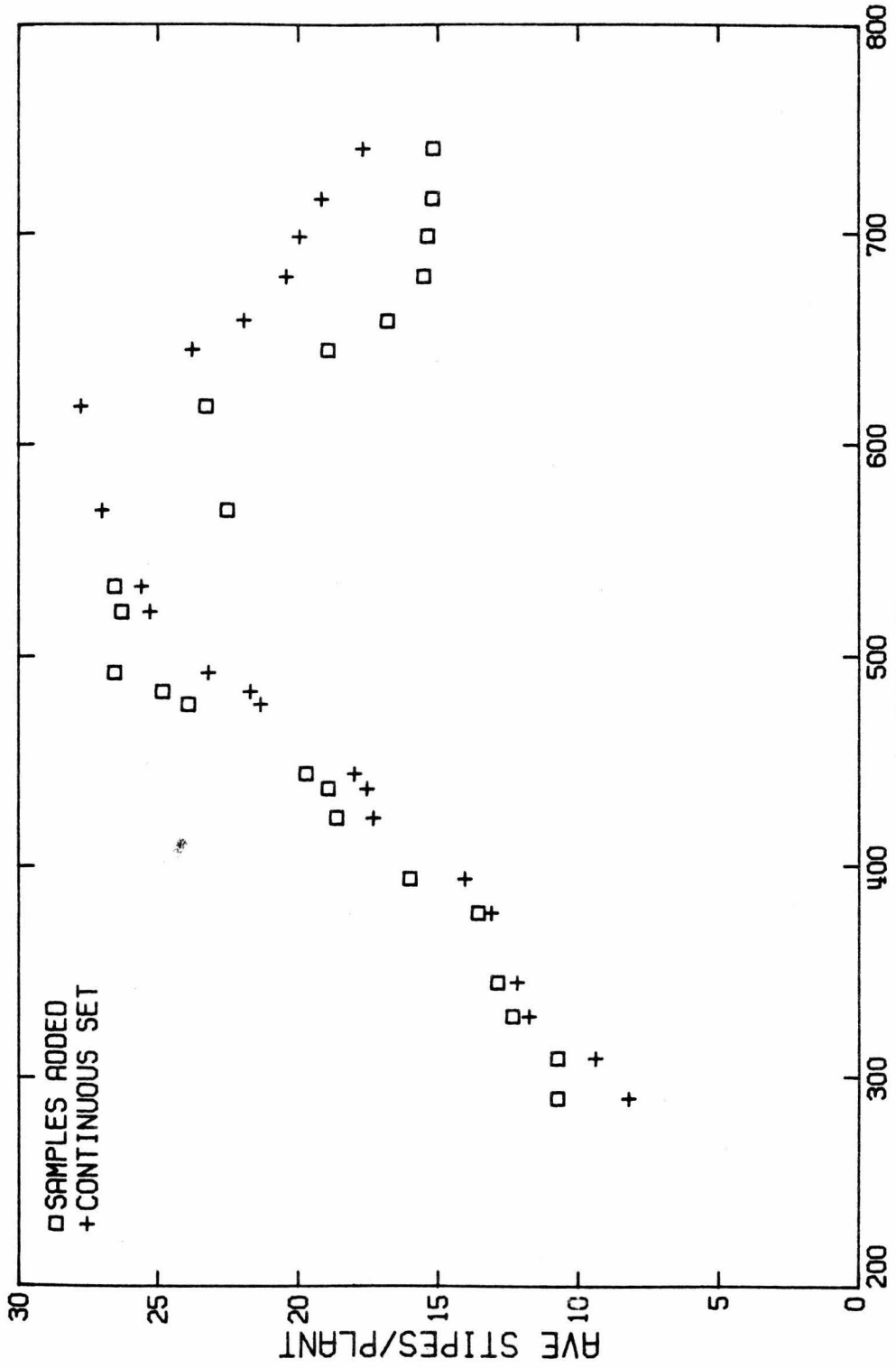


Figure 7. Average frond number along the 100 meter transect in Abalone Cove from October 17, 1974 to January 11, 1976.

Frond numbers are interpreted in two ways. The first approach included data only from those plants which survived the entire duration of the study. Among surviving plants, frond counts measure an initial size plus gains due to photosynthetic growth, minus losses due primarily to aging of individual fronds and also to physical hazards. These continuous average frond numbers indicate the vegetative growth history of a typical surviving sporophyte.

New frond production depends on advantageous conditions for photosynthesis. Frond life span, on the other hand, is set at six months by a seemingly predetermined age limit. The life span may actually be less, depending on physical stresses (see Introduction). Thus, many researchers (Miller and Geibel, 1973; Rosenthal, Clarke, and Dayton, 1974; Gerard, 1976) have used this interpretation of average frond numbers as an indication of recent well-being among surviving kelp plants. A time series of measurements must be available if frond numbers are used to evaluate vegetative growth. Average frond numbers should increase in response to beneficial growing conditions. Even normal frond aging will result in falling values when growth is slow.

The second interpretation of frond counts was an attempt to assess the average size of kelp plants in the study bed. This average was affected by the recruitment of juveniles and the loss of adults. When juveniles are added

to a population, the average size of individuals throughout the entire bed will decrease. Selective loss of the largest individuals will also lower average size. Other studies (North, 1971; Barrales and Lobban, 1975) have used bedwise average frond numbers to indicate concentrations of fronds within a bed.

An ideal sampling procedure could be outlined to produce bedwise average frond numbers. One could count stipes among a sample set chosen randomly each visit to the study site. Population changes due to recruitment and mortality would thus be included in the counts. This sampling method suffers a significant disadvantage. All information associated with individual plant continuity is ignored. It would be impossible to identify the mechanisms by which plants are removed from the population, for instance. Vegetative growth patterns would be obscured by reproductive influences.

My sampling method, while not ideal, approximates bedwise random sampling. Yet a sizeable surviving set was available to provide a body of continuous observations. I chose an initial random set of plants spaced evenly along a fixed transect. New plants were added to replace losses. Replacements were chosen without regard to size and might not have existed when the initial set was tagged. Delays occurred between the time a loss was noted and a replacement

was chosen (see Appendix A for individual stipe count histories). Thus, overall averages did not respond immediately to an influx of juveniles. Because a plant had to be lost before a new plant was tagged, bedwise frond numbers tended to underestimate the effect of new plant recruitment into the population.

The set of surviving plants in Abalone Cove (called the continuous set in Figure 7) was used to develop the average vegetative growth history. The complete tagged set (referred to as samples added in Figure 7) reflected frond number changes in the population including effects of recruitment and mortality. Furthermore, loss mechanisms were revealed as threats to specific tagged individuals became apparent.

Nineteen plants persisted through the duration of the study. Figure 7 shows that new fronds were steadily added by this continuous set until late summer 1975 (around day number 625). The initial average of 8.2 stipes per plant in October 1974 rose to a high of 27.7 early in September. The average among long-term survivors then fell to 17.7 by January 1976.

The complete tagged set to which samples were added averaged about forty individuals during each site visit. Bedwise averages taken from the complete set showed a pattern similar to that from the continuous set. Average frond

number in the bed as a whole rose from 10.7 at the start to 26.5 in June 1975 (around day number 510). It had fallen to 15.2 by January 1976.

The two records were similar but some important differences do appear. The average plant in the bed reached its peak in early June. Surviving plants, in contrast, continued to increase in size until September. The earlier peak together with lower averages after mid-summer (about day number 570) for bedwise values compared to the continuous set indicate that replacements were drawn from a population with smaller averages. In other words, a new generation of sporophytes was recruited during spring.

Somewhat larger bedwise averages compared to long-term survivors for the first half of the study further suggest selective destruction of large individuals. As larger plants were lost from the overall sample, the initial sizes of survivors became smaller. A discussion of loss mechanisms and the size distribution of lost plants is presented later in this chapter.

Only nineteen of fifty original tagged plants survived the entire study period. These increased from an average of 8.2 fronds one October to 23.8 the next. Given this low survival rate and the high growth rate, it seemed possible that the frond number from the continuous set represented the upper half of a standard logarithmic growth curve. This

set of survivors had a zero average frond number at some time in the past. If each of these sporophytes began life sometime during the first three months of 1974, averages for the continuous set would follow a rather smooth S-shaped curve. In fact, the spring of 1974 was marked by the appearance of a tremendous recruitment of sporophytes (North, 1974) confirming the successful restoration of Macrocystis in Abalone Cove. It is thus highly likely that the average frond numbers among long-term survivors follow a smooth rise from zero sometime between days 0 and 100 to a maximum after day 600, followed by a rapid decline. In other words, if a sporophyte is not lost to storms or grazed away by urchins or destroyed by some other external threat, it will show increases in frond numbers for about two years.

With this in mind I began an analysis to see if individual plants could be matched to a similar theoretical growth curve as the average values followed. North (1971) was able to do this for the growth of individual fronds. My analysis was not completely successful and is not presented in detail here. Individual plants showed a great deal of variability in frond number histories. Maximum numbers of stipes varied widely from plant to plant. Rates of frond addition and loss fluctuated too much for satisfactory matching to a common hypothetical curve.

One result of this theoretical growth curve analysis was interesting even though the overall analysis was inconclusive. I tried to fit each frond count record to the ideal S-curve. Most records were erratic but I made a qualitative, subjective fit anyway, estimating in each case where the zero frond count intercept would occur. This intercept marked the day on which each embryonic sporophyte began life. The birthdays of all plants observed during the study fell into a bimodal distribution in time. One group fell between day 100 and 200. The other group fell between 400 and 500 or roughly a year later. The analysis was qualitative but did suggest that two age groups of sporophytes were represented in my overall sample.

Rosenthal et al. (1974) wrote, "the number of living stipes on selected Macrocystis plants does not necessarily indicate the age of a kelp bed or the ages of plants within the bed." This statement might be true for mature beds which have passed through many generations and have reached steady state densities. The kelp bed in Abalone Cove was in the initial phases of restoration by 1973. Hence it is unlikely that steady state plant and frond densities had been reached at the time of my study. An increase of 4.8 fronds per plant occurred in the bedwise average from one winter's lows to the next (Figure 7). This difference was significant at the 95% level by student-t test. The increase might represent a gradual trend toward higher

levels around which seasonal patterns would eventually oscillate.

The age of individual plants in a bed is also open to debate. I was not able to show that individual Macrocystis sporophytes followed predictable ideal growth curves. It does seem likely, however, that the average of several plants from the same age group follows a logarithmic pattern.

Die-off in Macrocystis beds is common in southern California during late summer months both in terms of frond deterioration and canopy densities (Clendenning, 1971; McPeak, Fastenau, and Bishop, 1973). The bedwise frond number curve probably does represent a portion of a long-term cycling or oscillation around a steady state level. The oscillations result from three aspects of kelp ecology. First, recruitment of juveniles is most successful in the spring. Second, large adults are frequently lost to physical hazards. Third, even long-term survivors show a deterioration due either to aging or to poor growing conditions.

Chapter IV presents regression analyses which examine whether the deterioration observed among the continuous set can be correlated with growing conditions.

We can estimate net kelp plant productivity during spring 1975 from the observed average increase from 8.2 to 27.7 fronds per plant in 328 days. Average wet weight per frond is about 1 kg (North, 1971). Net frond increase

thus produced about 20 kg/plant/yr during the high growth period.

Frond production rates were calculated for each plant in the continuous set by dividing the change in frond number between observations by the time interval. Each of these rates was normalized by dividing it by the frond count for each plant at the start of the time period. This gave normalized production rates or the rates at which each single frond produced new fronds. Figure 8 shows the time sequence of normalized frond production rates as percent increase per day. Values are uniformly positive during the net growth phase prior to day 620. Net production was, of course, negative from then on. No smooth seasonal trend emerges from this plot.

An example is useful to help evaluate these rates. At a typical rate of 0.6% increase per day during the high growth period, a plant of 10 fronds would produce one new frond in about 20 days ($= 1/(10 \times 0.6 \times 10^{-2})$). At a higher rate, say 1%, a 20 frond plant would produce a new frond in 5 days ($= 1/(20 \times 1 \times 10^{-2})$).

Gerard (1976) reported net frond production at 1 to 2 fronds per plant per month for plants with fewer than 50 fronds. Using an average size of 18 fronds per plant for the continuous set, production averaged about 4 fronds per plant per month during the high growth period in Abalone

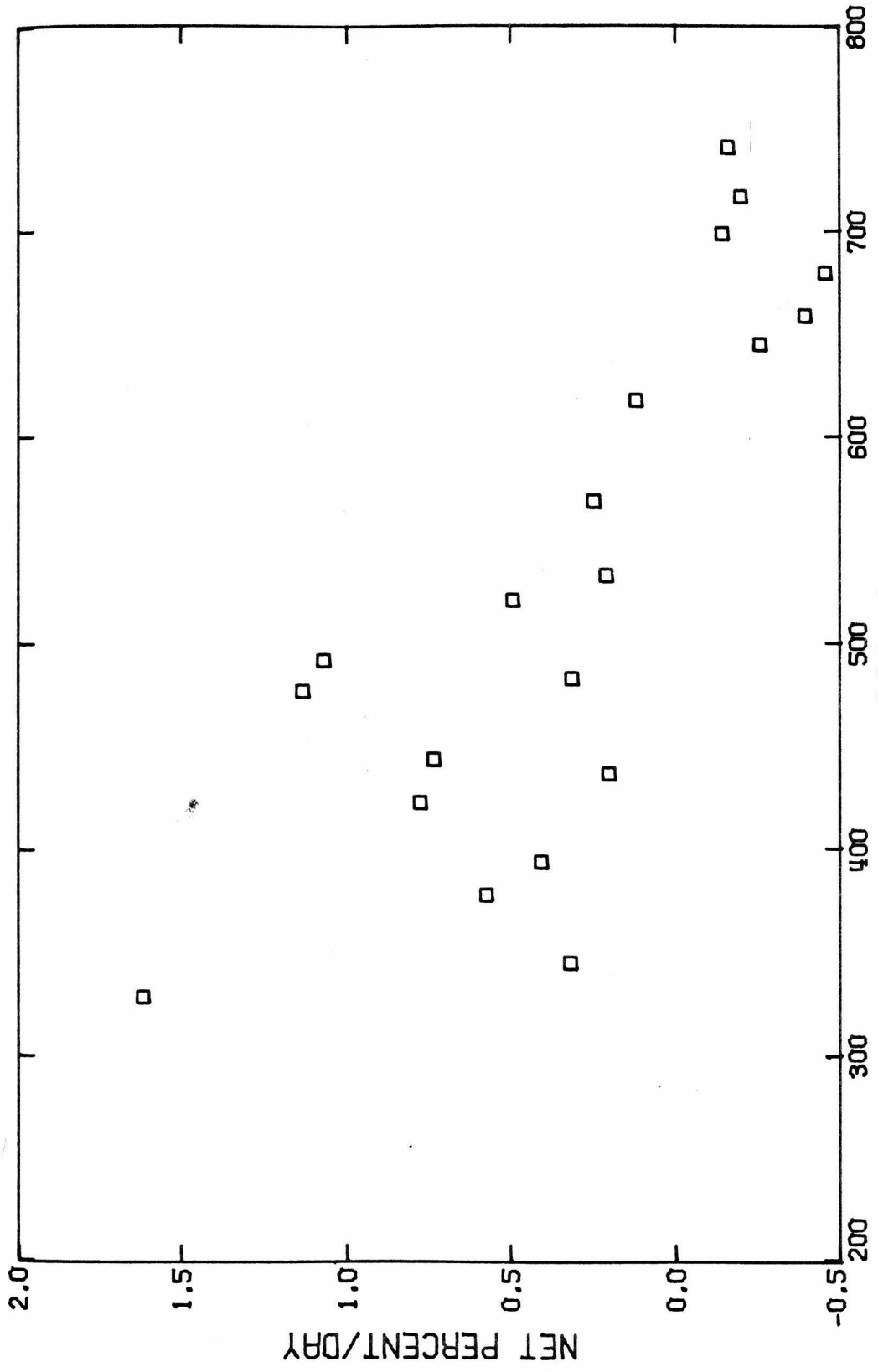


Figure 8. Normalized frond production rate along 100 meter transect in Abalone Cove from October 17, 1974 to January 11, 1976.

Cove. I have not included the period of slow growth or deterioration after day 620 because I do not know how long it lasts. The value of 4 fronds per plant per month is thus comparable to Gerard's value which includes low growth periods.

Productivity of the Abalone Cove bed as a whole can also be estimated. Bedwise average frond numbers rose from 10.7 to 26.5 in 202 days after the start of the study. An average frond weighs 1 kg. Population density was about 1 plant per square meter. Bedwise productivity was therefore about 30 $kg/m^2/yr$ during the early phase of the study. North's (1971) estimated range of wet weight productivity of 14 to 240 $kg/m^2/yr$ brackets the Abalone Cove value, as does Gerard's (1976) range of 4.8 to 36 $kg/m^2/yr$. Clendenning's (1971) reported a range of wet weight productivity as 5.7 to 28 $kg/m^2/yr$ very nearly included the value I estimated for Abalone Cove.

Bedwise productivity of 30 $kg/m^2/yr$ is somewhat higher than that of the continuous set at 20 kg/plant/yr if we apply the same plant density of 1 plant per square meter. The Abalone Cove bed was still in the early stages of recovery in 1974 and 1975. Recruitment of juveniles probably overbalanced the loss of adults during that time.

Table 1 lists individual plant losses I counted along the Abalone Cove transect. Fates of missing plants were

Table 1. Individual Macrocystis plants lost from the Abalone Cove transect 1974-1976. Arrows identify occurrences of major storm swell into Abalone Cove from the south.

Date	Day No.	Number of Plants Lost		Avg. Frond Count of Plants Lost	
		to storms	to urchins	to storms	to urchins
11-5-74	309	2	0	14.0	-
11-25-74	329 →	0	0	-	-
12-11-74	345	5	1	14.2	4.0
1-13-75	378	2	3	10.5	7.3
1-29-75	394	1	0	26.0	-
2-27-75	423 →	0	1	-	2.0
3-13-75	437 →	3	0	27.3	-
3-20-75	444 →	0	0	-	-
4-22-75	477	4	0	18.0	-
4-28-75	483	0	1	-	13.0
5-7-75	492 →	0	0	-	-
6-5-75	521	2	0	16.0	-
6-17-75	533	0	0	-	-
7-23-75	569 →	1	2	66.0	8.5
9-10-75	618 →	6	1	31.5	24.0
10-7-75	645	1	0	28.0	-
10-21-75	659	0	0	-	-
11-11-75	680	0	0	-	-
11-30-75	699	0	1	-	41.0
12-18-75	717	0	0	-	-
1-11-76	741 →	0	1	-	21.0
2-11-76	772 →	3	7	13.0	13.7
3-9-76	803	1	4	16.0	8.2

almost always clear. Site visits were usually only a few weeks apart. Consequently, a plant's sudden disappearance could be ascribed to storm removal. Urchins also threatened plants, but they move and graze slowly providing advance warning. A few plants were lost to a combination of urchin grazing and wave stress. Such losses have been counted as caused by urchins. Plants attacked by urchins at the holdfast never recovered. Urchins typically consumed all the accessible living material in the holdfast, severed the primary stipe, and set adrift the frond bundle. Therefore, the inception of attack by urchins sealed the plant's fate, leaving undecided only the time of destruction.

I did not systematically study predation on urchins by carnivores. Very little predation was observed in Abalone Cove.

Stress from water motion was the most important cause of whole plant loss. A total of 31 plants were lost to storms while 22 were destroyed by urchins. A statistically significant (95% confidence level by student-t test) difference existed between the average size of plants lost from these two processes. The average plant lost to waves consisted of 21.9 fronds. The average plant destroyed by urchins displayed 12.4 fronds. The 21.9 frond average size of plants lost to storms was also larger than the average

size (18.1 stipes) of all plants sampled during the study. Again this difference was significant at the 95% confidence level by student-t test.

The arrows in the second column of Table 1 indicate the occurrence of major south swells. Abalone Cove is protected from all directions except for waves coming from the south (see Figure 2). Unfortunately wave intensity was not measured. My observations indicated that swells associated with these periods were well above the average size for this area.

A series of three storms struck the study site during March and April 1975. The first took three plants from the sample. Seven days later on March 20 no plants were missing even though a sizable swell persisted throughout the week. A month later four plants were gone following the third period of high waves. April was also a time of rapid growth. During the thirty-two days between counts, the average frond number increased by more than 20% from 19.7 to 23.9 fronds per plant.

