The Effects of Discharges from the San Onofre Nuclear Generating Station on the Giant Kelp, *Macrocystis pyrifera*: I. Background Information and the Biology of Kelp

Final Report of the UCSB Kelp Ecology Project
for the Period
April 1978 through September 1987

Thomas A. Dean, Ph.D.
Marine Science Institute
University of California
Santa Barbara, California 93106
and
The Kelp Ecology Project Staff:
Larry Deysher
Fritz Jacobsen
Leilani Bost

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Table of Contents

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1.0 Introduction

1.1 Purpose

The UCSB Kelp Ecology Project has conducted studies at San Onofre since 1978. The primary goal of these studies has been to determine the effects of the San Onofre Nuclear Generating Station's (SONGS) Units 1, 2 and 3 on the giant kelp, Macrocystis pyrifera.

The final report for the project will consist of 2 documents. The first document is presented here and provides a description of the biology of kelp. It includes background information pertinent to the evaluation of the effects of SONGS. It is not intended to be an exhaustive review of the literature. More complete reviews have recently been published (Dayton, 1985; Foster and Schiel, 1985; North et al., 1986 . Schiel and Foster, 1986). This study focuses on the giant kelp, Macrocystis pyrifera, although much of the information on general life history attributes is also applicable to other laminarian algae, including the local subcanopy species Pterygophora californica. Studies in the San Onofre region are stressed because these are of direct interest in evaluating the effects of SONGS. An evaluation of the effects of SONGS on kelp will be presented in a separate document presented jointly with the USC Kelp Invertebrate Project and with ECOsystems Management Associates. A detailed description of our overall study plan and the underlying rationale for this plan are outlined later in this chapter. First, we present a brief overview of the life history of kelp, a history of the kelp forests

near SONGS and a description of these kelp forests in relation to other kelp forests in the region.

1.2 Life History of Kelp

The giant kelp, Macrocystis pyrifera, is a key species in the nearshore subtidal ecosystem in Southern California. The kelp forest habitat is structurally dominated by Macrocystis, which provides shelter and food for hundreds of animal species, including some which are valuable to both sport and commercial fisheries.

The life history of giant kelp consists of an alternation of generations between a microscopic gametophyte stage and the more familiar sporophyte stage (Fig. 1.1). Large sporophytes produce specialized reproductive blades called sporophylls, which are located near the base of the plant. Meiosis occurs in sporophylls, and the resulting haploid zoospores are released into the sea. Spores which are able to successfully settle onto hard substrates metamorphose into male and female gametophytes. Under favorable conditions, these produce sperm (antheridia) and eggs (oogonia), respectively. The diploid sporophyte results from the fertilization of an egg. Laboratory observations indicate that the egg and embryo are generally retained by the female gametophyte. The young sporophytes which grow from the female gametophyte initially develop into single blades. These plants continue to grow and produce the morphologically complex adults. Adult sporophytes can have over 100 fronds, many of which reach the water's surface from depths of 15 m.

For the purposes of this study, we have divided the macroscopic sporophyte portion of the life cycle into four different categories: 1) blade, 2) juveniles, 3) subadults, and 4) adults. For the most part, categories are based on morphological

characteristics of the plants that correspond roughly to size. Blade stage plants are those individuals large enough to be distinguished in situ as Macrocystis (approximately 2.5 cm) but which have not yet fully differentiated into two fronds. Juveniles are defined as plants with two or more fronds (usually approximately 40 cm in height) but with a height less than 1 m. Subadults are plants greater than 1 m in height but without haptera protruding from above the primary dichotomy (Fig. 1.1). Once these haptera appear, plants are classified as adults. Adult plants generally have 6 or more fronds, with the longest frond reaching to the surface from depths of 13 m.

1.3 A History of the Kelp Forests Near SONGS Prior to the Operation of SONGS Units 2 and 3

There are three kelp forests located along the coastline in the vicinity of SONGS (Fig. 1.2). These are San Mateo Kelp (SMK), 4 to 5 km northwest of SONGS, San Onofre Kelp (SOK), directly offshore of the generating station, and Barn Kelp (BK), about 11 km downcoast (southeast) of SONGS. The historical records of these forests have been reviewed previously (Deysher, 1978; Dean, 1980a; and SCE, 1981) and are summarized below.

The areal extent of kelp forests in the vicinity of SONGS has been mapped over the years using a variety of techniques including surveys of canopy areas by sextant triangulation, aerial photography, and mapping of subsurface plants by means of side-scan and downlooking sonar. Each method has its drawbacks and consequently the areas of kelp forest estimated by the various methods are not comparable in a quantitative sense (Dean, 1980a, p. 10). However, these records provide a semi-quantitative history of the sizes and shapes of the kelp forests.

The history of SOK, SMK and BK are summarized in aerial maps of canopy area (prior to December 1978) and areas of surface frond abundance (from December 1978 to 1982) (Fig. 1.3). A more detailed account of the size of the individual kelp forests from 1974 to the beginning of operations of SONGS Units 2 and 3 in 1983 is given in Figure 1.4.

In 1911, kelp forests were almost continuous along the coast line from San Diego to Point Conception, wherever suitable substrate existed, including the area under study. SMK, SOK, and BK apparently have persisted for over 40 years as indicated by surveys in 1934 and in the early 1950's (Deysher, 1978). In the 1958 and 1959 El Nino period, an estimated 90% of the kelp canopies (formed by fronds of adult sporophytes which reach the surface) located along the mainland coastline of Southern California disappeared (North, 1973). Canopies at SOK and SMK disappeared completely during this time and BK was reduced in size. It has been hypothesized that the die-off was related to either abnormally high water temperatures (North, 1971), extremely low nutrient concentrations (Jackson, 1977), or both. The die-off may also have been exacerbated by pollution (Wilson et al., 1978).

San Onofre Kelp and San Mateo Kelp did not become reestablished for more than 10 years after the die-offs, in 1970 and 1972 respectively. The kelp forests generally flourished for the next several years until another partial die-off of the forests occurred in the summer of 1976. Other Southern California kelp forests were also in a state of decline in the summer of 1976 (R. McPeak, Kelco Corp., personal communication), but the die-off of kelp was much more dramatic at SOK, SMK, and BK than elsewhere.

San Onofre Kelp and San Mateo Kelp began increasing in size again in 1977 a increased sharply in 1978 and 1979 following widespread recruitment events in the spring of 1978 and winter 1979. During these times, divers noted large numbers of blade stage Macrocystis throughout much of SOK and SMK, with densities of small plants generally exceeding 100/m² (Dean, 1979, p. 71). In "non-recruitment" years, densities of blades are less than 1/m².

not general for recruitment "events"

From late 1979 until early 1982, both SOK and SMK declined slightly. However, the most striking event to occur in the kelp forests near SONGS between 1979 and 1982 was the decline and eventual disappearance of BK during 1980. This was unexpected since BK had been the most persistent kelp forest on the coastline near SONGS from 1950 through 1980. Unlike SOK and SMK, BK persisted through the 1958-59 die-off. The decline in BK apparently began in the spring and summer of 1980. The sharpest period of decline was between June and November 1980, after which only a few scattered plants remained at the site. The cause of the die-off is not known, but several hypotheses exist. First, the kelp forest was comprised almost entirely of extremely large and, presumably, very old plants. There had not been any significant recruitment to the population in at least 5 years (based on diver observations) and probably longer (based on the large sizes of the holdfasts and large numbers of fronds per plant). The plants may simply have become old and senescent and reached the end of their normal life expectancy. However, there is no evidence that mortality rate of adult sporophytes increases with age, and similar events are unreported for other kelp forests in the absence of obvious contributing factors.

A second hypothesis is that adult plants were killed and further recruitment was restricted by heavy sedimentation within the kelp forest. Kuhn and Shepard

(1984) noted that there was extensive landslide activity and cliff erosion along the shoreline adjacent to Barn Kelp in February 1978 and again in February 1980. Enormous amounts of sediment were deposited offshore creating a series of sand bars. We noted extensive sand movement onto several of our stations in Barn Kelp. While some areas did not get covered with sand, a layer of fine sediments covered the kelp fronds and hard substrata in the region. We suspect that the die-off resulted from the direct burial and resulting death of adult plants, an increase in grazing pressure on the remaining individuals, an inhibition of recruitment due to the covering of much of the available hard substrata by sediments, and a lack of recruitment due to a declining source of spores.

Whatever the cause of the BK die-off, it is clear that it was unlike previous catastrophies in that it was obviously a very localized event. No other kelp forests from Point Conception to San Diego experienced such a decline at that time.

A major El Nino event occurred beginning in fall 1982. Associated with the El Nino were severe storms with exceptionally high surf in winter 1982-83. Many of the kelp forests were severely thinned by the storms (Dayton et al., 1984). The San Onofre and San Mateo Kelp forests were somewhat less affected by the storms than the others. Exceptionally high temperatures and low nutrients prevailed in Southern California kelp forests throughout most of the period from fall 1982 through fall 1984. A brief "relaxation" of this pattern occurred in spring 1983 when there was an intensive upwelling event. There was recruitment of kelp associated with the upwelling, but existing adult kelp grew slowly during 1983 and 1984 and canopies of kelp were severely depleted throughout Southern California at this time. The warm waters were also associated with a die-off of sea stars throughout Southern California kelp forests. During 1985 and 1986, oceanographic and climatological patterns returned to more normal conditions.

1.4 A Description of the Kelp Forest Communities in the SONGS Area

The substrate in the kelp forests near SONGS consists primarily of cobbles and boulders ranging from about 5 cm in diameter up to almost a meter in diameter. The cobbles are interspersed with patches of sand. Consolidated reef outcropping areas are rare except at Barn Kelp where some extensive reefs occur. The kelp forests in the vicinity of SONGS are dominated by a canopy of Macrocystis pyrifera and an understory of other algae, primarily Pterygophora californica and Cystoseira osmundacea; occasionally, large blooms of Desmerestia ligulata occur. Most of the giant kelp in these forests occurs between the depths of 10 m and 16 m. The inner margins of the kelp forests are bounded largely by sand. The outer margins are less clearly defined. Some portions are bounded by sand or by extensive aggregations of sea urchins on hard substrata.

The algal turf community is dominated by Acrosorium uncinatum and encrusting coralline algae. Although dominance is high, the species list of algae in these kelp forests is quite extensive given the lack of relief. Unpublished lists (R. Fay, personal communication) indicate that over 120 species of algae are present.

The principal macroinvertebrates in the kelp forests are the sea urchins, Strongylocentrotus franciscanus and Lytechinus anamesus, the sea stars Patiria miniata and Pisaster giganteus, the gorgonian coral, Muricea californica, and a variety of gastropod molluscs (Kelletia kelletii, Conus californicus, Pteropurpura festiva).

A brief description of the regional physical and chemical oceanographic factors that are most important to kelp is given below. A more complete description is given in Reitzel et al. (future publication).

Temperatures on the sea floor in the kelp forest range from 10°C to 20°C and average between 15°C and 16°C. Surface temperatures occasionally reach 23°C. Temperatures vary with depth, but daily mean temperatures are generally highly correlated among various locations at any given depth. Temperature stratification occurs regularly in the summer and fall. The upwelling of cool water occurs on an irregular basis but is most frequent in the spring. Nutrients (especially NO_2 and NO_3) are inversely correlated with temperature, with peaks in nitrogen occurring during upwelling events.

Irradiance reaching the sea floor in the kelp forest varies both temporally and spatially. Much of the spatial variability can be explained by changes in depth, shading by the kelp canopy, and proximity to fine sediments that can be resuspended by waves. Temporal variability is largely determined by changes in the extinction of light within the water column rather than changes in incident irradiance at the water's surface. Extinction rates are often higher near the bottom as the result of resuspension of sediments by waves. Irradiances (300 nm - 700 nm) on the sea floor in the kelp forests range from above 10 $E/m^2/d$ to undetectable levels (<0.05 $E/m^2/d$) but are generally between 1 and 2 $E/m^2/d$ (about 5% of surface irradiance).

Longshore currents in the kelp forest average about 4 cm/s. There is a strong tidal component to current speed and direction, but on average, currents run in the downcoast (equatorward) direction about 60% of the time. In the San Onofre Kelp forest, current directions tend to be canted inshore when currents are running downcoast and offshore when currents are running upcoast (poleward). The kelp forest itself can substantially alter current direction and reduce current velocity.

Waves are important both as a direct source of mortality to kelp and also indirectly due to the resuspension of bottom sediments. The San Onofre and San Mateo Kelp forests are substantially blocked from northerly swells by the Channel Islands (Pawka and Guza, 1983) and are more susceptible to the large southerly swells which tend to occur in late summer and fall.

1.5 Comparisons of Kelp Forests in the SONGS Area with Others in Southern California

There are few published descriptions of the kelp forests along the Southern California coast. However, based on the existing records and on personal diving experience, all 3 kelp forests in the SONGS area appear to be quite different from other forests in Orange and San Diego Counties. Most other kelp forests along this coastline are found growing on consolidated substrates rather than on cobble bottoms. Also, maximum densities of adult plants are lower at SOK and SMK than in other regions such as Pt. Loma, La Jolla and Del Mar. The average adult densities in canopy areas at SOK and SMK are approximately $0.1/m^2$ (Section 11.0), while in other forests densities are usually between 0.2 to $0.3/m^2$ (North, 1971, p. 46; Rosenthal et al., 1974; Dayton et al., 1984). We suspect that the differences in plants' densities are causally related to substrate availability.

SOK and SMK also differ from other forests in that the understory algal populations are not as diverse. In kelp forests elsewhere, Eisenia, Laminaria, Gelidium and other brown and red algae are important understory components (North, 1971, pp. 50-52; Neushul, 1971, p. 267). These species are relatively rare at SOK, SMK, and BK. SOK and SMK appear to have larger populations of urchins than elsewhere. Commercial urchin divers (Dave Roody, personal communication) indicate that none of the kelp forests between Pt. Loma and San Onofre has as large a population of red urchins, S. franciscanus, as SOK and SMK have. Our own diving

experience suggests that white urchins (Lytechinus anamesus) are much more abundant at SOK and SMK than elsewhere.

In spite of their dissimilarities, the kelp forests between La Jolla and SMK appear to undergo somewhat similar fluctuations in size, with peaks in abundance of Macrocystis occurring about every 3 to 4 years. North (1971, pp. 42 and 43) described this pattern for the kelp forests between Del Mar and Oceanside. The cycles appear to result from sporadic recruitment of Macrocystis. From 1978 through 1983, high densities of newly recruited plants appeared 3 times (in 1978, 1981, and 1983) at San Onofre and San Mateo Kelp forests with little or no successful recruitment in the interim periods (Dean, 1983). Rosenthal et al., (1974) noted two recruitment "events" in their 6-yr study at Del Mar. It also appears that these recruitment events may be somewhat synchronous among the kelp forests in San Diego and Orange counties. In the years that we noted good recruitment at San Onofre, Dayton (personal communication) also noted good recruitment at Pt. Loma. Similarly, dives made in the Laguna Beach area in 1981 suggested good recruitment occurred there as well as at San Onofre. In 1983, successful recruitment of kelp was prevalent all along the coastline from Palos Verdes to Pt. Loma, as indicated by a survey of kelp researchers in this region. However, the lack of recruitment in "off" years at Pt. Loma and La Jolla may not be as dramatic as in other San Diego area kelp forests. We have always been able to find a few newly recruited plants each summer at La Jolla and Pt. Loma while on occasion (e.g., 1980), there were no newly recruited plants at SOK (see Section 9.0).

The histories of the kelp forests in the southern portion of the Southern California Bight indicate that the large-scale patterns of kelp abundance may be driven by oceanographic conditions that exist over the entire area. For example,

the large-scale die-offs in El Nino years, such as occurred in 1958-59, and the recruitment events of 1978, 1981, and 1983, were all widespread phenomena. Superimposed on this large-scale picture are the changes brought about by more localized events. For example, the disappearance of BK in 1980 was an isolated event. Patterns of kelp abundance over time and space are thus a result of both "bight wide" and local events.

1.6 The Operation of the San Onofre Nuclear Generating Station

A general description of the San Onofre Nuclear Generating Station and the discharges from its 3 generating units is given in _____(pending MRC report). The generating stations are currently in operation and produce a maximum of 2,636 megawatts. Unit 1 was placed into operation in 1968. Once-through cooling water for Unit 1 is discharged through a single port about 800 m from shore and about 1 km from the San Onofre Kelp forest. Units 2 and 3 began low-level testing in 1982 and were first put into commercial operation in August 1983 and April 1984, respectively. Each of the latter units discharges about 830,000 gal/min of cooling water through diffuser-type discharge pipes. The diffusers run perpendicular to the shoreline and extend offshore 1,800 m to 2,500 m. Portions of the San Onofre Kelp forest are within 200 m of the diffusers. It is the discharges from Units 2 and 3 that are of primary concern with regard to possible adverse effects on kelp. Intakes for all 3 units are located, approximately 900 to 1,000 m offshore and at least 700 m from SOK.

1.7 History of the Project and Rationale for Our Approach

The Kelp Ecology Project was begun shortly after the founding of the Marine Review Committee (MRC) in 1975. Since 1978, the project has been contracted through the University of California, Santa Barbara. The primary purpose of the project has

been to determine the effects of SONGS on populations of kelp in the San Onofre Kelp forest. However, the project has undergone several shifts in emphasis. The first several years of the project were aimed at predicting the effects of Units 2 and 3 on the San Onofre Kelp forest. This approach was implemented by determining the effects of the existing Unit 1 discharge on various life-history stages of kelp. These studies involved transplanting the life-history stages of interest to stations at various distances from the Unit 1 discharge. Transplanting was necessary because there were no naturally-occurring kelp populations in the vicinity of Unit 1 at that time. The results of the Unit 1 studies were combined with observations on the life history of kelp in the SOK forest to make our predictions of the effects of Units 2 and 3 (Dean, 1980b). Briefly, our predictions indicated a potential reduction in the number of sporophytes produced from gametophytes and a reduction in the growth rate of juvenile plants when Units 2 and 3 began operating. These effects were primarily related to reductions in irradiation expected as a result of the operation of SONGS.

In 1980, we began to shift the emphasis from predicting the effects of Units 2 and 3 to the development of a pre-operational baseline, prior to the beginning of the operation of the new units. This baseline consists of life-history data gathered from both natural and experimental populations. The data are to be used in a Before-After/Control-Impact pairs (BACIP) design (Stewart-Oaten, 1984). Biological parameters were measured at stations near and far from the diffusers before the completion of Units 2 and 3 and were measured at these same stations after Units 2 and 3 became operational. We have defined the beginning of the operational period as January 1983, when Unit 2 first reached a level of 50% operating capacity. A significant change in a variable (relative to the control) after Units 2 and 3 began operation would indicate an effect of the power plant.

In the early phases of our pre-operational baseline studies, we emphasized using a station (or stations) in the upcoast portion of SOK as the "impact" site and a station (or stations) in the downcoast portion of SOK as the "control" site. However, predictions concerning the effects of SONGS on turbidity (Reitzel, 1980) indicated that SONGS Units 2 and 3 would have approximately equal impact at both up- and downcoast SOK. Thus, we were required to use stations in the nearby San Mateo and Barn Kelp forests as "control" sites.

The use of SMK and BK as controls presented several problems. First, we knew that the histories of the kelp forests (and especially BK) were quite different from one another. Second, the physical environment at SOK may be quite different from the other two kelp forests because SMK is located just offshore of a point of land (San Mateo Point) and BK is somewhat deeper, on average, than SOK. Thus, it did not appear as though SMK and BK would be ideal control sites. This point was even more strongly emphasized when BK disappeared in the summer of 1980.

The potential problems in a BACIP design created by the lack of an ideal control, along with other considerations (see Stewart-Oaten, 1981), caused us to redirect our approach. In 1981, we decided to continue to gather pre-operational data for BACIP, but also attempted to better understand the relationship between the physical/chemical environment and kelp. This "mechanistic" approach can be used to relate observed changes in biological parameters with changes in physical variables that may be altered by SONGS. In this way, we can demonstrate a potential SONGS' effect and also supply a direct causative link between the biological effects and SONGS operations. Therefore, our efforts over much of the last several years of the contract were aimed at developing mechanistic models for growth and mortality of kelp in its various life-history stages and, at the same time, providing data for the BACIP design. These mechanistic studies are the primary focus of this document.

Our general approach for both the mechanistic and BACIP studies was to deal with each life stage on an individual basis. We did this because the various life stages live in very different microenvironments and respond differently to various environmental factors (Neushul, 1978). For example, gametophytes live on the bottom where sedimentation is high and irradiance levels are relatively low. Adult plants, on the other hand, have most of their tissue in the upper portions of the water column where irradiance is relatively high and sedimentation is low. We could not simply assess the impact of SONGS following the fate of the adult kelp population because adult kelp are long-lived and recruitment is episodic. Although there may be impacts on recruitment, these may not be reflected in adult population densities for some time.

We have used different methods to study the different life-history stages. This was necessary because of both the large range in size displayed by the different life-history stages (from 5 μ to >15 m in height) and the large differences in the lengths of time a plant remains in the various stages (from several days to several years). The small gametophyte and sporophyte life stages were studied in the laboratory and in situ using "outplanting" techniques. Small plants were cultured in the laboratory and populations of known age, size and density were subsequently transplanted into the field. Outplanting techniques and laboratory studies were necessary because these life-history stages were too small to easily observe in the natural marine environment.

We studied the growth of juvenile sporophytes by transplanting laboratory-recruited plants or naturally-occurring plants which we obtained from various kelp forests. We used these sources because natural recruitment at SOK was rare and juveniles were not always available. The outplant and transplanting techniques also

allowed us to obtain control over many environmental factors. For example, we could study the growth of juveniles over several seasons at the same place and under similar conditions with regard to the density of competing adult Macrocystis and understory algal species. In addition, we were able to place plants at chosen locations so that we could obtain measures of growth, mortality, etc., under a wide range of environmental conditions.

The following chapters outline pertinent information on the biology of kelp with each life-history stage discussed in a separate chapter. These studies are combined with descriptions of the changes in physical factors, and with changes in kelp populations, especially with regard to the natural recruitment of kelp and subsequent changes in adult population densities. Evaluation of the effects of SONGS is based on the evidence compiled from all of these sources and, as indicated, is presented in a separate document.

Figure 1.1 A diagramatic representation of the Macrocystis pyrifera life cycle. The names of each life-stage and approximate size ranges are given. On adult and subadult plants, the various structures of the plant are labelled: (a) holdfast composed of haptera, (b) primary dichotomy, (c) sporophyll, (d) apical meristem or "scimitar blade," (e) frond, composed of: (f) stipe and (g) blade. The blade is made up of (h) lamina and (i) pneumatocyst.

Figure 1.1

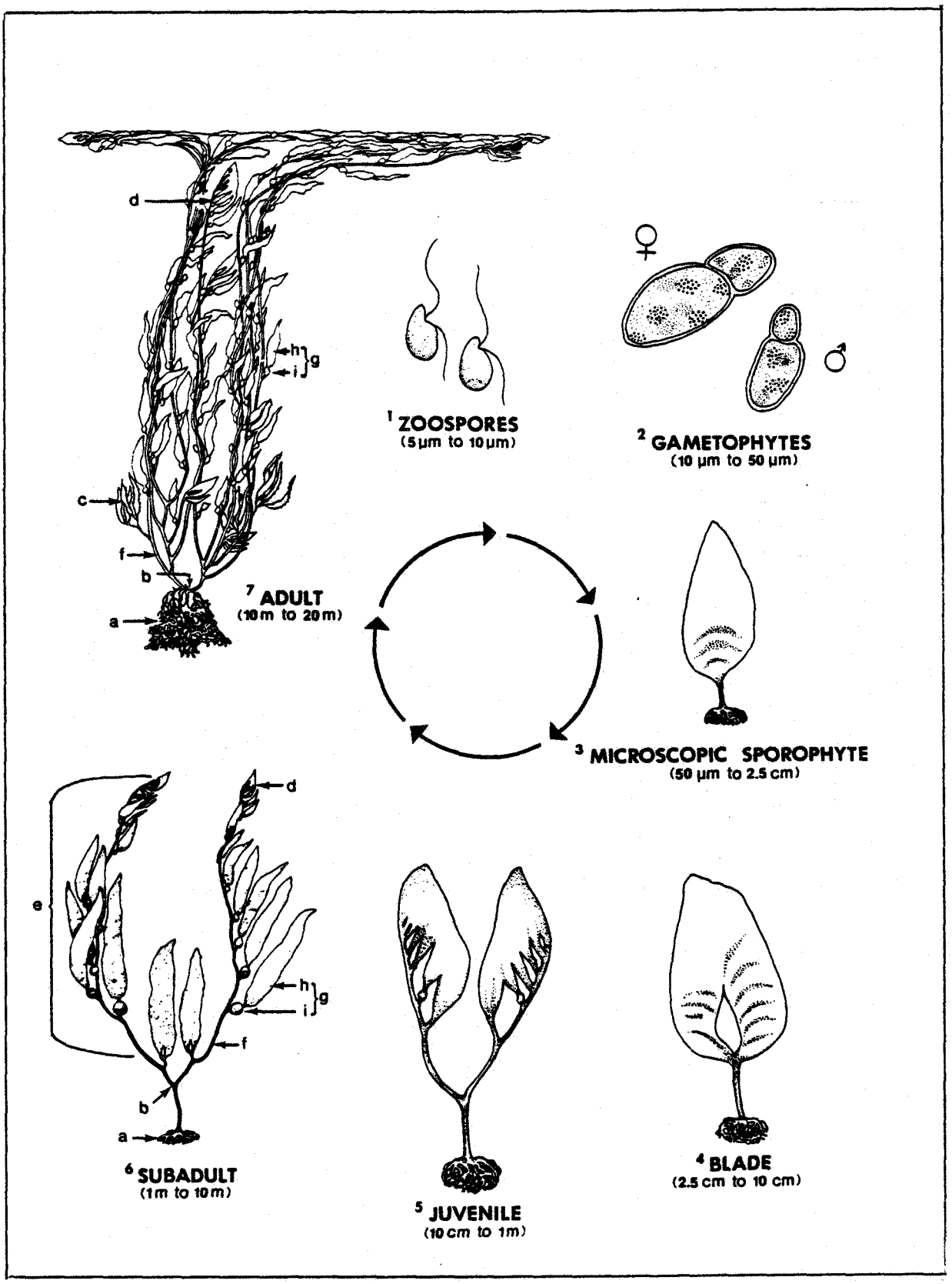

d
h
i
g
c
f
b
a
7 ADULT
(10 m to 20 m)
1 ZOOSPORES
(5 µm to 10 µm)
♀
♂
2 GAMETOPHYTES
(10 µm to 50 µm)
3 MICROSCOPIC SPOROPHYTE
(50 µm to 2.5 cm)
e
d
h
i
g
f
b
a
6 SUBADULT
(1 m to 10 m)
5 JUVENILE
(10 cm to 1 m)
4 BLADE
(2.5 cm to 10 cm)

Figure 1.2 Location of kelp forests and features of the San Onofre Nuclear Generating Station. Asterisks (*) denote SONGS' water intakes and circles (o) denote ends of the discharge pipes. Hatch marks along Units' 2 and 3 diffuser lines indicate areas over which water is discharged.

Figure 1.2

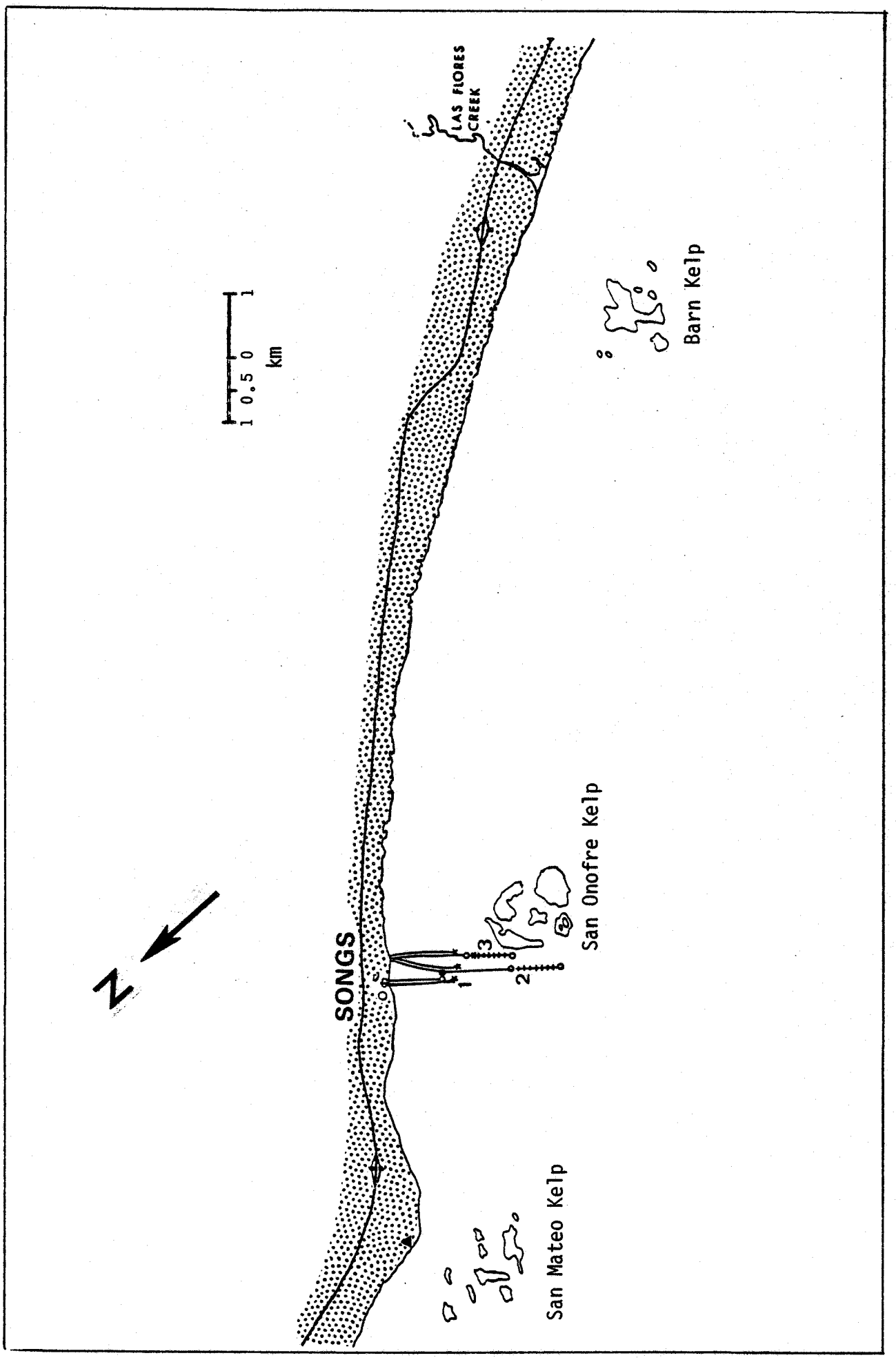

LAS FLORES CREEK
1 0.5 0 1
km
Barn Kelp
San Onofre Kelp
SONGS
1
2
3
San Mateo Kelp
N

Figure 1.3 Historical charts of the kelp forests in the San Onofre region: 1911-1972 from North (1973); March 1976 from Lockheed (1976); December 1976 from SCE (1978); December 1978-1982 from ECOsystems Management Associates, Inc. (Reitzel and Zabloudil, 1983). No estimates of forest size were available for Barn Kelp in 1970, but diver observations indicated its existence (North, 1973).