Two periods of south swells occurred in August and September 1975. The first removed six plants. The second episode was a particularly severe and long-lasting storm yet resulted in just one loss. During this twenty-seven day period the average frond number decreased almost 20% from 23.3 to 19.0 fronds per plant.

The third sequential series of south swells occurred in January and February 1976. Patterns associated with the earlier episodes reappeared. As ZoBell (1971) noted, weakly attached plants are removed by the first set of swells in a series.

Three important facts must be considered. First, weakly attached plants are removed early during extended stormy periods. Second, plants lost to storms tended to be larger than the average size plant in a bed. Third, plants lost to storms are larger than plants lost to the other most important hazard, urchin grazing. Apparently attachment strength of Macrocystis does not increase at the same rate as plant size. As a plant grows buoyancy and drag increase. To compensate for this the holdfast must expand and become more secure. Holdfast expansion depends on availability and suitability of substrate. In those cases where holdfast development is restricted the frond bundle can continue to expand eventually overcoming attachment strength. Hence drift plants tend to be large.

ZoBell reported a correlation of wave height with the volume of material washed ashore. An elementary hydrodynamic analysis (see Appendix C) shows that drag due to wave motion is more likely a function of the wave amplitude squared divided by the water depth.

Rosenthal et al. (1974) concluded that the entanglement of attached with drifting plants was an important cause of additional mortality for Del Mar. Occasionally I found plants moved to a new location on the transect with the anchoring rock still attached, but this was not a common occurrence. The relative shallowness of Abalone Cove might be an important difference from Del Mar in this regard. My transect included depths from 5 to 9 meters, whereas Rosenthal worked in depths of 14 to 20 meters. Plants in deeper waters grow longer and presumably have a larger probability of entanglement. Given similar plant densities and exposure time adrift, longer plants would intersect nearby individuals more frequently before they are washed free of the bed.

Urchin influence at my study site differed from Del Mar. Importance of urchin grazing has been a controversial issue. North (1974) noted in particular that importance of grazing varies from one location to another, nearby sewer outfalls can influence urchins, and dense urchin populations persist for many years. Abalone Cove is only slightly more than three miles from the Los Angeles County Sanitation Districts outfall system. Dense populations of urchins, Strongylocentrotus purpuratus and S. franciscanus persist there even though urchin control activities have been a major, continuing part of restoration programs by both the

Kelp Habitat Improvement Project and the Department of Fish and Game. The data in Table 1 clearly indicate the importance of urchins. 26% of the sample kelp population was lost to urchin attacks during the study.

These losses occurred primarily along the inshore portion of the transect. A significant but not troublesome population existed throughout the bed when the study began. Urchins were initially more dense in the shallow section of the transect. Subsequently numbers became very dense and animals began moving as a front into deeper water. The invasion destroyed 12 plants early in 1976.

Losses ascribed to urchins during the last months of this study were not representative of the entire Abalone Cove bed. By chance the transect was invaded by the only urchin front in the area. Had the line of tagged plants been located elsewhere, these large losses would not have been recorded. The 100 meter transect length did not give a truly representative statistical coverage of larger scale urchin movements in this particular case. Urchin grazing damage would nevertheless have been significant even if the moving front had not developed.

C. Grazing by fishes

1. Methods

Grazing estimates were made in conjunction with SCUBA surveys of tagged kelp plants on a 100 meter transect in

Abalone Cove. Numerical grazing estimates were assigned to each plant after making stipe counts. Estimates were subjective measurements of the amount of tissue missing. They were assigned when distinctive bite marks indicated that fishes were responsible. Values from one to three were used to characterize grazing damage in a pilot study. "One" meant light grazing. "Three" meant severe grazing damage was apparent. It was often difficult to decide which number to apply because damage levels fell between these few categories. I adopted a scale from zero to six in performing the main study. A value of six indicated practically all blade areas had been stripped. The need to expand the scale is indicative of the sensitivity of the measurement.

Opaleye Perch, Girella nicricans, and Halfmoon Perch, Medialuna californiensis, are the predominant fish grazers in southern California waters. Halfmoon were abundant in Abalone Cove during 1971-72 control efforts but in my counts they were outnumbered by Opaleye by almost an order of magnitude (see below). Opaleye tooth and jaw structure is unusual and highly specialized (Norris and Prescott, 1959). They leave a telltale bite mark. Halfmoon bites are not so easily recognized, but because they were less common, grazing estimates were relatively simple observations.

I have focused my studies on the growth and loss of kelp rather than on fish diets. Opaleye may derive more nutritional benefits from organisms which often encrust the algae than from the plant tissues (Williams and Williams, 1955; Follett, Gotshall, and Smith, 1960; Quast, 1971; Feder, Turner, and Limbaugh, 1974). I have considered only kelp tissue loss and have avoided the term herbivore in referring to these grazers.

Following stipe count and grazing survey I made a second swim along the transect to count grazing fishes. I employed the belt transect method described by Quast (1971). The number of Opaleye and Halfmoon sighted divided by the area swept (2 times visibility times length) measured areal density of these grazers.

2. Results and discussion

Grazing estimates were averaged over the set of surviving plants and over the set of all tagged plants (Figure 9). Averages were similar for the continuous set and for the set with new samples added to replace lost plants. High levels (averages greater than 2.0) prevailed from November 1974 until the following March. Recovery was rapid, reaching minimum values in June. Dates of the minimum grazing estimates corresponded to the maximum stipe counts (see Figure 7). The spring period of robust growth is apparently reflected in both grazing estimates

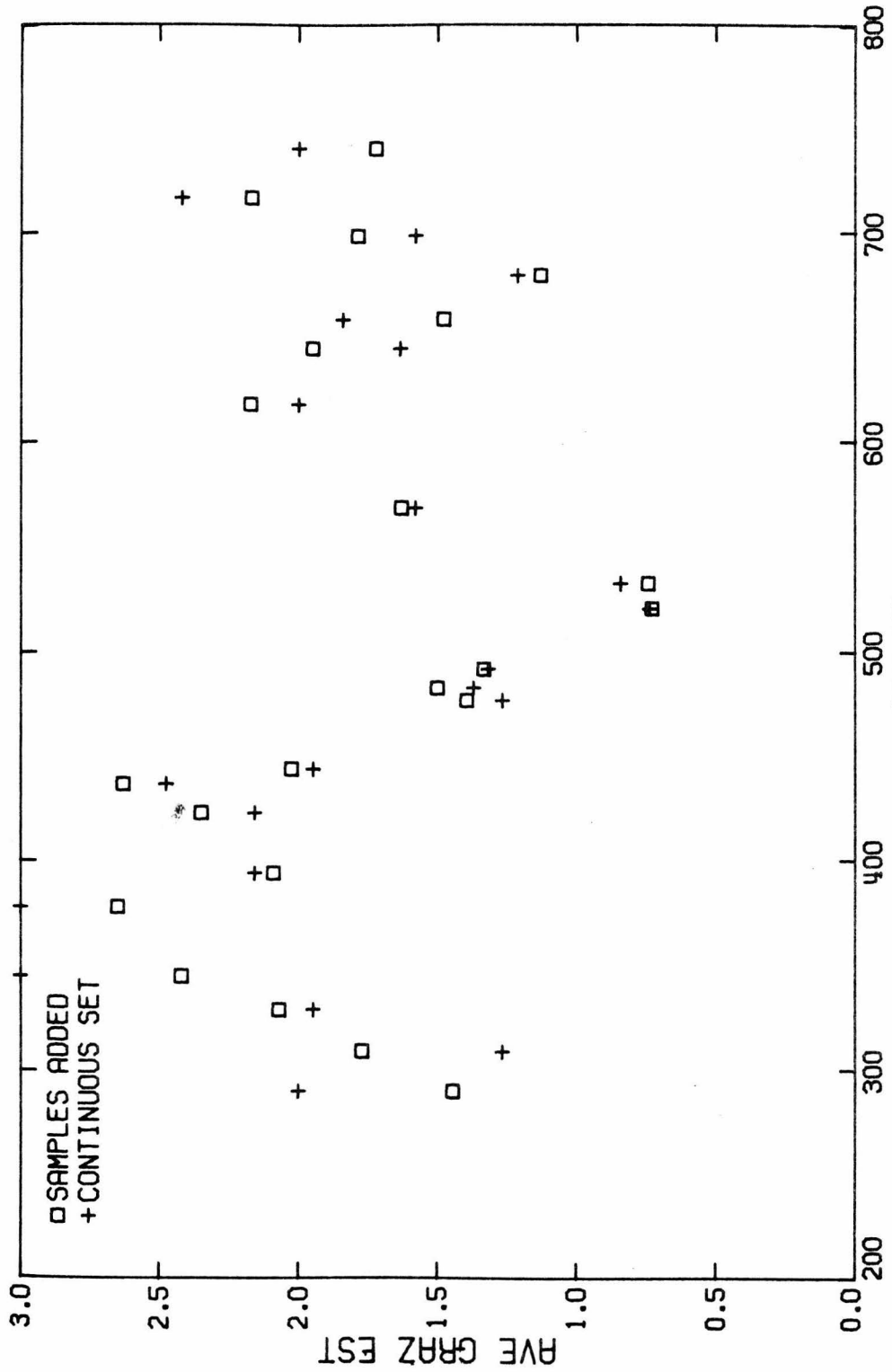


Figure 9. Average grazing estimates along 100 meter transect in Abalone Cove from October 17, 1974 to January 11, 1976. Zero indicates no apparent grazing. Six indicates total destruction of all blades.

and stipe counts. Grazing subsequently increased during summer and fall 1975.

The mean value of the grazing estimate for all plants from the entire study period was 1.8 with a standard deviation of 1.9. Clendenning (1971) reported that the blades constitute 62% of the weight of each frond, the balance being stipe and pneumatocysts. 6.0 represented total loss of blades. An average value of 1.8 would thus represent about 19% destruction of net production by grazing fishes. Mann (1973) reported that "herbivores did not consume more than 10% of the net production of the seaweeds" studied near shore in Nova Scotia. Khailov and Burlakova (1969) estimated that about 11% of gross production was consumed by herbivores after studying a macrophyte community in the Barents Sea. Grazing damage by my estimate in Abalone Cove was about twice that reported by these authors. This is probably due to the small size of the Abalone Cove bed in relation to the extensive Palos Verdes coastline.

Estimates of grazer density gathered by belt transect surveys are listed in Table 2.

These data show a high degree of variability. Similar variability is reflected in the reports of other workers who have used the belt transect method. Turner et al. (1964) reported 726 Opaleye/acre from one survey. Quast (1971) found average Opaleye density to be 40 fish/acre

TABLE 2

Density of grazing fishes along 100 meter transect in Abalone Cove 1974-76.

	Opaleye	Halfmoon
average	150 fish/acre	15.8 fish/acre
std. dev.	219 "	20.2 "
maximum	891 "	53.0 "
minimum	11.7 "	0 "

with counts ranging from 0 to 157 per acre after 17 surveys. Miller and Geibel (1973) reported densities of 96.3 Opaleye per acre from 106 surveys in 1969 and 23.9 Opaleye/acre from 73 surveys in 1970. They did not report ranges.

A concerted gill-netting program at Abalone Cove in 1971-72 captured more than 700 Opaleye and 500 Halfmoon during about one year (North, 1973). Numbers of netted fishes cannot be easily compared with densities I measured because the area covered by kelp in 1971-72 was quite small compared to 1974-76. Numbers of Opaleye and Halfmoon caught, however, suggest densities much higher than values I found. The discrepancy might not be real. Possibly large populations were attracted to the small bed in its early days. There were great difficulties in keeping plant populations from being totally destroyed. North

noted that the nets continued to catch grazers even after the populations appeared visually to be very low.

The spatial distribution of Opaleye is stongly influenced by schooling behavior. Opaleye tend to form loose aggregates or swarms. These clusters move unpredictably through kelp beds. Schools favor one locale for several weeks then suddenly shift to a new region. The habit of a shifting congregation rather than an even distribution leads to an erratic sequence of visual counts. The school may not be seen on the transect swim for a few sequential surveys so counts are low. Sometimes the school was encountered away from the visual range of the transect. In such cases samples showed grazing damage but the grazer density estimate was low. Other times swarms were repeatedly found occupying a part of the transect area. High variability resulted, as Table 2 shows.

Fish density might be more accurately estimated if sizes of areas occupied by these roving schools were known. If a characteristic length or area could be established, one could simply be sure to survey a region of adequate size. Attempts to use a photographic technique to measure grazer density turned out to be unsuitable for the turbid conditions normally present in Abalone Cove.

Shifting schooling behavior shown by Opaleye in Abalone Cove is not always seen elsewhere. Opaleye tend to be

solitary where Macrocystis canopies are sparse or absent. They remain close to the bottom, are somewhat sluggish and not particularly shy. In Abalone Cove and other beds where canopies are well-developed but isolated, Opaleye tend to swarm, swim in mid-water, and be very active and quite shy. Where full canopies extend along shore for long distances Opaleye schools seem to be formed less tightly. The fish may hover higher above the bottom, are less active and less affected by divers. These behavior patterns might be responses to kelp bed conditions, or to depth or turbidity or turbulence. They could be seasonal as well as age-related patterns.

CHAPTER III

LABORATORY STUDIES

A. Scope and Objectives

Experiments in this chapter measured losses of Macrocystis tissue to Opaleye grazing. This species, Girella nigricans, is responsible for most of the fish grazing discussed in the previous chapter. Fishes in a tank were fed a variety of Macrocystis tissues. Algal weight changes measured at the end of a feeding period represented grazing damage. Comparison of losses for each tissue type established a preference scale.

B. Methods

Specimen Opaleye Perch, Girella nigricans, were trapped near the end of the Kerckhoff Marine Laboratory pier. They were taken to the laboratory, anesthetized with Quinaldine, tagged, and weighed. Periodic reweighing during their captivity checked on their health.

The fishes were held in a 1.54 cubic meter (roughly 500 gallons) tank lined with white vinyl. They seemed to acclimate quickly to this large aquarium. Similar experiments in tanks of 1/6 this size were unsuccessful because subjects remained unsettled.

Plastic screens covered the tank to protect against vandals and to block some direct sunlight. Filtered sea water flowed continuously into the tank at about 5 gallons per minute. Constant flushing and the sunscreen kept water temperatures in the tank practically equivalent to ambient temperatures of the water source (Newport Bay). Air forced through a porous stone maintained dissolved oxygen levels when water pump failure interrupted normal flushing.

Fresh samples of Macrocystis were collected as needed from the kelp bed at Little Corona Beach near the marine laboratory. Sample fronds were then cut into sections about 1 meter long, a dimension chosen to suit tank scale. The short sections were then sorted into tissue grades. Samples included sporophylls, blades heavily encrusted by hydroids and bryozoans, mildly encrusted blades, clean blades, and growing tips (see Fig. 1). Each sample was then drained for thirty seconds and weighed.

Various combinations of tissue types were presented to the fish to see if some were favored. Approximately equal weights of each type were given to avoid bias. Weighted plastic clips held each piece secure against the Opaleye's jerks and pulls. Plastic mesh isolated controls of each tissue type from grazing pressure.

Feeding periods lasted 1 to 5 days. Kelp samples were removed from the tank, drained, and weighed. Differences, adjusted by changes in controls, gave the amount lost to grazing. Opaleye occasionally tear away pieces larger than bite-size. My concern was Macrocystis damage rather than Opaleye ingestion; so this experiment measured algal weight change whether or not lost material had been completely consumed.

Two sets of experiments involved groups of fish that were held for relatively short times. A third set employed another group for two months. This group received a supplement of frozen squid once every two weeks to insure their continued good health. Diatoms rapidly colonized tank walls and floor providing an additional diet supplement evidenced by profuse "kiss" marks where these growths had been cropped. Diatoms were far outweighed by Macrocystis in the diet.

C. Results and Discussion

Test diets were restricted to Macrocystis and associated epiphytes during 25 separate feeding periods. The mean weight loss corrected for changes in controls was 8.74 grams per fish per day. The standard deviation of these measurements was 5.67 grams per fish per day. Control

plant tissues increased an average of 3.8% per day in weight. (See Appendix for raw data.)

Research on fish feeding has shown that the daily maintenance ration ranges between 1% and 6% of body weight (Lagler, Bardach, and Miller, 1962; Cowey and Sargent, 1972). Larger, more mature individuals grow more slowly; so daily ingestion rates are in the lower half of this range for older fish (Brett, 1970). Individuals used here weighed 236 grams average, ranging from 182 grams to 293 grams. According to Hulbrock (1974) these would be 2 to 3 years old and fully mature. Thus the average 8.74 gr/fish/day equals 3.71 of body weight, a figure in agreement with the literature.

I previously mentioned that bits of kelp were torn away but left uneaten. The agreement of the loss rate with published feeding values tends to support my qualitative impression that these unconsumed fragments were a small fraction of the amount actually ingested. Even though the experiments focused on algal damage, some information has been gained about Opaleye feeding.

On the five occasions when squid was added to the diet, total consumption increased to 7.40% of body weight, i.e. mean 17.4 gr/fish/day and standard deviation 11.47 gr/fish/day. Algae constituted about 20% of the diet chosen by

the grazers. These values bear no relation to Opaleye diet in nature since a highly desirable meat resource is not commonly available. That such a supplement is desirable and unavailable in the sea is easily shown by the feeding frenzy that results when a diver breaks open a sea urchin exposing the delectable entrails.

Body weight of the fishes varied less than 2% during two months of study. All external signs indicated that the captives remained in good health throughout the series of experiments.

McPeak, Stephan, and North (1972) calculated a grazing rate of 100 grams per fish per day in Abalone Cove. They estimated a loss of 4000 kilograms of Macrocystis in 100 days, noting that about 1/2 the blades were stripped from 850 transplants thought to be less than 1 year old. They estimated the grazing population to average 400 fishes on the basis of their extensive gill-netting effort in the cove.

Other measurements of Opaleye populations made by Quast (1971), Turner et al. (1964), Miller and Geibel (1973), and myself (Chapter 2) show a high degree of variability. They were made by the visual belt-transect method which may not be suitable for counting schooling fishes like Opeleye. These data therefore cannot be used to judge McPeak's counts as too high to too low.

Quast (1971) measured an average Opaleye weight of 820 grams with an 11 fish sample. Turner et al. (1964) reported a size range which converts to 66 to 550 grams, based on a visual estimate of the school they encountered in the kelp bed near Canyon de las Encinas. My own experience is that Opaleye in Abalone Cove are of a larger average size than those used in the feeding experiments.

Using Quast's average weight and the grazing rate I measured, Opaleye would have consumed 32 grams per fish per day of the Macrocystis transplanted to Abalone Cove. This is about 1/3 the rate calculated by McPeak et al. It appears that my laboratory findings are well within an order of magnitude agreement with results from the field. This appears to be a satisfactory resolution, considering the uncertainties involved in the estimate by McPeak et al. Opaleye grazing can have a devastating effect on Macrocystis populations that are sparse, isolated, or in a slow growth period.

Table 3 shows Opaleye preferences for types of kelp tissue (raw data in Appendix). Entries in the table represent ratios of tissues chosen when simultaneously available. Each ratio's numerator is described by the column headings. Denominators are classified by row titles. As an example, when growing tips and heavily encrusted blades were given

Table 3. Macrocystis pyrifera tissue preference by grazing Girella nigricans held in aquaria - A/B

A / B	growing tips	clean blades	mildly encrusted blades	heavily encrusted blades	sporophylls
growing tips		0.81	0.55	2.01	0.10
clean blades	1.23		1.08	1.41	0.13
mildly encrusted blades	1.82	0.93		2.98	-
heavily encrusted blades	0.50	0.71	0.34		0.12
sporophylls	10.0	7.62	-	8.22	

at the same time in equal amounts, Opaleye consumed 2.01 times as much encrusted blade as growing tip. Each entry's reciprocal appears in the diagonally symmetric box.

Opaleye consistently chose heavily encrusted blades over other tissue types, supporting the contention that they require the organisms attached to kelp (Quast, 1971; Feder, Turner, and Limbaugh, 1974).

On the other hand, growing tips were preferred slightly over clean or mildly encrusted blades. This explains the impression reported by McPeak et al. (1972) that growing tips were grazed in favor of developed blades if the plants they observed were not heavily encrusted. In such a case the dietary needs fulfilled by encrusters must be found elsewhere.

Sporophylls are the least desirable portion of kelp plants. Sporophylls were compared to growing tips during just one feeding period and were not compared to mildly encrusted blades at all.

In summary, Opaleye preferred heavily encrusted Macrocystis blades. Growing tips were second choice, clean or mildly encrusted blades were third. Sporophylls were least preferred.

CHAPTER IV

STATISTICAL ANALYSIS

A. Scope and Objectives

This chapter develops mathematical relationships between environmental parameters and kelp growth. Equations from multiple linear regression analyses expressed average stipe counts as a function of sunlight, water temperature, fish grazing, and upwelling. Stipe counts and grazing data came from field studies discussed in previous chapters. Light, temperature, and upwelling data from other sources are described below.

The mathematical analysis indicated sense and relative importance of each environmental factor affecting kelp growth. Results were then interpreted in the context of current biological knowledge.

The derived regression equation also served to model a similar Macrocystis population. We hindcasted long-term growth patterns recorded at Point Loma, San Diego County. This exercise validated the analysis and also indicated some of its limits.

B. Methods

Our empirical model related average frond number (F) of a sample Macrocystis population to water temperature (T),

sunlight (L), upwelling (U), and fish grazing (G). I first hypothesized a basic equation of the form:

$$F(t) = aT(t) + bL(t) + cG(t) + dU(t) + k \qquad (1)$$

The coefficients, a, b, c, and d and the bias constant, k, are determined by multiple linear regression analysis (Draper and Smith, 1966). I subsequently modified the basic form (1) to improve the model and to assess the effects of other factors.

Average frond numbers from Abalone Cove (Figure 7) served as measured values of the dependent variable, F, in the regression equation. Regression of the continuous set frond numbers against environmental variables was an attempt to model the vegetative growth history of long-term survivors in Abalone Cove. Such analysis related the growth and aging of a typical plant to the parameters of its surroundings. Regressions using average frond numbers to which samples were added and lost during the study modeled the bedwise growth history. Bedwise models provided some insight into the effects of environment on recruitment and mortality.

Data were rearranged by linear interpolation to fall at regular intervals and were arbitrarily expanded from 23 to 30 points (Figure 10). These manipulations were justified by smoothness of the data and because each point

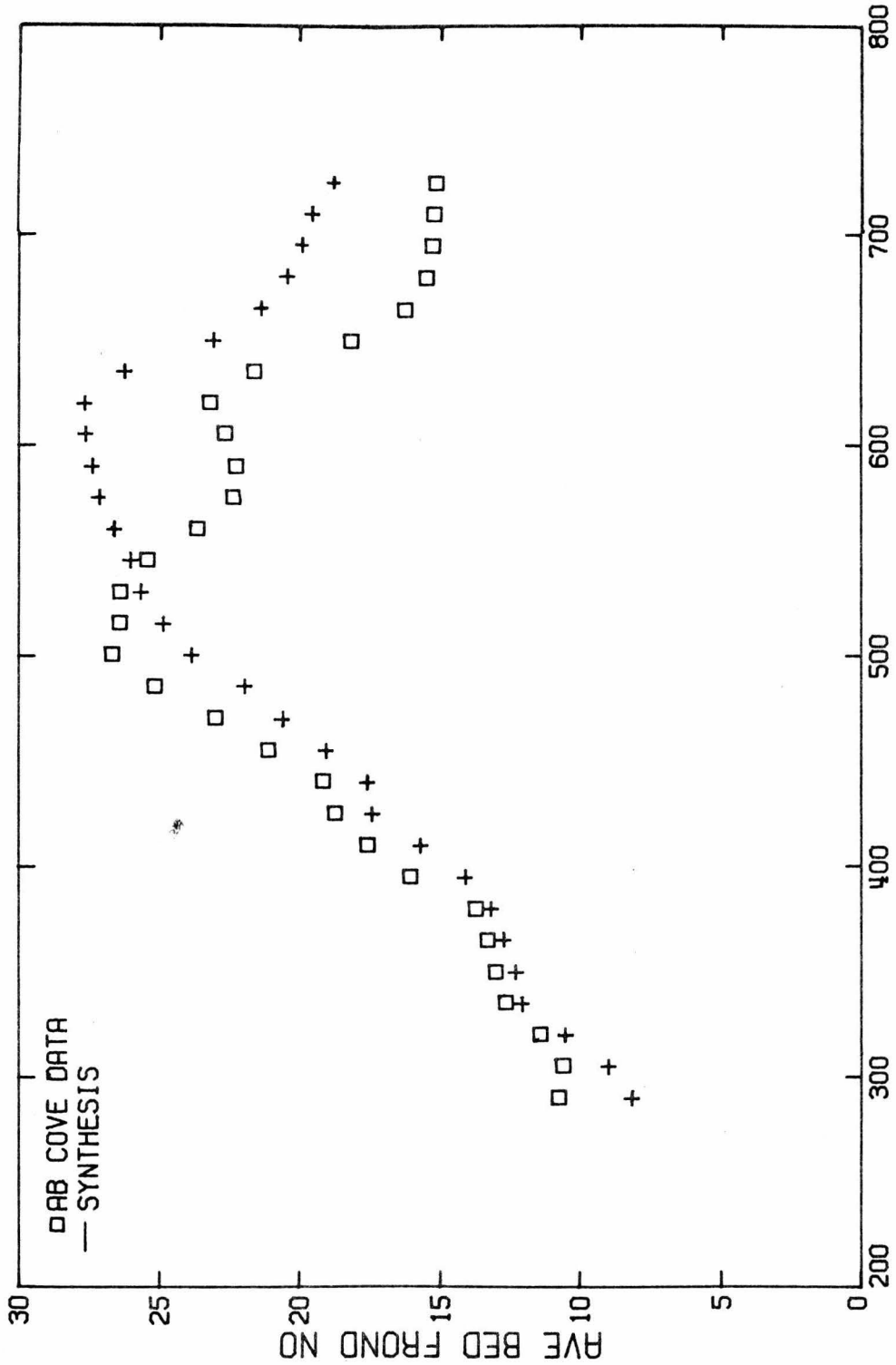


Figure 10. Average frond numbers along a 100 meter transect in Abalone Cove 1974-76. Data shifted by linear interpolation to fall at regular intervals.

was the mean of either 19 or 40 measurements for continuous or samples added data, respectively. Even spacing aided selection of independent variable data, T, L, and U. Increasing numbers of points provided additional degrees of freedom for regression.

Values of T, L, U, and G represented conditions existing in Abalone Cove at the time frond numbers were counted. I estimated grazing while making frond surveys. Temperature, upwelling, and light data were obtained from other researchers. Specific values and preparation of independent variables are described separately below.

Note that time (t) entered equation (1) as an index, relating each frond datum to the appropriate set of independent variable values. The time sequence also kept the analysis in the proper seasonal perspective.

Coefficients and constants were determined by regression after dependent and independent data had been selected. All regression calculations were done by digital computer using library algorithms. The right hand side of (1) was used to calculate synthetic or "predicted" average frond numbers, F'(t), which were then compared to measured values, F(t). Optimum coefficients and constant were determined by least squares, i.e., when

$$\sum_{t} (F(t) - F'(t))^2 = \text{minimum} \qquad (2)$$

The differences between measured and synthetic values, $F(t) - F'(t)$, are called residuals. The constant, k, is chosen so that the residuals have zero mean value. If the basic equation adequately models measured data, distribution patterns of the residuals will not contradict initial assumptions or suggest additional factors. If the residuals are normally distributed, the regression equation accounts for all except purely random variation in actual data. If these conditions were met by (1), for example,

$$F(t) = aT(t) + bL(t) + cG(t) + dU(t) + k + r(0,\sigma) \quad (3)$$

would give a good mathematical representation of the changes shown by the data. The term $r(0,\sigma)$ adds a component taken at random from a normal distribution with mean equal to zero and standard deviation, σ, equal to that of the residuals.

The accumulated environmental history may influence kelp growth. After examining the basic model (3), lag terms such as $T(t - \tau)$ can be added to the analysis to account for previous conditions. Time is divided into discrete elements τ days long.

The environmental variables are not strictly independent of one another. Water temperature is a function of light and upwelling. Upwelling is related to sunlight. Grazing is probably influenced by the other three. In

some cases the information contained in one variable to some extent will be contained in another. Thus it may not be necessary to include every variable in an adequate regression model. Consequently I used a stepwise regression technique to choose those factors which resulted in statistically significant improvement. Alternate forms can result from the stepwise procedure, depending on terms and lags included in the candidate set of variables.

A mathematically satisfactory regression model does not necessarily describe functional relationships. It merely mimics the data. The resultant terms and coefficients must be interpreted in the light of physical and biological knowledge. Alternate forms of the regression showing comparable representation of the data may provide insight into basic factors influencing the dependent variable.

To validate the analysis I applied one form of the regression model to conditions in the Point Loma kelp bed (San Diego County) from 1950 to 1969. During this period some distinct changes in the canopy occurred. Unusual temperature patterns were also recorded. I used the coefficients from the Abalone Cove regression along with pertinent independent variables for San Diego to hindcast a sequence of average frond numbers. Comparison of actual

records with calculated values confirmed some usefulness for the model and showed some of its limitations.

C. Independent Variables

1. Water temperature

Ideally, complete characterization of the temperature regime in Abalone Cove was desirable. Continuous, long-term monitoring was beyond my resources. Scripps Institution of Oceanography (SIO), however, measured surface water temperatures each morning at Santa Monica Pier for the period of interest (Figure 11). This site is about 28 kilometers north of Abalone Cove. List and Koh (1976) have demonstrated that lower frequency variations which are pertinent to this study, show highly correlated temperature behavior for two sites of this proximity. SIO also monitors temperatures much closer to the study site in Los Angeles Harbor. Limited water circulation and considerable human influence make these data less suitable.

Mean temperature at Santa Monica during 1975 was 15.5 degrees centigrade. The 18 year average from 1956 to 1973 was 16.4 degrees. Monthly means indicate that the entire study period was colder by about one degree than expected from earlier averages. Thus the pattern shown by data of Figure 11 can be considered typical but slightly cooler than normal. Kelp tends to grow better in cold water, so my values for average frond numbers may represent

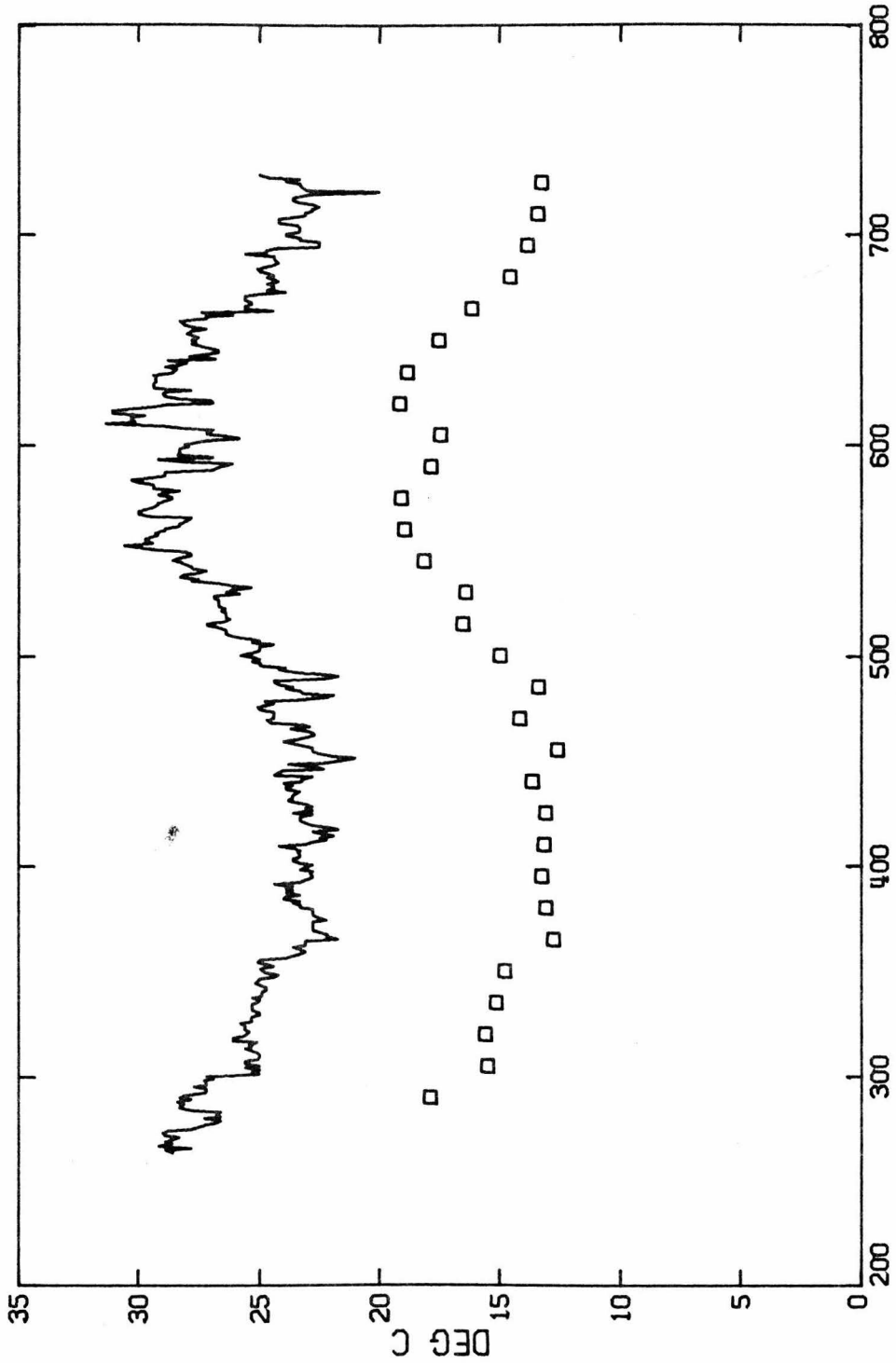


Figure 11. Surface water temperature at Santa Monica Pier, 1974-76. Solid curve, shifted up 10 deg C for display, shows daily measurements. Squares indicate digitally filtered values selected for regression purposes.

excellent environmental conditions. Variations due to extreme temperatures, however, are not expected.

The daily record of Figure 11 shows two characteristics described as typical by List and Koh (1976). Fluctuations tend to have greater amplitude in summer than winter. In addition a slight warming in mid-winter (days 350 to 400) often occurs in Southern California waters.

Abalone Cove is regarded as a local upwelling site (North, 1974). Santa Monica temperature data might not reflect upwelling conditions 28 kilometers to the south. This inadequacy should be eliminated by inclusion of upwelling indexes as an independent variable in the regression.

The daily temperature data contain unknown sampling errors. Any regular, discrete sampling of a continuous phenomenon introduces frequency aliases (Bendat and Piersol, 1971). Frequencies higher than one-half the sampling frequency will be confused with lower frequencies in the sample record. A visual example is the apparent reverse spin of a wheel in motion pictures. Temperature was measured once per day so that the folding or Nyquist frequency of the SIO data is 0.5 cycles per day. This is the highest frequency that can be defined by the data. Any temperature patterns occurring at frequencies higher than this will appear in the data but be confused with lower

frequency patterns. This could be a serious problem for temperature changes associated with internal waves (Summers and Emery, 1963).

Because energy of the aliased frequencies is also folded about the Nyquist frequency, some of the errors can be removed by digital filtering of the daily record. Low-pass filtering smooths the data removing a frequency band where aliasing is most likely.

Lowpass filtering also helps to justify use of Santa Monica Pier temperatures to describe Abalone Cove some distance away (List and Koh, 1976).

Smoothing the daily data is also desirable from biological considerations. While water temperature continuously influences kelp growth, it is unlikely that rapid fluctuations will influence frond counts. Some other measure of plant growth such as photosynthesis might show significant daily variation. But Figure 10 shows that average frond number varies noticeably only after many days or weeks.

Daily SIO temperature data were modified by a lowpass digital filter with half-power cutoff frequency of 1.43×10^{-2} cycles per day. In other words, the smoothed data contain only those temperature fluctuations occurring with a period greater than 21 days (reciprocal of half-power cutoff frequency).

Thirty points were chosen from the smoothed data (Figure 11) corresponding in time to the thirty points of the average frond count record (Figure 10). These temperature data were used in regression analyses to characterize water temperature regimes in Abalone Cove during my frond count surveys.

2. Sunlight

The United States Weather Bureau monitors ground-level solar radiation at Los Angeles International Airport. Cumulative daily values (obtained from the National Climatic Center of the National Weather Service, Asheville, North Carolina) are given in Langleys per day (Figure 12). These measurements were made approximately 21 kilometers north of Abalone Cove. As with temperature, only lower frequency components were pertinent to this analysis. It is thus assumed that these data correlate well with conditions at the study site.

These data correspond closely to sunlight variations recorded at the same site for the previous twenty years (Goodridge, 1973). Mean daily radiation in 1975 was 448 Langleys per day, exactly equal to the daily average from 1953 to 1973. Variations during the study period were qualitatively similar to earlier records. The depression seen in June (days 516 to 546) is a common phenomenon in Southern California. Daily averages for each month of our

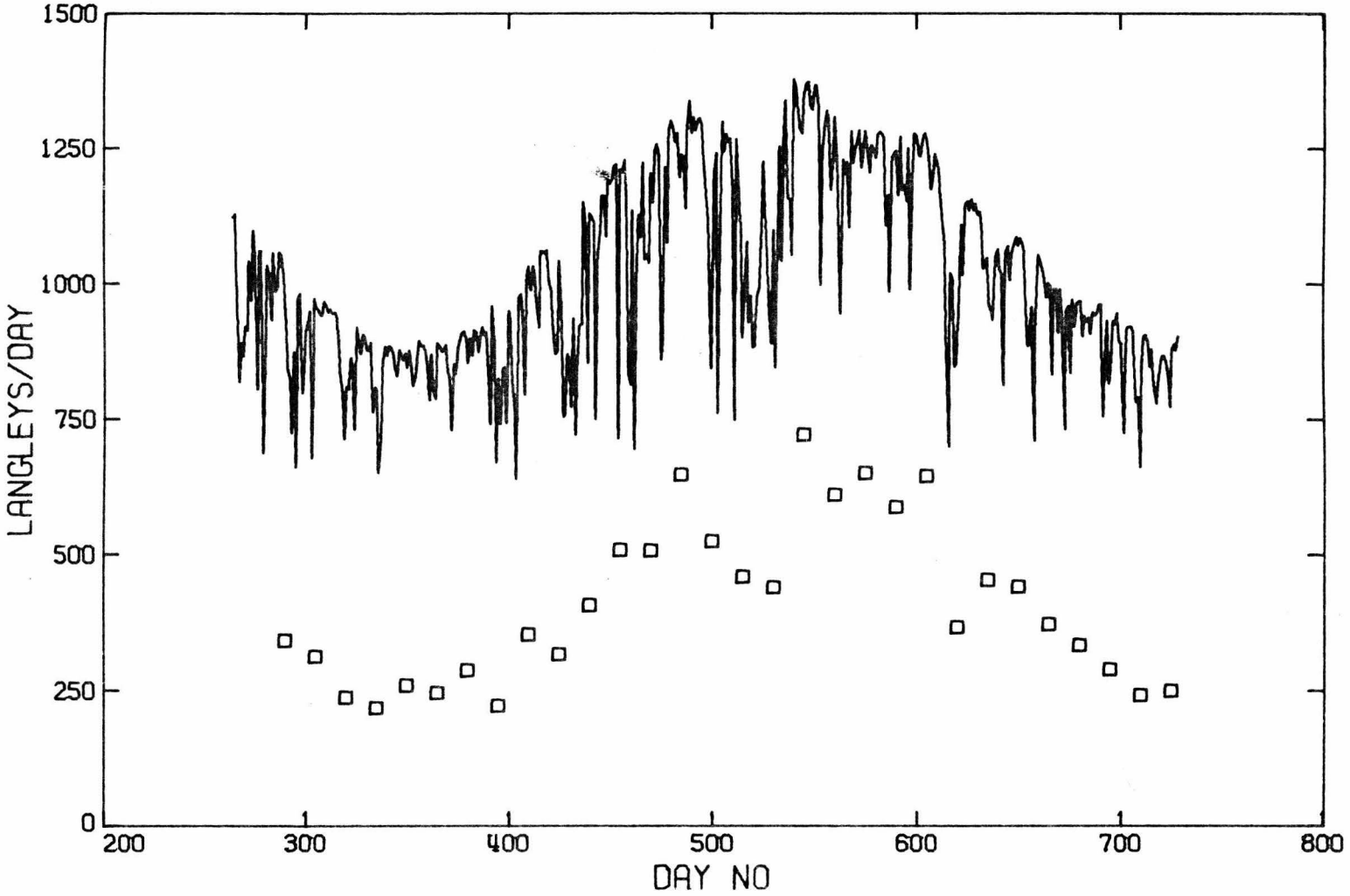


Figure 12. Solar radiation at ground level measured at Los Angeles International Airport by the U.S. Weather Bureau, 1974-76. Solid curve, shifted up 600 Langleys per day, shows daily values. Squares indicate lowpass filtered values selected for regression purposes.

study were within a few percent of values from previous years. Thus the study period can be considered typical in terms of sunlight.