Figure 1.3

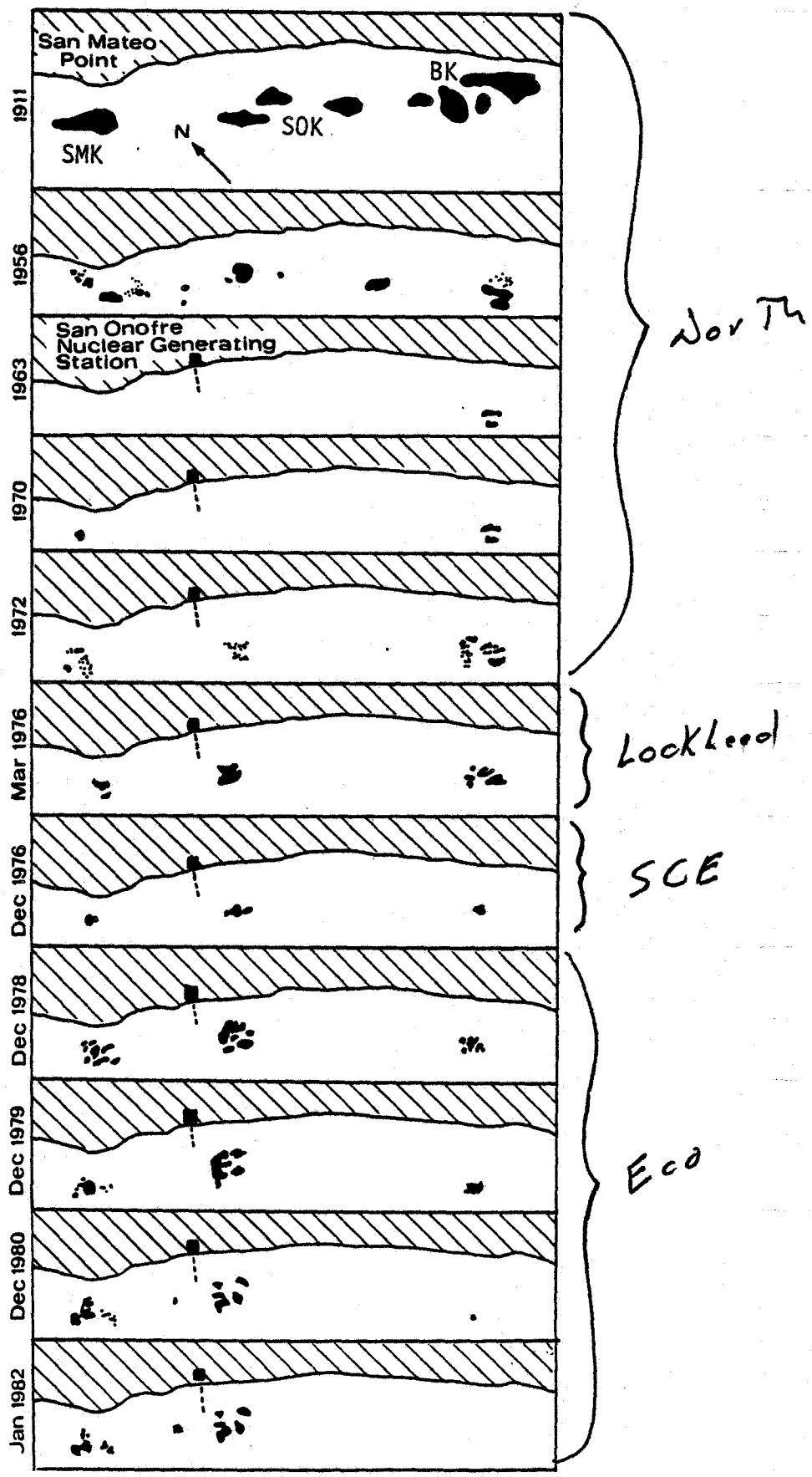
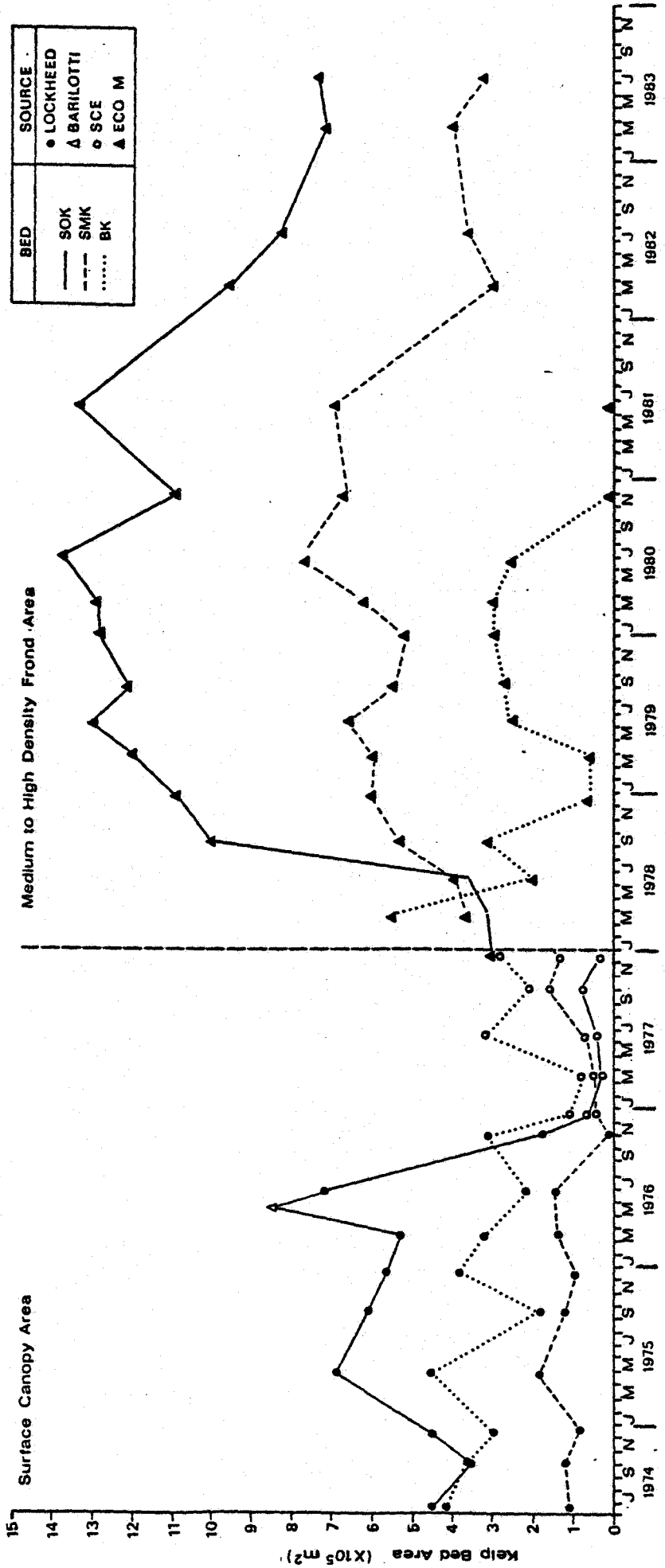

San Mateo Point
BK
SOK
SMK
N
1911
1956
San Onofre Nuclear Generating Station
1963
1970
1972
Mar 1976
Dec 1976
Dec 1978
Dec 1979
Dec 1980
Jan 1982
North
Lockheed
SCE
Eco

Figure 1.4 Fluctuations in kelp forest areas at SOK, BK, and SMK: June 1974 to October 1976 canopy area estimates from Lockheed (1976) except for May 1976 canopy area estimates from Barilotti (1978); December 1976 to December 1977 canopy area estimates from SCE (1978); December 1977 to July 1983 medium- to high-density frond area estimates from ECOsystems Management Associates, Inc. (Reitzel and Zabloudil, 1983).

Figure 1.4


Surface Canopy Area
Medium to High Density Frond Area
Kelp Bed Area (X10^5 m^2)
BED
SOK
SMK
BK
SOURCE
LOCKHEED
BARILOTTI
SCE
ECO M
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983

2.0 Production, Release, and Dispersal of Zoospores

Little is known about the temporal and spatial variability in release of zoospores from the sporophylls of adult kelp or the factors which influence production and release of spores. The only quantitative studies of zoospore release were conducted by Anderson and North (1967). They bagged sporophylls of Macrocystis in situ at various times of year and counted the numbers of zoospores released. Extremely high variability was noted among sites and among collection dates. There was no discernible seasonal trend and at least some spores were released in each month of sampling. In our studies at San Onofre, we collected sporophylls from adult plants on over 60 occasions and in all months. Viable zoospores were released on all occasions with the exception of fall of 1983 during the height of El Nino. At this time, finding sporophylls in the field was extremely difficult and the few sporophylls that were found released only a few zoospores. These data suggest that viable spores are produced and are available for release year-round except during extremely adverse conditions for kelp growth such as El Nino. However, the numbers of spores released may vary substantially from time to time.

Dispersal of zoospores by Macrocystis and other laminarian algae is limited. Zoospores quickly settle onto the bottom, probably within 12 hours of release (Neushul, 1978). New recruits of Macrocystis (Anderson and North, 1966) and other laminarian algae (Dayton, 1973; Paine, 1979; Sundene, 1982; Dayton et al., 1984; Santilices and Ojeda, 1984) are highest within close proximity to adults, suggesting poor dispersal. Also, Dayton et al. (1984) noted higher densities of recruits in locations "seeded" with sporophylls than at nearby control sites.

Although spores appear to disperse poorly, occasional longer-range dispersal is possible. Longer-range dispersal of Macrocystis pyrifera was graphically demonstrated by the colonization of an artificial reef near La Jolla, California. This reef was heavily colonized by M. pyrifera within a few months after emplacement (Davis et al., 1982), in spite of the fact that the nearest adult population was over 2 km away. Similarly, Fager (1971) found M. pyrifera recruits on artificial substrates placed on a sand bottom 2 km from the nearest adult population. Also, we have noted relatively high densities of spores on slides (Section 3.0) and cobbles (Section 4.0) collected from stations in SOK where densities of adult sporophytes were extremely low.

Longer-range dispersal is probably accomplished by drifting adult plants or by fragments of adults with sporophylls attached (Dayton, et al., 1984). Drifting adults have been traced several km from their origin (personal observations) and can probably retain sporophylls for up to several months while floating above the bottom (Dayton et al., 1984). Similar mechanisms of long-range dispersal have been documented for Sargassum muticum (Deysher and Norton, 1982) and suggested as a likely mechanism for other seaweeds (Dayton et al., 1984, Schiel, 1985). Dispersal by drifting adults or plant fragments is episodic and is likely to be most prevalent during periods of storms (Dayton et al., 1984).

3.0 Survival of Gametophyte Stages

3.1 Introduction

After settlement, zoospores quickly metamorphose into male or female gametophytes. A minimum of 10 to 12 days is required for gametophytes to undergo gametogenesis and to produce sporophytes (Deysher and Dean, 1984; Luning and Neushul, 1978, and Section 6.0). However, light, nutrient, or other environmental conditions in situ are often suboptimal for gametogenesis. Survival for longer than 2 weeks would greatly enhance the probability of successful recruitment as gametophytes could "wait out" periods when conditions are poor. Previous studies of survival of kelp gametophytes indicate that they can survive for several years in laboratory culture (Neushul, 1978). However, there have been no previous studies of the in situ rates of survival of Macrocystis gametophytes. In this section, we examine the effects of the age of gametophytes on survival and estimate survival rates.

We have examined the survival of gametophytes using two basic techniques. First, glass microscope slides were inoculated with zoospores of Macrocystis and outplanted to field sites. After periods of up to several months, the slides were collected and sporophytes on the slides were counted. The slides were then cultured in the laboratory under conditions optimal for sporophyte production, and re-examined approximately 3 weeks later for sporophyte density. Any increase in sporophyte density achieved in culture could be attributed to surviving gametophytes. Uninoculated controls were used to examine possible influences of natural spore settlement and were treated in the same manner as the inoculated slides.

A second method involved inoculating slides with zoospores and staining the gametophytes which developed from the spores with a fluorescent dye. The slides were then outplanted and collected after a period of several days to several weeks. The stained individuals remaining were then counted. Preliminary studies indicated that the stain had no adverse effects on survival and that the remaining stained gametophytes could be observed for several weeks after outplanting (see Dean, 1985, and Appendix A). However, more recent experiments have shown that the densities of stained gametophytes on slides greatly over-estimated the number of viable gametophytes that remained. Furthermore, the density of stained individuals observed prior to culturing did not correlate with the density of sporophytes produced after culture (see Appendix A for details and analyses). This was probably because the stained cell walls of the gametophytes remained on the slides for some time after the gametophytes had died or lost their viability. We have excluded analyses of stained gametophytes because of these methodological problems.

3.2 Methods

Frosted microscope slides (2.5 cm x 7.5 cm) inoculated with gametophytes were outplanted to field sites and later collected and cultured on 7 occasions in 1984 and 1985. The first two outplantings were preliminary studies conducted in San Mateo Kelp only (SMK45, Fig. 3.1 b). Substrates were outplanted on 30 November 1984 and 8 February 1985 and collected after 6 weeks. At approximately monthly intervals from April 1985 through August 1985, substrates were outplanted to SMK45, SOKD45, SOKD35, SOKU45, and SOKU35 (Fig. 3.1 a&b). These substrates were also collected after a period of 6 weeks.

In all experiments, slides were attached to 10 cm x 30 cm plexiglass plates using silicone sealant and the plates were attached to 90 lb cement anchors using

plastic cable ties (Fig. 3.2). Two to three plates were outplanted to each station on each outplant date. The slides used in culture were randomly selected from the pooled set of slides at each station. In most experiments, 4 slides were outplanted and later cultured. The actual number of slides observed varied from 1 to 5 at a given station and date (Table 3.1).

Uninoculated slides were put out at each station to assess the number of sporophytes produced from naturally settling gametophytes. Plates with uninoculated slides were placed on cement bags within 2 m of those holding inoculated slides.

In the laboratory, slides were first placed in filtered seawater with a germanium dioxide (GeO_2) concentration of 0.25 mg/l for 24 hrs. This procedure was used to eliminate diatoms, which can quickly overgrow laminarian gametophytes in culture. GeO_2 at this concentration and length of exposure has no adverse effects on laminarian gametophytes (Markham and Hagmeier, 1982). The slides were then placed into culture containers with 6ℓ of culture media (Provasoli's Enriched Seawater) which was aerated to prevent the formation of nutrient boundary layers. Cultures were maintained at 15°C and irradiances of 45 $\mu E/m^2/s$ using a 12-hr photoperiod. These conditions are optimal for sporophyte production (Luning and Neushul, 1978; Deysher and Dean, 1984, 1986; Section 6.0).

Densities of gametophytes on slides prior to outplanting were determined by choosing from 1 to 3 slides at random from each plate and counting the number of gametophytes on the slide. Counts were made from either 25 (in the Nov 1984 experiment) or 20 quadrats (in all other experiments), with each quadrat measuring 0.03 mm^2. Quadrats were selected haphazardly by moving the mechanical stage of the

compound microscope before examining a field of view. Counts achieved in this manner were similar to those in a random sampling of quadrats on a slide (Appendix B).

Slides were examined immediately after collection to determine if sporophytes were present. If so, the sporophytes were counted and removed prior to culturing. After 3 weeks, the slides were removed from culture. Sporophytes were counted on the entire upper surface (1875 mm^2) of each slide. Slides were divided into three 625 mm^2 sections to facilitate counting.

Survival of gametophytes was assessed by tabulating the initial densities of gametophytes and the final sporophyte densities for each outplanting. No statistical tests (e.g., comparing stations or outplant dates) were performed because the number of sporophytes produced in most cases was too low for use in meaningful testing. Percent survival after 6 weeks was computed as:

$$\text{Percent Survival} = 100 \times \frac{\left[(\bar{d}_i - \bar{d}_u)\right]}{\left[\bar{d}_g/2\right]}$$

where $\bar{d}_i$ is the mean density of sporophytes from inoculated slides, $\bar{d}_u$ is the mean density of sporophytes on uninoculated slides, and $\bar{d}_g$ is the mean initial density of gametophytes. We assumed that all sporophytes on uninoculated slides were from natural spore settlement and that equal numbers settled onto inoculated slides. We also assumed that the potential numbers of sporophytes on inoculated slides was one-half of the initial gametophyte density since male and female gametophytes are generally produced in a 1 to 1 ratio (Section 6.0).

A second study was performed in 1985 and 1986 that was specifically designed to test for the possible effects of the age of gametophytes on their survival. Two experiments were performed, in November 1985 through February 1986 and August through November 1986, at Barn Kelp (BK45). The times of the experiments were chosen because they were the least likely times of the year to encounter conditions that would allow production of sporophytes from gametophytes. We wanted the gametophytes to remain as such for 12 weeks so that we could test the effects of age on longer term gametophyte survival without the confounding effects of sporophytes being recruited *in situ* as the experiment progressed. The Barn Kelp site was selected in order to minimize the effects of natural spore settlement. Adult sporophytes of *Macrocystis* and other laminarian algae were rare at Barn Kelp, thereby reducing the likelihood of finding naturally settled gametophytes.

In each experiment, 3 sets of slides that were inoculated with gametophytes were put out at 3-week intervals for a period of 6 weeks (Table 3.2). Slides were collected at 3-week intervals until the end of the experiment, 12 weeks after the initial set of slides was put out. The slides were randomly selected from the pooled set of plates from each outplanting. The number of slides collected was increased as age (number of weeks after outplanting) increased (Table 3.2), in order to maintain reasonable sample sizes (in terms of total number of sporophytes counted) since the number of surviving gametophytes decreased with time.

Uninoculated slides were also put out and collected, according to an identical schedule to assess sporophyte production from natural spore settlement. Both inoculated and uninoculated slides were cultured and sporophytes on the slides were counted as described previously in this section.

The effect of age on survival was assessed by comparing survival of different aged populations over the same time period. For example, survival rates of 0, 3, and 6 week old gametophytes were compared over the period from 02 January 1986 to 26 January 1986. Statistical tests of differences in survival among age groups were made using prespecified contrasts with the SAS general linear model (GLM) procedure (SAS, 1982). The tests compared differences in the log-transformed values of sporophyte density at the beginning and end of a particular period among pairs of age groups. For cases involving only 2 age groups and 2 observation times, this is the same as testing for a significant time vs age interaction in a two-way ANOVA. The contrasts are equivalent to a comparison of the slopes of survival curves for different-aged populations. In cases where initial densities were for gametophytes, we assumed that the potential number of sporophytes produced would be one-half the number of gametophytes, since male and females are found in 1 to 1 ratios (Section 6.0). We, therefore, halved the gametophyte densities prior to the transformation and computation of differences in density. A constant of 0.0005 sporophytes/mm^2 was added to sporophyte density, per slide, prior to transformation, to avoid taking logs of zero values. This constant is equivalent to 1 sporophyte per slide.

In the age-survival experiments, sporophytes were produced in situ (prior to culture) on slides outplanted on 12 December 1985 and collected on 13 February 1986, and in all of the 1986 outplantings except the one collection of 06 November 1986 (Table 3.2). Therefore, we were unable to use these data in statistical analyses of the effects of gametophytes' age on survival.

The maximum densities of sporophytes observed on uninoculated slides were <6% of those observed on inoculated slides and the average was 1%. Therefore, the possible confounding effects of natural spore settlement were small and were ignored

in the statistical analysis. Half-lives reported are the number of days required for the population to be halved, given the estimated mortality rate. This is equivalent to:

$$\text{Half-life} = \frac{\ln (0.5)}{\text{mortality rate}}$$

Mortality rate was calculated as:

$$\frac{\ln \bar{d}_1 - \ln \bar{d}_2}{t_2 - t_1}$$

where $\bar{d}_1$ is the mean initial sporophyte density, $\bar{d}_2$ is the mean final sporophyte density, and $t_2 - t_1$ is the elapsed time, in days, between observations. Initial densities for gametophytes were assumed to be equal to one-half of the gametophyte density.

3.3 Results

Few viable gametophytes survived on slides outplanted for 6 weeks at SOK and SMK. A maximum of 0.07 percent and a mean of less than 0.001 percent of the female gametophytes produced sporophytes (Table 3.1). Although densities of sporophytes were too low for statistical comparisons, maximum survival rates appeared to occur in spring and were lowest in July and August (Fig. 3.3). There were no survivors at SMK45 in May, June, and August; at SOKD45 in July and August; and at SOKD35 in July and August. During times of peak abundance in April through June 1985, mean densities were highest at SOKU45 or SOKD35.

In the experiments conducted at Barn Kelp that examined the effect of age on survival, the survival of gametophytes that were 3 weeks old or older was significantly higher than that of younger populations (Table 3.3 and Fig. 3.4).

However, there were no significant differences among populations that were 3, 6, or 9 weeks old (Table 3.3). Half-lives of gametophytes during their first 3 weeks after outplanting averaged 2 days, while half-lives averaged 16 days for older populations of gametophytes (Table 3.4).

3.4 Discussion

The experiments outlined above suggest that mortality of newly settled gametophytes is extremely high (half-life ≈2 days), but that survival increases with age and eventually levels off at a half-life of about 16 days. The question remains whether the survival rates during the first several weeks were indicative of the survival rate of naturally settled zoospores or were an artifact of our experimental design. We suspect that survival rates of gametophytes on slides during the first 3 weeks after outplanting may indeed be lower than on natural cobbles. Some gametophytes are probably poorly attached to the slides and are quickly washed off when put into the sea. Survival rates of gametophytes older than 3 weeks appear to be reflective of survival under more natural conditions. Standing stocks of gametophytes on natural substrates in SOK and SMK decreased over time, in the absence of settlement, and the rate of decline on cobbles would indicate a half-life that was also on the order of several weeks (see Section 5.0).

Table 3.1 Percent survival of gametophytes on glass slides outplanted to various field sites on the dates indicated, and collected 6 weeks later. Methods of calculation for percent survival are given in the text. The values indicated with an asterisk was assumed to be 0 since densities on uninoculated slides were greater than on inoculated slides.

Station		Initial gametophyte density (#/mm2)		Inoculated sporophyte density (#/mm2)		Uninoculated sporophyte density (#/mm2)		Percent survival
		N	mean	N	mean	N	mean	
SMK45	30NOV84	3	746	4	0.0890	4	0.0043	0.023
"	08FEB85	3	855	4	0.0172	4	0.0096	0.002
"	25APR85	1	956	5	0.0142	2	0.0008	0.003
"	23MAY85	1	869	4	0.0003	4	0.0001	<0.001
"	20JUN85	2	823	4	0.0003	4	0.0000	<0.001
"	18JUL85	2	1031	4	0.0028	2	0.0016	<0.001
"	15AUG85	2	756	4	0.0000	4	0.0000	0.000
SOKD45	25APR85	1	1015	2	0.0333	3	0.0151	0.004
"	23MAY85	1	953	4	0.0952	4	0.0735	0.005
"	20JUN85	2	776	4	0.0168	4	0.0045	0.003
"	18JUL85	1	1080	2	0.0016	0	-	-
"	15AUG85	2	801	4	0.0001	0	-	-
SOKU45	25APR85	1	1034	3	0.2254	4	0.0268	0.038
"	23MAY85	1	853	4	0.4735	4	0.1803	0.069
"	20JUN85	2	762	4	0.0965	4	0.0301	0.017
"	18JUL85	2	813	4	0.0053	2	0.0016	<0.001
"	15AUG85	2	963	4	0.0088	4	0.0085	<0.001
SOKD35	25APR85	1	970	4	0.0159	4	0.0167	0.000*
"	23MAY85	1	1126	4	0.0453	4	0.0103	0.006
"	20JUN85	2	778	4	0.1617	4	0.0005	0.041
"	18JUL85	2	1137	1	0.0016	0	-	-
"	15AUG85	2	784	4	0.0004	0	-	-
							Mean =	0.011

Table 3.2 Mean densities (#/mm²) of sporophytes, number of slides sampled, and age (in days) of populations at the time of collection for slides inoculated with gametophytes and outplanted to Barn Kelp. Densities for Age = 0 are one-half of gametophyte densities. Values indicated with an asterisk are sums of sporophytes produced *in situ* plus those produced after culture. All other values reflect the numbers of sporophytes produced after culture.

Experiment #1 21 November 85 to 13 February 86

		Collection Date				
Outplant Date		21Nov85	12Dec85	02Jan86	26Jan86	13Feb86
21Nov85	Mean	530	1.987	0.047	0.029	0.009
	N	1	4	8	16	16
	Age	0	21	42	63	84
12Dec85	Mean	-	493	0.355	0.093	0.129*
	N		2	4	8	14
	Age		0	21	42	63
02Jan86	Mean	-	-	470	0.196	0.117
	N			1	4	8
	Age			0	21	42

Experiment #2 15 August 86 to 06 November 86

		Collection Date				
Outplant Date		15Aug86	05Sep86	26Sep86	14Oct86	06Nov86
15Aug86	Mean	254	0.788	0.511	0.179*	0.040*
	N	1	4	8	16	24
	Age	0	21	42	62	83
05Sep86	Mean	-	340	1.448	0.383*	0.145*
	N		2	4	8	15
	Age		0	21	42	62
26Sep86	Mean	-	-	260	0.212*	0.050*
	N			1	4	8
	Age			0	21	42

Table 3.3 Contrasts of survival rates of different aged populations of gametophytes observed over similar periods in time. The ages given are those at the beginning of the 3 week period over which survival was observed.

Time period	Age (weeks)	Percent survival	df	SS	F value	PR>F
12Dec85 to 02Jan86	0	0.07	1	13.03	30.12	<0.001
	3	2.37				
02Jan86 to 26Jan86	0	0.04	1	28.91	61.53	<0.001
	3	26.20				
05Sep86 to 26Sep86	0	0.43	1	12.95	6.74	0.022
	3	64.85				
02Jan86 to 26Jan86	0	0.04	1	37.76	80.35	<0.001
	6	61.70				
02Jan86 to 26Jan86	3	26.20	1	0.47	0.99	0.326
	6	61.70				
26Jan86 to 13Feb86	3	59.69	1	0.88	2.87	0.098
	9	31.03				

Table 3.4 Average half-lives of different aged populations of gametophytes on glass slides outplanted to Barn Kelp.

Age = 0 days

Dates	Days age	Half-life (days)
21Nov85 to 12Dec85	0	2
12Dec85 to 02Jan86	0	2
02Jan86 to 26Jan86	0	2
15Aug86 to 05Sep86	0	3
05Sep86 to 26Sep86	0	3
	Mean =	2.4 days

Age = ≥21 days

Dates	Days age	Half-life (days)
12Dec85 to 02Jan86	21	4
02Jan86 to 26Jan86	21	5
26Jan86 to 13Feb86	21	14
05Sep86 to 26Sep86	21	33
02Jan86 to 26Jan86	42	30
26Jan86 to 13Feb86	63	12
	Mean =	16.3 days

Figure 3.1 a & b Location of collection sites for gametophyte survival on cobbles in the San Onofre (3.1 a) and San Mateo (3.1 b) Kelp forests. Kelp density contours (#/100 m^2) are from downlooking sonar estimates of November 1985.

Figure 3.1 a

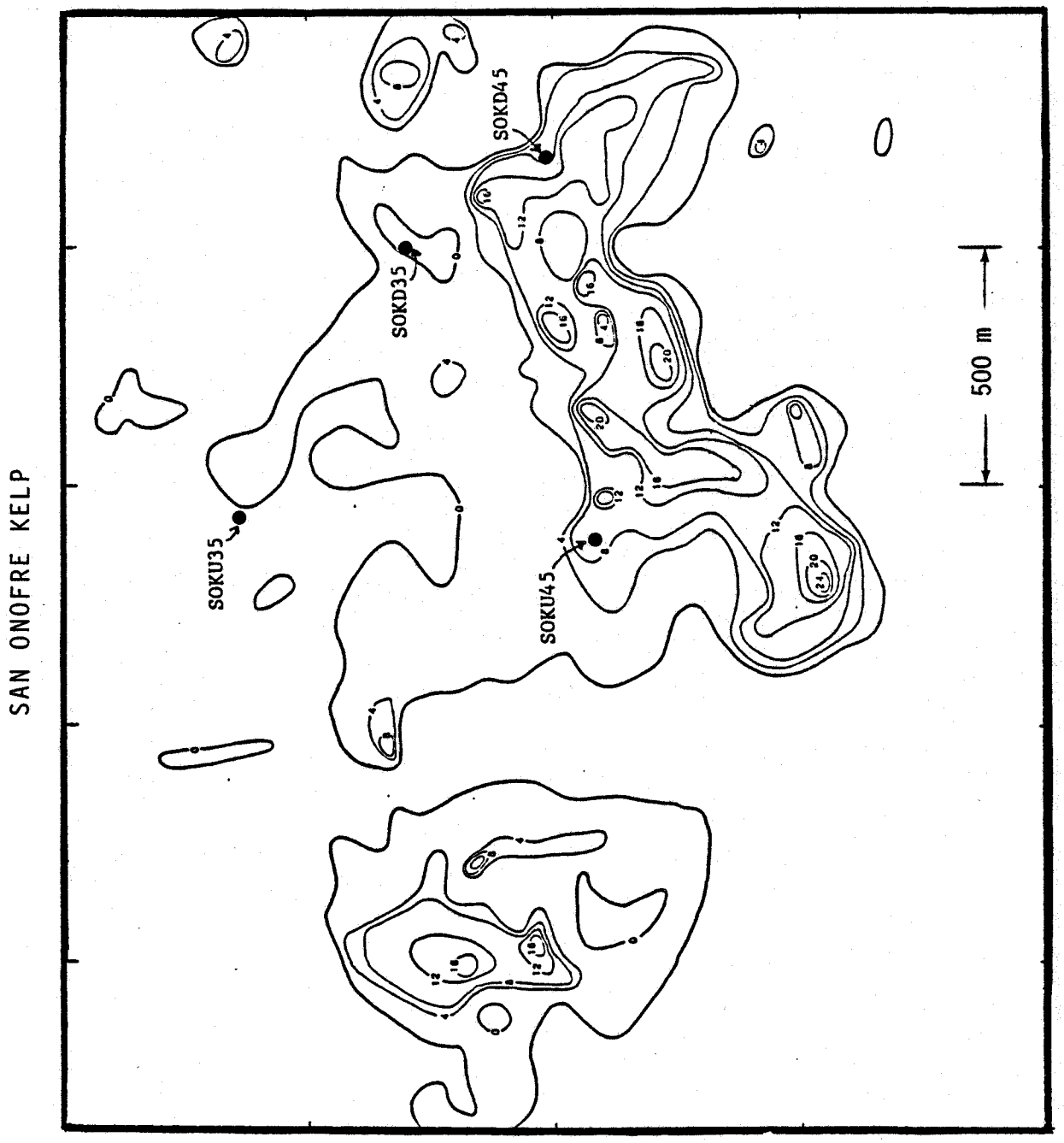


Figure 3.1 b

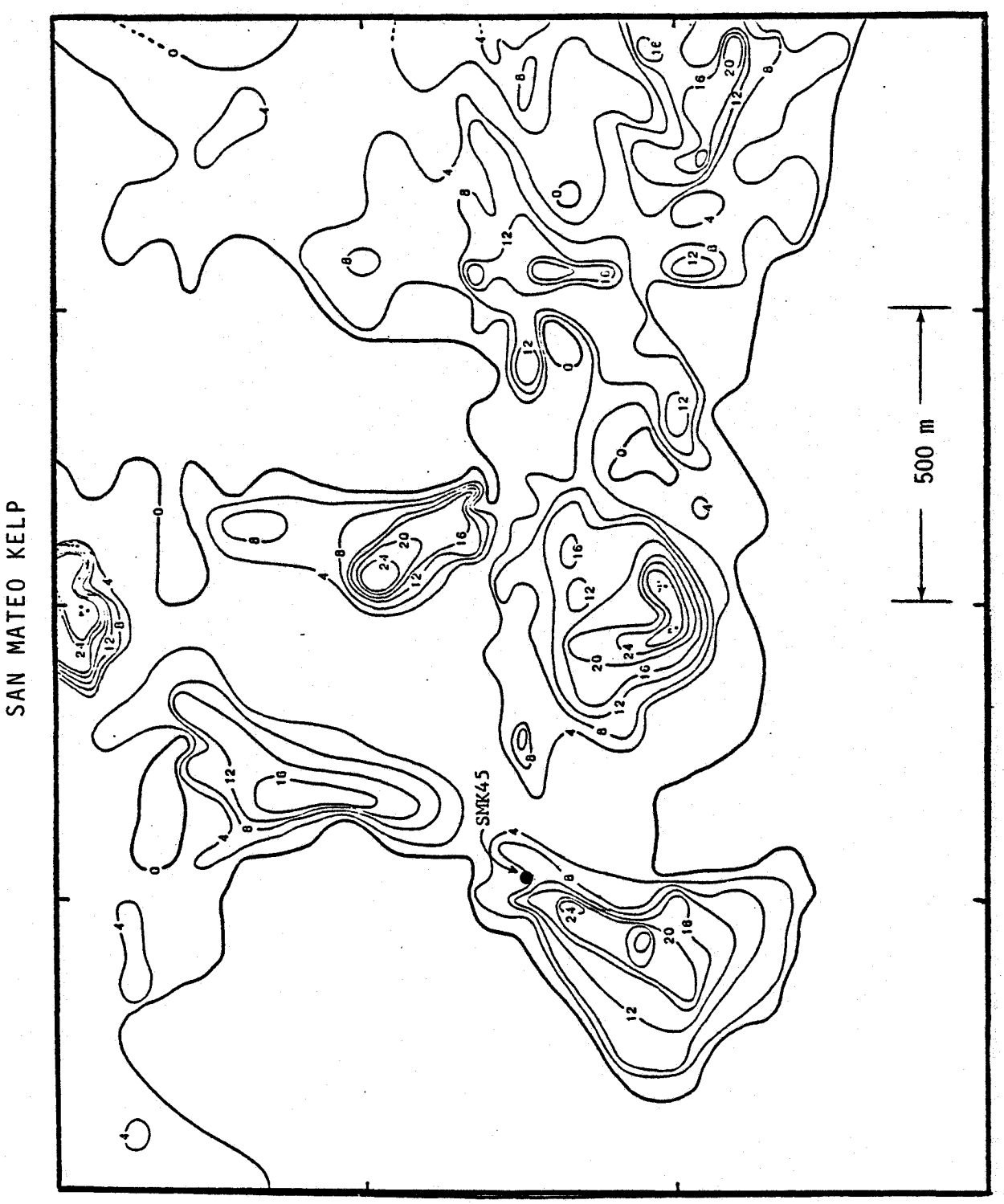


Figure 3.2 Diagram showing glass slides and anchoring device used in gametophyte survival studies and to determine settlement of gametophytes.