Because daily radiation is not a continuous parameter, frequency aliasing is not a problem. As with temperature, digital filtering that removes high frequency components helps make the light data applicable to Abalone Cove, 21 kilometers from the recording site. Average frond numbers, furthermore, do not reflect short-term fluctuations. Daily radiation data were treated with a lowpass digital filter with half-power cutoff frequency of 1.43×10^{-2} cycles per day (as applied to temperature data). Smoothed sunlight data thus included only variations with periods greater than 21 days.

The regression used thirty points from the filtered radiation data (Figure 12) corresponding in time to the average frond count record (Figure 10).

3. Grazing

Grazing was estimated in Abalone Cove at the same time that fronds were counted. Average estimates discussed in Chapter II (Figure 9) were rearranged by linear interpolation (Figure 13) to correspond to the frond count record used in the regression analysis (Figure 10). Plantwise

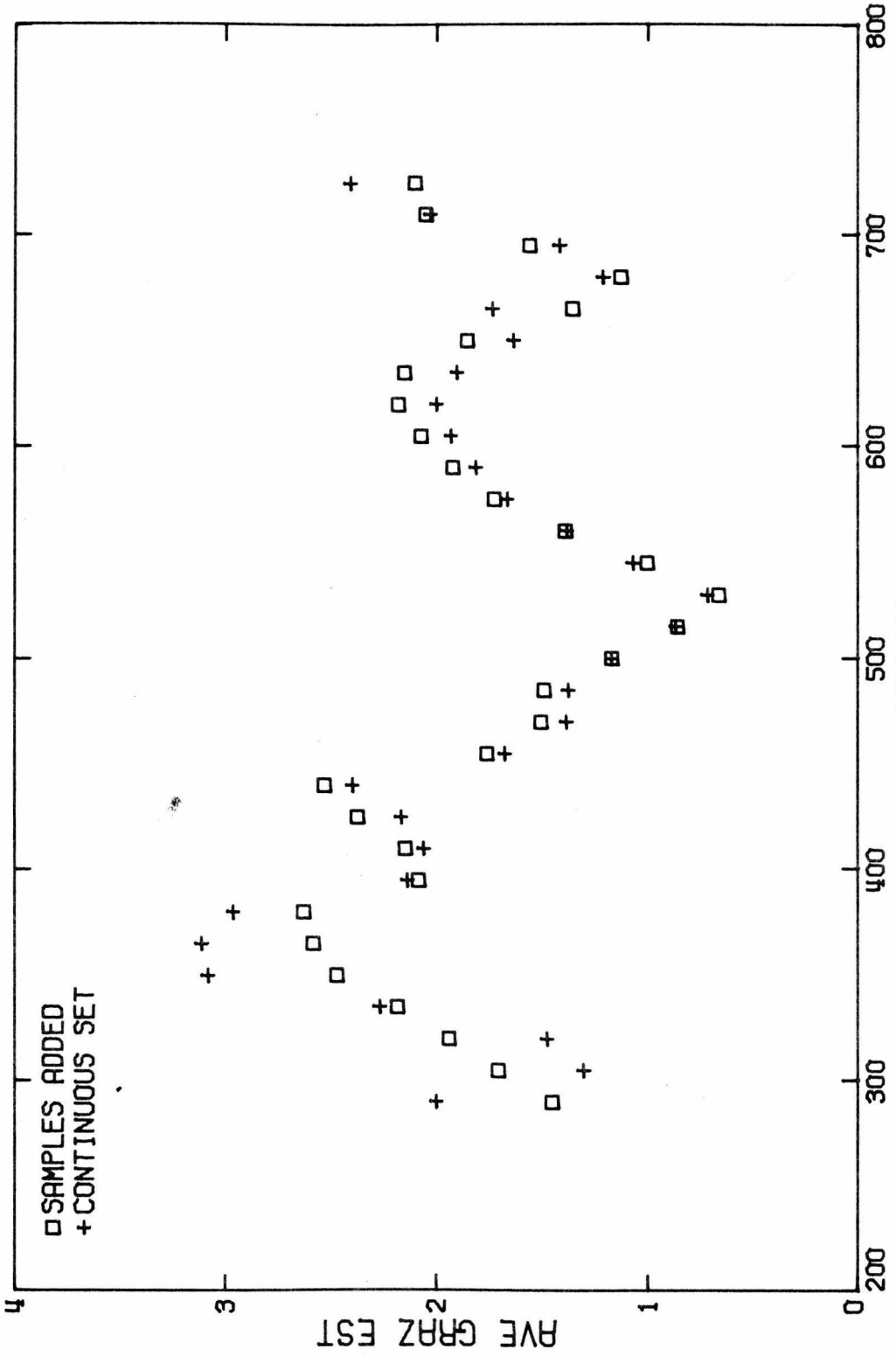


Figure 13. Average grazing estimates for Abalone Cove (see Figure 9) rearranged by linear interpolation to fall at equal time intervals.

(continuous set) and bedwise (samples added) averages were applied to appropriate frond number averages.

4. Upwelling

Variations in nutrient availability presumably have significant consequences for kelp growth. Spatial and frequency characteristics of these fluctuations in the sea are not available. Some general patterns, however, are known. Nitrates, phosphates, and other nutrients necessary for photosynthetic growth show higher concentrations below the euphotic zone. Thus periods or regions experiencing strong upwelling are usually characterized by high primary productivity (Wyrtki, Stroup, Patzert, Williams, and Quinn, 1976). California coastal waters, in fact, show this phenomenon (Kamykowski, 1974; Eppley, Sapienza, and Renger, 1976). Upwelled water can also contain trace constituents such as heavy metals which might have beneficial or deleterious effects depending on concentrations (Morgan and Jackson, in review).

Upwelling is an ocean current pattern resulting from winds. "Water in the surface layer of the ocean is driven offshore by the action of the wind, requiring replacement at the coast by upwelling of deeper water. Bakun (1973) computed monthly indices of wind induced coastal upwelling using surface atmospheric pressure fields to estimate the sea surface wind stress field" (Bakun, 1976). The

oceanographic theory behind these calculations was first developed in the early 1900's and is now referred to as Ekman transport theory (Sverdrup, Johnson, and Fleming, 1946). Smith's (1974) measurements of low-frequency upwelling currents on the Oregon continental shelf confirmed Bakun's index as a valid descriptor of broad scale upwelling.

The relationship between nutrient availability and deep water upwelling is yet another matter. Although nutrients generally increase with depth, there are still temporal and spatial variations. Furthermore, the fate of upwelled nutrients is complicated by advective mixing and biological uptake (Jackson, 1975).

The following regression analyses use Bakun's upwelling indices as an independent variable. Any correspondence between seasonal upwelling and kelp growth patterns must be carefully interpreted. The upwelling index is a theoretical estimate of deep water transport into shallower depths where kelp grows. When current research clarifies the relationship between upwelling and nutrient availability, these analyses can be interpreted in terms of nutrient variations.

Upwelling indices for the study period were supplied by Bakun as unpublished values (Figure 14). They refer to

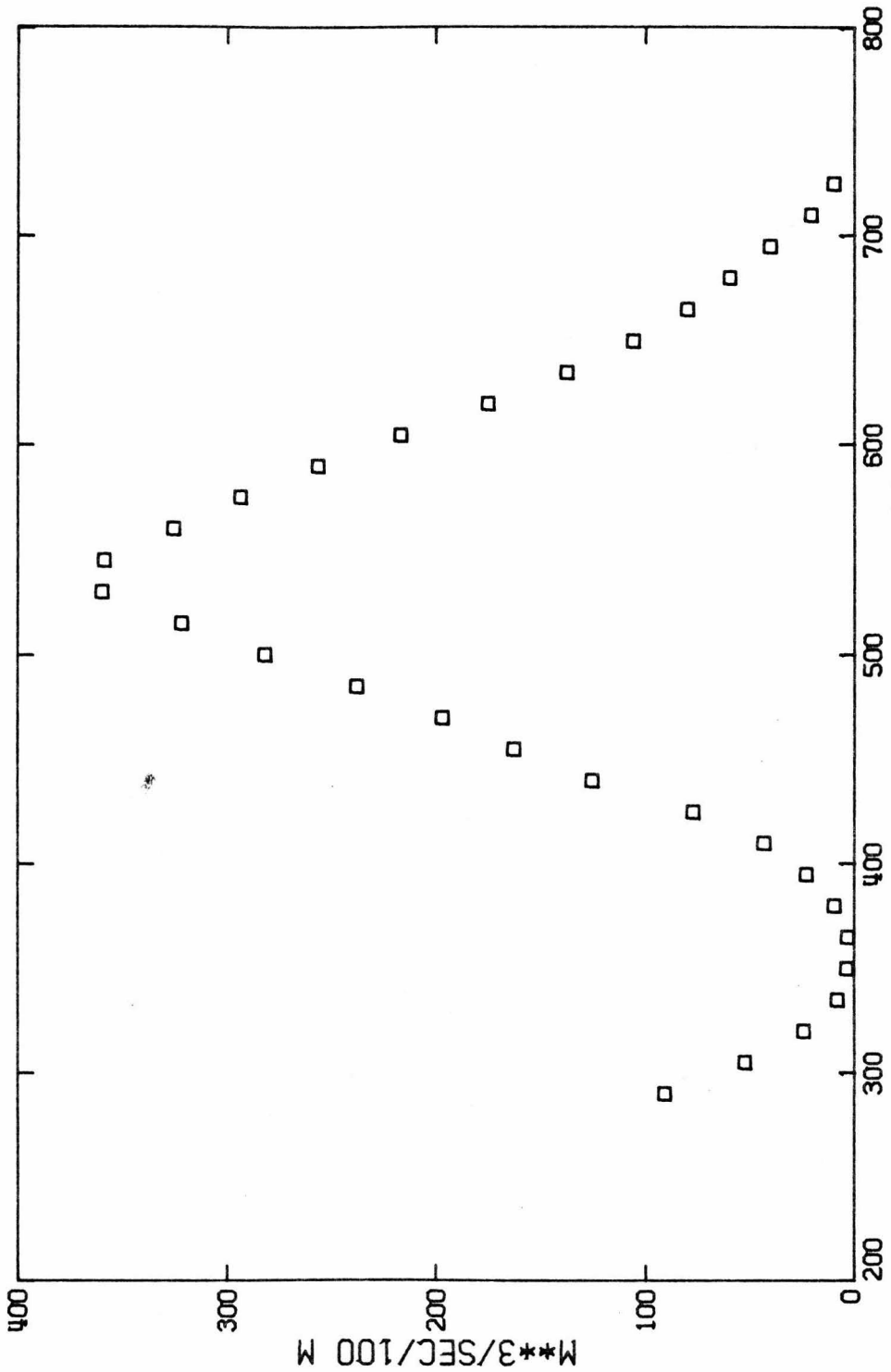


Figure 14. Monthly mean upwelling index at 33N, 119W, 1974-75. Rearranged by linear interpolation to correspond to regression intervals. (Values from Bakun, unpublished.)

a point off the southern California coast at lat. 33N, long. 119W. Units are metric tons per second per 100 meters of coastline. Indices indicate the average amount of water upwelled through the mixed layer each second along each 100 meters parallel to the coast. Due to theoretical uncertainties, magnitudes should not be considered as quantitative measures. They can be taken as indications of relative upwelling intensity in the area from one time to the next. Absolute magnitudes are not needed for the regressions.

Upwelling indices are calculated as monthly means. They are thus low frequency fluctuations as required by this analysis. Unlike temperature and sunlight data, upwelling values need no smoothing. Data were shifted by linear interpolation from mid-month timing to the spacing used in the regression. Likewise reduction from 30 day to 21 day spacing required an increase in the number of points. Some intermediate frequency variations (with periods between 21 and 30 days) may have been lost but monthly values were the best available.

The atmospheric conditions producing upwelling act across a broad geographic scale. Submarine topography and coastal orientation, especially in relation to dominant current patterns, could also influence upwelling behavior

at specific sites such as Abalone Cove. Geographical factors are constants. Site to site variation in the upwelling index will thus be consistent over time.

Annual average upwelling in 1975 was 17% greater than the annual average in the 20 years from 1948 to 1967. Values were less than corresponding monthly values during previous years only during 1974-75 winter months. Thus the study period was characterized by persistently higher upwelling than normal, a pattern supported by temperature data.

Table 4 lists numerical values of dependent and independent variables used in the regression analysis.

D. Analysis and discussion

1. Plantwise regressions.

The first model to be tested was proposed earlier in this chapter as equation (1):

$$F_P(t) = aT(t) + bL(t) + cG(t) + dU(t) + k \qquad (1)$$

The subscript P identifies average frond numbers from plants persisting throughout the study (Figure 10), the continuous set. The method of least squares produced the following coefficients and constant using data from Table 4.

a = 0.432

b = 0.0108

c = 0.196

d = 0.0232

k = 5.08

Table 4. Numerical values of dependent and independent variables used throughout regression analyses.

Day no.	Plantwise avg. frond no.	Bedwise avg. frond no.	Plantwise avg. graz. no.	Bedwise avg. graz. no.	Upw. index	Temp.	Light	Survivability
290	8.20	10.7	2.00	1.44	91.0	17.9	343.	100.
305	9.03	10.6	1.30	1.70	52.3	15.5	313.	96.5
320	10.5	11.4	1.47	1.94	24.5	15.6	237.	95.5
335	12.1	12.6	2.27	2.19	8.25	15.1	218.	93.2
350	12.3	13.0	3.08	2.47	3.75	14.8	260.	81.9
365	12.7	13.3	3.12	2.58	3.63	12.8	245.	77.1
380	13.2	13.7	2.96	2.63	10.0	13.1	288.	73.7
395	14.1	16.1	2.14	2.08	23.3	13.2	221.	75.9
410	15.8	17.6	2.06	2.15	43.4	13.1	354.	75.7
425	17.5	18.8	2.18	2.37	77.6	13.1	317.	74.7
440	17.6	19.1	2.40	2.53	126.	13.6	407.	69.4
455	19.1	21.1	1.67	1.76	162.	12.6	508.	68.0
470	20.6	23.0	1.38	1.50	197.	14.2	507.	64.8
485	22.0	25.2	1.37	1.48	238.	13.4	648.	61.5
500	23.9	26.7	1.17	1.17	282.	15.0	524.	61.2
515	24.9	26.4	0.865	0.856	322.	16.6	459.	60.1
530	25.7	26.4	0.714	0.662	360.	16.4	440.	59.4
545	26.0	25.4	1.07	1.00	358.	18.2	722.	59.6

Table 4 (Continued)

Day no.	Plantwise avg. frond no.	Bedwise avg. frond no.	Plantwise avg. graz. no.	Bedwise avg. graz. no.	Upw. index	Temp.	Light	Surviv-ability
560	26.6	23.7	1.38	1.38	325.	19.0	609.	59.5
575	27.1	22.4	1.66	1.72	294.	19.1	650.	58.6
590	27.4	22.3	1.81	1.92	256.	17.9	586.	56.0
605	27.6	22.7	1.93	2.08	217.	17.5	645.	52.6
620	27.6	23.2	2.00	2.18	175.	19.2	366.	49.1
635	26.2	21.6	1.90	2.15	138.	18.8	454.	49.4
650	23.1	18.2	1.63	1.85	106.	17.5	441.	53.6
665	21.4	16.3	1.73	1.35	79.9	16.1	372.	57.1
680	20.4	15.5	1.21	1.13	59.6	14.5	333.	56.6
695	20.0	15.3	1.41	1.56	40.2	13.8	289.	55.8
710	19.5	15.3	2.03	2.05	20.9	13.4	241.	55.3
725	18.7	1.52	2.41	2.11	10.0	13.2	249.	55.1

Average plantwise frond numbers synthesized with these coefficients and the same independent variables gave an unsatisfactory representation of the Abalone Cove observations. Only 62.4% of the variance in the data was accounted for by the fitted values ($R^2 = 0.624$).

The residuals from this model, the differences between each datum and its corresponding synthesized value, showed a distinct dependence on time. Frond numbers were overestimated in the early months and underestimated later. Some information related to time was not explained by this regression form. I tried an equation including time, represented by day number, as another independent variable:

$$F_p(t) = aT(t) + bL(t) + cG(t) + dU(t) + et + k \qquad (4)$$

In this case coefficients producing a least squares fit were:

a = 0.130

b = 0.00288

c = 0.192

d = 0.0336

e = 0.0275

k = -5.54

This model gave a much closer fit, explaining 93.6% of observed variance. Residuals now had an approximately

normal distribution, and showed no dependence on any model parameter or any other systematic pattern.

It is difficult to compare coefficients directly because of differing units and scales associated with each independent variable. Standard statistical tests for significance of coefficients indicate the validity and relative importance of each term. Differences between observed and fitted values must be normally distributed with mean zero to apply t-tests to residuals. Residuals from this model approximated a straight line when plotted on standard probability axes. Thus t-variables can be validly calculated:

$t_a = 0.834$

$t_b = 0.730$

$t_c = 2.93$

$t_d = 5.70$

$t_e = 12.1$

There were 30 data points and 5 independent variables giving 24 degrees of freedom. At the 95% confidence level t must be greater than 2.06. Thus we cannot reject the hypotheses that a=0 and b=0 based on available data. In other words, water temperature and sunlight could be eliminated from this model as statistically insignificant. An equivalent regression equation was therefore:

$$F_p(t) = cG(t) + dU(t) + et + k \qquad (5)$$

Coefficients change somewhat in the absence of temperature and sunlight data to:

$c = 2.07$

$d = 0.0385$

$e = 0.0281$

$k = -3.57$

Average frond numbers synthesized with this equation are plotted in Figure 15 in comparison with Abalone Cove values. Coefficient values and parameter magnitudes imply that each factor shared a different proportion in modelling plantwise frond numbers. Relative importance of each coefficient in explaining observed variance was:

$C_G = 3.32\%$

$C_U = 46.3\%$

$C_t = 50.3\%$

About half the change in size of surviving plants was apparently due to linear increase with time. Not surprisingly the plants grew. In addition to the increase with time there is a variation of roughly the same magnitude which is highly correlated with Bakun's upwelling index. Grazing estimates added a small but significant improvement to the model.