Figure 3.2

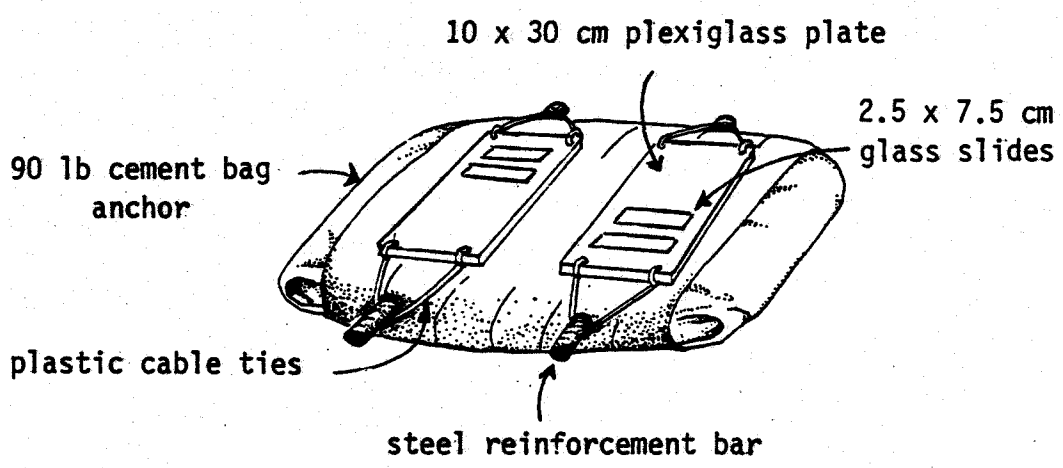

10 x 30 cm plexiglass plate
2.5 x 7.5 cm
glass slides
90 lb cement bag
anchor
plastic cable ties
steel reinforcement bar

Figure 3.3 Percent survival of gametophytes, on glass slides, outplanted for 6 weeks to field sites in SOK and SMK from November 1984 through August 1985.

Figure 3.3

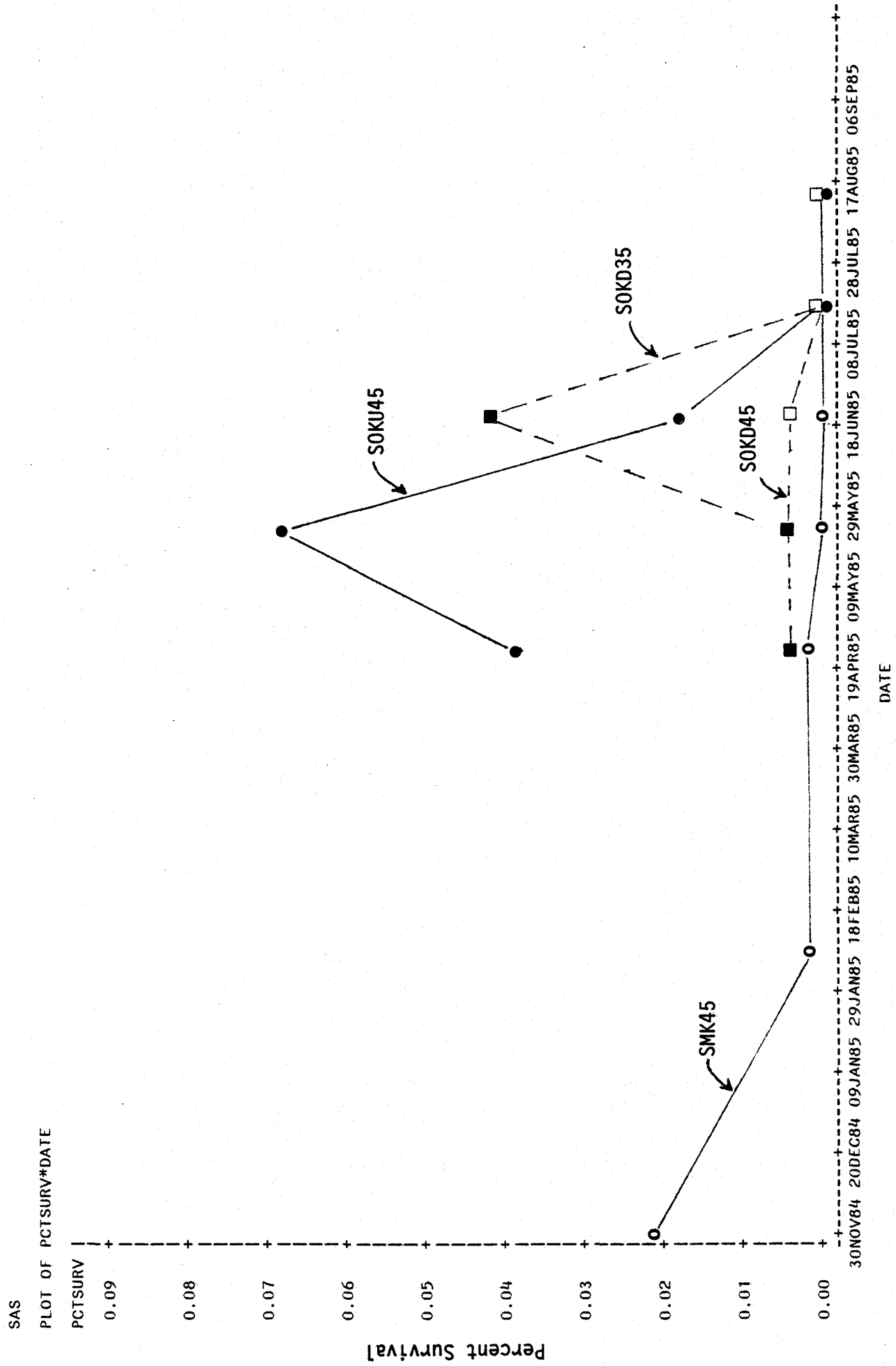
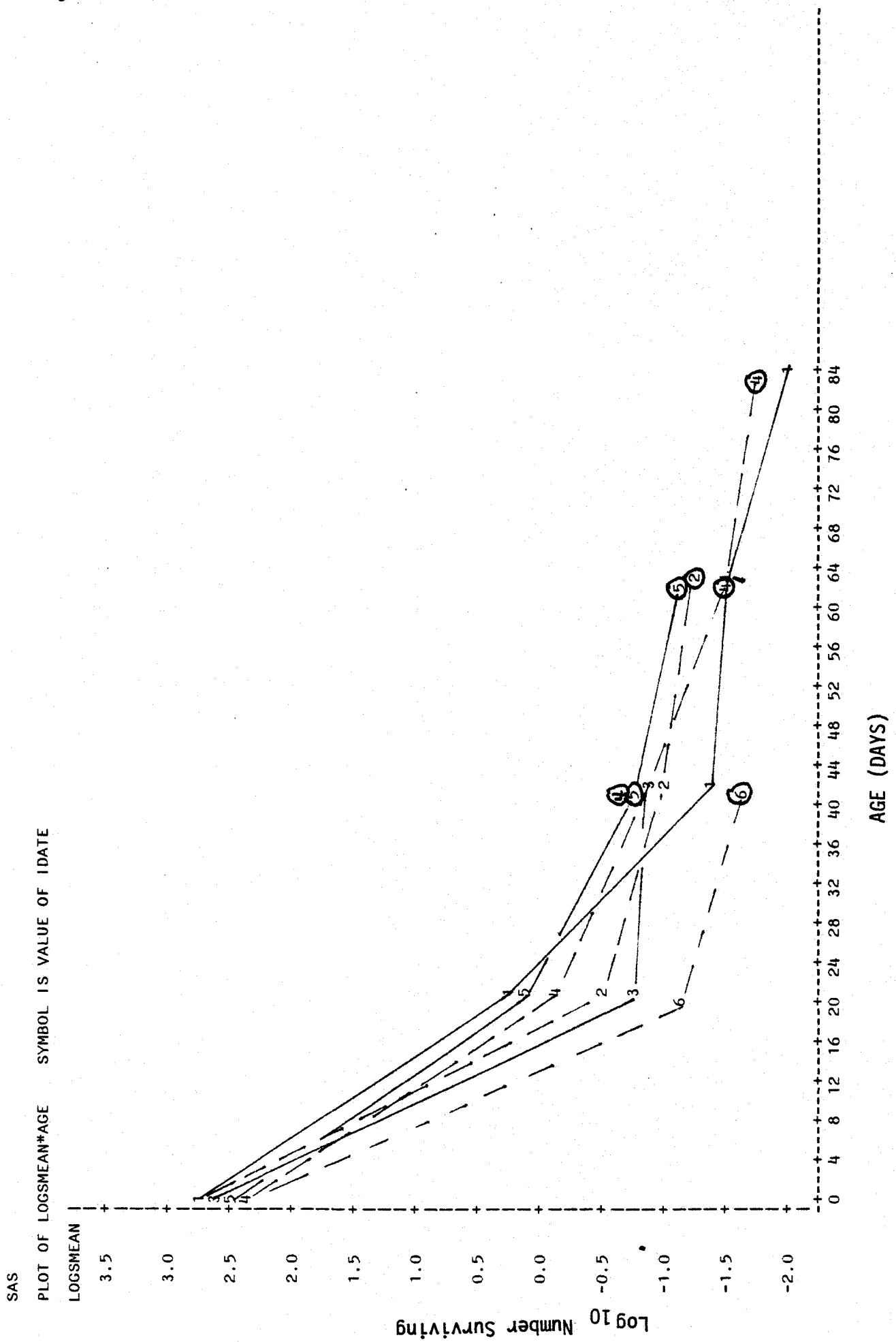

SAS
PLOT OF PCTSURV*DATE
PCTSURV
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Percent Survival
30NOV84 20DEC84 09JAN85 29JAN85 18FEB85 10MAR85 30MAR85 19APR85 09MAY85 29MAY85 18JUN85 08JUL85 28JUL85 17AUG85 06SEP85
DATE
SOKU45
SOKD35
SOKD45
SMK45

Figure 3.4 Survivorship curves for populations of gametophytes outplanted to Barn Kelp in 1985 and 1986. Circled points are sums of gametophyte and sporophyte densities; all others are for gametophytes only. Each point represents a mean of $\log_{10}$ transformed density per slide. The numbers represent the different outplant dates: 1 = 21 Nov 85, 2 = 12 Dec 85, 3 = 02 Jan 86, 4 = 15 Aug 86, 5 = 05 Sept 86, 6 = 26 Sept 86.

Figure 3.4


SAS
PLOT OF LOGSMEAN*AGE SYMBOL IS VALUE OF IDATE
LOGSMEAN
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Log 10 Number Surviving
0 4 8 12 16 20 24 28 32 36 40 44 48 52 56 60 64 68 72 76 80 84
AGE (DAYS)

4.0 In Situ Settlement Patterns of Gametophytes Standing Stock

4.1 Introduction

Standing stocks of gametophytes are dependent on the rate at which gametophytes settle onto the bottom and the rate at which they survive. In this section, we examine the spatial and temporal patterns of variability in settlement of gametophytes of laminarian algae (Macrocystis and Pterygophora). These data will later be examined in the document evaluating the effects of SONGS in order to assess the importance of gametophyte settlement patterns on the eventual patterns of recruitment by visible life stages.

4.2 Methods

Frosted glass microscope slides (25 cm x 7.5 cm) were placed at stations in SOK and SMK for 2-wk periods at approximately monthly intervals between November 1985 and July 1986. A total of 8 slides were placed at each station, during each sampling period. The slides were attached to 10 cm x 30 cm plexiglass plates which were secured to 90 lb cement bag anchors and steel bar cross members using plastic cable ties (Fig. 3.2, p. 3-17). The slides were collected after 2 weeks and returned to the laboratory for culture. Occasionally some slides were lost and as few as 5 of the 8 slides were collected in some cases. Culturing to the sporophyte stage was necessary because zoospores or gametophytes of laminarian algae could not be distinguished from those of other small algae.

Slides were cultured in the laboratory according to procedures outlined in Section 3.2. After 3 weeks in culture, the slides were removed and the entire upper surface area of each slide (1875 mm^2) was examined under a dissecting microscope at 20X. All all visible sporophytes were counted. For convenience in counting, slides

were divided into 3 equal sections and counts were made in each section. On one occasion (collection of 10 April 1986) densities were so high that subsampling was required. The subsampling consisted of counting sporophytes in twelve 16 mm^2 quadrats, sampled randomly on each slide.

Slides were placed at each of 5 stations: SMK45, SOKU45, SOKU35, SOKD45, and SOKD35 (see Fig. 3.1, p. 3-13 thru 3-15). At sites where there were adult sporophytes of Macrocystis present (SMK45, SOKU45, and SOKD45), slides were placed at the edge of an area cleared of kelp, approximately 40 m^2 in size, and within 10 m of an adult Macrocystis. There were no adult sporophytes within 50 m of the SOKU35 and SOKD35 sites, and adults were very scarce within 100 to 150 m of these stations.

Analyses of variance were used to test the hypothesis that densities of sporophytes on the slides did not differ among locations (stations) and times (collection dates). A two-way, fixed-effect model was used. All densities were log-transformed [ln (counts per slide + 1) / area of slide]. One-way analyses of variance and Duncan's multiple range tests (SAS, 1982) were used to test for differences among locations within a given time and among times within a given location.

We examined the relationship between settlement and physical factors by multiple regression of sporophyte density with irradiance, temperature, and maximum wave height. These physical factors were chosen because, in the laboratory, zoospore release is initiated by storing sporophylls in cold and darkness. Also, spore release seems facilitated by the rough handling of sporophylls, suggesting that the mechanical action of waves may cause release in the field. Methods used in the measurement of physical factors and in regression analyses are given in Appendices C

and D, respectively. Log-transformed values of mean sporophyte density on slides [ln (counts per slide + 1) / area of slide] were used as the dependent variable. Log-transformed values of mean irradiance, mean temperature, and maximum wave height observed in the 2-week exposure period were used as independent variables.

4.3 Results

Densities of sporophytes on slides varied significantly among locations and times (Table 4.1) and showed marked seasonal fluctuations at all stations peaking in late February or April (Fig. 4.1 and Table 4.2). At the time of peak abundance at most sites (April 1986), densities differed significantly among sites and were ordered as SMK45 > SOKU45 > SOKU35 > SOKD45 > SOKD35 (Table 4.3). SMK45 showed a more peaked distribution than the other sites. At the SOK stations, densities were generally high throughout the period from late February through early May while at SMK45, densities were low in late February, increased markedly in April, and declined rapidly in May. Extremely low abundances were observed at all sites in late May through August, with no sporophytes observed in June at SMK45 and SOKD45.

The peak in gametophyte settlement followed a period of poor underwater visibility and large swells that occurred in late February 1986. Sporophyte densities on slides were negatively correlated with irradiance over the 2-week outplant period (Table 4.4). Neither maximum wave height nor temperature explained a significant proportion of the variability in settlement. The relationship between irradiance and settlement was weak and resulted primarily from only a few instances of high settlement at low irradiance levels (Fig. 4.2).

4.4 Discussion

The distribution of sporophyte densities on slides indicates that either spore release, settlement, or survival rate of newly settled spores of laminarian algae was highest in late winter - early spring (February through early April) at most sites. In spite of our ability to release spores from Macrocystis in the laboratory at all times of the year, it is evident that spores did not settle in equal numbers between November 1985 and August 1986. Coupled with the relatively short-lived nature of gametophytes in situ (Section 3.4), this suggests that recruitment of laminarians is at times restricted by the number of available gametophytes. We could not establish in these studies whether the sporophytes observed were Macrocystis or other laminarian algae (Pterygophora or Laminaria), but the lack of sporophytes observed in fall of 1985 and summer of 1986 suggests that there were few gametophytes of any laminarian species settling.

The spatial patterns of abundance of sporophytes on slides was not strictly associated with the densities of surrounding adult plants. Although peaks in abundance were highest at SMK where adult densities were highest, we also observed relatively high abundances of sporophytes at SOKU35 where there were few adults nearby. While other studies indicate that dispersal abilities of spores are restricted during times of the year, this did not appear to limit dispersal in winter 1986. Over the period from February through April, approximately the same numbers of sporophytes were observed at SOKU35 (where adults were scarce) as at SOKU45 and SOKD45 (where adults were abundant) (Table 4.3).

The negative correlation between irradiance and densities of sporophytes on slides suggests that low light levels may promote zoospore release. We do not know whether this was a causative relationship or whether perhaps a seasonal cycle in

zoospore production happened to coincide with a period of low light in 1986. While low light may promote the release of zoospores, it is also apparent that the condition of the sporophylls varies over time. Large sporophyll bundles with dark sori were most evident after periods of upwelling that served to promote the growth of adult sporophytes. Strong zoospore release is therefore probably a function of the previous growth conditions of adult sporophytes in combination with such potential factors such as low light levels or storm activity.

Table 4.1 Two-way, fixed-effect analysis of variance examining the effects of time and location on the densities of gametophytes settling on glass slides at SOK and SMK.

SOURCE	DF	Type III SS	F value	PR>F
Time	9	1032.13	615.73	0.0001
Location	4	296.04	397.37	0.0001
Time*Location	35	461.35	70.77	0.0001

Table 4.2 Results of Duncan's multiple range tests comparing log-transformed densities of sporophytes among times (collection dates) at each location. In all cases, one-way ANOVAs of differences among times were significant at the P<0.05 level. Letters indicate groups of means (i.e., dates) dates that did not differ significantly at P<0.05.

LOCATION = SOKD45

DUNCAN GROUPING		MEAN	N	DATE
	A	-1.40	6	10APR86
	A	-1.49	8	08MAY86
	A	-1.54	8	27FEB86
	B	-2.72	8	21NOV85
	C	-3.90	8	07FEB86
	D	-4.60	8	02JAN86
	E	-5.38	8	30MAY86
	F	-7.33	8	24JUL86
	F	-7.60	8	26JUN86

LOCATION = SOKU45

DUNCAN GROUPING		MEAN	N	DATE
	A	-0.60	6	10APR86
	B	-1.71	8	27FEB86
C	B	-1.93	8	07FEB86
C		-2.28	8	02JAN86
	D	-2.92	8	21NOV85
	D	-3.01	8	26JUN86
	D	-3.21	8	08MAY86
	E	-4.41	8	30MAY86
	F	-5.02	6	28AUG86
	G	-5.88	8	24JUL86

LOCATION = SOKD35

DUNCAN GROUPING		MEAN	N	DATE
	A	-1.92	8	27FEB86
	B	-3.59	6	10APR86
	C	-4.08	8	08MAY86
	D	-4.98	8	02JAN86
	E	-5.98	8	07FEB86
	E	-6.23	8	30MAY86
	F	-6.95	8	24JUL86
G	F	-7.24	8	26JUN86
G	F	-7.33	8	21NOV85
G		-7.51	8	28AUG86

LOCATION = SOKU35

DUNCAN GROUPING		MEAN	N	DATE
	A	-0.88	6	10APR86
	A	-1.01	8	27FEB86
	B	-2.05	8	24JUL86
	B	-2.12	8	08MAY86
	C	-3.62	5	28AUG86
	D	-4.54	8	02JAN86
	D	-4.96	8	30MAY86
	E	-5.55	8	21NOV85
	F	-6.52	8	26JUN86

LOCATION = SMK45

DUNCAN GROUPING		MEAN	N	DATE
	A	0.33	6	10APR86
	B	-2.15	8	07FEB86
	C	-2.77	8	02JAN86
D	C	-2.92	8	08MAY86
D		-3.26	8	27APR86
	E	-4.47	8	30MAY86
	F	-6.04	8	21NOV85
	G	-7.42	8	24JUL86
	G	-7.50	7	28AUG86
	G	-7.60	8	26JUN86

Table 4.3 Results of Duncan's multiple range tests comparing log-transformed densities of sporophytes among locations during times of peak gametophyte settlement. In all cases one-way ANOVAs of differences among locations were significant at the P<0.05 level. Letters indicate groups of means (i.e., stations) that did not differ significantly at the P<0.05 level.

DATE = 27FEB86

DUNCAN GROUPING	MEAN	N	STACODE
A	-1.01	6	SOKU35
B	-1.54	8	SOKD45
B	-1.71	8	SOKU45
C	-1.91	8	SOKD35
D	-3.26	8	SMK45

DATE = 10APR86

DUNCAN GROUPING	MEAN	N	STACODE
A	0.33	6	SMK45
B	-0.60	6	SOKU45
C	-0.88	6	SOKU35
D	-1.40	6	SOKD45
E	-3.59	6	SOKD35

DATE = 08MAY86

DUNCAN GROUPING	MEAN	N	STACODE
A	-1.49	8	SOKD45
B	-2.12	8	SOKU35
C	-2.92	8	SMK45
C	-3.21	8	SOKU45
D	-4.08	8	SOKD35

Table 4.4 Summary of regression of log-transformed densities of sporophytes on settlement slides vs log-transformed values of mean irradiance, temperature, and maximum wave height.

SPOROPHYTE DENSITY VS IRRADIANCE TEMPERATURE, AND WAVE HEIGHT

R-SQUARE 0.19

VARIABLE	DF	PARAMETER ESTIMATE	T FOR HO: PARAMETER=0	PR > T
INTERCEPT	1	-23.04	-1.66	0.10
LOG IRRAD	1	-1.48	-2.62	0.01
LOG TEMP	1	7.29	1.38	0.18
LOG WAVE HEIGHT	1	-1.44	-1.01	0.32

SPOROPHYTE DENSITY VS IRRADIANCE

R-SQUARE 0.14

VARIABLE	DF	PARAMETER ESTIMATE	T FOR HO: PARAMETER=0	PR > T
INTERCEPT	1	-4.27	-12.08	0.00
LOG IRRAD	1	-0.99	-2.75	0.01

Figure 4.1 Mean density (#/mm^2) of sporophytes on glass slides. Slides were collected after 2 weeks exposure at various sites in SOK and SMK, and cultured for 3 weeks in the laboratory prior to counting. Collection dates are shown on the x-axis.

Figure 4.1

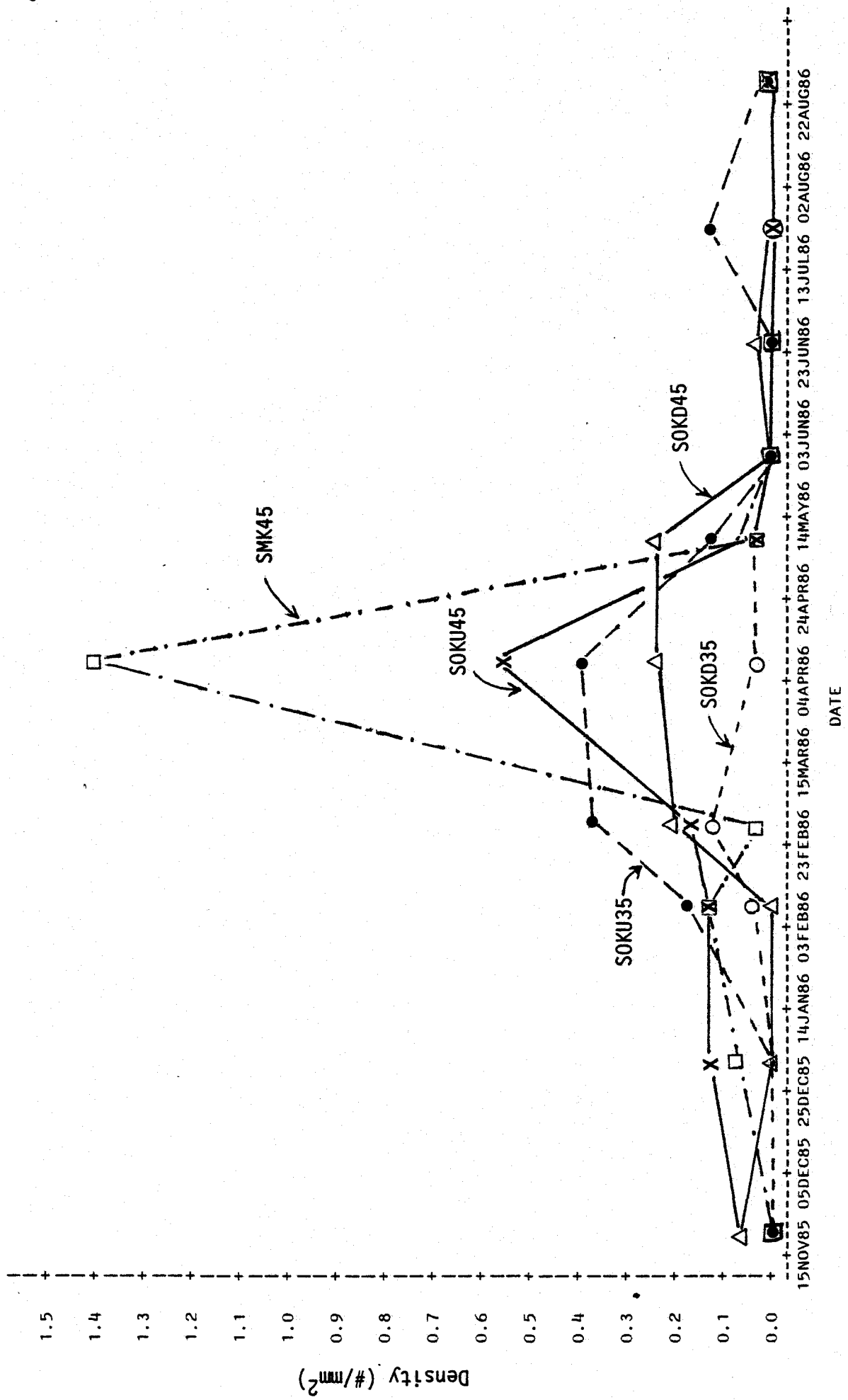
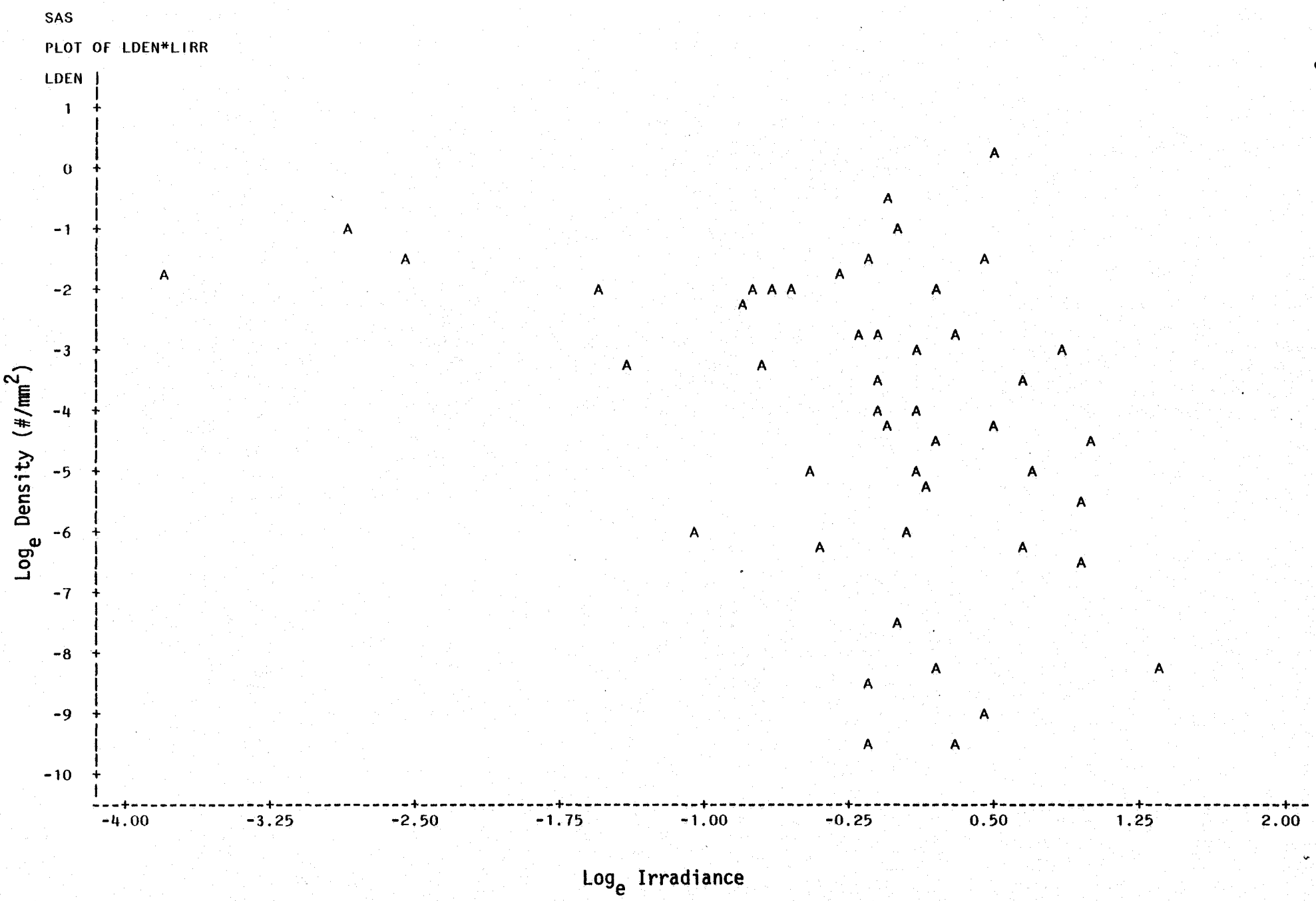

SMK45
SOKU45
SOKU35
SOKD45
SOKD35
Density (#/mm²)
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
15NOV85
05DEC85
25DEC85
14JAN86
03FEB86
23FEB86
15MAR86
04APR86
24APR86
14MAY86
03JUN86
23JUN86
13JUL86
02AUG86
22AUG86
DATE

Figure 4.2 Relationship between log-transformed densities of sporophytes on glass slides (collected after 2 weeks exposure and then cultured for 3 weeks in the laboratory) vs the log of the mean irradiance averaged over the 2-week exposure period.

Figure 4.2


SAS
PLOT OF LDEN*LIRR
LDEN
1
0
-1
-2
-3
-4
-5
-6
-7
-8
-9
-10
-4.00
-3.25
-2.50
-1.75
-1.00
-0.25
0.50
1.25
2.00
Log$_e$ Density (#/mm^2)
Log$_e$ Irradiance

5.0 Standing Stock of Microscopic Stages of Kelp on Natural Substrates

5.1 Introduction

Gametophyte and microscopic sporophyte life stages of kelp are not easily distinguished from sediments and other algae in the field. As a result, little is known of the distribution of these life stages (either temporal or spatial) within kelp forests. Knowing these distribution patterns is important in two ways. First, in order to interpret the causes for temporal and spatial distributions of macroscopic recruits. Second, to establish whether these patterns result from gametophyte availability or from subsequent sporophyte production and survival. Here, we examine the distribution patterns of gametophytes and microscopic sporophytes of laminarian algae on cobble substrates collected from various sites in SMK, SOK, and BK.

5.2 Methods

Cobbles, measuring approximately 6 to 10 cm in diameter, were collected from various field sites in SOK, SMK, and BK (BK) on 14 occasions between March 1985 and July 1986. Five replicate cobbles were collected from each station. Cobbles were placed into 25ℓ plastic buckets, brought to the surface, and returned to the laboratory cold room for culture. Culture conditions were as described for slides in Section 3.2 except that cultures were maintained in 25ℓ trash cans. Cobbles remained in culture for a period of approximately 3 weeks (19 to 22 days). A separate trash can culture was maintained for each group of 5 cobbles.

The first 5 collections of cobbles made between March 1985 and September 1985 were preliminary surveys to examine the feasibility of the sampling and culture method. In each survey, cobbles were collected from SMK, SOKU and SOKD. Cobbles

were also collected at BK in June and September 1985. The exact sampling location differed among these early surveys (Table 5.1). In order to standardize the sampling procedure and to maximize the likelihood of finding gametophytes, we selected cobbles that were not overgrown with invertebrates or other algae and that were located within 1 m of an adult plant. In each of the 9 subsequent surveys conducted at approximately monthly intervals between November 1985 and July 1986, cobbles were collected from stations used for gametophyte settlement, gametophyte outplant, and sporophyte outplant studies (see Sections 3.0, 6.0 and 7.0): SOKU45, SOKD45, SOKU35, SOKD35, and SMK45 (Fig. 5.1). The offshore sites at SOK and SMK (SOKD45, SOKU45, and SMK45) were located near the edges of patches of adult Macrocystis. The area immediately surrounding each collection site was cleared of adult kelp and understory algae (Cystoseira, Pterygophora, and Acrosorium) in November 1985 and kept clear of new recruits by removing them approximately monthly. The nearest adult plants were 7 m away from each offshore collection site. At the inshore stations (SOKU35 and SOKD35) there was essentially no adult kelp, with the nearest adults plants located more than 50 m away.

Cobbles were collected from seven additional stations in November 1985, February 1986, and May 1986, in order to more closely examine spatial patterns of gametophyte abundance and to determine the effects of densities of adult Macrocystis on gametophyte standing stock (Fig. 5.1). At 3 of these stations (SOKU45CL, SOKD45CL, and SMK45CL) adult Macrocystis and understory algae (Cystoseira Pterygophora, and Acrosorium) were cleared within a 15 m radius of the collecting sites in October 1985. At the three canopy stations (SOKU45CN, SOKD45CN, SMK45CN), no clearings were made and there were adult kelp within several meters of the collection sites. Cobbles were also collected from BK45. There were no adult Macrocystis within 50 m of our collection site and the nearest canopy of adult kelp was approximately 11 km away at SOK.

Stations labelled SOKDCN2 and SMKCN2 were used in place of SOKD45CN and SMKU45CN during the November 1985 collection (Table 5.1). These pairs of stations were in close proximity to one another within their respective kelp forests and, therefore, and the canopy stations at SOKU or SMK were considered as equivalents for statistical purposes. For convenience sake, the station names for SOKDCN2 and SMKCN2 were relabelled as SOKD45CN and SMK45CN in tables of statistical output.

Cobbles collected in April 1986 had larger sporophytes than would be expected if all were gametophytes at the beginning of the laboratory culture period. We suspected that microscopic sporophytes were present when cobbles were collected and as a result, we collected 5 additional cobbles from each station beginning in May 1986 and examined these for sporophytes without culturing. The uncultured cobbles were kept in filtered seawater in the laboratory and examined within several days of collection. No attempt was made to obtain quantitative estimates of mean size of sporophytes on uncultured cobbles, but notes were kept as to approximate mean size and maximum size of sporophytes on each cobble.

Both cultured and uncultured cobbles were examined at 8 to 20x under a dissecting microscope and all visible sporophytes were counted. The perimeter of each cobble was then traced and the approximate surface area of the cobble determined using a planimeter. Various species of laminarian algae (of which *Macrocystis pyrifera*, *Pterygophora californica*, and *Laminaria farlowii* are found locally) are indistinguishable from one another when very small. As a result, the numbers of sporophytes counted represent the sum of all laminarian algae present on cobbles.

Analyses of variance were used to test the hypothesis that densities of sporophytes differed among locations (stations) and times (collection dates). A two-way, fixed-effect model was used. All densities were $\log_e$ transformed ($\ln(\#/100\ cm^2 + 0.01)$). The constant of 0.01 was chosen since it approximated represented the lowest non-zero density obtainable. One-way analyses of variance and Duncan's multiple range tests were used to examine differences among locations within a time and among times within a location. Separate analyses were performed for the five preliminary collections made between March and September 1985, for those collections made between November 1985 and July 1986 from 5 designated sites, and for the 3 dates (Nov 1985, Feb 1986, and May 1986) when cobbles were collected from 12 sites.

We also tested the hypothesis that density of surrounding adults affected gametophyte standing stock, using a nested ANOVA. The differences among 4 different adult density groups and three stations within these groups were examined. The groups included: (1) canopy stations with high densities of adults nearby (SOKD45CN, SOKU45CN, SMK45CN), (2) cleared canopy stations with high densities of adults but no adults in close proximity to our sampling sites (SOKD45CL, SOKU45CL, and SMK45CL), 3) cleared edge with moderate densities of adults, and adults within 7 m of the collection site (SOKD45, SOKU45, and SMK45), and (4) areas with no adult kelp within 50 m (SOKD35, SOKU35, and BK45). Separate analyses were performed for each of the 3 times (November 1985, February 1986, and July 1986) that all of these stations were sampled.

5.3 Results

Gametophyte standing stock, as indicated by densities of sporophytes on cobbles that were cultured in the laboratory varied among times (in all analyses) and among

locations (in all but the preliminary sampling in 1985, Table 5.2). Densities at most sites followed a distinct seasonal trend with peaks occurring in late February to April and nadirs occurring in summer and fall (Fig. 5.2, and Tables 5.3 and 5.4). Peaks generally appeared later at SOKD35 and SOKD45 than at SMK45 and SOKU stations. Spatial patterns varied among the times. In the 27 February 1986 collection, densities among the 5 sites which were sampled monthly were ordered as SMK > SOKU45 > SOKU35 > SOKD45 > SOKD35 (Table 5.5). By April 10, there were no significant differences among these sites and all had mean densities greater than 100/cm^2.

Cobbles collected within close proximity to adults generally had higher densities of gametophytes than those collected from stations where there were few adults (Table 5.6). However, the degree of effect changed with time, probably as the result of variability in wave action. In a calm period in November, densities of sporophytes were extremely low at stations where there were few adults nearby. Following intense storms in February, only sites that were 50 m or more from adult sporophytes (the zero density group) had gametophyte densities that were significantly lower than at stations where there were high densities of adults. At the same time, stations in SOK relatively distant from adults (SOKU35), had higher densities of sporophytes than some stations which were located nearer to stands of adult kelp (SOKD45). By May 1986, during another relatively calm period, densities of gametophytes on cobbles were once again ordered according to nearby adult densities (Table 5.6).

Microscopic sporophytes began to appear on uncultured cobbles in April shortly after peaks in abundances of gametophytes. Densities of sporophytes differed among locations and times (Table 5.7). Highest densities were observed in the collections of May 1986 (Fig. 5.3), but differences among times within a station were generally

not significant at $P<0.05$ (Table 5.8). Densities of sporophytes declined after May as sporophyte size increased. We did not measure all of the sporophytes on cobbles, but noted approximate average and maximum sizes per cobble. From 05 May until 25 July 1986, average sporophyte length increased from approximately 0.5 mm to between 5 and 10 cm, and the maximum length increased from 6 mm to 17 cm.

Patterns of sporophytes on uncultured cobbles differed markedly from the patterns observed for gametophytes (as inferred from data on cultured cobbles and settlement slides, Fig. 5.3). In May 1986, densities of sporophytes on uncultured cobbles were highest at SOKD45 and SMK45 (Table 5.9 and Fig. 5.3). Very few sporophytes were observed at SOKU45 and almost none were observed at SOKU35, even though gametophyte densities were high at these two stations.

5.4 Discussion

Spatial and temporal patterns of abundance of sporophytes on cobbles cultured in the laboratory were similar to patterns observed on slides used for the estimation of spore settlement. Peaks in sporophyte abundance on both substrates occurred in late February to April, during which time the densities of sporophytes at different locations were ordered as SMK > SOKU sites > SOKD stations. These similarities indicate that patterns in standing stocks of gametophytes on natural substrates are determined largely by patterns of settlement of spores or survival of gametophytes shortly after settlement. There was no indication of accumulation of gametophytes on cobbles. Rather, gametophyte standing stock on cobbles declined when settlement declined and also was near zero at times when settlement was near zero. This corroborates our other observations and experiments (Section 3.0) which indicate that gametophyte stages are not long-lived <u>in situ</u>. The data from cobbles collected and later cultured also agree with the settlement data in suggesting that

at times of peak gametophyte abundance in late winter 1986, propagules of laminarian algae were widely dispersed and were relatively abundant at most stations (including SOKU35) even though densities of surrounding adult sporophytes were sometimes low.

Peaks in sporophyte density on uncultured cobbles followed peaks in gametophyte density by approximately 1 to 3 months. It appears that most of these sporophytes were produced from spores (and subsequently gametophytes) which settled onto the cobbles between late February and April. Very few small sporophytes were observed after June, following a sharp decline in the number of gametophytes found on both slides and cultured cobbles in May. Thus, it appears that temporal patterns in the successful recruitment of sporophytes was governed, in part, by the availability of gametophytes.

Very different spatial patterns were observed for sporophytes on uncultured cobbles vs gametophytes on both slides and cultured cobbles. Densities of both gametophytes and sporophytes were similarly high at SMK, but spatial patterns within SOK differed. Higher densities of gametophytes were observed at SOKU sites while higher densities of sporophytes were observed at SOKD sites. Clearly, a lack of recruitment of sporophytes at SOKU was caused by either a lack of production of sporophytes from gametophytes or poor survival of microscopic sporophytes, and not by a lack of availability of gametophytes. Good sporophyte recruitment occurred at SOK in spite of poor gametophyte settlement and resulted from exceptionally good sporophyte production and survival. (This discussion will be persued further in a document evaluating the effects of SONGS).

Table 5.1 Sampling schedule for cobbles used in gametophyte standing stock assessment. In cases where sampling stations differed from location names, sampling station names are put in parentheses. Station locations are given in Fig. 5.1. Transect location names are indicated by (Txx) and transect locations are shown in Section 9.0.

COLLECTION DATE	LOCATION											
	SOKD45	SOKU45	SMK45	BK45	SOKD35	SOKU35	SOKD45CL	SOKD45CN	SOKU45CL	SOKU45CN	SMK45CN	SMK45CL
15MAR85	X(T24)	X(T9)	X									
22APR85	X(T11)	X(T9)	X(T17)									
10JUN85	X(T11)	X(T9)	X(T17)	X								
23JUL85	X(T24)	X(T4)	X(T17)									
03SEP85	X(T11)	X(T9)	X(T17)	X								
21NOV85	X	X	X	X	X	X	X	X(SOKDCN2)	X	X	X(SMKCN2)	X
02JAN86	X	X	X		X	X						
07FEB86	X	X	X		X	X						
27FEB86	X	X	X	X	X	X	X	X	X	X	X	X
10APR86	X	X	X		X	X						
08MAY86	X	X	X		X	X						
29MAY86	X	X	X	X	X	X	X	X	X	X	X	X
26JUN86	X	X	X		X	X						
24JUL86	X	X	X		X	X						

Table 5.2 Results of two-way, fixed-effect ANOVA comparing sporophyte densities on cobbles collected from different locations (stations) and times (collection dates). All cobbles were cultured in the laboratory for 3 weeks. Separate analyses were performed for cobbles collected between March 1985 and September 1985 at 2 SOK and 1 SMK station, between November 1985 and July 1986 at 4 SOK and 1 SMK stations, and in November 1985, February 1986, and May 1986 at 8 SOK, 3 SMK, and 1 BK station.

15 March 1985 to 03 September 1985 - 3 Stations

SOURCE	DF	TYPE III SS	F VALUE	PR > F
TIME	3	114.84	18.40	<0.001
LOCATION	2	7.21	1.73	0.188
TIME*LOCATION	6	8.46	0.68	0.669

21 November 1985 to 24 July 1986 - 5 Stations

SOURCE	DF	TYPE III SS	F VALUE	PR > F
TIME	8	677.75	38.12	<0.001
LOCATION	4	252.00	28.35	<0.001
TIME*LOCATION	32	521.16	7.33	<0.001

21 November 1985, 27 February 1986, and 29 May 1986 - 12 Stations

SOURCE	DF	TYPE III SS	F VALUE	PR > F
TIME	2	344.17	68.54	<0.001
LOCATION	9	523.17	23.15	<0.001
TIME * LACATION	18	550.92	12.19	<0.001

Table 5.3 Results of Duncan's multiple range tests comparing log-transformed densities (#/100 cm**2) of sporophytes on cobbles, among preliminary survey dates dates in 1985, at each location. One-way ANOVAs indicated significant differences among dates at SMK and SOKU but not at SOKD. Letters indicate groups of means (i.e., dates) that did not differ significantly at P<0.05.

LOCATION = SMK

DUNCAN GROUPING	MEAN	N	CDATE
A	5.07	5	15MAR85
A	5.07	5	22APR85
A	4.12	5	10JUN85
B	1.33	5	03SEP85
B	1.04	5	23JUL85

LOCATION = SOKD

DUNCAN GROUPING	MEAN	N	CDATE
A	5.48	5	10JUN85
A	5.11	5	22APR85
A	4.96	5	23JUL85
B A	4.66	5	15MAR85
B	2.66	5	03SEP85

LOCATION = SOKU

DUNCAN GROUPING	MEAN	N	CDATE
A	4.88	5	15MAR85
A	4.71	5	22APR85
A	4.12	5	10JUN85
B	1.68	5	23JUL85
B	0.88	5	03SEP85

Table 5.4 Results of Duncan's multiple range tests comparing log-transformed densities of sporophytes on cobbles among collection dates for each location. Letters indicate groups of means (i.e., dates) that did not differ significantly at $P<0.05$.

LOCATION = SOKD45

DUNCAN	GROUPING		MEAN	N	CDATE
	A		4.97	5	10APR86
B	A		4.78	5	08MAY86
B	C		3.06	5	29MAY86
D	C		2.62	5	02JAN86
D	C	E	1.35	5	24JUL86
D		E	1.18	5	26JUN86
		E	0.36	5	27FEB86
		E	0.00	5	21NOV85
		E	0.00	5	07FEB86

LOCATION = SOKU45

DUNCAN	GROUPING		MEAN	N	CDATE
	A		9.24	5	27FEB86
	B		6.57	5	10APR86
	B		6.57	5	08MAY86
	C		3.68	5	26JUN86
D	C		3.39	5	24JUL86
D	C		3.26	5	29MAY86
D	C		2.68	5	07FEB86
D	E		1.50	5	21NOV85
	E		0.40	5	02JAN86

LOCATION = SOKD35

DUNCAN	GROUPING	MEAN	N	CDATE
	A	5.85	5	10APR86
	B	2.69	5	08MAY86
	B	2.28	5	26JUN86
C	B	1.98	5	29MAY86
C	B	1.11	5	24JUL86
C	B	1.10	5	07FEB86
C		0.20	5	21NOV85
C		0.00	5	02JAN86
C		0.00	5	27FEB86

LOCATION = SOKU35

DUNCAN	GROUPING	MEAN	N	CDATE
	A	4.70	5	10APR86
	A	4.27	5	27FEB86
	A	3.91	5	08MAY86
	B	0.52	5	26JUN86
	B	0.43	5	07FEB86
	B	0.17	5	21NOV85
	B	0.15	5	24JUL86
	B	0.15	5	29MAY86
	B	0.00	5	02JAN86

LOCATION = SOKD45CL

DUNCAN	GROUPING	MEAN	N	CDATE
	A	6.956	5	27FEB86
	A	4.258	5	29MAY86
	B	1.369	5	21NOV85

LOCATION = SOKU45CL

DUNCAN	GROUPING	MEAN	N	CDATE
	A	9.54	5	27FEB86
	B	3.88	5	29MAY86
	B	3.34	5	21NOV85

Table 5.4 continued

LOCATION=SOKD45CN

DUNCAN GROUPING	MEAN	N	CDATE
A	7.167	5	27FEB86
A	5.553	5	29MAY86
B	0.915	5	21NOV85

LOCATION=SOKU45CN

DUNCAN GROUPING	MEAN	N	CDATE
A	7.34	5	21NOV85
B	5.01	5	29MAY86
B	3.66	5	27FEB86

LOCATION = SMK45

DUNCAN GROUPING	MEAN	N	CDATE
A	10.57	5	27FEB86
B	6.03	5	07FEB86
B	4.93	5	10Apr86
B	4.46	5	08May86
C	2.85	5	29May86
D C	1.58	5	26Jun86
D	1.20	5	24Jul86
D	0.72	5	02Jan86
D	0.27	5	21Nov85

LOCATION = SMK45CN

DUNCAN GROUPING	MEAN	N	CDATE
A	9.48	5	27FEB86
B	7.06	5	21NOV85
C	2.90	5	29MAY86

LOCATION = SMK45CL

DUNCAN GROUPING	MEAN	N	CDATE
A	8.9493	5	27FEB86
B	5.0705	5	21NOV85
C	2.5420	5	29MAY86

LOCATION=BK45

DUNCAN GROUPING	MEAN	N	CDATE
A	2.648	5	29MAY86
A	2.152	5	27FEB86
A	0.551	5	21NOV85

Table 5.5 Results of Duncan's multiple range tests comparing log-transformed densities of sporophytes on cobbles among locations on 27 February 1986 and 10 April 1986, times of peak density. Letters indicate groups of means (stations) that did not differ significantly at P<0.05. Twelve stations were sampled in February and only 5 were sampled in April.

COLLECTION DATE = 27FEB86

DUNCAN GROUPING			MEAN	N	STACODE
	A		10.568	5	SMK45
B	A		9.55	5	SOKU45CL
B	A		9.48	5	SMK45CN
B	A		9.25	5	SOKU45
B	A		8.95	5	SMK45CL
B			7.17	5	SOKD45CN
B			6.96	5	SOKD45CL
	C		4.27	5	SOKU35
	C		3.66	5	SOKU45CN
	C	D	2.15	5	BK45
		D	0.36	5	SOKD45
		D	0.00	5	SOKD35

COLLECTION DATE = 10APR86

DUNCAN GROUPING	MEAN	N	STACODE
A	6.57	5	SOKU45
A	5.85	5	SOKD35
A	4.97	5	SOKD45
A	4.93	5	SMK45
A	4.70	5	SOKU35

Table 5.6 Nested analysis of variance of log-transformed densities of sporophytes on cobbles collected from locations differing in adult sporophyte density and at 3 stations within those locations. Separate analyses were performed for the November 1985, February 1986, and May 1986 samplings. Results of contrasts among adult density groups are also given. Letters indicate groups of means (density groups) that did not differ signficantly at P<0.05.

November 1985

Source	df	Type III SS	F value	PR > F
Adult density	3	235.34	71.06	0.0001
Location (DENGRP)	8	173.01	19.59	0.0001

Contrast group	Mean	N	Adult density
A	5.1053	15	high
B	3.2589	15	medium
C	0.5915	15	low
C	0.3045	15	none

February 1986

Source	df	Type III SS	F Value	PR > F
Adult density	3	332.65	26.22	0.0001
Location (DENGRP)	8	457.75	13.53	0.0001

Contrast group	Mean	N	Adult density
A	8.4833	15	medium
B	6.7684	15	high
B	6.7245	15	low
C	2.1403	15	none

May 1986

Source	df	Type III SS	F Value	PR > F
Adult density	3	65.69	7.86	0.0002
Location (DENGRP)	8	44.96	2.02	0.0641

Contrast group	Mean	N	Adult density
A	4.49	15	high
B A	3.56	15	medium
B	3.06	15	low
C	1.59	15	none

Table 5.7 Two-way, fixed-effect analysis of variance of log-transformed densities of sporophytes, on cobbles collected from various locations in SOK and SMK, vs time (collection date). Sporophyte densities were determined without culturing.

SOURCE	DF	TYPE III SS	F VALUE	PR > F
TIME	3	17.39	3.64	0.016
LOCATION	4	90.16	14.16	<0.001
TIME * LOCATION	12	46.43	2.43	0.010

Table 5.8 Results of Duncan's multiple range tests comparing log-transformed densities of sporophytes on uncultured cobbles. Tests compare sampling dates for each station. Letters indicate groups of means (i.e., dates) that were not significantly different at P<0.05.

LOCATION=SOKD45

DUNCAN GROUPING	MEAN	N	CDATE
A	2.919	5	08MAY86
A	2.717	5	26JUN86
A	1.982	5	29MAY86
A	0.766	5	24JUL86

LOCATION=SOKD35

DUNCAN GROUPING	MEAN	N	CDATE
A	4.3632	5	08MAY86
B	2.1527	5	29MAY86
B	1.6504	5	24JUL86
B	0.2743	5	26JUN86

LOCATION=SOKU35

DUNCAN GROUPING	MEAN	N	CDATE
A	0	5	08MAY86
A	0	5	24JUL86
A	0	5	26JUN86
A	0	5	29MAY86

LOCATION=SOKU45

DUNCAN GROUPING	MEAN	N	CDATE
A	0.6201	5	26JUN86
A	0.4985	5	29MAY86
A	0.1845	5	24JUL86
A	0.0000	5	08MAY86

LOCATION=SMK45

DUNCAN GROUPING	MEAN	N	CDATE
A	2.6973	5	08MAY86
A	2.2343	5	24JUL86
A	2.0176	5	29MAY86
A	0.2980	5	26JUN86

Table 5.9 Results of Duncan's multiple range tests comparing log-transformed densities of sporophytes on uncultured cobbles. Tests compare locations within each sampling date. Letters indicate groups of means (i.e., stations) that were not significantly different at P<0.05.

COLLECTION DATE = 08MAY86

DUNCAN GROUPING	MEAN	N	STACODE
A	4.3632	5	SOKD35
A	2.9186	5	SOKD45
A	2.6973	5	SMK45
B	0.0000	5	SOKU35
B	0.0000	5	SOKU45

COLLECTION DATE = 29MAY86

DUNCAN GROUPING			MEAN	N	STACODE
	A		3.0438	5	SMK45CL
	A		2.8780	5	SOKU45CL
B	A		2.5068	5	BK45
B	A	C	2.1527	5	SOKD35
B	A	C	2.0176	5	SMK45
B	A	C	1.9824	5	SOKD45
B	A	C	1.6876	5	SOKD45CN
B	A	C	1.4773	5	SMK45CN
B		C	0.4985	5	SOKU45
B		C	0.3345	5	SOKD45CL
		C	0.0000	5	SOKU35
		C	0.0000	5	SOKU45CN

COLLECTION DATE = 26JUN86

DUNCAN GROUPING	MEAN	N	STACODE
A	2.7173	5	SOKD45
B	1.2980	5	SMK45
B	0.6201	5	SOKU45
B	0.2743	5	SOKD35
B	0.0000	5	SOKU35

COLLECTION DATE = 24JUL86

DUNCAN GROUPING		MEAN	N	STACODE
	A	2.2343	5	SMK45
B	A	1.6504	5	SOKD35
B	A	0.7664	5	SOKD45
B		0.1845	5	SOKU45
B		0.0000	5	SOKU35

Figure 5.1 a and b. Location of collection sites for cobbles in the San Onofre (5.1 a) and San Mateo (5.1 b) Kelp forests. Kelp density contours (#/100 m^2) are from downlooking sonar estimates of November 1985.

Figure 5.1 a

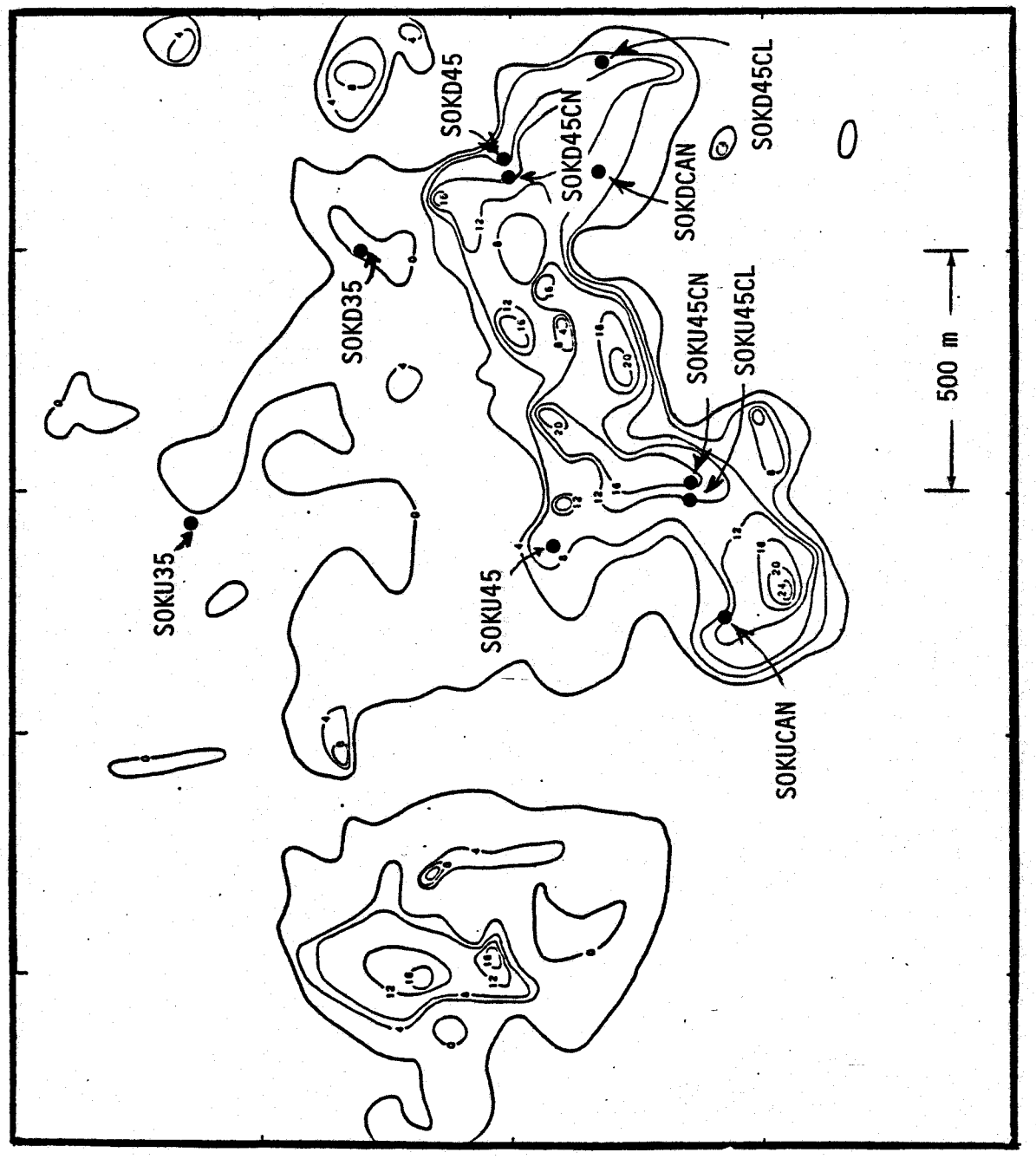

SAN ONOFRE KELP
SOKU35
SOKD35
SOKD45
SOKD45CN
SOKDCAN
SOKD45CL
SOKU45
SOKU45CN
SOKU45CL
SOKUCAN
500 m

Figure 5.1 b

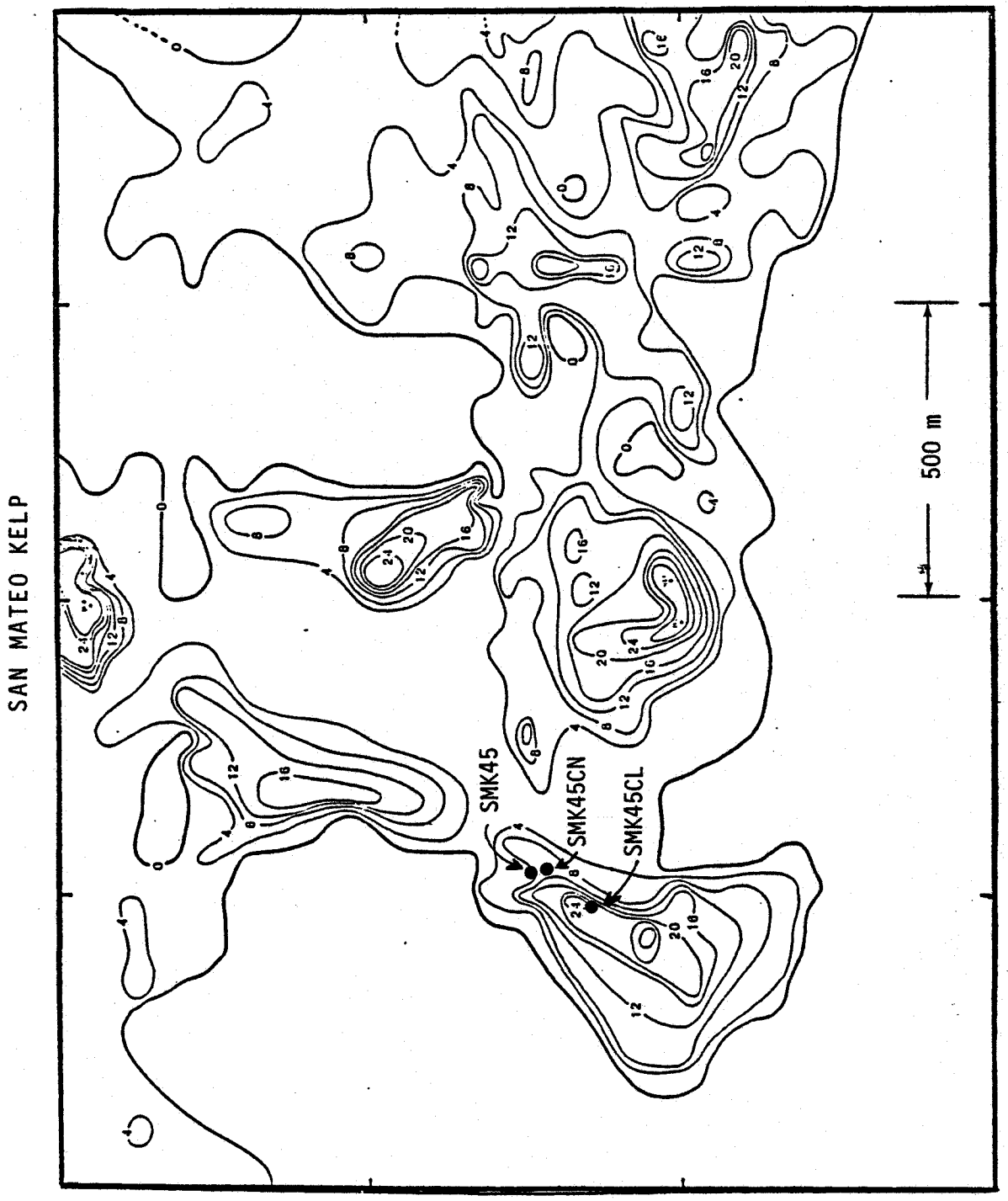


Figure 5.2 Mean density (log (#/100 cm^2 + 0.01)) on cobbles collected from sampling stations in at SOK, SMK, and BK and cultured in the laboratory for 3 weeks. Mean values ± 1 standard of error are given. Collection dates are shown on the x-axis.