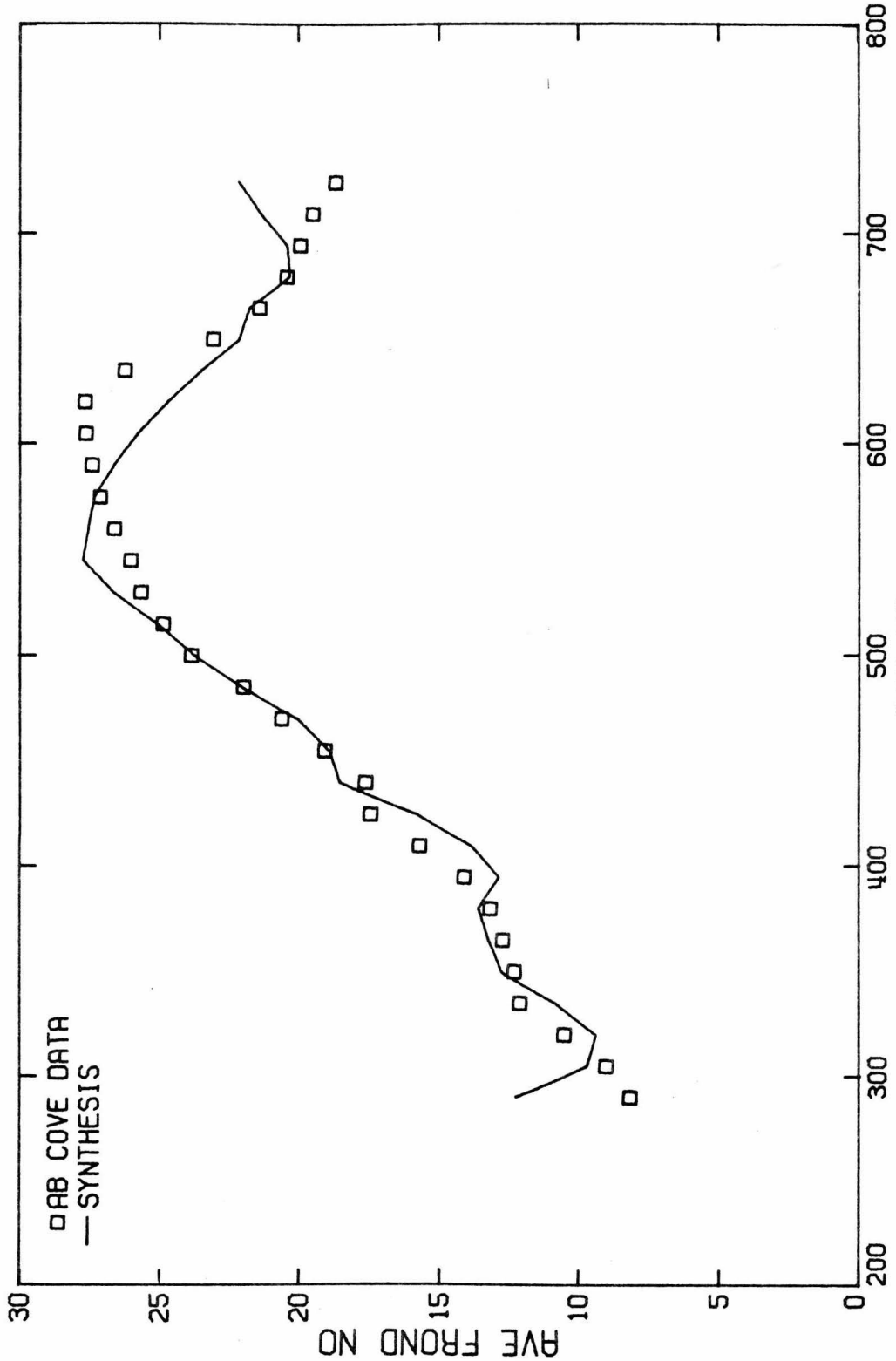


Figure 15. Average plantwise frond numbers fitted by regression equation (5)
$F_p(t) = cG(t)+dU(t)+et+k.$

Environmental variables might have had a delayed effect on kelp growth. A model of the form:

$$F_p(t) = aT(t) + bL(t) + cG(t) + dU(t) + et + fT(t-\tau) + gL(t-\tau) + hG(t-\tau) + iU(t-\tau) + k \quad (6)$$

might provide a closer representation of growth data. Here the independent variables included water temperature during the observation period, $T(t)$, as well as temperature during the previous period, $T(t-\tau)$ where τ is the time between observations. Light, grazing, and upwelling index for the previous period are also included.

Some terms in the proposed model will contribute significantly to the regression while others will not. Terms with no statistical value complicate calculations and interpretation of results. A modified statistical procedure called stepwise regression made it possible to choose from a candidate set only those independent variables making significant contributions. The eight variables on the right side of (6) were considered candidates.

The best regression form that included only independent variables significant at the 95% level (by partial F-test of the least significant variable included) was:

$$F_p(t) = aT(t) + dU(t) + hG(t-\tau) + et + k \quad (7)$$

with:

$a = 0.455$

$d = 0.0329$

$h = 1.96$

$e = 0.0252$

$k = -7.95$

This regression form gave a slight improvement in fit as shown in Figure 16. Here 95.6% of observed variance was reproduced by synthesized values.

Contributions made by each term were:

$C_T = 3.33\%$

$C_U = 44.3\%$

$C_G = 4.29\%$

$C_t = 48.1\%$

Time and upwelling were again used in about equal proportions to model most of the variance. Grazing was again included in a small but significant way. Grazing estimated during the previous time period was used in preference to more recent values. Water temperature, referred to the current time period, was now included in small proportion with the other variables to provide a statistically significant improvement in fit.

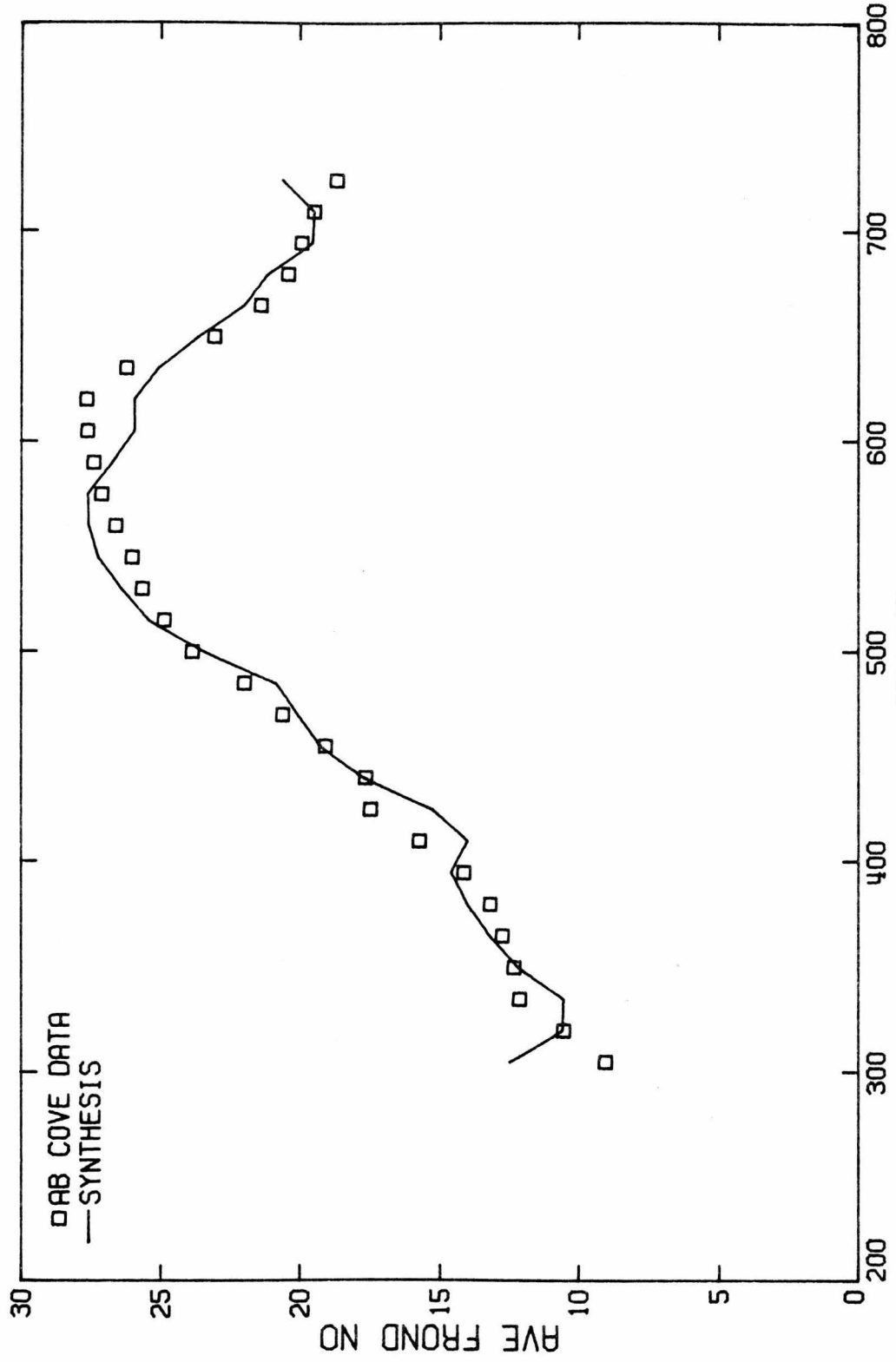


Figure 16. Average plantwise frond numbers fitted by regression equation (7)
$F_p(t) = aT(t)+dU(t)+hG(t-\tau)+et+k$.

2. Bedwise regressions

Bedwise average frond numbers (noted in Figure 10 as samples added) were the dependent variable for further regressions based on equation (1). A linear time factor was added to the basic form as had been done with plantwise analyses:

$$F_B(t) = aT(t) + bL(t) + cG(t) + dU(t) + et + k \qquad (8)$$

The subscript B identifies bedwise frond numbers. Least squares coefficients with data from Table 4 were:

$a = -0.653$

$b = -0.00310$

$c = 2.53$

$d = 0.0534$

$e = 0.00963$

$k = 13.4$

This model's correlation coefficient was $R^2 = 0.916$; so the fit was good. Residuals showed a roughly normal distribution justifying the calculation of t-variables to test the significance of coefficients.

$t_a = 4.33$

$t_b = 0.788$

$t_c = 3.42$

$t_d = 8.90$

$t_e = 4.39$

With 24 degrees of freedom, t greater than 2.06 is required for acceptance at the 95% level. We therefore cannot reject the hypothesis that b=0. Sunlight data did not contribute significantly to this regression as was the case with plantwise data.

It was difficult to justify the linear term in time. The term added a straight line component which geometrically rotated synthesized values counterclockwise, improving the model fit. This suggested physically, however, that frond number of the bed as a whole would increase indefinitely. The steady increase of the plantwise frond number is acceptable because a plant's life is limited. The life of a bed should be much longer if not indefinite. Whereas a plant might show steady growth over its lifespan, frond density in the bed should level off. The physical mechanism for reducing bedwise frond numbers was shown previously to be related to the mortality of large individuals and replacement by succeeding generations.

I replaced time as an independent variable in the regression equation with a variable termed "survivability." Survivability was defined as 100 times the number of tagged plants surviving at any observation time divided by the total number of plants tagged up to that time, expressed as a percentage. Survivability among Abalone Cove samples

was plotted versus time in Figure 17. This function represented a concise history of plant loss and sample addition for our study.

The analysis using equation (8) with survivability (S) replacing time (t) resulted in normally distributed residuals, allowing valid calculation of t-variables. The coefficient b in the sunlight term proved insignificant at the 95% level. Thus the equation:

$$F_B(t) = aT(t) + cG(t) + dU(t) + eS(t) + k \qquad (9)$$

provided a good fit ($R^2 = 0.937$) without the problem of continuing increase with time. Thus, synthetic frond numbers slightly more closely resembled Abalone Cove values (Figure 18) compared to the linear time factor. Least squares coefficients for this model were:

$a = -0.550$

$c = 1.53$

$d = 0.0424$

$e = -0.109$

$k = 26.0$

Contributions of each term were:

$C_T = 7.74\%$

$C_G = 2.78\%$

$C_U = 74.2\%$

$C_S = 15.2\%$

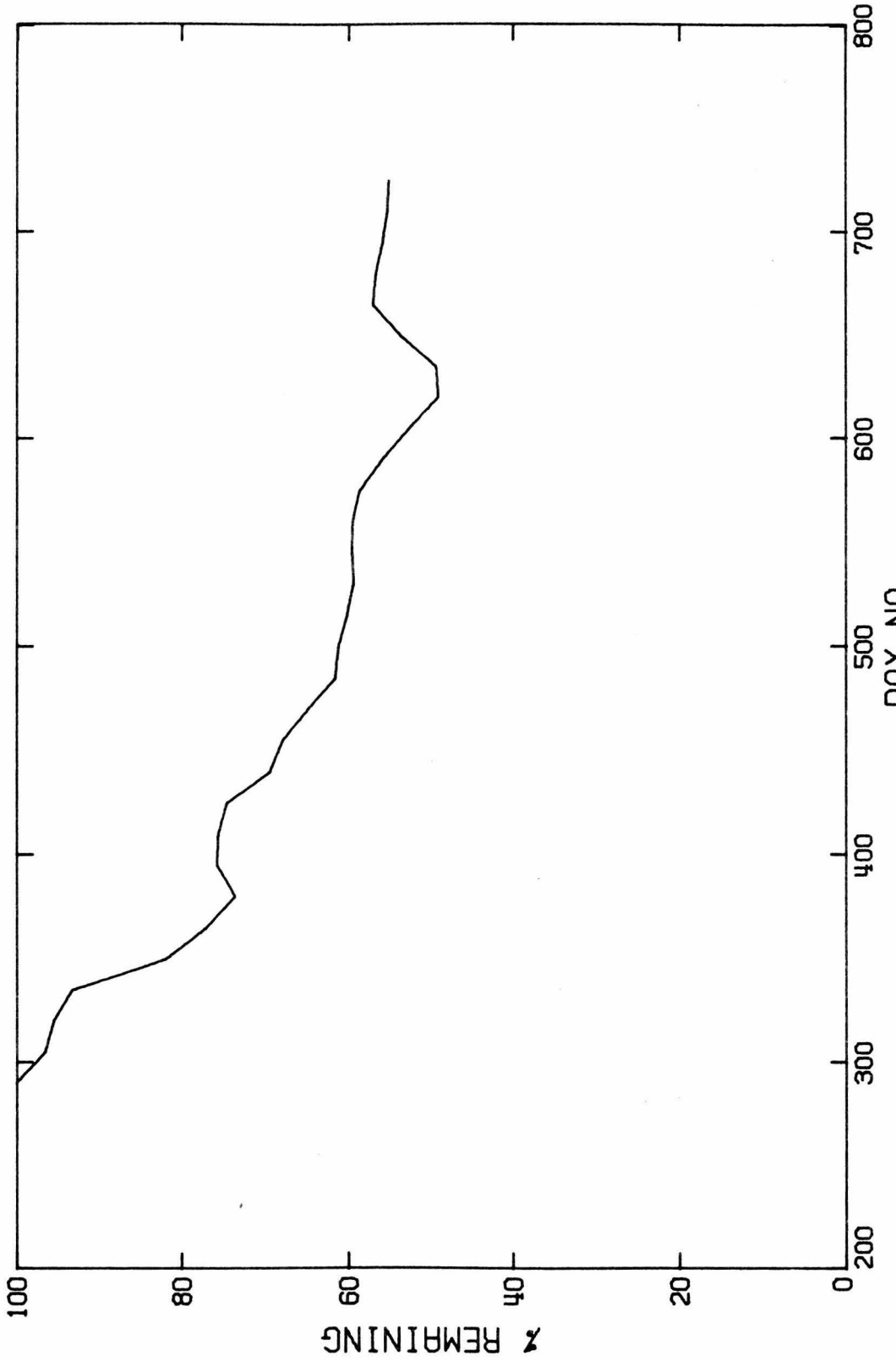


Figure 17. Abalone Cove survivability function (see text for definition).

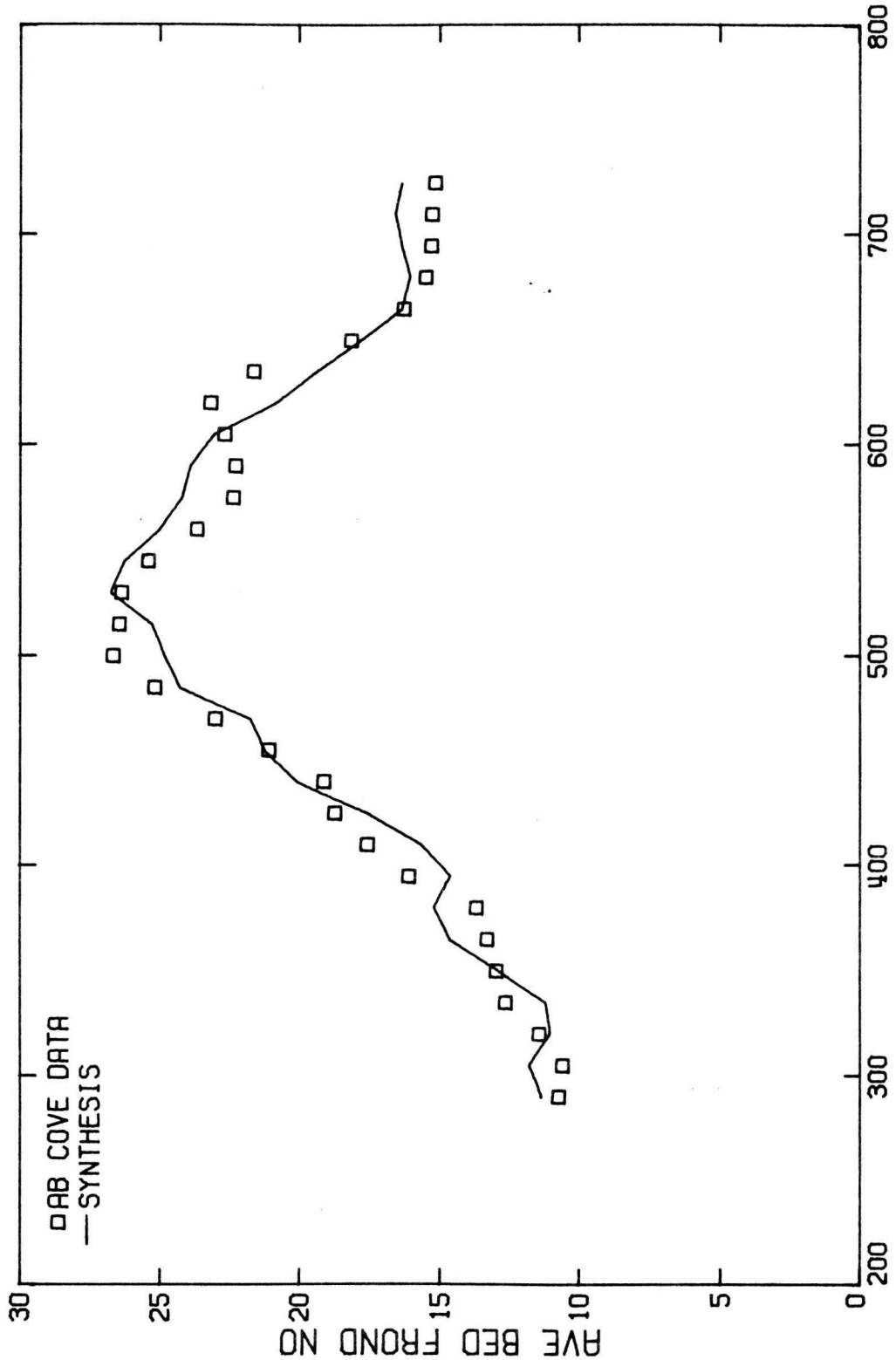


Figure 18. Abalone Cove bedwise frond numbers fitted by regression equation (9) $F_B(t) = aT(t)+cG(t)+dU(t)+eS(t)+k$.

Upwelling index played the dominant role in the synthesis of theoretical frond numbers. Survival function was next most important at about 15% of the overall mixture. Water temperature came in at a still smaller proportion. Grazing estimates accounted for less than 3% of the composite.

3. Interpretation

Multiple linear regression analysis established three satisfactory models (Table 5) of kelp growth observed in Abalone Cove. More than 90% of the variation in average frond numbers was reproduced by these mathematical forms for both plantwise and bedwise statistics. Regression is an abstract technique, identifying statistical similarities. It does not prove physical relationships, but it can suggest biological mechanisms or support those already suspected.

Bakun's (1976) upwelling index contributed a large fraction of the theoretical composite in all three models. The upwelling term had a positive coefficient for both plantwise and bedwise models, indicating that increasing frond production correlated with periods of strong upwelling.

A linear time function was very influential in describing the growth of individual plants. It provided about half the shape of these models. This could be a first

TABLE 5

Regression models (5), (7), and (9) with percent contributions of significant terms	R^2
$F_P(t) = 0.0385\ U(t) + 2.07\ G(t) + 0.0281\ t - 3.57$ 46.3 3.32 50.3	0.933
$F_P(t) = 0.0329\ U(t) + 1.96\ G(t-\tau) + 0.455\ T(t) + 0.0252\ t - 7.95$ 44.3 4.29 3.33 48.1	0.956
$F_B(t) = 0.0424\ U(t) + 1.53\ G(t) - 0.550\ T(t) - 0.109\ S(t) + 26.0$ 74.2 2.78 7.74 15.2	0.937

approximation or a coarse substitute for the standard S-shaped growth curve mentioned in Chapter II. It seemed likely that individual plants in a constant, adequate environment would follow an exponential growth pattern. Fluctuations in the environment would then cause deviations from the ideal shape. Attempts to match individual plant histories to an idealized growth curve were unsuccessful as discussed previously. Success with regression analysis and its emphasis on steady growth with time revives the idea of a standard plant growth pattern and recommends further study of the question.

Survivability data provided a time substitute for modelling frond numbers in the bed as a whole. Its influence was less important than in the plantwise models. The survivability coefficient was negative because higher frond numbers corresponded to lower survivability values. When new plants were added to the sample, survivability was declining due to plant losses made up by addition of new specimens. This replacement tended to reduce stipe counts. In other words, about 15% of the shape of the bedwise frond number history was attributable to the replacement of lost samples with new, smaller individuals.

Fish grazing estimates added 3 to 4 percent to the theoretical mixture in each case. Each grazing term coefficient was positive. Larger grazing values

corresponded to improved growth of both individual plants and overall bed averages. Higher estimates from Abalone Cove were less than 3 on a scale of 0 to 6 (Figure 13). Such moderate values might well be beneficial. As shown in Chapter III, Opaleye in aquaria fed preferentially on older, heavily encrusted blades. If the same behavior occurred in the field, Opaleye might perform a pruning service. Removal of older, encrusted tissue would enhance light penetration to clean, more highly productive parts. North and Hubbs (1968) mentioned the possibility that kelp canopy harvesting similarly improved productivity by allowing better light penetration.

Plantwise growth simulations were improved when grazing data were shifted backwards for one time period. The lag between tissue removal and the appearance of new fronds was consistent with the pruning effect and a delay introduced by our procedures (new fronds entered the counts only after they reached one meter above the holdfast).

Sunlight was conspicuous by its absence from the models. Kelp obviously requires light for growth, but the mathematics did not require sunlight data to reproduce growth data, at least not when the other independent variables were provided. Sunlight data and upwelling index were well correlated with each other (r_{UL} = 0.870), both

showing seasonal peaks in summer and low values in winter. Upwelling index thus provided much the same information as sunlight data would. Upwelling data apparently had a marginal advantage over sunlight so that it was preferentially included in the models and sunlight became mathematically superfluous. It is also possible that the difference between light available on sunny days and on short or cloudy days is less important to kelp growth than the difference between the effects of strong and weak upwelling.

Water temperature and upwelling index were not highly correlated ($r_{UT} = 0.598$), even though upwelling can strongly affect temperatures. Currents and climatic factors both locally and at great distances influence water temperatures. Thus there would be temperature variations from season to season in Abalone Cove even in the absence of local upwelling.

Water temperature data played a significant role in plantwise simulation only when lagged grazing data were included. The coefficient was positive, matching warm water with faster plant growth. The temperature term was negative in the bedwise model, on the other hand, matching cold water with increasing frond counts in the bed as a whole. North (1971) showed higher vegetative growth in

warm water, although extremely warm water can be harmful. Several investigators (McPeak, 1973; North, 1974; Foster, 1975) have found increased recruitment during cold water periods. Thus the mathematical analysis was in agreement with the known biological relationships.

E. Sample application

Accurate correspondence between observed and synthesized frond number established validity of multiple linear regression models of the Abalone Cove study. The resultant models should produce similar correspondences when appropriate environmental data are used to synthesize frond numbers at some other time and location. Successful simulation of growth at another site would assure that the model expresses fundamental biological relationships between environmental conditions and kelp growth.

Long-term records of average frond numbers in other kelp beds were unfortunately not available. Aerial surveys have been taken regularly, showing canopy extent of many sites. Records of the Pt. Loma bed in San Diego County, for example, show two patterns which might be comparable to bedwise frond count fluctuations (Figure 19). The canopy practically disappeared between 1956 and 1960. Recruitment in 1964 was highly successful and much of the canopy recovered. These patterns were observed in surveys of many southern California kelp beds.

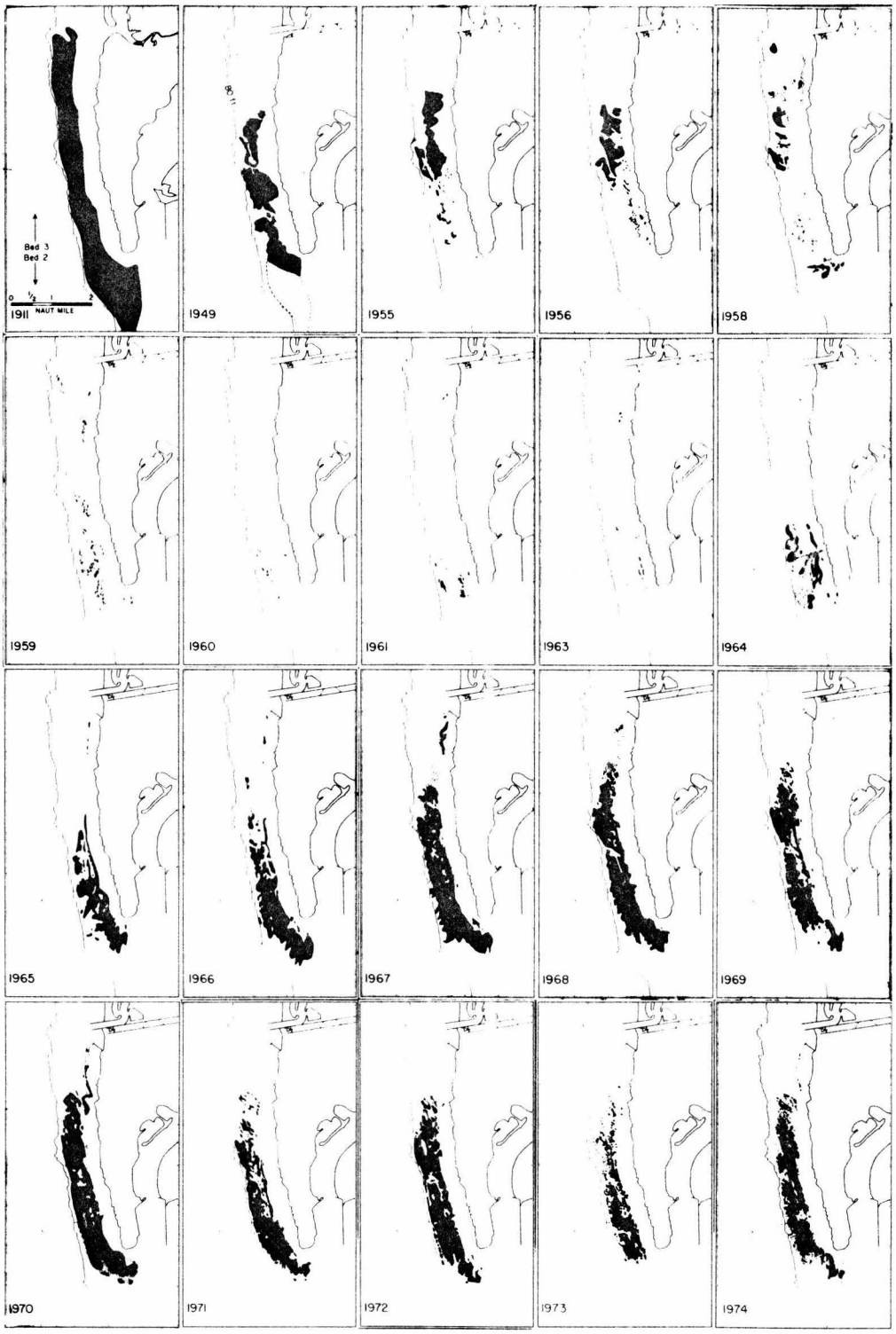


Figure 19. Historical charts of the Point Loma kelp bed. Kelp shown as black. (from North, 1974)

We can use the Abalone Cove model to hindcast a synthetic bedwise frond count record for Point Loma during these years. We substituted environmental conditions pertinent to Point Loma with terms and coefficients determined from the Abalone Cove study. If the simulation were to show similar patterns, the fundamental soundness of the model would be corroborated.

Surface temperatures from 1950 to 1969 were provided by the Ocean Records Group of the Institute of Marine Resources, Scripps Institution of Oceanography (Figure 20). These are monthly means of daily measurements at the SIO pier, about 16 kilometers north of the Pt. Loma bed. Winter months from 1956-57 through 1958-59 were abnormally warm (months 80 to 112).

Bakun (1973) calculated monthly upwelling indices for the same twenty year period (Figure 21). The center of the calculated upwelling field was about 125 kilometers east and slightly north of Pt. Loma. The same field was used in the Abalone Cove regressions. This was the closest to Pt. Loma for which upwelling has been calculated. Characterization of conditions at this great a distance was reasonably justified because the index is computed from broad-scale meteorology. The summer of 1964 (month 174) showed the highest index value during the twenty year

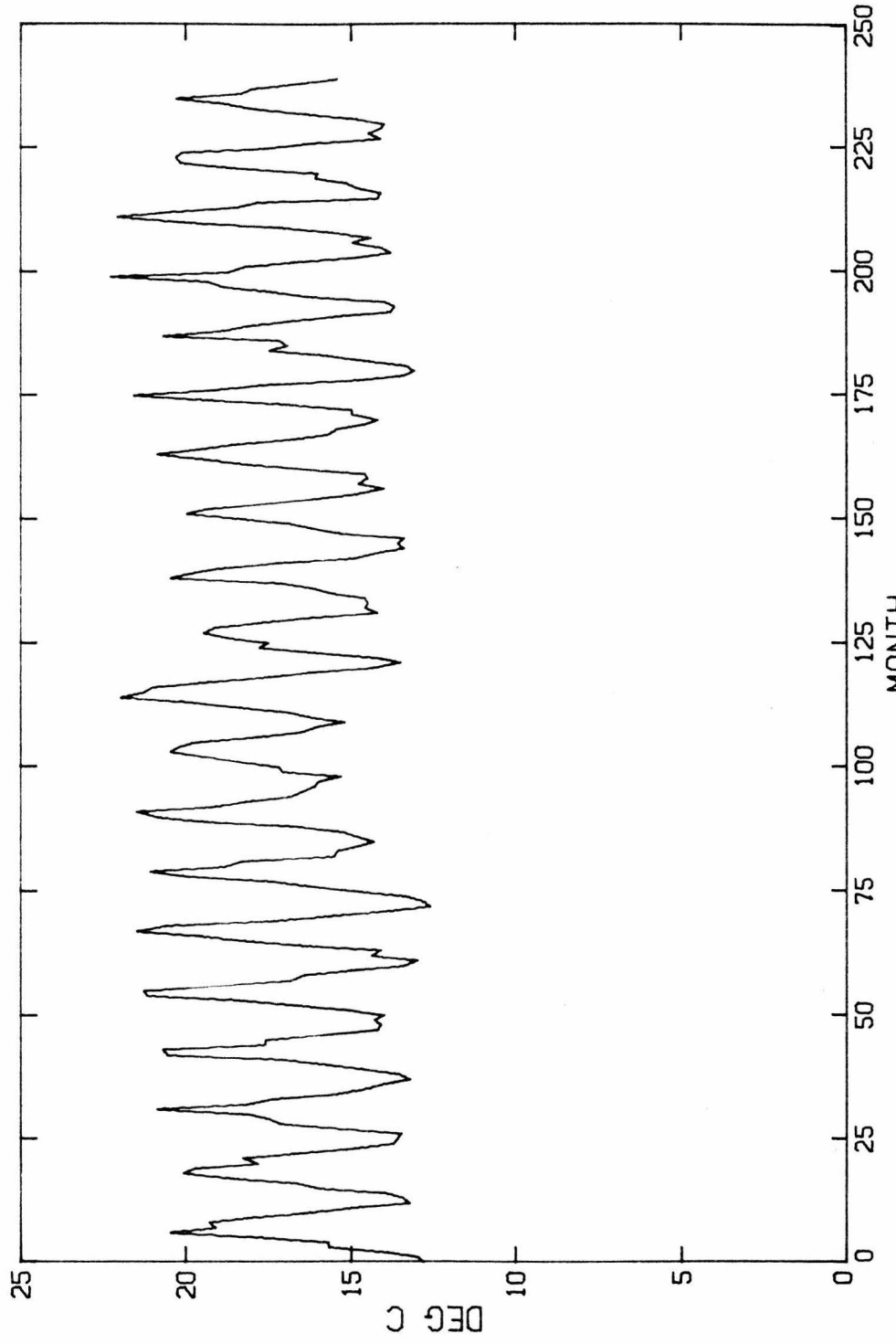


Figure 20. Surface water temperature at Scripps Pier 1950 to 1969. Monthly means of daily measurements.

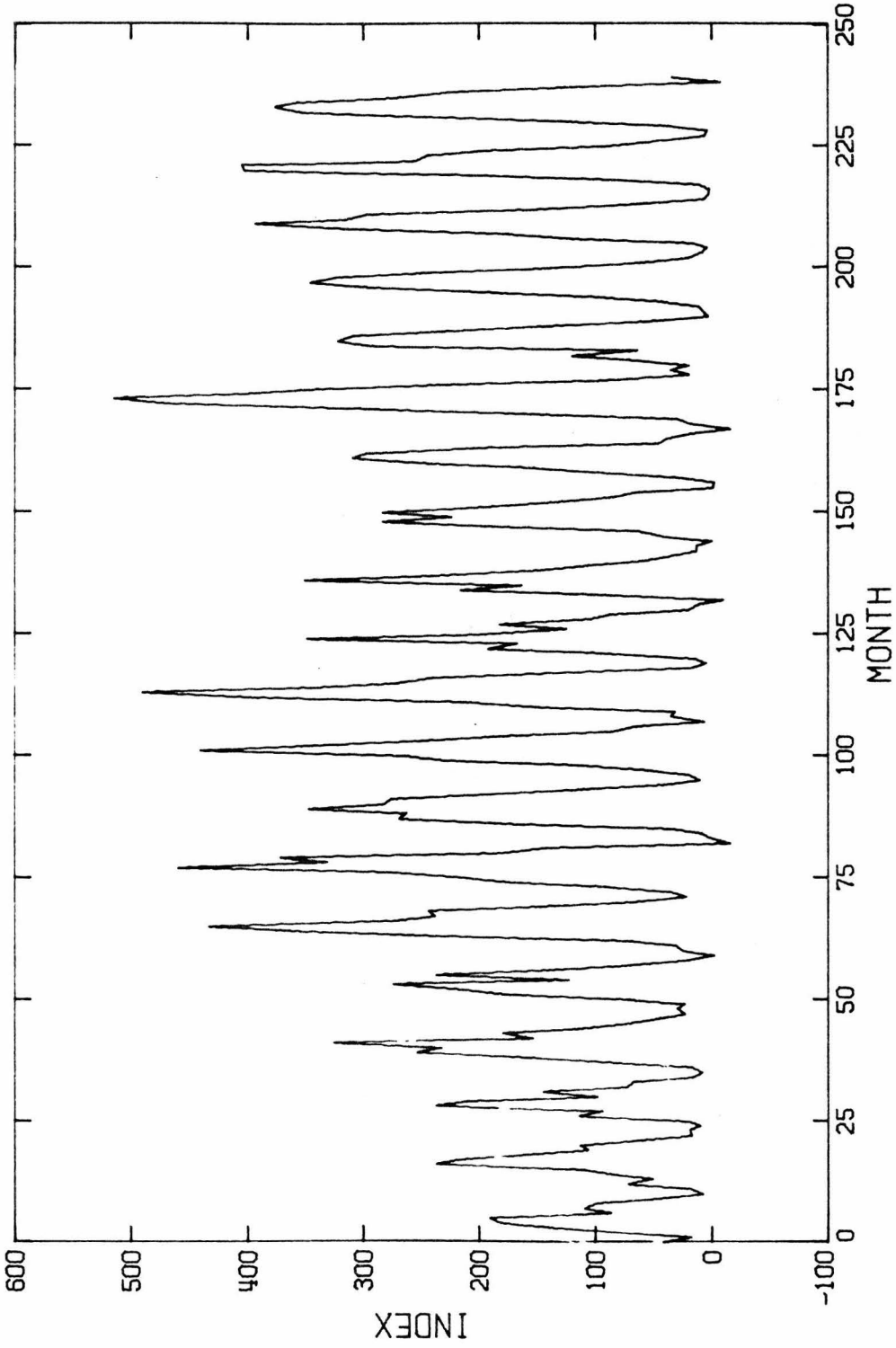


Figure 21. Monthly mean upwelling index 1950 to 1969. Calculated for the location 33N, 119W. (Bakun, 1973)

period. Unlike the detrimental temperature conditions from 1956 to 1959, upwelling seems to have been well developed then.

No estimates of fish grazing were available for Point Loma. For this simulation grazing was held constant and equal to zero.

No survivability function was available either. I noticed that bedwise frond numbers from Abalone Cove had a high serial correlation. That is, the value at one moment was fairly close to the value from the previous observation time. The survivability function served in the Abalone Cove model to account for a time related bias in residuals that seemed related to plant mortality and recruitment. The survivability function was a way to describe the sampling history and how it might have affected frond counts. An autocorrelation term might serve the same role for the Point Loma simulation. I hypothesized a regression form for Point Loma as follows:

$$F_B(t) = aF_B(t-\tau) + bU(t) + cT(t) + dG(t) + k \qquad (10)$$

Least squares coefficient and constant were determined for this equation using Abalone Cove frond numbers and environmental data.

$a = 0.812$

$b = 0.0138$

$c = -0.503$

$d = 0.908$

$k = 7.90$

This model gave a good synthetic representation of Abalone Cove bedwise frond numbers (Figure 22), accounting for 96.9% of observed variance ($R^2 = 0.969$).

Separate term contributions for this version were:

$C_{F_b(t-\tau)} = 66.2\%$

$C_T = 8.78\%$

$C_U = 21.7\%$

$C_G = 3.43\%$

Much of the role played by upwelling index was taken over in this model by the auto correlation term $F_B(t-\tau)$. Upwelling index and frond numbers were closely correlated ($r_{UF} = 0.929$). Lagged frond numbers thus supplied much of the information that upwelling index itself had given to the composite.

A random term, $r(0,\sigma)$ was added to equation (10) to represent the unexplained variance difference between simulated values and observed data. These residuals were

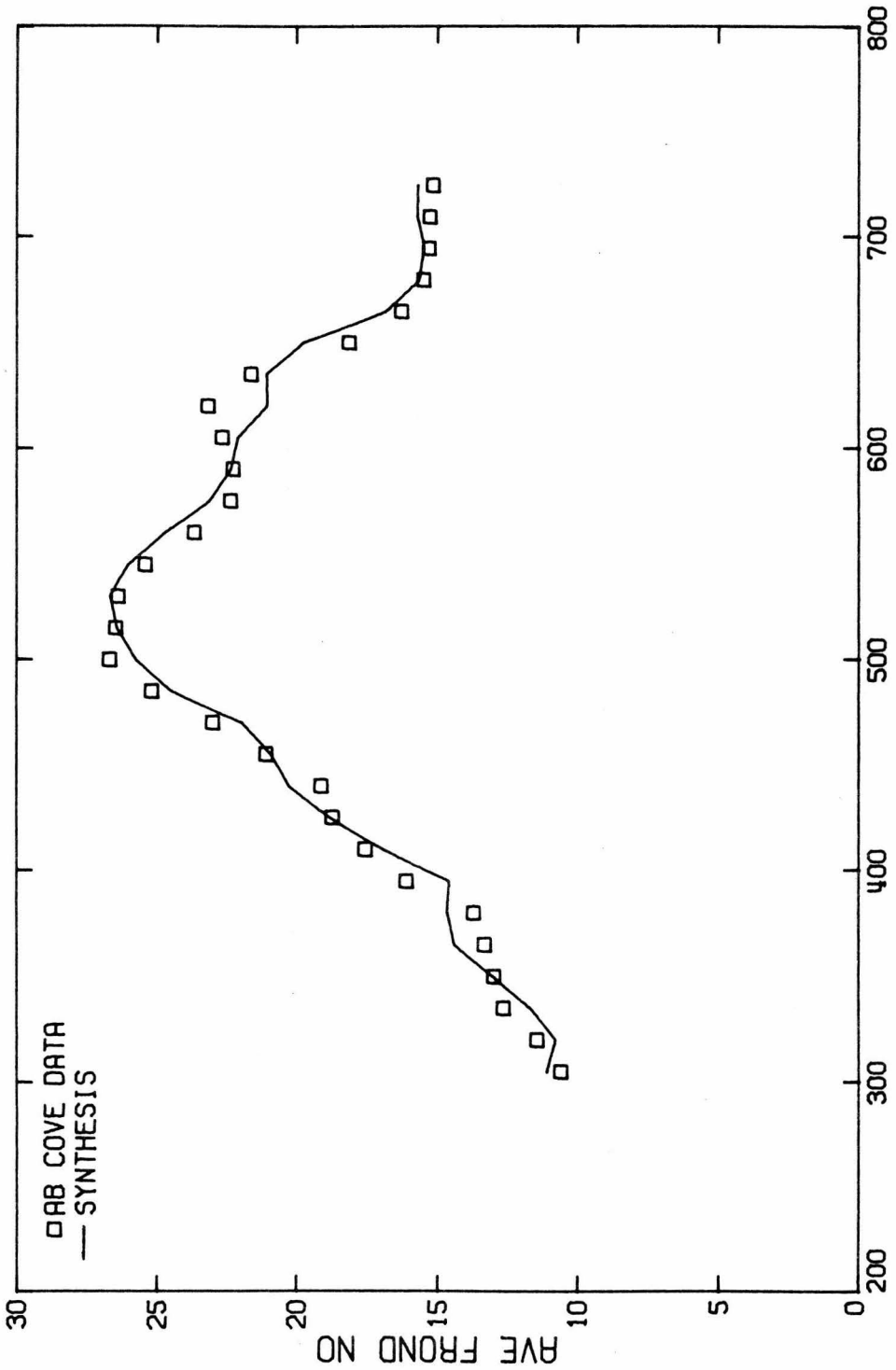


Figure 22. Synthesized average frond numbers from regression equation (10).
$F_B(t) = aF_B(t-\tau) + bU(t) + cT(t) + dG(t) + k.$

normally distributed with zero mean. Standard deviation, σ, was 0.844 again from Abalone Cove data.