Figure 5.2

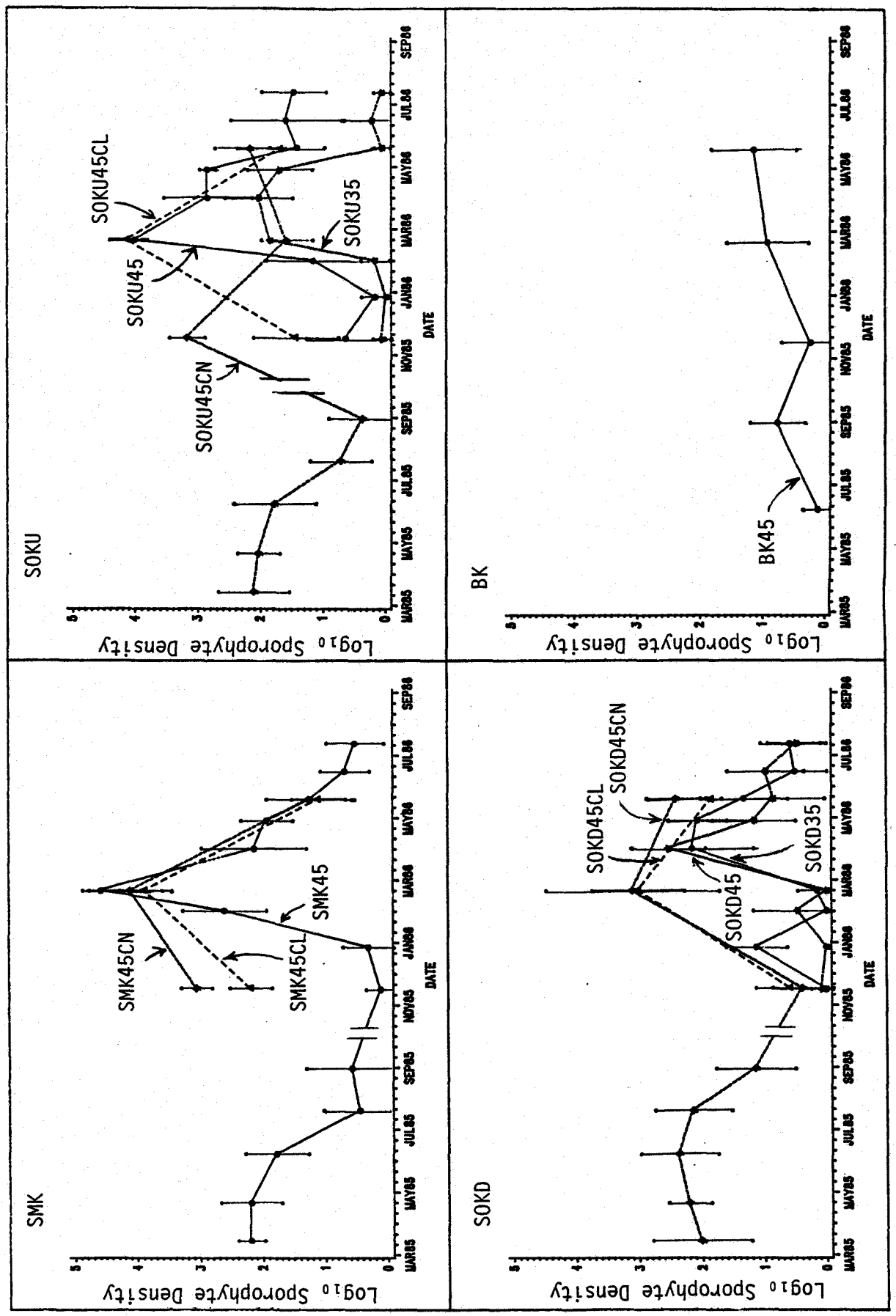
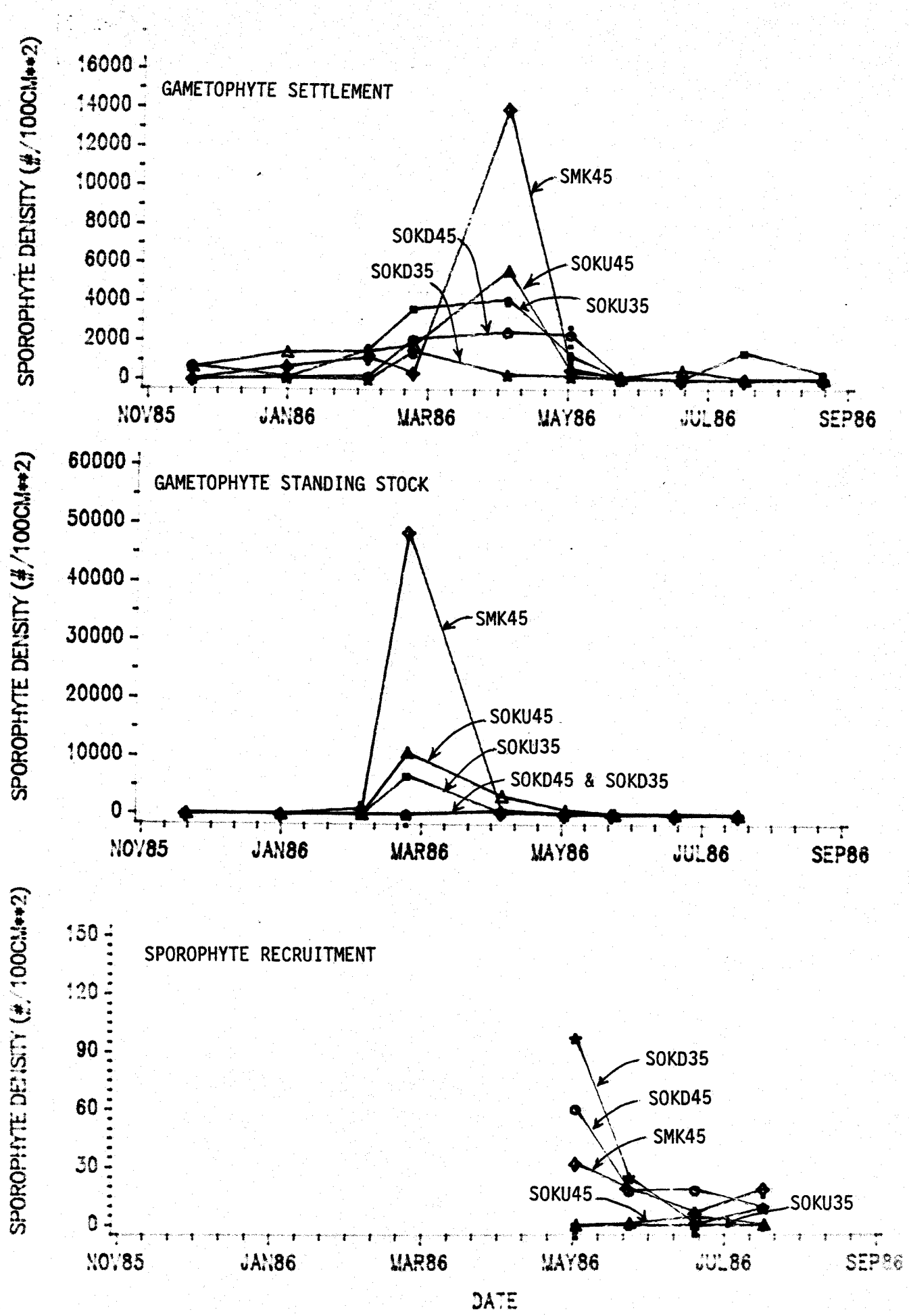

SOKU
SOKU45CL
SOKU45
SOKU35
SOKU45CN
BK
BK45
SMK
SMK45CN
SMK45
SMK45CL
SOKD
SOKD45CL
SOKD45CN
SOKD35
SOKD45
Log10 Sporophyte Density
DATE
MAR85
MAY85
JUL85
SEP85
NOV85
JAN86
MAR86
MAY86
JUL86
SEP86

Figure 5.3 Mean density (log #/100 cm^2) of sporophytes on glass slides after 2 weeks field exposure and 3 weeks in culture (gametophyte settlement), on cobbles after 3 weeks in culture (gametophyte standing stock), and on cobbles examined without culturing (sporophyte recruitment). Collection dates are indicated on the x-axis.

Figure 5.3


GAMETOPHYTE SETTLEMENT
SPOROPHYTE DENSITY (#/100CM**2)
16000
14000
12000
10000
8000
6000
4000
2000
0
SMK45
SOKD45
SOKD35
SOKU45
SOKU35
NOV85
JAN86
MAR86
MAY86
JUL86
SEP86
GAMETOPHYTE STANDING STOCK
SPOROPHYTE DENSITY (#/100CM**2)
60000
50000
40000
30000
20000
10000
0
SMK45
SOKU45
SOKU35
SOKD45 & SOKD35
NOV85
JAN86
MAR86
MAY86
JUL86
SEP86
SPOROPHYTE RECRUITMENT
SPOROPHYTE DENSITY (#/100CM**2)
150
120
90
60
30
0
SOKD35
SOKD45
SMK45
SOKU45
SOKU35
NOV85
JAN86
MAR86
MAY86
JUL86
SEP86
DATE

6.0 Production of Sporophytes from Gametophytes

6.1 Introduction

A primary goal of our studies at San Onofre has been to define the relationships between various physiochemical factors and gametogenesis in the giant kelp, Macrocystis pyrifera. An especially important aspect of these relationships is the set of critical boundaries for various factors within which gametogenesis can occur. For example, the lower threshold for irradiance is important because a potential effect of the operation of SONGS Units 2 and 3 is increased turbidity in the vicinity of the San Onofre kelp bed. Increased turbidity could lower irradiance levels on the bottom to the point where gametogenesis would not occur, thereby preventing the recruitment of sporophytes. It is important, therefore, to establish the relationships with gametogenesis in order to assess whether changes in the physiochemical regime at San Onofre are adversely affecting sporophyte recruitment.

The small size of the gametophyte generation of Macrocystis pyrifera makes the direct study of their biology in the field difficult. Laboratory studies on this stage have been conducted for many years (see Kain, 1979, for review of literature), but only recently has a coherent view begun to emerge of how the various physicochemical factors interact to control gametogenesis (Luning, 1980). The primary reason for this lack of clarity has been is that many of the studies used gametophyte growth as the biological variable by which physiochemical factors were assessed. Gametophyte growth, however, responds very differently than gametophyte fertility to the same suite of environmental factors. Luning and Neushul (1978), for example, found that two to three times more irradiance was required to induce fertility than was required for maximum growth of gametophytes. Therefore, studies assessing the effects of physicochemical factors on gametophyte growth would reach

very different conclusions than those assessing fertility. Gametophyte fertility is the more revelant ecological parameter to use with respect to the gametophyte generation and has been exclusively used in all of our studies of gametophyte response to physiochemical factors. This chapter describes a series of both laboratory and field experiments which examine the effects of irradiance, temperature, nutrient concentrations, and seston flux on sporophyte production in Macrocystis. Quantitative relationships between sporophyte recruitment and these physicochemical factors are provided.

6.2 Laboratory Studies of Effects of Irradiance

6.2.1 Introduction

A number of recent studies have investigated the importance of light quantity and quality in controlling laminarian gametogenesis. Luning and Dring (1972, 1975) demonstrated that a critical dosage of blue light (360 - 500 nm) is necessary for gametogenesis in Laminaria saccharina, and that this blue light response is independent of photosynthesis. Luning and Neushul (1978) investigated the irradiance and temperature requirements for gametogenesis in Macrocystis pyrifera and eight other laminarian species from California. They found that gametogenesis in Macrocystis pyrifera showed a linear dependence on quantum irradiance from 10 to 60 $\mu E/m^2/s$ with no fertility at 5 $\mu E/m^2/s$. They also showed that Macrocystis gametophytes, like gametophytes of Laminaria saccharina, became fertile only in blue light, with 50% fertility induced by a blue light dose of 2.6 E/m^2. Luning (1980) emphasized the dependence of gametophyte fertility on quantum dose rather than instantaneous irradiance (photon flux density) in his work on three species of Laminaria.

Our own laboratory work on the relationship between Macrocystis gametophyte fertility and irradiance consisted of two studies. The first study, conducted in 1980, describes the lower critical irradiance for fertility and the interactive effects of instantaneous irradiance (photon flux density) level and quantum dose on this process. This study was conducted at a constant temperature of 15°C since previous studies (Luning and Neushul, 1978) showed that 15°C was an optimum temperature for sporophyte production. However, Luning (1980) showed that the relationship between irradiance and fertility in gametophytes of Laminaria saccharina was temperature dependent. This potential interaction between irradiance and temperature led us to conduct a second study in 1984 in which the critical irradiance level was investigated over a temperature range of 11° to 20°C. This second study is described in the following section on temperature effects (Section 6.3)

The purpose of the first study was to determine the lower critical light requirements for gametogenesis. The determination of this lower light limit required an assessment of the interaction between quantum dose and instantaneous irradiance in controlling gametogenesis. Luning and Neushul (1978) showed a linear relationship between blue light dose and fertility in a dosage range from 1.0 to 5.0 E/m^2. Fifty percent fertility was induced by 2.6 E/m^2, provided solely by blue quanta at a rate of 10 to 20 $\mu E/m^2/s$. However, they also found that gametophytes grown in a continuous white light regime (20% blue), at an instantaneous irradiance of 5 $\mu E/m^2/s$ did not become fertile even when the blue light quantum dose reached 2.4 E/m^2. The linear relationship developed with blue light in these studies predicted that a fertility of approximately 40% should have occurred at this dosage. It appeared, therefore, that the instantaneous rate at which gametophytes received a specified quantum dose also influenced gametogenesis.

6.2.2 Methods

The zoospores used to produce gametophytes for this laboratory experiment were obtained from adult sporophytes in the San Onofre kelp forest. Fertile sporophylls were collected by divers, stored in plastic buckets filled with seawater, and transported back to the laboratory, with care taken to minmize increasing the water temperature above ambient. The sporophylls were carefully rinsed with filtered seawater to remove detritus and diatoms attached to the surface and then stored overnight in moist towelling at 15°C. Zoospores were released the following morning by placing the sporophylls into seawater that was previously filtered through a 0.2 µm filter. The resulting zoospore solution was diluted to produce an inoculation solution with a zoospore concentration of approximately 1.0×10^4 spores/ml. Zoospore concentration was determined with a hemocytometer.

The zoospores were inoculated onto glass coverslips (22 x 22 mm) to obtain a density of approximately 150 gametophytes/mm^2. These coverslips had a 2 mm diameter glass tube cemented perpendicularly to one corner to facilitate handling. Inoculation of coverslips was conducted in a constant temperature room at 15°C. The coverslips were inoculated for 24 hours in Pyrex baking dishes containing 1.5 liters of the inoculation solution. After inoculation, four coverslips were placed in each culture vessel which contained 250 ml of Provasoli's enriched seawater (PES) nutrient medium (Provasoli, 1968).

Three photoperiod regimes were used in these experiments: 24:0 LD (light-dark), 12:12 LD, and 8:16 LD. Five to six instantaneous irradiance levels were used in each photoperiod. These levels were selected as to produce equal daily quantum dosages between photoperiod treatments. The proper irradiances were obtained by placing the culture vessels at varying distances from daylight fluorescent bulbs

(Westinghouse F40D 40W). These daylight fluorescent bulbs had approximately 27% of their quantum output in the blue portion of the spectrum (360 - 500 nm) (Gaines, 1977). This blue quantum output is approximately 7% higher than that of cool-white bulbs which are commonly used in algal culture experiments. Irradiances were measured with a LI-COR model LI-185 quantum meter. Two culture vessels, each with 4 coverslips, were placed at each designated irradiance and photoperiod treatment. Gametophyte cultures in the 24:0 LD photoperiod were maintained in a constant temperature room and the 12:12 and 8:16 LD photoperiods were maintained in a low temperature incubator (Lab-Line Instruments). The experiments were run during two separate times. The first used the 24:0 LD and 12:12 LD photoperiods, and the second used 24:0 LD and 3:16 LD photoperiods. All cultures were grown at 15°C.

One coverslip was removed from each irradiance treatment approximately every three days for fertility measurements. Seven sets, of 25 female gametophytes each, were scored for fertility on each coverslip. Gametophytes were chosen randomly on the coverslips by moving the mechanical stage of the microscope haphazardly before viewing. Fertility was designated by the appearance of sporophytes of two cells or larger, attached to the female gametophyte. Sporophyte appearance, rather than egg production, was used as an indicator of fertility because egg production was difficult to observe and define.

6.2.3. Results

The time course of fertility under the various quantum irradiances for the three photoperiods is shown in Figure 6.1. The minimum time necessary for production of sporophytes was 10 days from zoospore settlement. At quantum irradiances above 5 $\mu E/m^2/s$, sporophyte production increased rapidly after the 10 day lag period in all three photoperiods. In the 12:12 and 24:0 LD photoperiods,

greater than 80% fertility was reached in approximately 20 to 28 days at all irradiances above 5 $\mu E/m^2/s$, but this level of fertility was delayed until approximately 28 to 35 days in the 8:16 LD photoperiod. Sporophyte production rates in general were slightly depressed in the 8:16 LD photoperiod as compared to the 12:12 and 24:0 LD photoperiods. There was little sporophyte production (<50%) at irradiances of 3 $\mu E/m^2/s$ or less in all three photoperiods.

The relationship between the sporophyte production rate (expressed as the time to 50% fertility) and the daily quantum dose for each of the 3 photoperiods are shown in Figure 6.2. The time to 50% fertility was determined from a regression of points in the linear portion of each curve in Figure 6.1. The general pattern observed was the presence of lower critical dosage and the presence of a lower critical dosage below which sporophytes were not produced and a quick leveling off of production rates, at near maximum levels, as irradiances increased. The exact form of these functions, however, varied with photoperiod. The lower critical dosage was approximately 0.2 $E/m^2/d$ in the 8:16 and 12:12 LD photoperiods, and was approximately 0.4 $E/m^2/d$ in the 24:0 LD photoperiod. The sporophyte production rates reached near maximum levels at at about 0.8 $E/m^2/d$ in the 24:0 and 12:12 LD photoperiods, but production rates continued to increase at irradiances up to 1.8 $E/m^2/d$ in the 8:16 LD photoperiod.

The differences in the curves of sporophyte production rate vs quantum dosage for the various photoperiods appear to be due to a nonlinear accumulation of quanta into the daily dosage at various instantaneous quantum irradiance levels. At lower irradiance levels there is a critical threshold below which irradiance did not contribute to the effective irradiation dose for gametogenesis. Gametophytes in the 24-hr photoperiod, for example, never reached 50% fertility at daily irradiation

levels less than 0.4 $E/m^2/d$ (instantaneous rates <5 $\mu E/m^2/s$) but gametophytes in the 12:12 and 8:16 LD photoperiods reached 50% fertility at irradiation levels as low as 0.15 $E/m^2/d$ (3 $\mu E/m^2/s$) and 0.25 $E/m^2/d$ (8 $\mu E/m^2/s$), respectively. These differences between photoperiods appear to be related to the inability of gametophytes to effectively utilize low instantaneous irradiances. The gametophytes in the 24-hr photoperiod at an irradiance of 3 $\mu E/m^2/s$ were apparently unable to utilize the radiant energy received. The threshold is therefore between 3 and 5 $\mu E/m^2/s$ and we estimate it at 4 $\mu E/m^2/s$.

At higher irradiance levels, the accumulation of quanta into the effective quantum dose appears to saturate at instantaneous irradiances between 5 and 10 $\mu E/m^2/s$. This saturation of sporophyte production at higher irradiances is especially evident in the 8:16 LD photoperiod (Fig. 6.2). Gametophytes cultured in this photoperiod at irradiation doses greater than 0.4 $E/m^2/d$ (instantaneous rates >10 $\mu E/m^2/s$) took 4 to 9 days longer to reach 50% fertility than gametophytes cultured under the same daily quantum dose in the 12:12 LD photoperiod which had lower instantaneous irradiances. This suggests that gametophytes in the 8:16 LD photoperiod were able to utilize only a portion of the irradiation dose they received.

The saturating irradiance level was more precisely estimated by using different saturation values between 5 and 10 $\mu E/m^2/s$ and calculating the quantum dose required to achieve gametogenesis by 50% of the gametophytes (critical dose). It is assumed that none of the irradiance above the saturation level is able to be utilized by the gametophytes. The premise was that all treatments (instantaneous irradiance x photoperiod) should yield equivalent total dosages once the appropriate saturation level was applied. Therefore, the saturation level that produced the lowest

coefficient of variation in total dose among treatments was deemed the most appropriate. We did this using all laboratory data obtained at either 12:12 LD or 8:16 LD photoperiods (those normally encountered in the field) at all irradiance levels above the estimated threshold level of 0.4 $\mu E/m^2/s$. The resulting values of total quantum dose showed little variability even though instantaneous rates and total doses without saturation levels applied varied greatly. The smallest coefficient of variation in total dose was obtained for a saturation level of 6 $\mu E/m^2/s$. The average critical dose using this 6 $\mu E/m^2/s$ saturation level was 3.9 E/m^2.

While we have expressed these results in terms of total quanta (400 - 700 nm), we know that gametogenesis is a function of only the blue light portion of the spectrum. The blue portion represented 27% of the total quanta for the light source used in our study (Gaines, 1977). Using this relationship of total quanta to blue quanta, we can express the threshold level, saturation level, and total dose in terms of blue quanta. This conversion yields values of 1.1 $\mu E/m^2/s$ for the threshold irradiance level, 1.6 $\mu E/m^2/s$ for the saturating irradiance level, and 1.1 E/m^2 for the total blue dose required for gametogenesis by 50% of the sporophytes.

6.2.4 Discussion

Both the instantaneous rate at which irradiance is received and the total irradiation dose received by gametophytes are important for the process of gametogenesis. The instantaneous threshold is approximately 1.1 $\mu E/m^2/s$ of blue light and the saturation level is 1.6 $\mu E/m^2/s$. The narrow range in threshold and saturation values indicates that the relationship between irradiance and gametogenesis is essentially a step function. Novaczek (1984) has described a similar step function response for gametogenesis in the brown alga Eklonia.

Threshold and saturation levels are important in interpreting gametogenesis in the field. Instantaneous irradiances on the bottom in the San Onofre kelp forest are occasionally below the threshold level and are often above the saturation level (Fig. 6.3).

We have described a definitive saturation level for gametogenesis, but there appears to be some accumulation of usable quanta above this level. This is indicated by the increasing rate of gametogenesis with increasing irradiance, especially in the 8:16 LD photoperiod (Fig. 6.1). However, only a small proportion of available quanta above 0.6 $\mu E/m^2/s$ are apparently utilized. This is suggested by the small variance in total dose required to achieve 50% fertility, assuming a saturation level of 0.6 $\mu E/m^2/s$.

While it is convenient to express results in terms of total quanta (400 - 700 nm), these values are not very useful in comparing results among lab and field studies or among lab studies that used different light sources. Gametogenesis responds to blue light and because the proportion of total quanta that are blue vary among light sources, it is best to convert values to blue quanta before comparison.

As previously indicated, it is probable that sporophyte production is dependent on a variety of physicochemical factors and that these factors interact to control sporophyte recruitment. A temperature of 15°C, which has been shown to be in the optimal range for gametogenesis in *M. pyrifera* (Luning and Neushul, 1978) was used in this study. Luning (1980) demonstrated that the total irradiation dosage necessary for gametogenesis in *Laminaria saccharina* increases exponentially as temperature increases. This potential interaction between temperature and irradiance in the control of *Macrocystis* fertility is explored in the following section.

6.3 Laboratory Studies on the Effects of Temperature and Interactive Effects of Irradiance and Temperature

6.3.1 Introduction

Previous laboratory studies on Macrocystis pyrifera gametophytes showed that the optimal temperature range for gametogenesis was between 12° and 17°C and that no gametogenesis occurred at 7° and 20°C (Luning and Neushul, 1978). This was also the general pattern they found for gametogenesis in 4 other species of Laminariales occurring in southern California. Work on Laminaria saccharina by Luning (1980) showed that the irradiance dose for 50% fertility increased almost exponentially in the temperature range between 10° and 18°C. Based on this previous research and on the range in temperatures observed in situ at SOK, we chose the temperature range of 11° to 20°C in which to investigate temperature effects on gametogenesis and the potential interactive effects with irradiance.

6.3.2 Methods

Gametophytes were grown on glass microscope slides at a density of approximately 150 female gametophytes/mm². Procedures for inoculating the slides with gametophytes were identical to those used in the irradiance experiments described in Section 6.2. Germanium dioxide (0.5 mg/l) was added to the inoculation solution to control diatom contamination since contamination is prevalent at the high temperatures used in these experiments (Lewin, 1966; Markham and Hagmeier, 1982). The growth medium for the gametophyte cultures, however, did not contain GeO_2. The use of GeO_2 at similar concentrations and durations has been shown to have no effects on the development of other laminarian algae (Markham and Hagmeier, 1982).

The gametophytes were grown in PES media (Provasoli, 1968) in plexiglass culture containers (37 x 9 x 21 cm) with a volume of 6 ℓ. The medium was changed once after 3 weeks of the 6 week culture period. Ten slides were positioned at mid-depth in each container by a removable acrylic frame, which allowed for easy transfer of the slides from the inoculation solution to the culture container. The slides were attached to the frame with a thin bead of silicone grease. The medium in the culture containers was circulated by an air bubbler on the bottom of the container.

The irradiance regimes used in the experiments ranged from 2.9 to 30 $\mu E/m^2/s$ (spherical irradiance 400 - 700 nm) (Table 6.2). The desired irradiance levels were obtained by adjusting the distances between the lights and the containers and by shading the containers with various grades of window screen. Irradiances were measured underwater at the level of the glass slides with a LI-COR quantum meter (model 182) fitted with a spherical underwater quantum sensor. Spherical irradiance was used in this study because the gametophytes grown on the clear glass slides received light from all directions within the culture container. This configuration was different from the previous laboratory study in which the gametophytes were grown on the bottom of small culture containers and received light only from above. Irradiance in that study, therefore, was measured with a flat plate, cosine-corrected sensor. A 10:14 (light:dark) photoperiod was maintained yielding daily irradiation doses of 0.1 to 1.1 E m^2/d (Table 6.2). Irradiation levels on the bottom in southern California kelp forests are often below 1 $E/m^2/d$ (Dean, 1985).

Ten temperatures, 11° to $20^{\circ}C$ at one degree intervals, were used in each of the irradiance treatments. This is approximately the range of temperatures observed on the bottom in southern California kelp forests (Dean and Jacobsen, 1984). The

temperatures were maintained within a range of $\pm 0.2^{\circ}C$ by keeping the coldroom temperature at $10^{\circ}C$ and elevating the temperature of the medium in each culture container to the appropriate level with an aquarium heater controlled by an electronic thermostat system.

One culture container was maintained at each of the 70 temperature-irradiance treatments. Replication of the treatments was accomplished by conducting the entire experiment on two separate occasions. Therefore, error due to variability within treatments was confounded with possible differences among zoospores collected from different sources at different times. The first experiment was inoculated on 25 January 1984 and the second on 4 April 1984. The zoospores used in both of the experiments were obtained from sporophylls collected from 3 to 5 randomly selected plants in the San Onofre kelp forest.

Gametophytes were sampled on two randomly selected slides from each container during each sampling period. On each slide, 5 haphazardly chosen sets of 25 females were scored for production of both eggs and sporophytes. In the first experiment, gametophytes were sampled at 14, 21, 28, 35, and 42 days after inoculation, and in the second experiment they were sampled after 21, 35, and 42 days.

The time required for 50% of the female gametophytes to produce sporophytes was determined from a least squares regression of fertility with time in the period from 14 days to either the first occurrence of 100% fertility or the end of the experiment. The regression was bounded at 14 days because there is a latent period, of approximately 10 to 14 days after zoospore settlement, during which no fertility will occur even under optimal conditions (Luning and Neushul, 1978; Section 6.2).

6.3.3 Results

Differences in fertility in the two experiments were tested by ANOVAs across all temperatures at the 0.60 $E/m^2/d$ irradiation level, between 11° and 15^oC at 0.25 $E/m^2/d$, and across all irradiations at 20^oC. Under all other conditions, fertility was either near 100% or 0% in both experiments. The second experiment had slightly lower fertility at the lower temperatures at the 0.25 $E/m^2/d$ irradiance level, than the first experiment (Table 6.3). In all other cases, differences among experiments were not significant.

The minimum daily quantum dose at which female gametophytes produced sporophytes (i.e., the threshold level) was 0.25 $E/m/^2/d$ at temperatures up to 15^oC and slightly higher at temperatures above 15^oC (Fig. 6.4). At temperatures between 11° and 15^oC, differences in fertility at the 0.25 $E/m^2/d$ irradiance level were not significant (Table 6.3). All cultures except those at 19° and 20^oC had nearly 100% fertility at irradiances above 0.25 $E/m^2/d$ (Fig. 6.4). At 0.60 $E/m^2/d$ percent fertility differed among temperatures, but only the fertilities in cultures at 20^oC were significantly different than those at lower temperatures (Table 6.4).

The time to 50% fertility, which provides an index of how rapidly gametogenesis occurs, showed the same general trends as maximum fertility. At irradiances near the threshold level (0.25 $E/m^2/d$), it took slightly less time for 50% fertility at 11° and 12^oC than at temperatures between 13° and 19^oC. At 20^oC, the development time was generally longer than at lower temperatures (Table 6.5).

6.3.4 Discussion

The various relationships between gametogenesis and irradiance such as the minimum irradiance threshold, the level for 50% fertility, and the saturation

irradiance, agreed well between the two experiments as well as with the results of previous laboratory experiments which were conducted at 15°C (Section 6.2). The irradiance level required for 50% fertility in a 12:12 LD photoperiod 0.4 E/m²/d in our previous experiments (Section 6.2) and was between 0.25 and 0.60 E/m²/d (at 15°C) in these experiments.

The strong interaction between irradiance and temperature in Laminaria spp. (Luning, 1980) was not observed in Macrocystis pyrifera. Some interaction was noted in the slightly greater fertility at 0.25 E/m²/d at temperatures below 15°C and in the slightly lower fertility at irradiances between 0.60 and 1.1 E/m²/d at 20°C. However, these effects were small compared to the exponential increase in the irradiance dose required for 50% fertility with increasing temperature observed in L. saccharina.

One surprising result was that sporophytes were produced at temperatures up to 20°C. Previous laboratory studies (Luning and Neushul, 1978) indicated that the upper temperature limit for gametogenesis in this species was between 17° and 20°C. However, we found 100% fertility at 19°C when light levels were at or above 0.92 E/m²/d and greater than 70% at 20°C under the same irradiance regimes. These differences were not due to irradiance since the irradiance level used by Luning and Neushul (60 µE/m²/s or 2.15 E/m²/d) was well above the level at which we observed high levels of fertility. The differences in the results of these two studies may have been due to genotypic variability among kelp populations in different regions with respect to temperature tolerances. Luning and Neushul (1978) used gametophytes produced from sporophytes in the Santa Barbara areas, whereas our gametophytes came from a population approximately 300 km to the south.

The occurrence of 100% sporophyte production at temperatures above 17°C also differs from the results of our gametophyte field studies (Section 6.5) in which very low sporophyte production occurred at temperatures above 16.3°C even when irradiance levels were high. The data from this laboratory study suggest that the lack of sporophyte production in the field outplants was not simply due to higher temperatures, but possibly due to a factor that correlated with temperature, such as nutrients. The role of both macronutrients and micronutrients in controlling gametogenesis is discussed in the following section.

6.4 Laboratory Studies on the Effects of Nutrients

6.4.1 Introduction

A number of studies have shown that nutrients are an important factor regulating gametogenesis in Macrocystis pyrifera and other laminarian species. Kuwabara and North (1980) conducted an elegant study in which Macrocystis gametophytes were cultured in a totally defined artificial medium. In this study, the essential micronutrients for gametogenesis were defined and various quantitative relationships between fertility and these micronutrients were determined. However, nitrogen was maintained at 20 µM, a high concentration relative to average levels in nearshore waters of southern California, due to limitations of the experimental design. The concentration at which nitrogen limits gametogenesis, therefore, was not defined in this study. In a study of Laminaria saccharina from British Columbia, Hsiao and Druehl (1971, 1973a) found that the optimum nitrogen concentration at which gametophytes produced sporophytes in laboratory culture was 600 µM. This concentration is more than 100 times the normal nitrogen concentration in that species' natural habitat. The authors ascribed this high optimum concentration to various artifacts associated with the culture methodology. Therefore, even though nitrogen has been shown to be an important

factor in gametogenesis of various laminarian species, the quantitative relationships in this process are not well known.

The results of our laboratory studies on the relationships between temperature, irradiance, and gametogenesis in Macrocystis, presented in the previous section, show that under optimal nutrient conditions populations of gametophytes can have 100% sporophyte production at temperatures up to 19°C. This is in contrast to the results of the field outplant studies which show a significant negative correlation between sporophyte production and temperature, at temperatures between 11 and 18°C, with few sporophytes produced at temperatures above 16°C (see section 6.5).