I hypothesized that this equation:

$$F_B(t) = 0.812\ F_B(t-\tau) - 0.503\ T(t) + 0.0138\ U(t) + r(0,0.844) + 7.9 \qquad (11)$$

could be used to hindcast the kelp canopy fluctuations seen at Point Loma from 1950 to 1969. Observation interval, τ, was set at 30 days. Temperature and upwelling indices were appropriate for Point Loma as mentioned above.

Inclusion of the random term allowed a Monte-Carlo type simulation in which each set of values selected from the random distribution yielded a different synthetic record. Repetitive calculation of different synthetic records gave a distribution of possible results.

An initial seven-year period was pre-calculated for each record to obtain an unbiased, initial $F(t-\tau)$ from $F_0 = 25$.

Figure 23 shows the distribution of 50 Monto-Carlo simulations. The solid curve represents the mean. Dashed curves show the mean plus or minus one sigma.

During 1956 synthetic frond number averaged about 20 over the year. The average during 1958 was down to about 14. This 30% loss, though large, was not as dramatic as

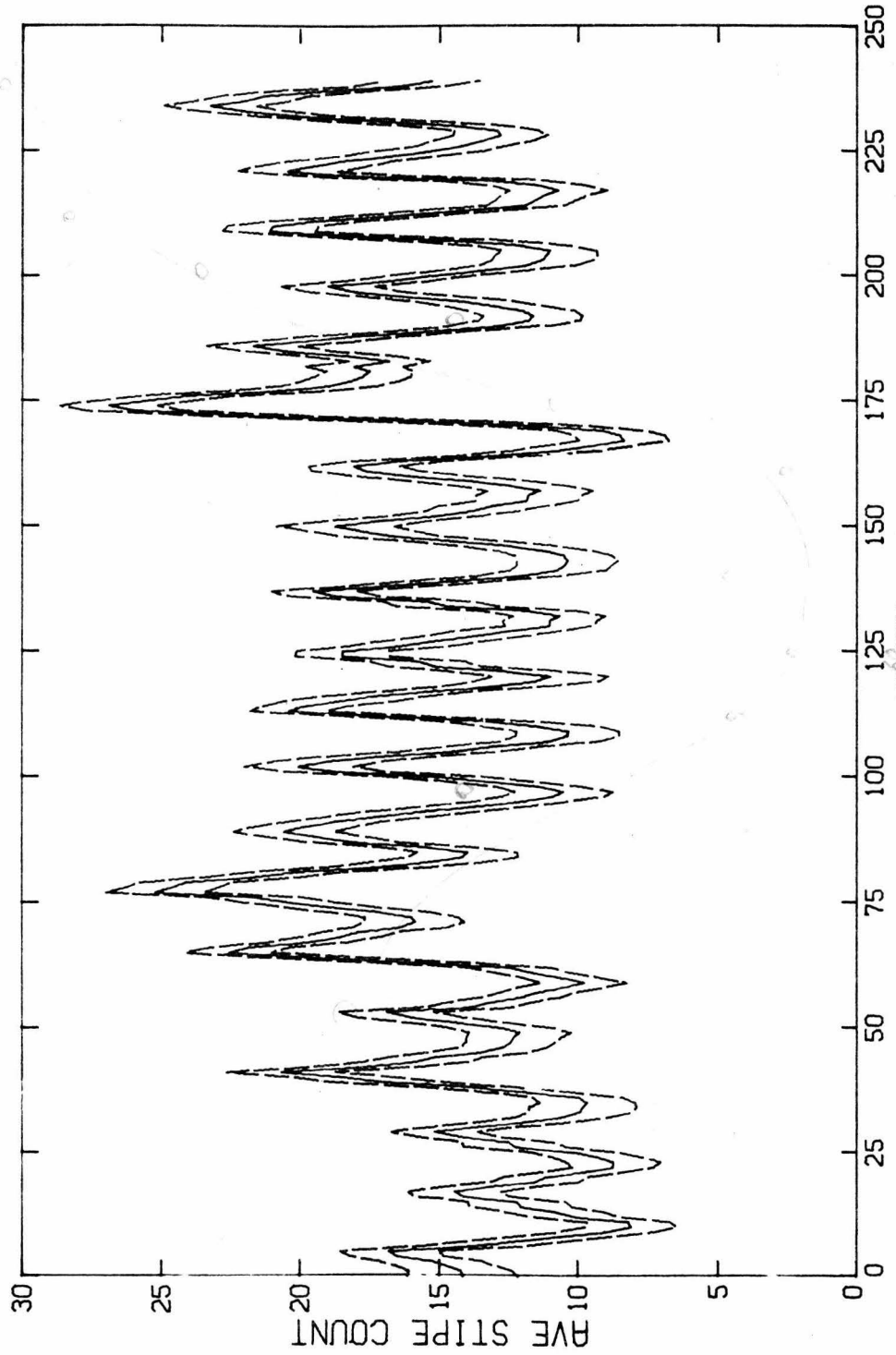


Figure 23. Synthesized average frond numbers for the Point Loma kelp bed, 1950 to 1969. Solid curve shows mean of 50 Monte-Carlo simulations. Dashed curves show mean plus and minus one sigma.

the nearly total destruction witnessed in aerial surveys. Warm winter temperatures detracted from good growing conditions. Relatively high upwelling, on the other hand, stimulated some growth.

Two factors could have contributed to the difference between observed and simulated fluctuations. Severe storms could remove enough plants to affect canopy coverage significantly. Losses of large numbers of plants would also reduce reproductive capacity of the kelp bed. Likewise, fish grazing was not considered in the simulation. Grazing has a small and probably beneficial effect on kelp growth at normal kelp and fish population densities. If kelp density were reduced and plants further stressed by warm water, fish grazing could overwhelm kelp productivity (North, 1973).

We have assumed that frond number is proportional to a linear function of grazing. When the fraction of kelp tissue destroyed is high, this assumption is probably not valid. The regression model is safely applied only within the range used to generate the equation coefficients. As with each independent variable, extrapolation beyond a moderate range may be hazardous due to the linear hypothesis.

The rapid increase in synthetic frond number in 1964 corresponded well to canopy recovery at Point Loma. Temperatures were normal that year, but upwelling was very high.

The model seemed able to hindcast the basic trends. Yet it failed to estimate intensity of the reaction. Given the linearity restriction and the omission of influences of plant recruitment and mortality, this simulation essentially supported findings from the Abalone Cove analysis. Upwelling and water temperature play the major roles in determining the seasonal patterns of plant growth. Fish grazing, normally a lesser factor, should be considered whenever possible.

The Pt. Loma simulation exemplifies another basic belief fundamental to this study. Various aspects of Macrocystis development fall into specific frequency response ranges. The changes observed within these ranges are driven by environmental changes in the same ranges. Kelp response to sudden or rapid fluctuations occurring within days can be observed in changes shown by individual blades or fronds (Figure 24). One example of short-term frond reaction is internodal elongation. The longer duration seasonal patterns are manifested as whole plant changes. I have used average frond number to describe plant reactions. Environmental changes lasting many years will be reflected in parameters encompassing an entire bed.

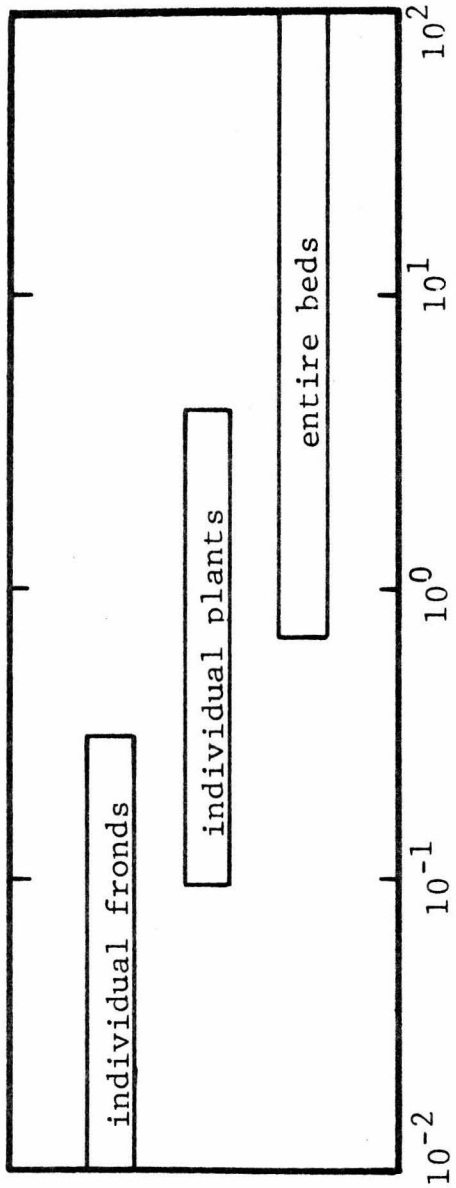


Figure 24. Range of observable reaction times for growth or population studies in Macrocystis pyrifera

Semi-permanent effects might be reflected in differences between regions in plant density or canopy coverage.

The four-factor linear model successfully described month-to-month growth patterns in Abalone Cove. It was less suited for modelling twenty year patterns.

CHAPTER V

SUMMARY AND CONCLUSIONS

This study investigated relationships between certain environmental influences and seasonal growth patterns in a selected population of Giant Kelp, Macrocystis pyrifera. I hypothesized that the growth history over several months could be expressed as a quantitative function of appropriate environmental factors. A method was chosen for deciding which factors were most influential. The method was applied to the data with good success.

Frond counts among kelp plants in Abalone Cove, Los Angeles County, were surveyed for sixteen months. Observations of a sample population along a fixed 100 meter transect were made at approximately three week intervals using SCUBA.

I counted numbers of fronds in each plant in a sample population which was occasionally supplemented with new individuals to replace lost specimens. A subset of nineteen plants survived from the beginning to the end of the study. Frond counts averaged over this set of surviving plants depicted the vegetative growth of a typical plant. An average plant increased from 8.2 to 27.7 fronds in 328 days. Net frond increases thus produced about 20 kg/plant/yr during the high growth period. Net frond production of about 4 fronds per plant per month was of the same order

of magnitude as the values reported by Gerard (1976). Normalized production rates between 0 and 1 frond/frond/day were also similar to Gerard's measurements which were taken near Monterey, California.

Average frond numbers from the overall, supplemented sample rose from 10.7 at the start in November to 26.5 in June, then fell to 15.2 the following January. Bedwise productivity was about 30 $kg/m^2/yr$ during the early phase of the study, assuming a population density of 1 plant per square meter. This rate was within the ranges reported by North (1971) and Gerard (1976) and was of the same order of magnitude as values reported by Clendenning (1971).

The average long-term survivor steadily increased in size from the start of the study in November until the following September. Bedwise averages, in contrast, began to decrease in early June. The earlier peak together with lower average values after mid-summer for bedwise values compared to the continuous set indicate that replacements were drawn from a population with smaller average sizes. In other words a new generation of sporophytes was recruited during spring.

Many tagged plants were lost entirely during the study. Thirty-one of the eighty-four marked plants were removed by stresses due to wave motion. Plants lost to

storm-induced waves tended to be larger than the average plant in the sample. Attachment strength can be overcome when buoyancy and drag increase as plants grow. In some cases plants were fastened to individual rocks whose anchoring weight was exceeded. In other cases holdfast development was impaired by unsuitable substrate.

A similar study in San Diego County (Rosenthal, et al. 1974) found that entanglement between drifting and attached plants was a major factor in whole plant losses. Only a few plants were entangled with drifters in my study. Abalone Cove was relatively shallow so that plants were possibly somewhat short and less likely to tangle with their neighbors.

Twenty-two of the eighty-four marked plants were destroyed by sea urchin grazing. Urchin damage did not cause significant losses in Rosenthal et al.'s study. Palos Verdes historically supports dense urchin populations (North 1974). Localized and migrating urchin fronts do develop despite human efforts to control their numbers. Such an invasion caused most of the losses along the Abalone Cove transect.

The underwater surveys provided opportunities to assess impacts of fishes grazing on Macrocystis. Bite marks displayed by each sample plant were recorded. Average grazing damage ranged from light to moderate during the study. An estimated 19% of net productivity was

consumed by fishes. Other studies (Mann, 1973; Khialov and Burlakova, 1969) estimated that herbivores consumed 10% to 11% of macrophyte productivity.

A belt transect was monitored during each visit to estimate the population of Opaleye Perch and Halfmoon Perch, the two common grazers. Visual counts of Opaleye far outnumbered Halfmoon. Opaleye population estimates, however, were highly variable due to variable schooling and erratic shifting of concentrations from place to place within the bed.

Opaleye in an aquarium consumed about 9 grams of Macrocystis per day per fish. This represented about 4% of body weight. Daily maintenance rations vary from 1% to 6% according to Lagler, Bardach, and Miller (1962) and Cowey and Sargent (1972). Experimental Opaleye were somewhat smaller than commonly seen in the field. Thus consumption rates greater than 9 grams per day per fish might be expected in kelp beds.

Opaleye showed a significant preference for older, heavily encrusted blades in the aquarium study. They also preferred squid or urchin entrails, items not normally available in their natural diet. This indicates that they actually prefer the encrusting organisms and not the algal tissues. Growing tips were next eaten most often, followed by clean or mildly encrusted, mature blades. Thus algal

tissue possibly provides some nutritive value. Sporophylls were the least desirable portion of kelp plants.

I selected water temperature, sunlight, fish grazing, and upwelling for mathematical analysis as the major factors controlling kelp growth. Daily measurements of surface temperature at Santa Monica Pier showed that the study period was slightly cooler than usual but otherwise normal. Variations in daily solar radiation at Los Angeles International Airport corresponded approximately to the previous twenty years. The upwelling index, calculated by Bakun (1976) from meteorologic data for the area, indicated that more deep water was brought into coastal surface waters than in an average year. My own estimates of fish grazing varied from light to moderate. They could not be compared to other situations because similar grazing surveys have never been made. Thus overall environmental conditions were slightly better than average for kelp growth during the study.

Linear regressions successfully synthesized frond numbers which closely resembled observed values. Plantwise frond counts were built up of a linear combination of time, Bakun's upwelling index, and grazing estimates. The largest proportion of the modelling was shared by time and upwelling index. Grazing played a minor but valid part. Modeled values fitted observations more closely (regression

coefficient improved from R^2=0.933 to 0.956) when frond numbers were correlated with grazing estimates from the preceding time interval.

The analysis suggested that sporophytes were growing steadily. The basic growth rate was increased or retarded as upwelling conditions improved or degraded. Fish grazing in moderation was a beneficial factor, possibly a pruning function, whose effects were realized after a time lag.

Bedwise frond counts were also successfully synthesized (R^2 = 0.937). Bedwise values required a linear combination of upwelling index, water temperature, fish grazing estimates, and a survivability function. Upwelling index provided almost three quarters of the model's shape. The survivability function supplied information about recruitment and mortality. Development of a new generation each spring tends to add a seasonal pattern to the frond count history and to reduce overall average size. Mortality of large plants further reduced the average size in the bed.

Sunlight data did not add statistically significant improvement to either plantwise or bedwise models. Sunlight and upwelling index were closely correlated during the study so the inclusion of upwelling index in each model probably supplied the information necessary to represent sunlight's obviously important role.

One model developed from Abalone Cove data was used to hindcast changes observed in the Point Loma kelp canopy from 1950 to 1969. The simulation predicted a noticeable drop in frond number from 1956 to 1959. Warm winter water during that time actually caused the virtual elimination of kelp at Point Loma. The simulation also showed a dramatic rise in frond number in 1964, the year that major recovery began at Point Loma.

This model application supported our confidence in the fundamental accuracy and utility of the regressions. Long-term kelp growth patterns can be quantitatively expressed as functions of a few principal environmental factors. On the other hand, the specific parameter chosen to measure growth (in this case average frond number) imposed restrictions on the frequency of the phenomenon under study. Certain aspects of Macrocystis growth vary over days to weeks. Others can be observed only in studies lasting years.

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Appendix A. Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	1	2	3	4	5	6	7	8	9	10	11	12
10-17-74	12	4	13	9	9	16	12	17	6	10	13	14
11-5-74	S	10	12	7	10	21	14	21	6	12	13	17
11-25-74		13	19	7	12	21	17	20	10	11	17	23
12-11-74		13	16	6	13	22	S	S	10	10	19	23
1-13-75		13	15	U	U	22			11	16	22	20
1-29-75		16	20			31			17	19	24	20
2-27-75		24	25			37			24	19	33	26
3-13-75		25	24			39			18	18	S	11
3-20-75		24	29			43			16	18		12
4-22-75		28	39			44			13	22		8
4-28-75		25	40			52			U	24		8
5-7-75		27	41			49				24		10
6-5-75		35	43			66				26		14
6-17-75		37	43			66				26		15
7-23-75		39	43			S				27		17
9-10-75		37	S							32		17
10-7-75		31								30		16
10-21-75		36								23		15
11-11-75		36								23		15
11-30-75		31								28		15
12-18-75		31								34		13
1-11-76		28								30		9
2-11-76		U								27		5
3-13-76										32		10

Appendix A. (cont.) Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	13	14	15	16	17	18	19	20	21	22	23	24
10-17-74	19	8	6	4	3	21	9	2				
11-5-74	21	12	8	4	4	6	12	S	2	13	3	14
11-25-74	19	15	14	8	5	6	13		2	16	3	16
12-11-74	17	11	14	7	5	S	16		3	S	4	19
1-13-75	26	16	18	10	4		17		U		5	19
1-29-75	S	21	25	10	2		4				4	21
2-27-75		30	32	10	U		4				6	28
3-13-75		S	41	11			6				7	29
3-20-75			40	13			6				10	30
4-22-75			S	15			7				12	36
4-28-75				14			8				11	38
5-7-75				13			11				11	38
6-5-75				12			12				14	41
6-17-75				15			13				14	41
7-23-75				20			14				17	44
9-10-75				16			20				24	48
10-7-75				15			14				23	44
10-21-75				17			16				26	38
11-11-75				16			13				28	34
11-30-75				14			12				21	35
12-18-75				13			10				18	36
1-11-76				11			11				22	28
2-11-76				U			4				22	U
3-13-76							1				35	

Appendix A. (cont.) Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	25	26	27	28	29	30	31	32	33	34	35	36
10-17-74												
11-5-74	45	5	6	11	2	2	2	9	2	4	2	3
11-25-74	36	5	4	9	2	4	3	13	3	5	2	4
12-11-74	37	4	U	9	2	3	5	14	4	5	3	7
1-13-75	44	6		14	2	6	5	S	5	7	3	S
1-29-75	44	5		16	2	7	6		6	9	2	
2-27-75	57	3		19	2	12	6		8	13	2	
3-13-75	59	4		17	2	15	8		9	13	1	
3-20-75	63	6		20	2	15	8		10	11	1	
4-22-75	82	S		21	5	20	S		15	16	3	
4-28-75	88			22	5	21			15	17	3	
5-7-75	87			22	6	25			15	18	4	
6-5-75	95			23	7	28			17	17	7	
6-17-75	89			21	7	28			18	16	7	
7-23-75	90			18	9	32			25	23	9	
9-10-75	S			16	11	35			24	28	8	
10-7-75				26	12	36			29	S	11	
10-21-75				20	10	35			27		9	
11-11-75				19	11	36			26		8	
11-30-75				21	11	33			23		9	
12-18-75				21	14	32			21		12	
1-11-76				21	12	30			24		14	
2-11-76				16	S	37			19		15	
3-13-76				22		38			23		22	