These results suggest that some factor related to temperature, but not temperature itself, is controlling the observed correlation between temperature and sporophyte production in the field. Several studies have shown that nitrogen is correlated with temperature in kelp forests in southern California (Jackson, 1977; Zentara and Kamykowski, 1977; Reitzel and Zabloudil, 1984; Zimmerman and Kremer, 1984). Nitrogen levels are generally low (<1 μM) at temperatures above 16°C (Fig. 6.5) in the nearshore waters off San Onofre. This relationship suggests that low nitrogen levels may be responsible for the lack of sporophyte production in warm waters. The purpose of this laboratory study was to explore the relationships between nutrients (especially nitrogen) and gametogenesis under optimal conditions of temperature and irradiance.

6.4.2 Methods

The procedures used to inoculate the gametophyte cultures were identical to those used in the above studies (Section 6.3). The basic culture medium was natural seawater enriched with various nutrient additives. We collected the seawater from

0.5 m below the sea surface and approximately 15 km offshore to ensure that the unenriched water had a low nitrogen concentration. The water was filtered through a 0.2 µm capsule filter to eliminate diatoms and other phytoplankton. The gametophytes were grown on glass slides in 6 ℓ culture vessels that were aerated from the bottom. The large volume-to-sample ratio and the continuous movement of the medium in the culture vessels eliminated any potential problems of nutrient depletion.

This study consisted of a series of 3 experiments in which the findings of each experiment were more fully explored and tested in the next experiment. Two replicate culture vessels were used for each of the treatments except for the third experiment in which there was only one vessel per treatment. Two slides were randomly sampled from each container and 5 groups of 25 haphazardly chosen sets of female gametophytes were sampled for fertility on each slide.

The objective of the first experiment was to determine if additions of nitrogen, or nitrogen and iron, to offshore surface seawater would be sufficient to induce gametogenesis. The control seawater used in this study had a total nitrogen ($NH_4^-+NO_2^-+NO_3^+$) concentration of 0.4 µM. Additions of nitrogen, as $NaNO_3$, were made to this control seawater to yield concentrations of 5 and 10 µM total nitrogen. In the field outplant experiments, high levels of sporophyte recruitment were observed when average nitrogen concentrations ranged from 2 to 6 µM.

In a second treatment, iron and nitrogen were both enhanced with additions of $FeCl_3$, EDTA, and Tris buffer along with the $NaNO_3$. Nitrogen concentrations were again adjusted to 5 and 10 µM the other constituents were added in concentrations normally found in PES growth medium (Table 6.6). Similar concentrations of $FeCl_3$,

EDTA and Tris, and nitrogen along with the addition of nitrogen, have been shown to be sufficient to stimulate gametogenesis in Lessonia nigrescens (Hoffman and Santelices, 1982). These compounds are also important components of the PES media which we routinely used to induce gametogenesis in laboratory culture (Table 6.6). The final treatment in the first experiment was the addition to control seawater of the complete set of PES additives in which the nitrogen concentration was adjusted to produce a final concentration of 10 µM. PES media normally has a total nitrogen concentration of over 660 µM.

A second set of experiments was performed to test for the effects of varying nitrogen and phosphorus concentrations when all other components of PES medium (phosphorus, metals, vitamins, EDTA and Tris) were kept constant. We assumed that factors other than nitrogen would not be limiting in this case. The nitrogen concentrations used ranged from 0.4 to 7.0 µM. In this experiment, we also examined the effects of additions of nitrogen and phosphorus to seawater. Nitrogen and phosphorus were added in ratios normally encountered in coastal waters of southern California (Jackson, 1977). The highest nitrogen (7 µM) and phosphorus (2.8 µM) concentrations are similar to levels observed in coastal southern California during strong upwelling events (Jackson, 1977). The control sea water had a total nitrogen concentration of 0.4 µM.

The third experiment was designed to serve three purposes. The first was to confirm the findings of the second experiment, which showed that gametogenesis was being stimulated at much lower nitrogen levels than expected; the second was to test for possible effects of the addition of the three PES vitamins and the third purpose was to address the possibility that additional nitrogen was being supplied to the gametophytes by nitrogen-fixing bacteria present in the culture system. A factorial

design was used in this experiment in which we had 3 levels of treatment: (1) control seawater (nitrogen concentration = 1.9 μ/M), (2) seawater and metals + 25 μM Na-glycerophosphate, (3) seawater and metals + 25 μM Na-glycerophosphate + 660 μM $NaNO_3$. Each of these treatments was crossed with vitamin and antibiotic (penicillin and chloramphenicol) treatments and their respective controls. Differences among factors and the interactions among factors were examined with a three-way, fixed-effect ANOVA.

6.4.3 Results

The only treatment in the first experiment to produce fertile gametophytes was the addition of PES medium with 10 μM N (Table 6.7). The addition of neither nitrogen nor nitrogen and iron by themselves was sufficient to stimulate gametophyte production.

In the second experiment, all of the treatments in which vitamins, metals and phosphorus were added induced fertility (Table 6.8). Even the treatment in which no nitrogen was added to the culture produced fertility in 68% of the female gametophytes. There was no significant difference in sporophyte production among nitrogen levels when PES components (vitamins, metals, Tris, and phosphate) were added. The addition of only phosphate and nitrogen, at various concentrations, produced a maximum of only 4.0% fertility.

The results of the third experiment confirmed that gametophytes could produce eggs without additions of nitrogen or vitamins, when other PES components were added to the seawater (Table 6.9). As high as 90% of the female gametophytes became fertile in control seawater (0.4 μM nitrogen) to which only metals and phosphorus and antibiotics were added. In the overall analysis, neither the vitamin nor the

antibiotic treatment had a significant effect on gametophyte fertility. However, the treatments with antibiotics had greater fertility than those without in the cases when no nitrogen was added to the culture medium. The causes of this difference are not known, but may be related to bacterial uptake of nitrogen in the no antibiotic treatment and subsequent competition between bacteria and gametophytes for nutrients. However, these results suggest that bacterial supply of nitrogen was not an unimportant source of these nutrients for gametophytes.

6.4.4 Discussion

These laboratory experiments have shown gametogenesis to be less dependent on nitrogen concentrations than was first believed, and that other micronutrients or an interaction between macro- and micronutrients, may be equally if not more important for gametogenesis. The important role of micronutrients, especially trace metals, in gametogenesis of laminarian gametophytes has been shown in two laboratory studies. Kuwabara and North (1980) cultured gametophytes in a precisely defined artificial media (Aquil) and established 9 elements (N, P, Mn, Fe, Co, Cu, Zn, Mo, and I) as being essential for fertility. The minimum concentration needed to produce sporophytes was found for eight of these elements, but was not established for nitrogen because of limitations in a complex experimental design.

Motomura and Sakai (1984) cultured gametophytes of two Laminaria species in a widely used artificial medium ($ASP_{12}NTA$) and found that iron was limiting gametogenesis in the normal formulation of this medium. This finding is important because it explains the results of an earlier study by Hsiao and Druehl (1973a) that showed an optimal nitrogen concentration for gametogenesis in Laminaria sacharrina of 600 µM. Hsiao and Druehl used the same basic media (ASP_2) as Motomura and Sakai, and it appears that the high nitrogen requirement that they demonstrated was the result of iron limitation.

The same type of interaction between micronutrients and macronutrients (nitrogen and phosphorus) appears to be influencing gametogenesis in Macrocystis pyrifera. Our laboratory studies showed that when high levels of trace metals and phosphorus were supplied, nitrogen levels as low as 0.4 µM/l were adequate to induce gametogenesis. When trace metals were not added to the culture, even relatively high nitrogen and phosphorus concentrations (10 µM N and 3 µM P) were not sufficient for gametogenesis.

This interaction was also suggested by the results of a field nutrient experiment conducted in the fall of 1981 (Section 6.5). In this experiment, gametophyte-outplant substrates were put into the field at SMK (0, 2, 4, and 6 m above the bottom), both with and without Osmocote fertilizer. This fertilizer provides nitrogen, phosphorus, and potassium but no trace elements. The average temperature during the two outplants was above 16°C and natural nitrogen levels were near 1.0 µM. Sporophyte recruitment was greater on the fertilized substrates but still low compared to outplants conducted at other times, when temperatures were lower and nitrogen levels were approximately the same as those on the fertilized substrates. It appears that other nutrient constituents, such as trace metals, which are associated along with nitrogen in colder, upwelled water (Anderson, 1978) water are necessary to induce high densities of sporophytes from gametophytes.

The relative importance of the different micronutrients to fertility, and the quantitative relationships between nutrient concentrations and fertility, however, are not yet known. The laboratory studies conducted by Kuwabara and North (1980) allowed the calculation of the free ion concentration of each of the trace metals in the culture media. In most cases the free ion concentration was much lower than the analytical concentration. This was due to the presence of the chelator, EDTA, which

binds with metal ions. Various organic molecules in nearshore seawater also act as chelators and it is therefore difficult to determine the concentrations of trace metals which would be available to the gametophytes.

6.5 In Situ Studies of Production of Sporophytes from Gametophytes

6.5.1 Introduction

The field studies of sporophyte production from gametophytes have had two primary objectives. The first was to serve in the "BACIP" analyses as a direct assessment of any impacts of SONGS on this critical life stage of Macrocystis. The second objective was to develop general quantitative relationships between the production of sporophytes and various physicochemical variables. These relationships will allow us to link the physical regime of the discharge plume with any observed changes in the pattern of sporophyte recruitment in the local kelp forests. The relationships developed in these field studies also serve to validate the results of the various laboratory studies discussed in the previous sections. BACIP results will be presented elsewhere (Vol. II, The Effects of SONGS). Here, we investigate the mechanistic relationships between in situ recruitment of sporophytes and physicochemical factors.

6.5.2 Methods

Outplant and Culture Techniques

The primary experimental tools in this study were artificial substrates that were inoculated with Macrocystis pyrifera zoospores in the laboratory and outplanted to the field stations. These inoculated substrates provided a defined population of gametophytes from which the recruitment of sporophytes could be quantified. The substrates consisted of plexiglass plates (30.5 x 10.2 x 0.6 cm) onto which pieces of nylon line (10 cm long, 0.64 cm diameter) were fastened with plastic cable ties.

This arrangement allowed for the simultaneous inoculation of a large number of sampling units which could then be individually removed from the substrate for transport back to the laboratory for analysis. Nylon line was chosen as the artificial substrate because dense sporophyte recruitment onto this substrate was noted on many occasions within the San Onofre kelp forest.

Zoospores used in the inoculations were obtained from adult Macrocystis pyrifera in SOK. Fertile sporophylls were collected, placed in plastic buckets filled with seawater, and immediately returned to the laboratory to avoid large changes in water temperature over ambient. In the laboratory, the sporophylls were carefully rinsed with filtered seawater to remove excess mucus and diatoms, stored overnight in moist towelling at 15°C, and then allowed to release zoospores in filtered seawater. The zoospore solution was diluted to produce an inoculation solution with a zoospore concentration of 1.0×10^5 spores/ml. Zoospore concentrations were determined with a hemacytometer.

Inoculation of substrates was conducted in a constant temperature room at 15°C. Substrates were inoculated for 24 hours in Pyrex baking dishes containing 1.5 liters of the inoculation solution. After inoculation, the substrates were stored overnight in filtered seawater until outplanting to the field the next day.

The initial gametophyte density for each outplant was estimated by taking 1 to 3 substrate lines from each plate, immediately before the plates were outplanted to the field. The newly settled gametophytes were censused in 10 quadrats of 0.03 mm^2 at 400X using a dipping cone objective fitted with an epi-illumination system. This system provides for high magnification of objects on opaque backgrounds.

The substrates were transported into the field 36 hours after the start of inoculation. They were transported in black plexiglass containers stored in insulated chests. This method of transport was designed to protect the gametophytes from large temperature changes and exposure to direct sunlight.

Field Stations and Sampling Schedule

We attached the outplant plates along with instruments used to measure physical factors on an array of racks at each station (Fig. 6.6). This type of rack has been used since 1979. (An earlier rack design was used at SOKD45 in 1977 and 1978, see Fig. 5.2 in Dean, 1980a). The plates were kept in position by PVC frames attached to a stainless steel cable that was anchored to the bottom by a 23 kg steel plate. Plates were placed on the bottom and 2 m above the bottom at each of the stations. In addition, plates were also placed at 4 m and 6 m above the bottom at the SMK45 station during 1981 and 1982. The rationale for the placement of the substrates in the water column was to provide a wider range of physicochemical regimes than would be available directly on the bottom. Therefore, even though the natural habitat for sporophytes is on the bottom, the use of substrates at 2, 4 and 6 meters above the bottom aided in describing the relationships between sporophyte recruitment and the various environmental factors measured.

The field stations used in the gametophyte outplants varied between experiments. The station at SOKD45 was used continuously since 1977, the station at SOKU45 was added in June, 1979, and the control station at BK55 was added in August, 1980. Additional stations at SOKD35, SMK45, and SMK-CAN were added in August, 1981, and a station at SOKU35 was added in October, 1985. A complete description of the stations included used for outplant is given in Appendix E. Various combinations of stations and depths were used because these samples were part of an evolving BACIP

design (see Section 1.0) and because, in later outplants, we increased the number of stations and depths sampled in order to obtain a wider range of physicochemical variables.

The number of replicate plates at each field station varied between outplants. During the initial outplants, 3 plates, each with 30 lines, were placed at each depth. In later outplants, the number of plates was reduced to 2, and the number of lines was reduced to 14 and, finally, to 7 per plate. These changes in sample size were due to a reduction in the number of times each outplant was sampled. We retained 2 plates on 2 separate racks to insure that some data from each station were obtained in the event of loss of one of the racks. From October to December 1981, on the bottom, we placed 4 plates, each consisting of 14 lines, to increase the chances of detecting sporophytes. The 2 extra bottom plates were discontinued in 1982 because they didn't provide any additional information on recruitment. Uninoculated plates were paired with inoculated plates to detect any natural recruitment of Macrocystis that might have confounded our outplant results.

As indicated, the sampling schedule for the gametophyte outplant substrates varied between outplants. During the initial outplants, substrates were sampled periodically during the course of the outplant experiment. Beginning in 1981, gametophyte outplant experiments were censused for recruited sporophytes only once, after an outplant period of approximately 42 days. This 42-day period was selected because the maximum sporophyte densities, in the outplants that were collected periodically, had occurred at between 35 and 45 days from the date of outplanting (Fig. 6.7). The distributions are peaked because sporophyte densities on the outplant substrates were the result of a dynamic balance between sporophyte recruitment and sporophyte mortality. The 42-day time period is adequate for most

gametophytes to produce sporophytes and have them grow to a size (even under sub-optimal conditions) that could be censused at 12 to 20x under the microscope. Very little sporophyte recruitment could be expected after 42 days, because of the low survival rate of gametophytes in situ. Gametophyte survival experiments (Section 3.0) showed that the average half-life of gametophytes was approximately 16 days. The 42-day outplant interval, therefore, was long enough to maximize the recruitment additions to density, even under suboptimal environmental conditions when gametogenesis could have been but still short enough to minimize the mortality reductions from the final sporophyte density.

During the initial outplants, which were sampled on several occasions, lines were removed from the plates in the field by divers and returned to the laboratory for censusing. In later outplants, entire plates were collected and the lines were removed in the lab. In both cases, substrates were transported back to the lab in black plexiglass containers filled with seawater. These containers were kept cool and protected from direct sunlight. In the lab, lines were stored in the dark at 2°C until sampled. All lines were observed "live", i.e., without fixation or chemical preservation.

The methods used for censusing the substrate lines also evolved over the course of the gametophyte outplant studies. In the first two outplants, 9 Nov 1977 and 23 June 1978, an attempt was made to quantify both gametophyte and sporophyte densities on the outplant substrates. Gametophytes were counted with a dipping cone objective on a compound microscope fitted with an epi-illumination system. The recruited sporophytes were observed with a standard dissecting microscope. Direct censusing of gametophytes, however, was abandoned because gametophytes were often obscured by sediment particles on the lines. In all later experiments, only recruited sporophytes were sampled.

Censusing of sporophytes during the initial gametophyte outplant was done in small quadrats, 1 to 10 mm^2 in size. However, the variance in the estimate of sporophyte density using this quadrat size was unacceptably high because of the patchy distribution of sporophytes on the lines. This variance was reduced in later outplants by increasing the quadrat size. In outplants since August 1978, each line was considered a separate sampling unit with an area of 500 mm^2. This 500 mm^2 area is the entire upper half of the line's surface. Sporophytes on the lines were counted at a magnification of 12 to 20X.

Uniformity of the Inoculation

One of the assumptions of this study was that the zoospores settled evenly on all lines on a plate, and between all plates in a single outplant. This assumption was tested by random sampling of gametophyte densities, on from 6 to 8 lines, on each of 3 plates, in a preliminary inoculation conducted on 7 October 1977. Gametophyte counts were taken from five to seveteen 0.03-mm^2 quadrats on each line. Differences in log-transformed densities among plates, and among lines within a plate, were tested using a nested ANOVA.

Effects of Transporting

The effect of transporting the gametophytes into the field were monitored during the first outplant experiment in November 1977. Two lines were removed from each of two plates in the laboratory prior to outplanting. The plates were then taken into the field and returned on the same day and two more lines were removed from each plate. All lines were then cultured for 13 days in the laboratory and, after culture, sporophytes were counted in each of six 0.03-mm^2 quadrats per line. Log-transformed density in each quadrat were averaged per plate and used as the criterion variable. We tested the hypothesis that densities did not differ significantly among treatments using a Student's t-test.

Effects of Density of Gametophytes

The inoculation procedure was designed to provide uniformity among outplantings. However, initial densities of gametophytes on lines sometimes varied by more than twofold. The possible effect of initial density on sporophyte production was examined during an outplant experiment in June 1981. One plate was inoculated with approximately 7 times the normal density of gametophytes and outplanted to SOKD45 along with 2 plates inoculated with normal densities. Two lines per plate were collected prior to outplanting and the number of gametophytes were counted in ten 0.03-mm^2 quadrats on each line. After 6 weeks, the plates were collected and sporophytes were counted on each of 7 lines per plate. The hypothesis that the sporophyte production rate differed among treatments was tested with a two-way, fixed-effect ANOVA, using time (at the beginning or end of the observation period) and treatment (normal initial density or 7x initial density) as the classes. Log-transformed densities per rope (ln [density + 0.2]) were used as the criterion variable. A significant interaction in this analysis would suggest an effect of initial density on the rate of sporophyte production *in situ*.

Sporophyte Recruitment and Physical Factors

The relationships between sporophyte recruitment and the various physicochemical factors were determined with multiple regression analyses (SAS, 1982). Sporophyte recruitment was expressed as the proportion of female gametophytes producing sporophytes. The log-transformed values of sporophyte recruitment were used as the dependent variable in the regression. This was computed as:

$$\text{Sporophyte recruitment} = \log_e\left[(\bar{D}_{42}/(\bar{I}_0/2)) + (1 \times 10^{-6})\right]$$

where $\bar{D}_{42}$ is the average sporophyte density approximately 42 days after outplanting

and I_0 is the average initial density of gametophytes. The $\bar{D}_{42}$ value was the mean sporophyte density from the collection date closest to 42 days after outplanting; collections made less than 38 days, or more than 46 days after outplanting were omitted. The initial density was divided by 2 so that only female gametophytes were taken into account for this calculation. The assumption of an equal proportion of male and female gametophytes was tested in a laboratory experiment in which the sex of gametophytes, cultured under optimum conditions, was determined after 7 days. The proportions of male and female gametophytes did not differ significantly from one another (Table 6.10).

The independent variables used in the analyses were mean temperature, irradiation, and seston flux rate (accumulation of sediments in plastic tubes). Details of methods of measurement for each of these factors are given in Appendix C. These variables were the overall means of the daily values measured during the time that the outplants were in the field irradiation was put into these analyses as a dummy variable with a value of 1 for mean irradiation levels above 0.4 $E/m^2/d$ and a value of 0 for means below this threshold level. This dummy variable was used because the laboratory studies had shown that the relationship between irradiance and gametophyte fertility was essentially a step function, in which fertility quickly reached a saturation level at irradiation levels above the critical threshold level of 0.4 $E/m^2/d$ (Section 6.2.3). Nitrogen values were not included in this regression model because nitrogen was measured too infrequently. Nitrogen values are correlated with temperature and daily nitrogen values may actually be better estimated by daily temperatures than by less frequently measured nitrogen concentrations (Zimmerman and Kremer, 1984).

We have used total quanta (400 - 700 nm of light) in our analyses even though gametogenesis responds only to blue light. In SOK, total quanta are highly correlated with the blue fraction ($R^2 = 0.91$) and the blue fraction can, therefore, be estimated from the total quanta using the equation (given in Reitzel et al., 1985, p.110):

$$\text{Blue irradiance} = e^{(-1.17 + 1.17 \log \text{total irradiation})}$$

We have also used total daily dose of quanta received by gametophytes, even though the total quanta utilized depends on the instantaneous rate at which quanta are received, as well as the total dose received. Gametophytes have threshold and saturation levels of 1.1 $\mu E/m^2/s$ blue light and 1.6 $\mu E/m^2/s$ blue light, respectively. Figure 6.8 shows the relationship between total daily dose ($E/m^2/d$), as used in our analysis, vs the total dose of blue light received over 42 days given the above threshold and saturation levels. The blue dose threshold (1.1 E/m^2) required for production of sporophytes by 50% of the gametophytes in the laboratory is equivalent to a daily dose of total irradiation (400 - 700 nm) of 0.4 $E/m^2/d$ over 42 days. This value was used as the threshold value in our regression analyses.

In some outplant experiments, a full complement of daily mean measurements of temperature and irradiation was not available because of instrument failure and other causes. We eliminated all outplantings from our analyses that had less than 21 days of temperature data or less than 28 days of irradiation data. Using a finite sampling distribution (Cochran, 1977), we calculated that given 21 days of temperature data, the true 42-day mean temperature could be estimated to within $\pm 0.2^{\circ}C$ for 68% of the time or $\pm 0.3^{\circ}C$ for 95% of the time. For irradiation, 28 days of data yielded estimates of 42-day means within ± 0.15 $E/m^2/d$, 68% of the time, and within ± 0.20 $E/m^2/d$, 95% of the time.

Initial analyses were performed to determine whether a log-transformed or untransformed regression model fit the data best. It was determined that a model with $\log_e$-transformed dependent and independent variables had the highest overall R^2.

A preliminary regression analysis was also run to further verify the threshold value used for setting the irradiation dummy variable (Table 6.11). In this test, the irradiation value was varied from 0.2 $E/m^2/d$ to 0.8 $E/m^2/d$, with each value assumed to be the threshold and used in setting the irradiation dummy variable to either 0 or 1. A threshold value of 0.4 $E/m^2/d$ produced the highest R^2 in the regression model. This threshold is the same as that found in our laboratory studies on irradiance effects (Section 6.2).

The regression analyses were first performed using all physicochemical variables measured on outplants at all of the kelp bed stations in the period before SONGS Units 2 and 3 began operations (November 1977 - December 1982) and from only the SMK45 station in the operational period (January 1983 - July 1986). Data from stations in SOK during the operational period were omitted because of possible confounding effects of SONGS on the "normal" physiological processes. Only those stations located at depths greater than 8 m were used in these regression analyses. Data from shallower sites (7 to 8 m), sampled in conjunction with our studies of the effects of Unit 1, were not included because these stations were not within the usual depth range for kelp at San Onofre, and because little physicochemical data was available for these sites. Separate analyses were performed for each sample depth (0 m and 2 m above the bottom) and for both depths combined. The variables which were not significant at $P < 0.10$ were eliminated and the analysis was rerun using only the significant factors as independent variables. A detailed description

of methods used for measuring physicochemical factors and this selection procedure are given in Appendices C and D.

Nutrient Enrichment Studies

The effects of nutrients on sporophyte recruitment were tested in a field experiment in which the levels of nitrogen and phosphorus were elevated in the vicinity of outplanted gametophytes. Nitrogen levels were elevated above ambient with a commercially available slow-release inorganic fertilizer (Osmocote®, Sierra Chemical Co., Milpitas, CA). This fertilizer is a blend of ammonium nitrate and phosphate salts (26% N and 11% P) which is pelletized and coated with a semipermeable polymer film. These experiments used nylon line substrates attached to plexiglass plates as described previously. The fertilizer was placed in a nylon mesh covered tray and attached to a cut-out plate, thereby forming the bottom of the plate (Fig. 6.9). The unfertilized plates had a solid plexiglass bottoms.

Water samples for nitrogen determinations were collected at weekly intervals during the experiments. Samples were drawn by vacuum pressure through perforated polyethylene tubes which alternated with the nylon line substrates on the outplant plate (Fig. 6.9). The samples were collected in acid-washed glass bottles and were immediately taken back to the boat where they were filtered and frozen on dry ice. Analyses for NO_3^-+ NO_2^- and NH_4^+ were performed by ECOsystems Management, Inc. The fertilizer trays were replaced immediately after the weekly water samples were taken.

The nutrient enrichment experiments were put into the field on 6 August and 10 September 1981. Both experiments were conducted at the SMK 45 station. Each experiment consisted of 4 outplant arrays (Fig. 6.6) with plates at 0, 2, 4, and 6 m

above the bottom. Plates on half of the arrays were fertilized while plates on the other 2 arrays served as unfertilized controls. The unfertilized arrays were located approximately 10 m from the fertilized arrays. Preliminary experiments indicated that this was far enough away from the treatments to avoid any contamination by drift of the fertilizer (Section 10.2.5). Each plate with inoculated lines was paired with an uninoculated plate at each depth on each array. The uninoculated plate served as a control to monitor the natural recruitment of sporophytes. One line was sampled from each plate prior to outplanting and gametophytes were counted in ten 0.03-mm^2 quadrats per line. After approximately 6 weeks in the field, 7 lines were collected from each plate and the number of sporophytes one each line were counted as above. The gametophyte substrates from the two experiments were collected on 16 September and 22 October 1981, respectively.

A three-way, fixed-effect analysis of variance was used to test for differences in nitrogen concentrations among depths above the bottom, treatments (fertilized vs control), and experiments (outplant dates). A three-way interaction term was not included because there were insufficient degrees of freedom for a full rank model. Differences in sporophyte density among fertilized and unfertilized control treatments and among depths were tested with a two-way, fixed-effect ANOVA; separate tests were performed for each experiment. Depths at which most observed densities were zeros (6 m in the first experiment and 0 m in the second) were eliminated from the analyses. Means per plate, of log transformed densities per line (ln [density + 0.017]) were used as the criterion variables. The constant 0.017 was added to the density prior to transformation to avoid taking logs of zero and represents the smallest possible non-zero density.

6.5.3 Results

Preliminary Experiments

Preliminary studies conducted in 1977 indicated that there were no significant differences in gametophyte densities among plates, or among lines within plates, following inoculation (Table 6.12). Also, we found no significant effect of transporting substrates on the eventual number of sporophytes produced (Table 6.13) and there was no significant effect of initial gametophyte density on subsequent sporophyte recruitment (Table 6.14).

The sporophyte densities on the uninoculated control lines were always considerably less than those on the inoculated substrates. The maximum density for the controls was approximately 10% of the maximum for the inoculated substrates, and when recruitment on inoculated lines exceeded $0.01/mm^2$, control densities averaged less than 4% of those on the inoculated substrates (Appendix F). Natural settlement of zoospores on the substrates, therefore, appeared to be an insignificant factor in these experiments.

Seasonal Trends

The proportion of gametophytes producing sporophytes was extremely variable among experiments. The only consistent seasonal trend was low sporophyte recruitment at both 0 and 2 m above bottom during July, August, and early September (Fig. 6.10). A Chi-square analysis of recruitment (Table 6.15) showed significantly fewer than expected instances of high (>0.1%) sporophyte production in outplants put into the field between July and September; both on the bottom ($\chi^2_{1\ df} = 4.18$, $p<0.05$), and at 2 m above the bottom ($\chi^2_{1\ df} = 9.55$, $p<0.005$). There were also significantly more than the expected number of instances of high sporophyte production in outplants made in April to June, on the bottom only ($\chi^2_{1\ df} = 21.0$, $P <$

.005). Recruitment of sporophytes was lower on the bottom than at 2 m above bottom (paired t-test, P = 0.02, df = 126).

Relationship to Physicochemical Factors

The results of the regression analyses of sporophyte recruitment vs physicochemical variables are given in Table 6.16. Mean densities and means for physicochemical data are given in Appendix G. As described previously in the Methods section, a series of regressions was run in which independent variables that were found not significant at $P < 0.10$ were eliminated in successive steps. Only the final regression results (with those independent variables significant at $P < 0.10$) are presented here. The significant independent variables for the substrates at 0 m above the bottom were temperature, and irradiation. At 2 m above the bottom, only temperature was significant. The R^2 values for 0 m and 2 m above bottom regressions were both 0.24. The regression analysis for both depths combined found temperature, seston flux, and irradiation to be significant. The R^2 for this model was 0.29. The coefficients for temperature and seston flux were negative and the coefficient for irradiation was positive.

We further investigated the relationship between sporophyte production and temperature and irradiation by plotting the proportions of gametophytes producing sporophytes against both temperature and irradiation (Fig. 6.11). There were no sporophytes produced at temperatures above 18.1°C, and two-thirds of the outplants in which temperatures were above 17.6° did not produce sporophytes. The highest sporophyte recruitment (>1 % of gametophytes) occurred at temperatures below 15.8°C. The lowest irradiation level at which any sporophytes were produced was 0.1 $E/m^2/d$, at the SMKCAN station (0 m) during the outplant of 13 May 1982. The sporophyte density in this outplant was 0.03 sporophytes/cm^2 or 0.00011% of the outplanted

gametophytes. This was one of only two cases in which sporophytes were produced at an average irradiation of less than 0.25 $E/m^2/d$. The other case was at SOKD45 (0 m), in the outplant of 22 April 1982 in which an average density of 0.07 sporophytes/cm^2 (0.00027% of gametophytes) was observed. Relatively high proportions (>0.1%) of gametophytes produced sporophytes only when temperatures were below 16.3°C and irradiation levels were above 0.4 $E/m^2/d$. At temperatures approaching 16.3°C, higher recruitment levels were observed only at higher irradiation levels, suggesting a possible interactive effect of temperature and irradiation on sporophyte production.

Nutrient Enrichment Studies

The nutrient enrichment field experiments were designed to separate the effects of nutrients and temperature on sporophyte recruitment from outplanted gametophytes. They provided a unique set of conditions in which a high nutrient environment occurred during a time of high temperatures, a situation that would not be expected to occur under natural conditions. The nitrogen concentration in the vicinity of the enriched substrates was significantly greater than ambient during both experiments (Table 6.17 and Fig. 6.12). There was no significant difference in the degree of nitrogen enrichment between experiments, but nitrogen levels increased with depth in both experiments. The reasons for this phenomenon remain unclear, but it may have been due to higher current velocities near the sea surface which caused more rapid advection and diffusion of the fertilizer. Temperature and irradiation levels were relatively high (>16.6°C and >2.3 $E/m^2/d$, respectively) during these experiments and both decreased with depth (Table 6.18).

Mean sporophyte densities were significantly higher on the enriched substrates than on the unfertilized controls in each of the experiments (Table 6.19 and Fig.

6.13). In the first experiment, sporophyte recruitment on enriched substrates decreased with distance from the bottom, in a manner similar to nitrogen concentrations. However, in the second experiment, sporophyte densities were not significantly different at 2, 4, and 6 m (Table 6.19), and were higher there than at 0 m (Fig. 6.13). This may have been because of relatively low levels irradiation recorded during the second experiment and possible interactions between light and nutrient uptake. Although there were unexplained interactions among depths and experiments, it is clear that fertilizing the substrates increased the sporophyte production even at the high temperatures observed during these experiments.

While the addition of nitrogen and phosphorus increased sporophyte production, the levels of recruitment that we observed on fertilized substrates were low compared with the maximum densities observed, at some other times, on unfertilized substrates. Sporophyte densities reached 12/cm^2 on fertilized substrates put out into the field on 10 September 1981 at 6 m above the bottom, compared with densities of >50/cm^2 (>0.1% of gametophytes producing sporophytes) in some fertilized substrates put into the field when at times temperatures were less than 15.8°C.

6.5.4 Discussion

Results of the <u>in situ</u> studies presented here corroborate the basic relationships between sporophyte production and physicochemical factors observed in the laboratory studies. Sporophyte production was a function of irradiance, temperature, and seston flux. The irradiation dose required for 50% fertility of gametophytes in the laboratory (1.1 E/m^2 blue light) is equivalent to a daily total dose of irradiation (400 - 700 nm) of 0.4 E/m^2/d over a 6-wk period in the field. Sporophyte production in the field was generally restricted to irradiation levels

above 0.4 $E/m^2/d$. Occasionally, recruitment occurred at lower irradiation levels but this was infrequent and densities of sporophytes produced were low (<0.1%). The few exceptions to the 0.4 $E/m^2/d$ threshold that we observed may have been due to our inability to accurately measure irradiation at low levels in the field. Anomalously low irradiation values can result from the irradiance sensor being covered up by kelp or sediments. Such occurrences are most likely to occur during stormy periods when ambient levels of irradiation are already low.

Temperature explained the highest proportion of the variability in sporophyte recruitment in our field studies. The highest densities of sporophytes occurred at temperatures below 15.8°C and the upper temperature limit for sporophyte production by more than 0.1% of female gametophytes (a density of approximately 50 sporophytes/cm^2) was 16.3°C. Laboratory studies on Macrocystis pyrifera gametophytes showed that good recruitment occurred at temperatures of up to 19°C in the laboratory. Thus, we expected that high densities of sporophytes would have been produced in the outplant experiments at temperatures up to 19°C. The low fertility values at temperatures at 16.3°C and above suggest that some factor correlated with temperature, such as nutrient availability, was acting to inhibit recruitment at high temperatures. The results of the nutrient enrichment experiment support this conclusion. The enrichment of nitrogen and phosphorus in the vicinity of the gametophyte populations increased sporophyte recruitment, albeit at low densities, at temperatures up to 18.1°C. It appears that the significant effect of temperature in the regression analyses is a reflection of the correlation of temperature with nitrogen and other micronutrients (Jackson, 1977; Zentara and Kamykowski, 1977; Zimmerman and Kremer, 1984; Reitzel and Zabloudil, 1984). Because of this correlation and the high frequency temporal variability observed in nutrient levels, hourly temperature records may provide a better estimation of nitrogen

availability than bi-weekly nitrogen samples (Zimmerman and Kremer, 1984). The case for temperature serving as a proxy for nutrients is further supported by the similarity of the upper temperature boundary for greater than 1% sporophyte production (16.3°C), and the temperature level (~16.5°C) above which nitrogen concentration is uniformly low (Fig. 6.5). Although temperature may not be the factor controlling recruitment, it serves as a relatively good index variable because it is more easily measured than the nutrient components of upwelled water, such as nitrogen and various trace minerals which are essential to gametogenesis (Kuwabara and North, 1980).

Abrasion and burial by sediments are known to be sources of mortality for kelp gametophytes (Devinny and Volse, 1978). Small amounts of sediment can preclude the effective settlement of zoospores and kill gametophytes already attached to the substrate. In the laboratory study of Devinny and Volse (1978) a layer of sediment as small as 8 mg/cm² was sufficient to reduce zoospore survival by about 90%. For gametophytes already attached on the substrate, a sediment layer of 107 mg/cm² (approximately 450μ thick) was enough to reduce survival by 90%. Lack of sedimentation, therefore, appears to be very important for survival of the gametophyte stage. However, it is difficult to extrapolate these quantitative relationships into the field where sediment cover is temporally variable and, therefore, difficult to measure. In our experiments, vertical seston flux explained little of the variability in sporophyte recruitment and was a significant factor in our regression analyses only when 0 and 2 m above bottom depths were combined. The lack of a stronger effect may have been due to a negative correlation between seston flux and irradiation (Dean, 1985). It may also be that vertical flux of seston, as measured by seston tubes, correlates only roughly with the covering of gametophytes by sediment.

The relationship between sporophyte recruitment, temperature, and irradiation developed in our field studies, suggested that there may have been some interaction between irradiation and temperature (or nutrients) such that higher irradiation levels were required for gametogenesis at higher temperatures. However, the laboratory studies showed no such interaction between temperature and irradiation, at least over the range of temperatures observed in the field (12.7° to 18.4°C). There may be some interaction between nutrients and irradiation, as suggested by irradiance-dependent nitrate uptake in the sporophyte stage (Wheeler, 1979; Gerard, 1982b). On the other hand, the suggested interaction may be an artifact due to the lack of low irradiation values observed at higher temperatures (Fig. 6.11).

Although proper temperature and irradiation levels are necessary prerequisites for the recruitment of sporophytes, not all outplantings made during periods of high irradiation and low temperature resulted in high levels of recruitment. This lack of recruitment could have been caused by a number of different factors. One likely cause could have been variability in the temperature-nitrogen relationship. Sometimes, periods of low temperature are associated with low nitrogen because the nitrogen in the upwelled water is quickly used up by phytoplankton (Reitzel and Zabloudil, 1984). Therefore, even though temperatures are in the proper range for recruitment, nutrients may not be present in concentrations sufficient to stimulate gametogenesis. For example, at temperatures between 14.5° and 15.5°C, the probability that the NO_2^-+ NO_3^- levels would exceed 1 µM is only 0.29 (based on data given in Fig. 6.5). Other factors that could have precluded recruitment include various biological processes that were not directly assessed in this study. One factor that could be especially important is grazing. The effect of this biological factor was minimized in our studies by the design of the outplant racks which raised substrates off of the bottom slightly. Furthermore, when it did occur, grazing

appeared to be very patchy both in space and time. Some of the outplant plates had lines which suffered obvious grazing damage, but in none of these cases did all of the lines on plates suffer damage. Therefore, biological effects could have been expected to increase the variance in the relationships that we observed, but not to significantly alter the relationships themselves.

Table 6.1 Irradiation dose required for fertility by 50% of the gametophytes under various assumed saturation levels of irradiance. Dosages are the product of the number of daylight hours, the instantaneous irradiance, the number of days to 50% fertility, and the proportion of instantaneous irradiance that could be utilized given the assumed saturation level.

Photo-period (L:D)	Instantaneous Irradiance (µE/m**2/s)	Days to 50% Fertility	50% fertility dose with no saturation (E/m**2)	50% fertility dose with assumed saturation level (E/m**2) — Assumed saturation level (µE/m**2/s) 10	9	8	7	6	5
12:12	40	14.5	25.1	6.2	5.6	5.0	4.4	3.8	3.1
12:12	20	14.3	12.4	6.2	5.6	4.9	4.3	3.7	3.1
12:12	10	15.6	6.7	6.7	6.1	5.4	4.7	4.0	3.4
12:12	5	17.8	3.8	3.8	3.8	3.8	3.8	3.8	3.8
8:16	60	18.7	32.3	5.3	4.8	4.3	3.8	3.2	2.7
8:16	30	22.4	19.4	6.5	5.8	5.2	4.5	3.9	3.2
8:16	15	24.5	10.6	7.1	6.4	5.6	4.9	4.2	3.5
8:16	8	28.4	6.5	6.6	6.6	6.6	5.7	4.9	4.1
			Mean	6.0	5.6	5.1	4.5	3.9	3.4
			C.V.	17.6	16.3	16.5	13.7	12.3	13.1

Table 6.2 Quantum irradiance levels measured with a spherical sensor (4π), and daily quantum dose for a 10:14 (light:dark) photoperiod.

Irradiance	
4π ($\mu E/m^2/s$)	Dose ($E/m^2/d$)
2.9	0.10
6.7	0.25
16.5	0.60
22.5	0.81
25.6	0.92
29.0	1.04
30.0	1.10

Table 6.3 Summaries of ANOVAs testing differences in the percent fertility of female gametophytes between experiments and temperatures. All the values for percent fertility were arcsine-transformed for the analyses. No interaction term is included because there were insufficient degrees of freedom for a full rank model.

A. Replicates at all temperatures at 0.60 $E/m^2/d$.

Source	DF	Type III SS	F value	PR>F
Temperature	9	1.67	8.28	0.005
Experiment	1	0.02	1.26	0.299

B. Replicates at temperatures between 11 and 15°C at 0.25 $E/m^2/d$ (all replicates between 16 and 20°C were 0)

Source	DF	Type III SS	F value	PR>F
Temperature	4	0.08	0.96	0.517
Experiment	1	0.20	9.60	0.036

C. Replicates at all irradiances at 20°C.

Source	DF	Type III SS	F value	PR>F
Irradiance	6	5.32	16.99	0.002
Experiment	1	0.02	0.30	0.603

Table 6.4 Results of ANOVA testing for differences in the mean percent fertility at various temperatures under a daily irradiation of 0.60 $E/m^2/d$. Letters indicate groups of means (temperatures) that did not differ significantly at $P<0.05$. All percent fertilities were arcsine transformed for the analysis. Data from the two experiments were pooled since previous analyses showed no significant experiment effect.

Analysis of Variance				
Source	DF	SS	F	PR > F
Temperature	9	1.706	8.18	0.0035
Error	8	0.185		
Total	17	1.891		

Temperature (°C)	% Fertility	Duncan Group
11	93	A
12	97	A
13	99	A
14	100	A
15	100	A
16	93	A
17	100	A
18	96	A
19	86	A
20	26	B

Table 6.5 Days to fifty percent fertility under the various irradiance and temperature regimes. Values of greater than 42 days were extrapolated. The cases in which the projected time to 50% fertility exceeded 300 days are designated with a "∞". The daily irradiance dose (DID) is in $E/m^2/d$.

DID ($E/m^2/d$)	Temperature (^oC)									
	11	12	13	14	15	16	17	18	19	20
0.10	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞
0.25	76	73	∞	∞	∞	∞	∞	∞	∞	∞
0.60	34	32	32	31	29	33	30	31	31	72
0.81	26	26	24	26	24	28	28	28	28	31
0.92	24	21	24	24	22	26	27	26	27	28
1.04	28	28	28	28	28	30	20	30	26	28
1.10	26	22	22	25	25	31	19	22	30	32

Table 6.6 Concentrations of the various components of PES nutrient medium (Provasoli, 1968) as added to filtered seawater.

Component	Concentration
Nitrogen (Sodium nitrate)	660.00 µM
Phosphorus (Na-glycerophosphate)	25 µM
Tris	660.00 µM
Vitamins	
Cyanocobalamin (B_{12})	1.6 µg/ℓ
Biotin	0.8 µg/ℓ
Thiamine	20 µg/ℓ
Trace Metals	
Fe-EDTA	7,200.00 µM
Zinc	0.80 µM
Manganese	7.30 µM
Cobalt	0.17 µM
Boron	185.00 µM
Iodine	0.12 µM

Table 6.7 Percent fertility of gametophytes grown in various culture media with added nitrogen (as NO_3). A dash indicates that the treatment combination was not included in the experimental design.

Culture Media	Nitrogen Concentration (μM)		
	0.4	5	10
Control seawater	0	0	0
Seawater + Fe-EDTA and Tris	0	0	0
Seawater + Fe-EDTA, other metals, Tris, vitamins and phosphorus	-	-	100

Table 6.8 Percent fertility of gametophytes grown in various culture media with added nitrogen (as NO_3). An ANOVA was performed on the 4 treatments in which 25 µM of phosphorus were added. All percent fertilities were arcsine-transformed for the analysis.

	Nitrogen Concentration (µM)			
Culture media	0.4	2	5	7
Control Seawater	0	-	-	-
0.4 µM P	-	4.0	0	-
1.6 µM P	-	0	0	-
2.8 µM P	-	-	-	0
25 µM P + metals, vitamins, and Tris	68.0	92.2	96.0	97.6

Analysis of Variance
(Micronutrient treatments only)

Source	df	SS	F	PR > F
Nitrogen level	3	929.2	5.1	0.076
Error	4	242.6		

Table 6.9. Percent fertility of gametophytes in the various culture media with and without vitamins and antibiotics added. The ANOVA was performed on the mean arcsine-transformed percent fertility from each culture container. No interaction term was generated since only one replicate container was used per treatment.

	Control Seawater	
	Vitamins	No Vitamins
Antibiotics	0.0	0.0
No Antibiotics	0.0	0.0

	Metals & Phosphorus	
	Vitamins	No Vitamins
Antibiotics	90.8	86.0
No Antibiotics	19.6	20.4

	Metals & Phosphorus & Nitrogen	
	Vitamins	No Vitamins
Antibiotics	93.2	80.4
No Antibiotics	100.0	100.0

Analysis of Variance

Source	df	SS	F	PR > F
N, P & Metals	2	1.76	15.8	0.0026
Antibiotic	1	0.10	1.82	0.22
Vitamins	1	0.002	0.04	0.84
Error	7	0.39		

Table 6.10 Differences in the proportions of male and female gametophytes in laboratory cultures. The t-test was made on the differences in log-transformed densities of male and female gametophytes observed in 0.03 mm 2 quadrats on slides from laboratory cultures. Untransformed means (#/mm²) are tabulated below.

Sex	Mean	N	t	PR > t
Males	17.6	24	-1.04	0.31
Females	18.1	24		

Table 6.11 Comparison of the regression models which used using different values for the critical threshold of the irradiation dummy variable. The analyses used log-transformed values of temperature and seston flux, as well as dummy variable for irradiation, as independent variables. The R^2 is for the complete model and the P value is the significance level of the irradiation variable alone.

Threshold Irradiation ($E/m^2/d$)	R^2	P
0.2	0.26	0.035
0.3	0.28	0.007
0.4	0.29	0.001
0.5	0.26	0.034
0.6	0.26	0.034
0.7	0.26	0.110
0.8	0.26	0.153

Table 6.12 Summary of a nested analysis of variance testing the uniformity of initial gametophyte density on plates, and on lines within plates, used in the gametophyte outplant experiments. Densities were log-transformed (ln density).

Source	df	SS	F	PR > F
Plate	2	0.172	0.38	0.69
Line (plate)	18	4.600	1.13	0.33

6.13 Student's t-test examining the effect of transporting inoculated substrates on subsequent sporophyte production. The test compared transported and control plates. The variate used in the test was the mean, on each plate, of the log-transformed density in each quadrat (ln [density + 33]).

Outplant Date	Days in Culture	Control (C) or Transported (T)	N	Sporophyte density (#/cm^2)	t	PR > F
28 Nov 77	13	T	2	22.08	0.06	0.96
		C	2	24.83		

Table 6.14 Summary of analysis of variance examining the effects of initial gametophyte density on sporophyte production. Mean initial densities (#/cm²) and the proportion of gametophytes producing sporophytes after 6 weeks are given. The analysis used log-transformed values of mean density per line (ln [density + 0.2]).

Treatment	Initial gametophyte density	% gametophytes producing sporophytes
Normal density	223.5	0.0018
7x normal density	1470.2	0.0070

ANOVA SUMMARY

Source	df	SS	F	PR > F
Treatment	1	5.065	6.15	0.021
Time (initial or final)	1	194.071	235.74	<0.001
Treatment*time	1	2.641	3.21	0.086

Table 6.15 Chi-square analysis of recruitment data from gametophytes outplant experiments at both 0 m and 2 m above the bottom. The three recruitment classes are based on the percentage of female gametophytes producing sporophytes.

	Bottom Recruitment classification		
	0%	> 0 ≤ 0.1%	> 0.1%
JAN-MAR	6	8	1
APR-JUN	7	19	15
JUL-SEP	13	15	1
OCT-DEC	11	25	2

Overall $\chi^2 = 24.2$, $p < 0.005$

	2 m above the bottom Recruitment classification		
	0%	> 0 ≤ 0.1%	> 0.1%
JAN-MAR	0	7	8
APR-JUN	3	26	15
JUL-SEP	6	21	4
OCT-DEC	4	17	16

Overall $\chi^2 = 13.0$, $p < 0.05$

Table 6.16 Results of multiple regression analyses with the sporophyte recruitment (see p. 6-28 of text) as the dependent variable. Log-transformed temperature and seston flux, and a dummy variable for irradiation, were used as independent variables. The analyses included data from all stations during the SONGS pre-operational period, and from SMK45 during the operational period. Only the significant independent variables are presented in this table.

0 m

Overall $R^2 = 0.24$
N = 86

Source	Parameter Estimate	t	PR > T
Intercept	36.74	3.28	0.002
Log Temperature	-18.46	-4.38	<0.001
Irradiation dummy	2.70	3.70	<0.001

2 m

Overall $R^2 = 0.24$
N = 90

Source	Parameter Estimate	t	PR > T
Intercept	39.40	4.27	<0.001
Log Temperature	-17.79	-5.23	<0.001

All Depths

Overall $R^2 = 0.29$
N = 160

Source	Parameter Estimate	t	PR > T
Intercept	37.01	4.87	<0.001
Log temperature	-18.08	-6.39	<0.001
Log seston flux	-0.61	-3.70	<0.001
Irradiation dummy	2.35	3.32	0.001

Table 6.17 Summary of analyses of variance of concentrations of total nitrogen ($NO_2^- + NO_3^- + NH_4^+$) from the nutrient enrichment experiments. Three-way interactions were not included because of insufficient degrees of freedom.

Total Nitrogen				
Variance Source	df	SS	F	PR > F
Experiment	1	46.3	3.1	0.08
Treatment	1	251.2	17.0	<0.01
Depth	3	172.4	3.9	0.01
Exp x Treat	1	10.9	0.7	0.39
Exp x Depth	3	68.1	1.5	0.21
Treat x Depth	3	89.6	2.0	0.11
Error	126	1857.6		

Table 6.18 Summary of physical factors observed during the two nutrient enrichment experiments at SMK45. Dashes indicate that no data were available.

	06 August 1981		10 September 1981	
Depth	Temperature (^{o}C)	Irradiation ($E/m^2/d$)	Temperature (^{o}C)	Irradiation ($E/m^2/d$)
0 m	-	-	16.9	2.3
2 m	16.6	6.1	-	-
4 m	-	8.6	-	-
6 m	18.4	11.1	18.1	-

Table 6.19 Analyses of variance of densities of sporophytes on fertilized and control lines at different depths. Separate analyses were performed for experiments of 06 August 1981 and 10 September 1981. The first analyses included only 0, 2, and 4 m depths (distance above bottom) while the second included 2, 4, and 6 m depths. Densities of sporophytes on each line were log-transformed (ln [density + 0.017]) and then averged over each plate for use as variates in the analyses.

06 August 1981

Variance source	df	SS	F	PR > F
Treatment (with or without fertilizer)	1	9.237	9.89	0.026
Depth	2	18.376	9.84	0.019
Treatment*depth	2	0.86	0.46	0.655

10 September 1981

Variance source	df	SS	F	PR > F
Treatment (with or without fertilizer)	1	26.786	10.23	0.019
Depth	2	9.086	1.74	0.254
Treatment*depth	2	2.267	0.51	0.625

Figure 6.1 Fertility of Macrocystis gametophyte vs time for each of the three photoperiod regimes (light:dark): 24:0, 12:12, and 8:16. The quantum irradiances ($\mu E/m^2/s$) used for the cultures are listed with each photoperiod.

Figure 6.1

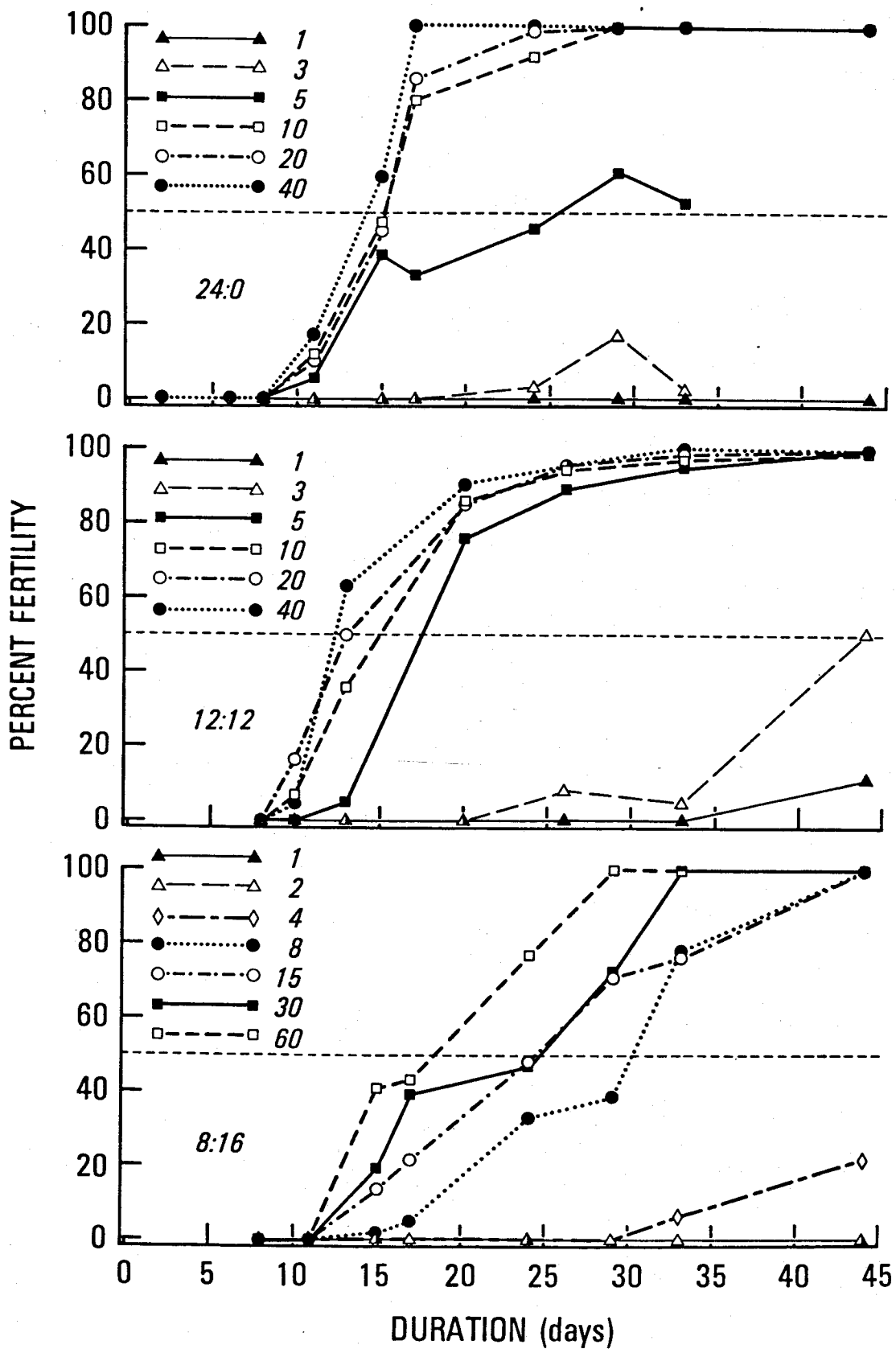

PERCENT FERTILITY
DURATION (days)
24:0
12:12
8:16
1
3
5
10
20
40
2
4
8
15
30
60
0
20
40
60
80
100
0
5
10
15
20
25
30
35
40
45

Figure 6.2 Relationship between the number of days to reach 50% fertility and daily quantum dose for each of 3 photoperiods. Numbers in parentheses represent the instantaneous quantum irradiance for each trial.

Figure 6.2

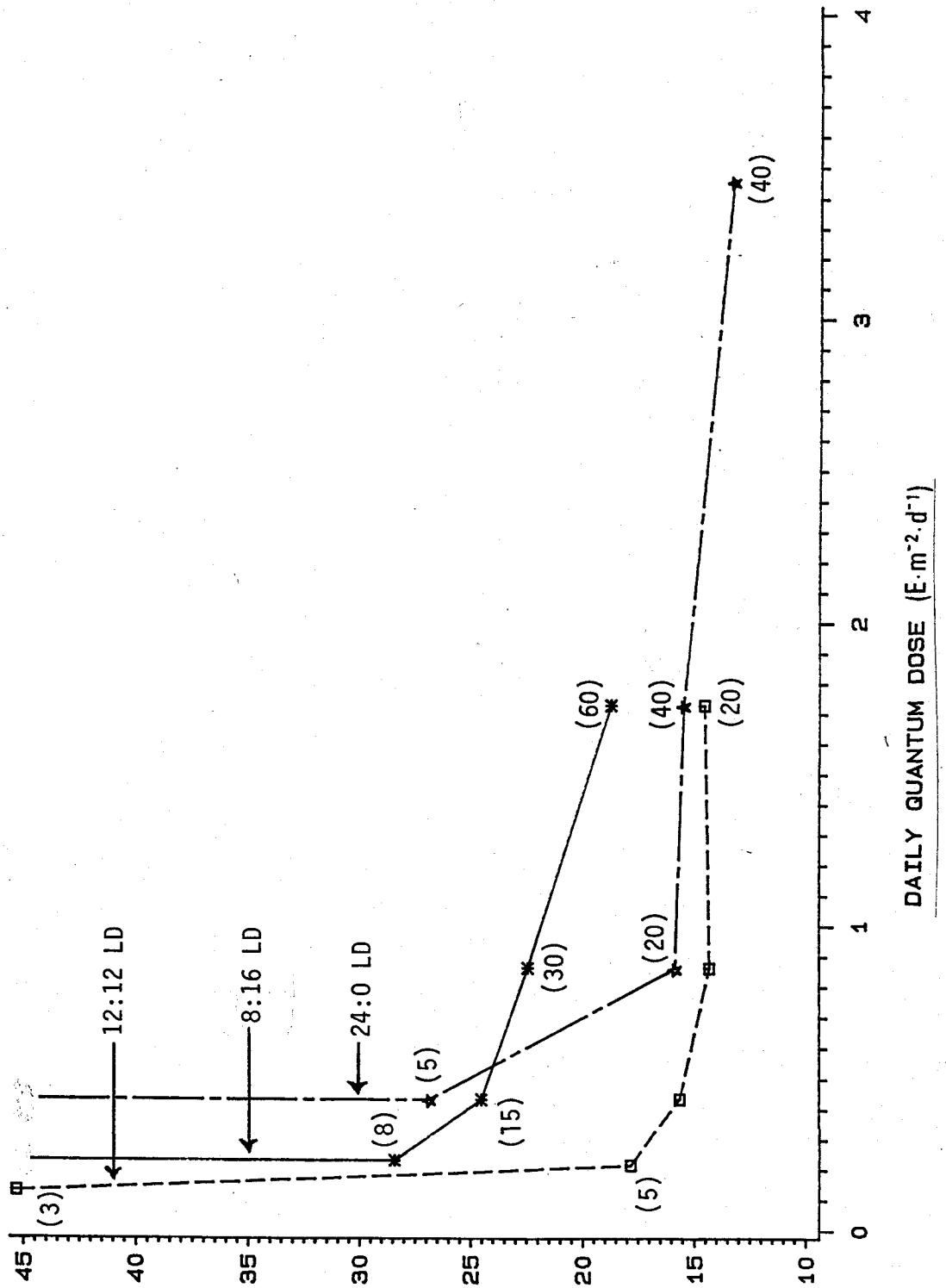

Days to 50 Percent Fertility
45
40
35
30
25
20
15
10
0
1
2
3
4
DAILY QUANTUM DOSE (E·m⁻²·d⁻¹)
12:12 LD
8:16 LD
24:0 LD
(3)
(8)
(5)
(15)
(30)
(60)
(5)
(20)
(40)
(20)
(40)

Figure 6.3 Distribution of blue quantum irradiance on the bottom (15 m depth) in the San Onofre kelp forest during November 1983. The quantum irradiance values plotted ($\mu E/m^2/s$) are the mean irradiances in each 1-hr interval during the day. The vertical bars are ± 1 SD about the mean. The horizontal reference lines indicate threshold (lower dashed line) and saturation levels (upper dashed line) for gametophyte fertility.

Figure 6.3

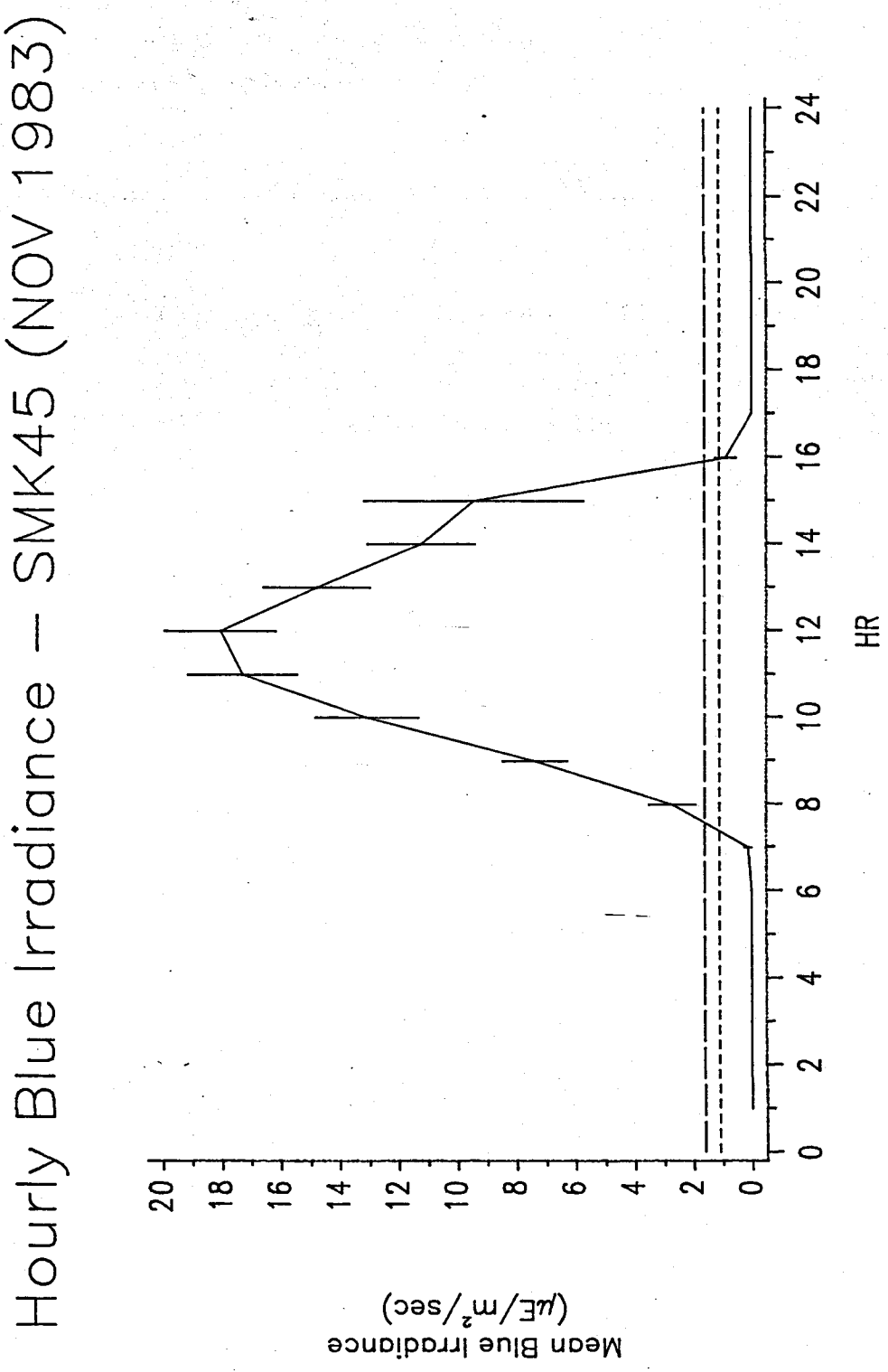

Hourly Blue Irradiance — SMK45 (NOV 1983)
Mean Blue Irradiance
(μE/m²/sec)
20
18
16
14
12
10
8
6
4
2
0
0
2
4
6
8
10
12
14
16
18
20
22
24
HR

Figure 6.4 Mean fertility of gametophytes (percent of female gametophytes producing sporophytes) cultured under various irradiance and temperature regimes during a 42-day culture period. Vertical bars are one standard error of mean fertility between the two experiments (n=2).