Appendix A. (cont.) Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	37	38	39	40	41	42	43	44	45	46	47	48
10-17-74												
11-5-74	2	5	17	15	8	20	7	15	15	11	22	11
11-25-74	4	8	20	20	12	23	9	11	15	10	30	13
12-11-74	4	6	21	20	S	23	8	9	13	11	29	12
1-13-75	6	8	21	21		6	6	8	16	14	29	9
1-29-75	7	13	24	25		6	6	11	19	14	32	11
2-27-75	10	15	29	31		4	8	7	15	15	39	12
3-13-75	10	22	29	34		0	5	7	13	15	44	10
3-20-75	8	19	34	36		0	5	5	14	13	43	13
4-22-75	14	25	40	38		6	5	7	21	13	51	17
4-28-75	14	27	39	39		6	9	8	22	14	49	19
5-7-75	14	27	41	43		7	10	12	26	12	53	21
6-5-75	14	30	40	46		7	13	11	20	12	53	23
6-17-75	15	30	38	43		8	12	8	20	9	51	21
7-23-75	14	31	39	38		8	11	U	24	U	56	19
9-10-75	14	37	45	35		S	S		U		44	26
10-7-75	15	32	45	30							12	25
10-21-75	15	23	42	28							12	25
11-11-75	10	18	41	25							8	23
11-30-75	12	19	U	22							6	26
12-18-75	12	13		20							6	24
1-11-76	9	8		15							7	19
2-11-76	6	2		U							S	24
3-13-76	7	U										30

Appendix A. (cont.) Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	49	50	51	52	53	54	55	56	57	58	59	60
10-17-74												
11-5-74	21	11										
11-25-74	27	14										
12-11-74	33	14	8									
1-13-75	32	14	12									
1-29-75	37	15	16	9	14	14	11	14	33	18	27	
2-27-75	46	16	19	14	18	19	14	19	30	15	25	34
3-13-75	45	17	S	16	21	20	16	19	26	11	30	39
3-20-75	45	17		18	22	19	18	20	26	12	30	38
4-22-75	46	23		S	22	29	23	27	36	14	31	44
4-28-75	48	23			24	28	26	28	39	15	29	43
5-7-75	51	26			22	27	29	30	39	14	30	49
6-5-75	48	30			24	27	S	33	36	19	24	54
6-17-75	50	34			23	28		31	28	17	23	53
7-23-75	51	33			21	26		35	37	18	18	51
9-10-75	53	30			21	25		S	34	19	10	49
10-7-75	40	11			18	20			23	18	5	50
10-21-75	30	12			14	18			21	13	4	50
11-11-75	33	6			8	14			14	18	4	38
11-30-75	37	4			6	14			9	19	3	32
12-18-75	31	3			6	16			9	21	3	28
1-11-76	33	5			7	16			13	U	1	23
2-11-76	27	7			4	12			10		U	11
3-13-76	41	6			U	8			12			1

Appendix A. (cont.) Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	61	62	63	64	65	66	67	68	69	70	71	72
10-17-74												
11-5-74												
11-25-74												
12-11-74												
1-13-75												
1-29-75												
2-27-75	9											
3-13-75	7											
3-20-75	8											
4-22-75	4											
4-28-75	3											
5-7-75	3											
6-5-75	S	15	2									
6-17-75		13	1									
7-23-75		14	1	6	2	8	4	4	4	2		
9-10-75		18	1	7	S	7	6	9	10	4		
10-7-75		15	1	8		7	13	12	11	4	9	13
10-21-75		15	2	10		5	13	11	17	5	7	12
11-11-75		15	2	12		5	11	13	23	5	10	14
11-30-75		15	2	11		5	12	15	24	6	9	17
12-18-75		19	1	18		4	13	12	20	6	10	21
1-11-76		19	1	16		3	10	19	27	7	12	20
2-11-76		21	2	18		3	10	27	24	3	11	S
3-13-76		17	4	17		4	8	36	U	U	11	

Appendix A. (cont.) Stipe counts of tagged kelp plants along a fixed 100 meter transect in Abalone Cove. "S" indicates lost plant assigned to storm damage. "U" indicates lost plant assigned to sea urchin grazing.

	Plant number											
Date	73	74	75	76	77	78	79	80	81	82	83	84
10-17-74												
11-5-74												
11-25-74												
12-11-74												
1-13-75												
1-29-75												
2-27-75												
3-13-75												
3-20-75												
4-22-75												
4-28-75												
5-7-75												
6-5-75												
6-17-75												
7-23-75												
9-10-75												
10-7-75	3	9	28	6	7							
10-21-75	6	12	27	7	6	4	9	5	12	35	3	5
11-11-75	6	11	27	10	9	6	8	5	12	29	5	7
11-30-75	4	8	29	12	8	8	9	7	10	36	5	9
12-18-75	5	9	27	11	7	8	7	6	14	38	5	12
1-11-76	6	7	24	12	10	6	6	8	15	38	6	13
2-11-76	11	U	16	14	15	6	U	11	10	33	8	10
3-13-76	12		S	18	19	7		13	5	37	8	15

Appendix B. Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	1	2	3	4	5	6	7	8	9	10	11	12
10-17-74	2	4	2	2	2	0	0	2	4	2	0	0
11-5-74		1	2	1	1	2	2	2	2	1	1	2
11-25-74		1	2	3	0	1	1	1	1	1	1	1
12-11-74		1	1	2	2	0			2	2	0	4
1-13-75		5	1			0			1	0	0	4
1-29-75		2	2			0			1	0	1	1
2-27-75		0	0			1			2	0	0	1
3-13-75		0	0			0			2	0		4
3-20-75		2	0			3			2	0		0
4-22-75		1	1			0			2	0		1
4-28-75		0	0			0				0		2
5-7-75		2	2			0				0		2
6-5-75		1	2			0				0		0
6-17-75		0	1			0				0		0
7-23-75		0	0							0		0
9-10-75		0								2		4
10-7-75		0								0		3
10-21-75		4								1		2
11-11-75		0								2		1
11-30-75		0								0		1
12-18-75		2								0		2
1-11-76		0								0		3
2-11-76										0		6
3-13-76										0		4

Appendix B. (cont.) Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	13	14	15	16	17	18	19	20	21	22	23	24
10-17-74	0	0	0	2	2	2	2	5				
11-5-74	2	1	1	1	1	2	1		4	0	3	1
11-25-74	2	0	2	1	3	3	0		6	1	2	2
12-11-74	3	0	0	4	3		1		6		1	1
1-13-75	0	1	1	3	4		3				4	2
1-29-75		0	0	0	6		2				0	0
2-27-75		0	2	4			4				0	0
3-13-75			4	5			5				2	0
3-20-75			2	3			5				0	0
4-22-75				2			1				2	0
4-28-75				2			1				1	0
5-7-75				3			0				0	0
6-5-75				2			0				0	0
6-17-75				1			0				0	0
7-23-75				0			0				0	0
9-10-75				3			4				0	1
10-7-75				2			0				0	1
10-21-75				4			2				0	2
11-11-75				0			0				0	0
11-30-75				2			1				0	2
12-18-75				4			1				1	1
1-11-76				3			0				0	1
2-11-76							4				3	
3-13-76							6				0	

Appendix B. (cont.) Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	25	26	27	28	29	30	31	32	33	34	35	36
10-17-74												
11-5-74	3	2	5	3	0	0	3	2	0	4	0	2
11-25-74	1	2	6	2	3	5	4	1	2	4	6	6
12-11-74	3	4		6	6	5	6	1	3	3	6	6
1-13-75	1	2		3	2	5	5		3	5	6	
1-29-75	1	4		0	0	4	4		4	2	6	
2-27-75	0	5		3	2	2	6		4	4	6	
3-13-75	0	6		4	5	0	5		1	2	2	
3-20-75	0	6		4	2	0	2		1	0	2	
4-22-75	0			1	4	1			0	0	3	
4-28-75	0			0	2	1			0	1	2	
5-7-75	0			1	2	1			1	0	0	
6-5-75	0			0	2	0			0	0	0	
6-17-75	0			0	2	0			0	0	3	
7-23-75	0			4	2	4			1	1	5	
9-10-75				0	4	3			0	5	1	
10-7-75				5	0	4			2		2	
10-21-75				4	0	1			0		0	
11-11-75				1	2	1			0		1	
11-30-75				2	2	2			0		3	
12-18-75				4	1	1			3		5	
1-11-76				2	2	0			3		1	
2-11-76				1		3			3		2	
3-13-76				5		3			2		3	

Appendix B. (cont.) Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	37	38	39	40	41	42	43	44	45	46	47	48
10-17-74												
11-5-74	0	3	0	2	3	3	5	3	0	2	1	2
11-25-74	4	4	0	0	4	3	4	0	2	2	1	0
12-11-74	4	4	1	2		5	2	2	2	2	0	1
1-13-75	4	2	0	0		6	5	6	1	2	1	4
1-29-75	3	2	0	1		6	6	5	5	5	3	6
2-27-75	0	2	0	0		6	6	6	5	6	2	6
3-13-75	2	0	2	0		6	6	6	5	6	1	6
3-20-75	0	0	0	2		6	5	6	4	6	1	6
4-22-75	0	0	0	1		0	6	6	2	5	2	1
4-28-75	0	0	0	2		0	5	6	3	5	2	3
5-7-75	0	0	1	0		0	4	5	4	3	2	3
6-5-75	0	1	0	0		0	2	2	0	5	2	4
6-17-75	1	0	0	0		2	3	0	2	5	1	3
7-23-75	2	1	1	2		4	4		5		2	4
9-10-75	1	2	2	0							1	1
10-7-75	0	2	2	1							1	0
10-21-75	0	0	0	0							4	3
11-11-75	0	1	0	0							5	2
11-30-75	1	0		1							4	3
12-18-75	5	2		2							3	4
1-11-76	4	5		1							4	2
2-11-76	1	6										2
3-13-76	6											3

Appendix B. (cont.) Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	49	50	51	52	53	54	55	56	57	58	59	60
10-17-74												
11-5-74	1	2										
11-25-74	1	1										
12-11-74	1	1	0									
1-13-75	1	5	0									
1-29-75	2	5	0	0	0	1	0	2	5	0	1	
2-27-75	0	5	0	1	0	3	0	0	3	2	0	0
3-13-75	5	5		0	0	0	0	0	4	4	4	0
3-20-75	4	5		2	0	0	0	0	2	1	0	0
4-22-75	1	3			3	1	0	0	1	0	0	0
4-28-75	3	5			0	0	0	0	1	0	2	0
5-7-75	3	5			0	0	0	1	2	0	0	1
6-5-75	1	1			0	0		0	1	1	0	0
6-17-75	3	2			0	0		0	2	0	2	0
7-23-75	1	2			0	0		0	3	1	4	0
9-10-75	5	6			1	0			5	5	5	1
10-7-75	3	5			2	0			4	0	6	0
10-21-75	2	6			3	0			3	1	5	1
11-11-75	1	6			3	0			0	0	6	0
11-30-75	2	4			5	0			5	2	0	0
12-18-75	0	5			2	0			6	2	6	1
1-11-76	1	6			4	1			5		6	2
2-11-76	0	6			1	0			1			5
3-13-76	1	4				5			4			6

Appendix B. (cont.) Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	61	62	63	64	65	66	67	68	69	70	71	72
10-17-74												
11-5-74												
11-25-74												
12-11-74												
1-13-75												
1-29-75												
2-27-75	2											
3-13-75	6											
3-20-75	6											
4-22-75	6											
4-28-75	6											
5-7-75	6											
6-5-75		0	0									
6-17-75		0	4									
7-23-75		2	5	0	0	2	1	2	0	5		
9-10-75		4	0	0		4	5	4	0	1		
10-7-75		2	2	1		3	0	0	0	2	6	0
10-21-75		2	3	0		0	1	0	0	0	3	0
11-11-75		2	0	0		1	0	1	0	0	0	1
11-30-75		3	5	0		6	0	1	0	0	0	0
12-18-75		1	2	1		6	2	1	1	0	3	0
1-11-76		0	0	0		0	2	0	0	0	1	0
2-11-76		0	5	1		0	2	0	0	2	2	
3-13-76		2	4	2		4	6	0			4	

Appendix B. (cont.) Fish grazing estimates for tagged kelp plants along a fixed 100 meter transect in Abalone Cove. Scale range from zero to six. Zero indicates no grazing evident. Six indicates removal of all blades.

	Plant number											
Date	73	74	75	76	77	78	79	80	81	82	83	84
10-17-74												
11-5-74												
11-25-74												
12-11-74												
1-13-75												
1-29-75												
2-27-75												
3-13-75												
3-20-75												
4-22-75												
4-28-75												
5-7-75												
6-5-75												
6-17-75												
7-23-75												
9-10-75												
10-7-75	4	0	5	5	5							
10-21-75	0	2	3	3	6	0	0	0	0	0	0	0
11-11-75	2	0	1	2	5	0	3	0	0	1	1	1
11-30-75	0	0	4	4	2	4	5	4	0	3	0	1
12-18-75	5	0	1	2	1	1	4	0	2	2	2	2
1-11-76	6	0	2	2	4	0	6	0	1	0	5	0
2-11-76	2		0	2	3	0		3	0	1	6	3
3-13-76	2			4	1	5		0	2	1	6	2

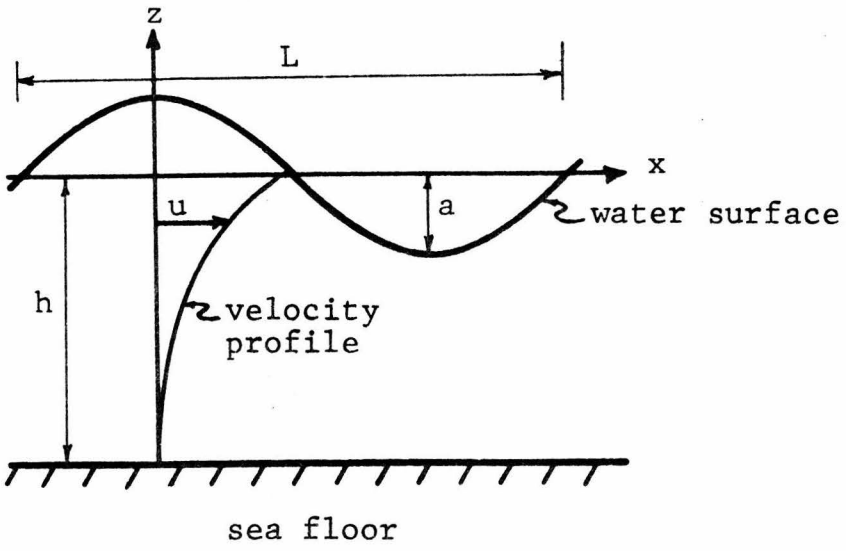
APPENDIX C

HYDRODYNAMIC FORCES ON KELP PLANTS

These notes show theoretical considerations (ref. Estuary and Coastline Hydrodynamics, A. T. Ippen, McGraw-Hill Book Co., New York, 1966) of the force on a kelp plant resulting from wave induced water motions.

Assume:

1. The plant is very flexible and buoyant.
2. Skin friction drag coefficient is constant, not a function of Reynold's number.
3. Skin friction drag dominates form drag. (This is not the case with the Palm Kelp, Eisenia arborea (Charters, Neushul, and Barilotti, 1969).)
4. Maximum force occurs under the peak of the wave.



Definitions - see sketch above:

$H = 2a$ = wave height = 2 · wave amplitude

L = wave length

T = wave period

u = horizontal component of water velocity

$k = \frac{2\pi}{L}$ = wave number

$\sigma = \frac{2\pi}{T}$ = wave angular frequency

C = phase velocity = celerity = $\frac{L}{T}$

B = plant surface area (skin friction area)

L_p = characteristic plant length

ρ = water density

C_f = drag coefficient

g = gravity constant

By dimensional analysis the wave force, F, has the form

$$F \sim C_f \frac{\rho}{2} B L_p u^2 \qquad (1)$$

Checking the dimensions the right hand side of (1) shows

$$\frac{M}{L^3} \cdot L \cdot L \cdot \frac{L^2}{T^2} = \frac{ML}{T^2}$$

which are the dimensions of force. We can express the horizontal velocity component, u, as

$$u = \frac{agk}{\sigma} \cdot \frac{\cosh k(h + z)}{\cosh kh} \cdot \sin (kx - \sigma t) \qquad (2)$$

where

$\frac{\cosh k(h + z)}{\cosh kh}$ = vertical decay of velocity profile

This is a non-dimensional factor and is to be integrated over depth, z. We also have

$\sin (kh - \sigma t)$ = phase angle = 1. under wave peak.

Therefore the velocity under the peak, u_p, is

$$u_p = \frac{agT}{L}$$

Then the maximum force, F_p, varies as follows:

$$F_p \sim C_f \frac{\rho}{2} B L_p \left(\frac{agT}{L}\right)^2$$

If wavelengths range from L = 200 feet to 1000 feet and water depths range from h = 10 feet to 50 feet, shallow water principles apply, namely

$$C^2 = \left(\frac{L}{T}\right)^2 = gh$$

So that

$$F_p \sim \frac{a^2}{h}$$

If waves are not impeded by the sea floor, deep water principles apply.

$$C^2 = \left(\frac{L}{T}\right)^2 = gh = \frac{gL}{2\pi}$$

In this case

$$F_p \sim a^2 L$$

Appendix D. *Macrocystis* consumption by Opaleye in an aquarium. A = growing tips. B = clean blades. C = mildly encrusted blades. D = heavily encrusted blades. E = sporophylls. F = frozen squid. Table entries represent the amount of tissue missing at the end of each feeding period multiplied by percent change in controls. Units are grams per day per fish.

Feeding period	# of fish	Temp	A	B	C	D	E	F	Total algae	Total plus squid
3/14 to 3/15	24		1.55	3.73		3.55	0.15		8.98	
3/25 to 3/26	24			0.98		3.28	1.72		5.98	
5/13 to 5/15	14			0.79	0.62	5.64			7.05	
5/15 to 5/19	14	16.3		0.97	1.09	1.61			3.67	
5/27 to 5/28	14	18.5	4.50						4.50	
6/3 to 6/5	14	18.3	1.40			2.20			3.60	
8/22 to 8/26	6	15.8	2.27		2.17			3.74	4.44	8.18
8/26 to 8/27	6	16.3	-1.25		6.52				5.27	
8/27 to 8/29	6		5.82		2.88				8.70	
8/29 to 9/2	6	18.3	6.34		1.72				8.06	
9/2 to 9/3	6	18.2	3.32		14.70				18.02	
9/3 to 9/5	6	18.7	1.76		0.56			34.67	2.32	36.99
9/5 to 9/8	6	19.2	1.52		0.55				2.07	
9/8 to 9/9	6	19.1	0.10			14.17			14.27	
9/9 to 9/10	6		1.97			2.17			4.14	
9/15 to 9/16	6	19.0	3.07	6.78					9.85	
9/16 to 9/17	6	19.1	2.10	0.60				9.18	2.70	11.88
9/17 to 9/20	6		1.19	2.13					3.32	
9/22 to 9/23	6	18.3		12.85		10.57			23.42	
9/23 to 9/24	6	19.8		6.35		11.23			17.58	
9/24 to 9/26	6			2.08		14.00			16.08	
9/26 to 10/1	6	18.8		1.48		1.98			3.46	

Appendix D. (cont.) Macrocystis consumption by Opaleye in an aquarium. A = growing tips. B = clean blades. C = mildly encrusted blades. D = heavily encrusted blades. E = sporophylls. F = frozen squid. Table enties represent the amount of tissue missing at the end of each feeding period multiplied by percent change in controls. Units are grams per day per fish.

Feeding period	# of fish	Temp	A	B	C	D	E	F	Total algae	Total plus squid
10/3 to 10/6	6	18.5		4.03				13.89	4.03	17.92
10/7 to 10/9	6	17.3		0.81	0.88	1.79			3.48	
10/9 to 10/10	6			1.60	1.72	3.45			6.77	
10/10 to 10/13	6	18.5		9.32	0.67	0.20			10.20	
10/13 to 10/14	6	18.8				4.99	1.61		6.60	
10/14 to 10/15	6					12.83	3.05		15.88	
10/15 to 10/16	6	19.0		5.69			1.84		7.53	
10/16 to 10/20	6	19.8		1.64			0.84	9.44	2.48	12.22
Average									7.82	17.46