Figure 6.4

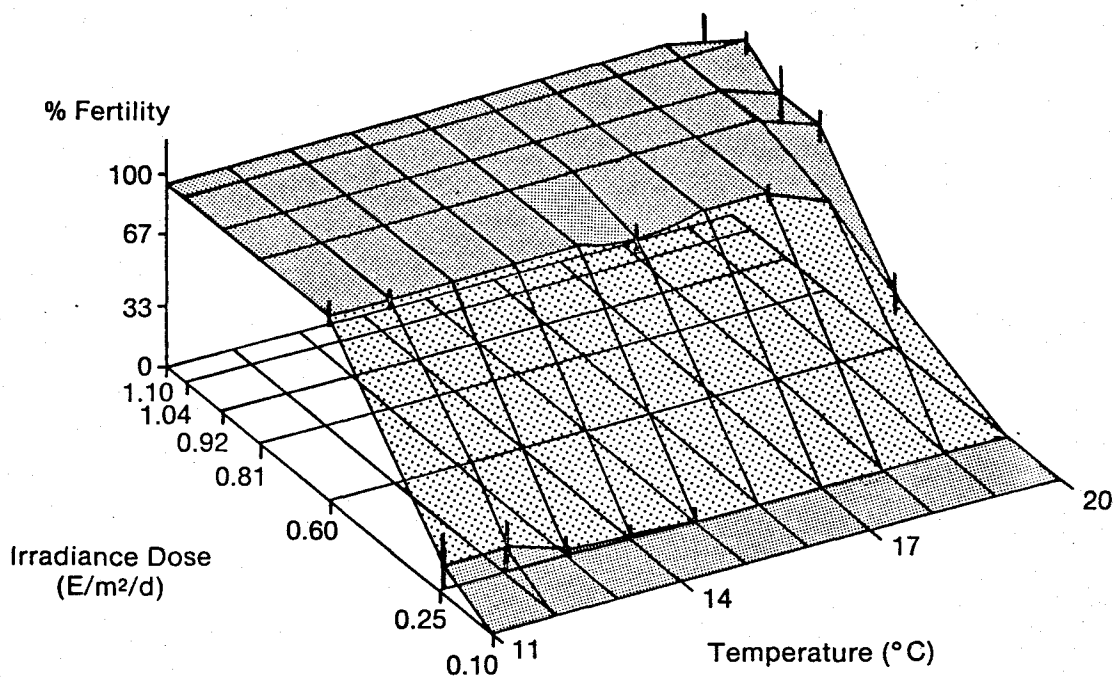

% Fertility
100
67
33
0
1.10
1.04
0.92
0.81
0.60
0.25
0.10
Irradiance Dose
(E/m²/d)
11
14
17
20
Temperature (°C)

Figure 6.5 Relationship between temperature and total nitrogen concentration in the nearshore waters (depth contours from 9 to 20 m) off of San Onofre. Water samples were taken at depths throughout the water column. A "1" indicates one observation; a "2" indicates two observations, etc.

Figure 6.5

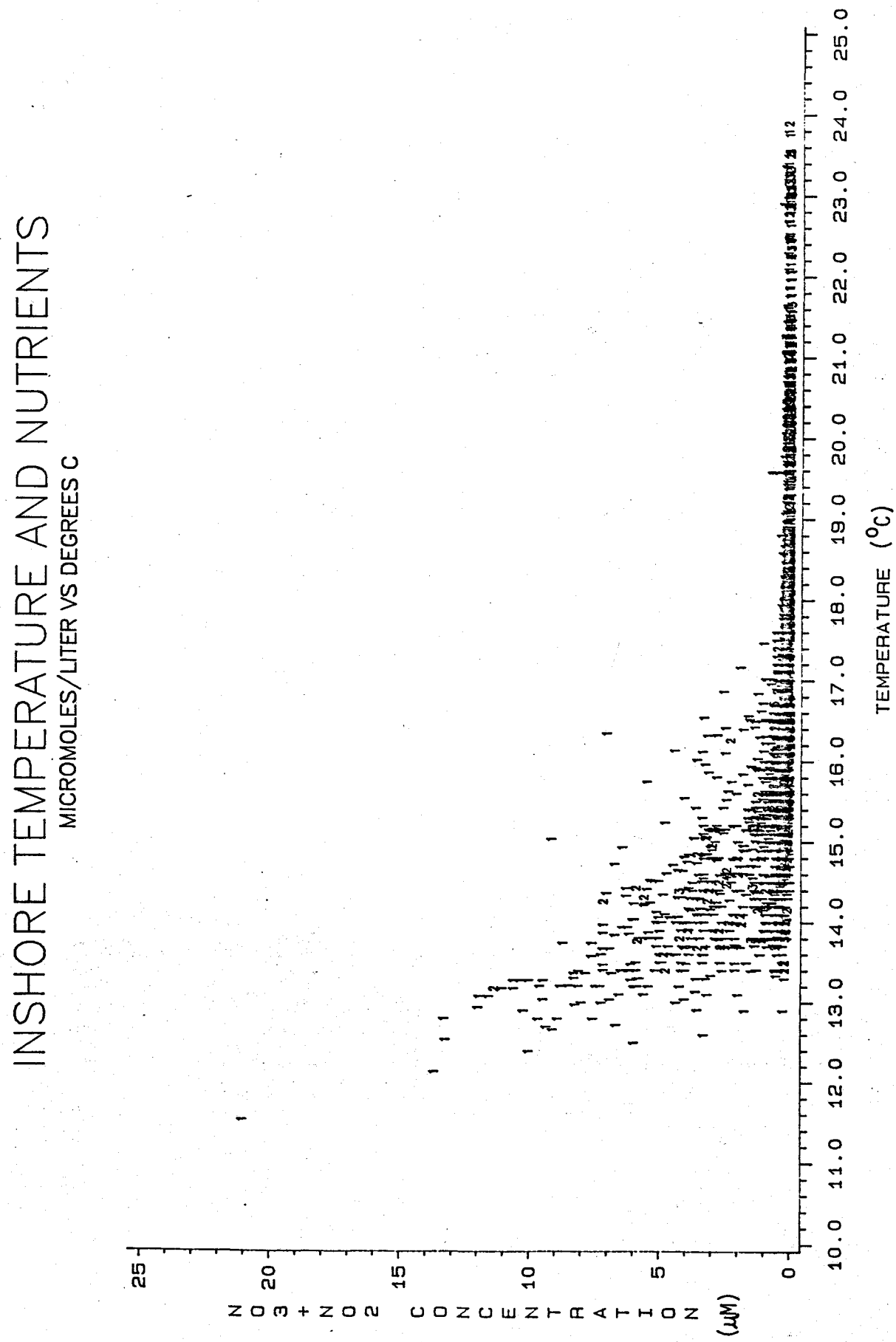

INSHORE TEMPERATURE AND NUTRIENTS
MICROMOLES/LITER VS DEGREES C
NO3+NO2 CONCENTRATION (µM)
25
20
15
10
5
0
10.0
11.0
12.0
13.0
14.0
15.0
16.0
17.0
18.0
19.0
20.0
21.0
22.0
23.0
24.0
25.0
TEMPERATURE (°C)

Figure 6.6 Design of outplant array showing the racks holding outplant substrates on the bottom and at 2 m above the bottom. This design has been used since January 1979. The instrumentation used for measuring physical variables is also shown.

Figure 6.6

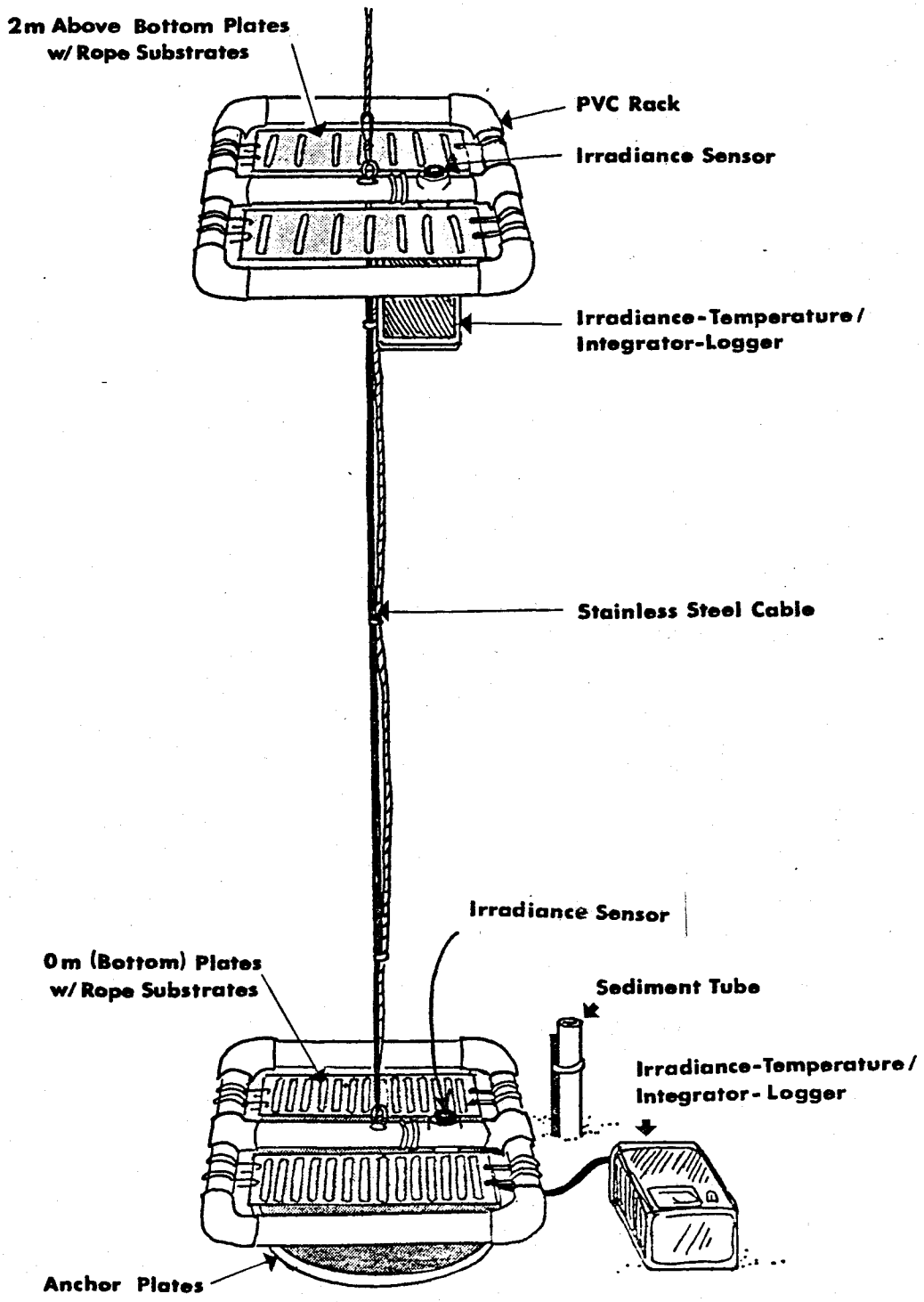

2m Above Bottom Plates
w/ Rope Substrates
PVC Rack
Irradiance Sensor
Irradiance-Temperature/
Integrator-Logger
Stainless Steel Cable
Irradiance Sensor
0m (Bottom) Plates
w/ Rope Substrates
Sediment Tube
Irradiance-Temperature/
Integrator-Logger
Anchor Plates

Figure 6.7 Relationship of mean sporophyte density (#/cm^2) with duration of outplanting on 0 m and 2 m gametophyte outplant substrates. Densities are means from all offshore outplant experiments conducted between November 1977 and January 1982 that were sampled more than one time. Durations are grouped into 5-day intervals for plotting.

Figure 6.7

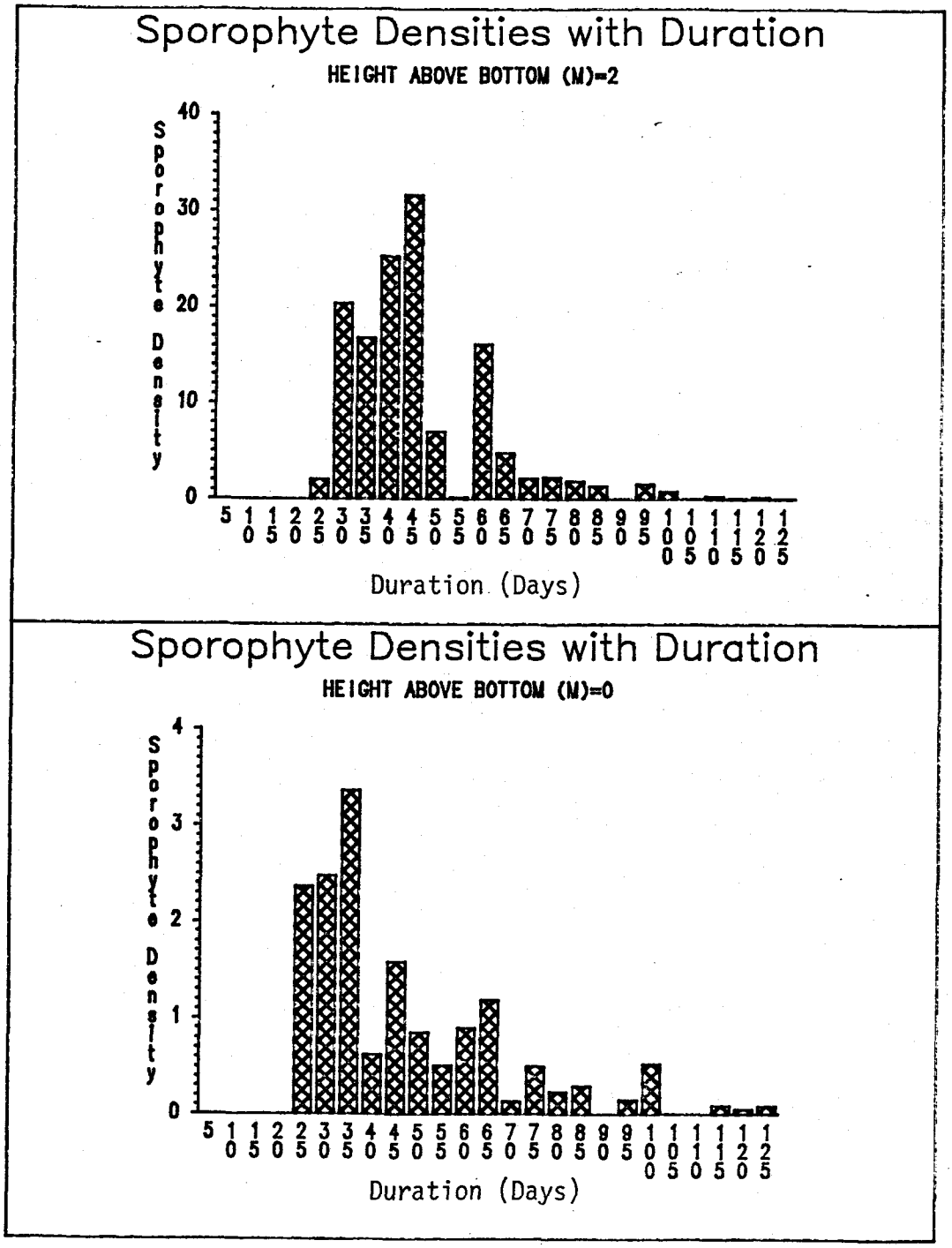

Sporophyte Densities with Duration
HEIGHT ABOVE BOTTOM (M)=2
Sporophyte Density
0
10
20
30
40
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120 125
Duration (Days)
Sporophyte Densities with Duration
HEIGHT ABOVE BOTTOM (M)=0
Sporophyte Density
0
1
2
3
4
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120 125
Duration (Days)

Figure 6.8 Relationship of blue irradiation dose (400 - 500 nm) received over the duration of each experiment (~42 days) to total daily irradiation (400 - 700 nm). Blue dose values were calculated by converting all hourly values of total irradiance to blue light values (using the equation given on 6-30), applying the threshold and saturation levels (1.1 and 1.6 $\mu E/m^2/s$, respectively), summing the hourly values for each day, and multiplying by 42. The plot and the regression analyses used data from 1981 through 1986 that were measured at gametophyte outplant stations.

Figure 6.8

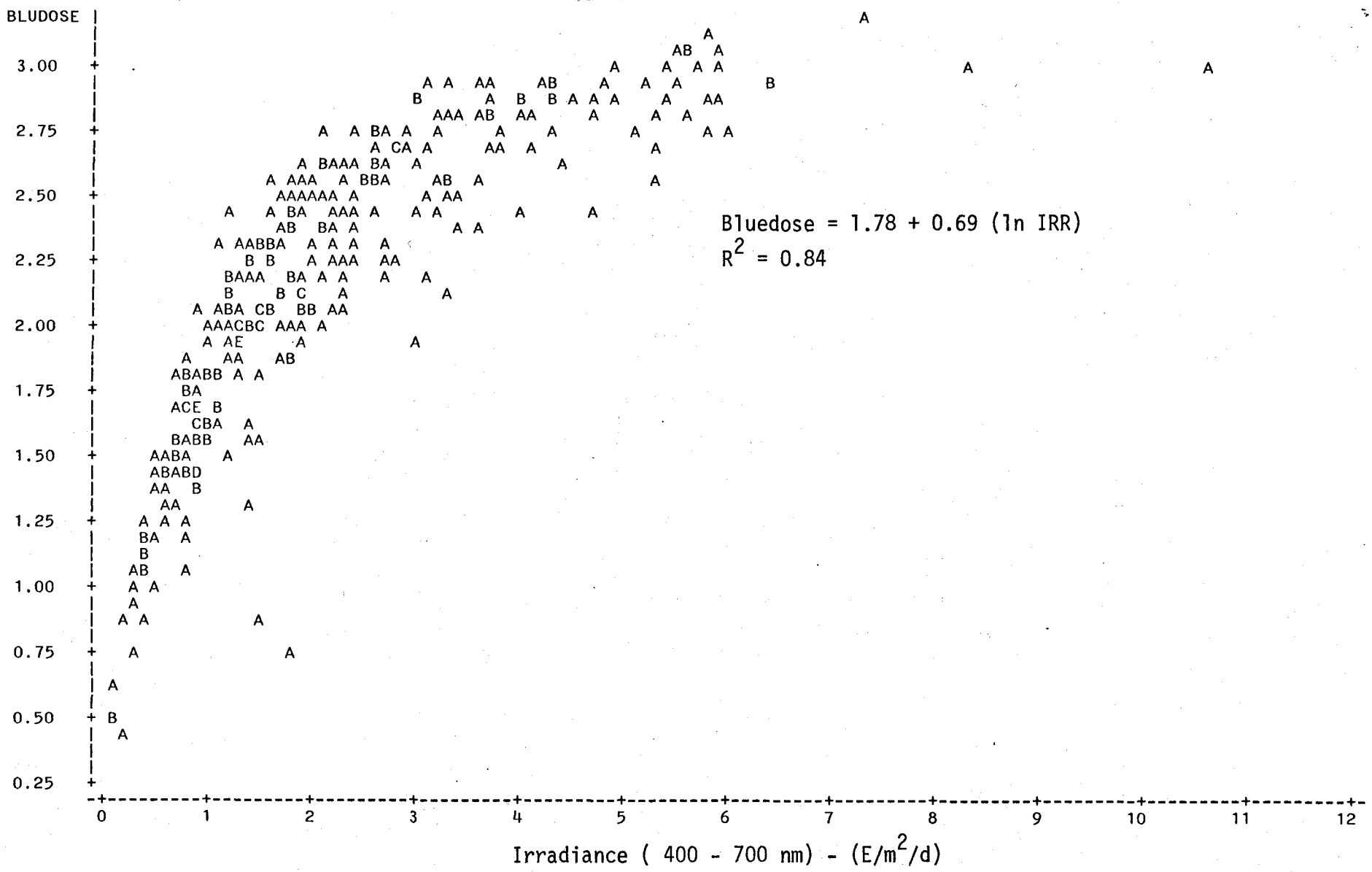

BLUDOSE
3.00
2.75
2.50
2.25
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0
1
2
3
4
5
6
7
8
9
10
11
12
Bluedose = 1.78 + 0.69 (ln IRR)
R^2 = 0.84
Blue Light Dose ($E/m^2/42d$)
Irradiance (400 - 700 nm) - ($E/m^2/d$)

Figure 6.9 Diagram of the fertilized substrate and nitrogen sampling device used in the nutrient enrichment experiments.

Figure 6.9

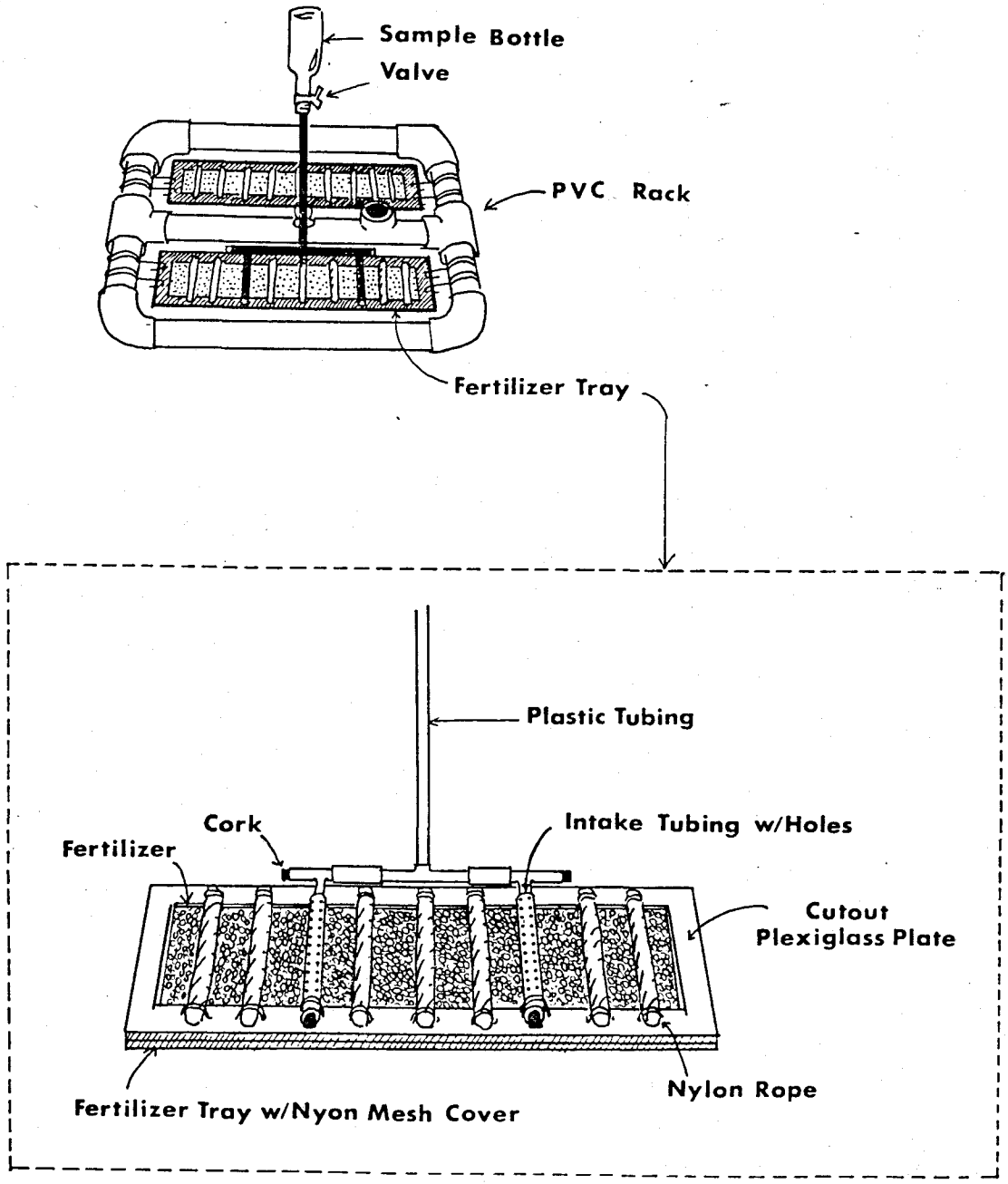

Sample Bottle
Valve
PVC Rack
Fertilizer Tray
Plastic Tubing
Cork
Intake Tubing w/Holes
Fertilizer
Cutout
Plexiglass Plate
Nylon Rope
Fertilizer Tray w/Nyon Mesh Cover

Figure 6.10 Mean percentage of female gametophytes producing sporophytes at each station during each of the outplant experiment in the SONGS Units 2 and 3 pre-operational period (September 1977 to December 1982). The means are plotted at the date on which the gametophytes were outplanted to the field.

Figure 6.10

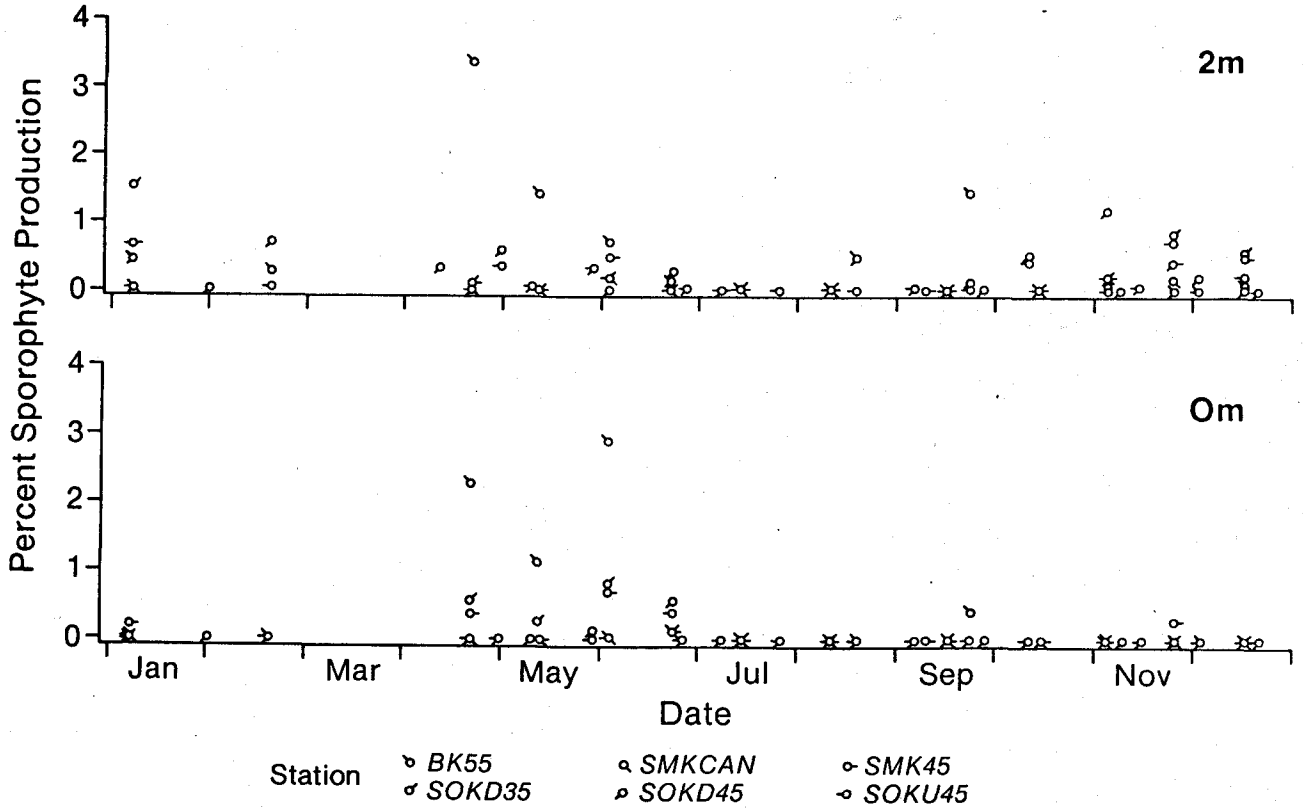

Percent Sporophyte Production
2m
Om
0
1
2
3
4
Jan
Mar
May
Jul
Sep
Nov
Date
Station
BK55
SOKD35
SMKCAN
SOKD45
SMK45
SOKU45

Figure 6.11 Plot of the mean proportion of female gametophytes producing sporophytes vs mean temperature and irradiation values during the outplant period. Means are for both 0 m and 2 m above the bottom, at all kelp forest stations in the SONGS Units 2 and 3 pre-operational period and SMK45 in the operational period. Lines are drawn designating temperature and irradiation boundaries for given levels of sporophyte production.

Figure 6.11

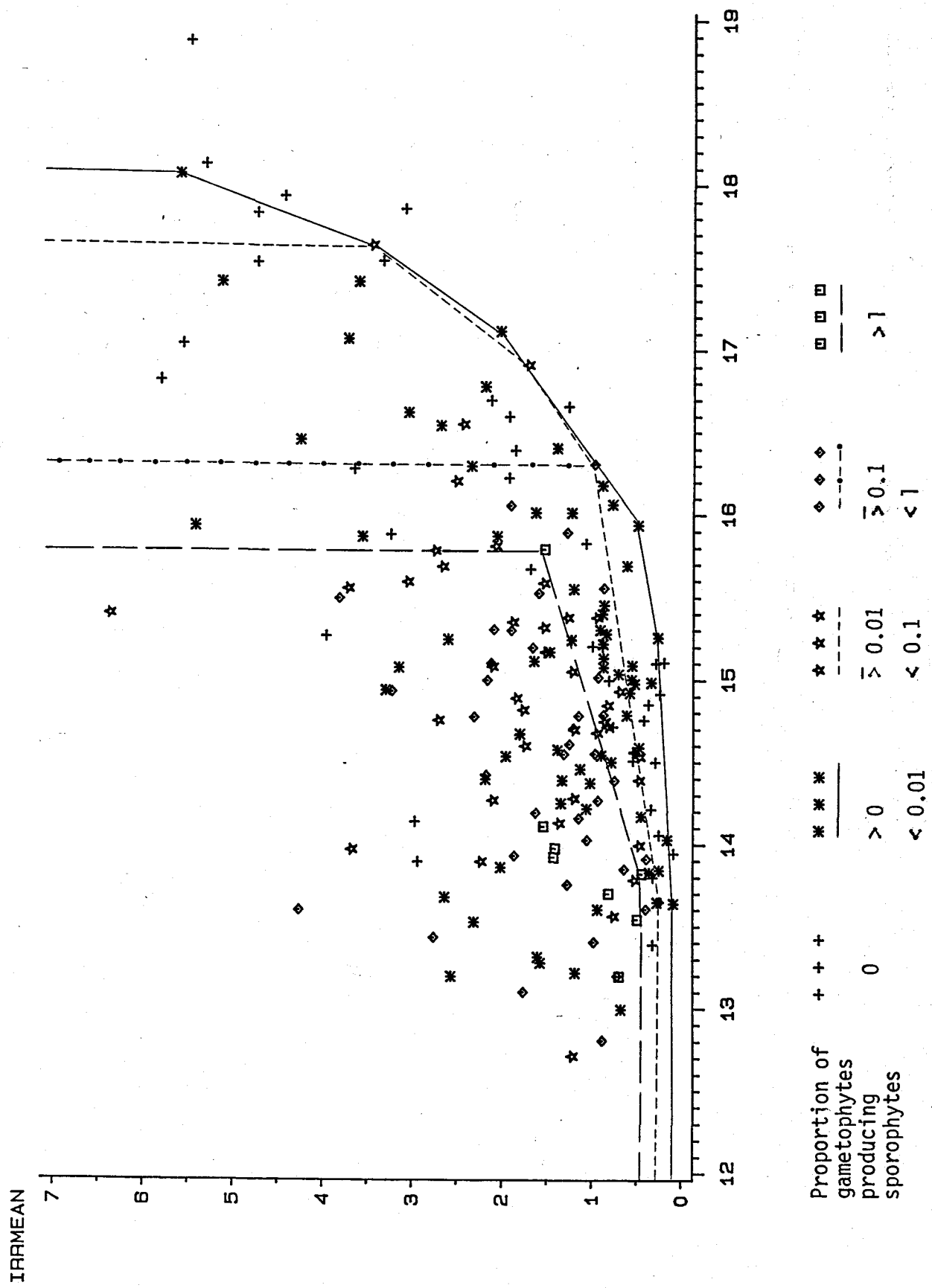

IRRMEAN
7
6
5
4
3
2
1
0
12
13
14
15
16
17
18
19
Mean Irradiation (Einsteins/M**2/Day)
Proportion of gametophytes producing sporophytes
+ + +
0
> 0
< 0.01
≥ 0.01
< 0.1
≥ 0.1
< 1
> 1

Figure 6.12 Average total nitrogen levels on the fertilized (enriched) and unfertilized (control) gametophyte outplant substrates at 0, 2, 4 and 6 m above the bottom in the two nutrient enrichment experiments. Vertical bars are ± 1 standard error of the mean. These experiments were outplanted to SMK45 on 6 August (A) and 10 September (B) 1981.

Figure 6.12

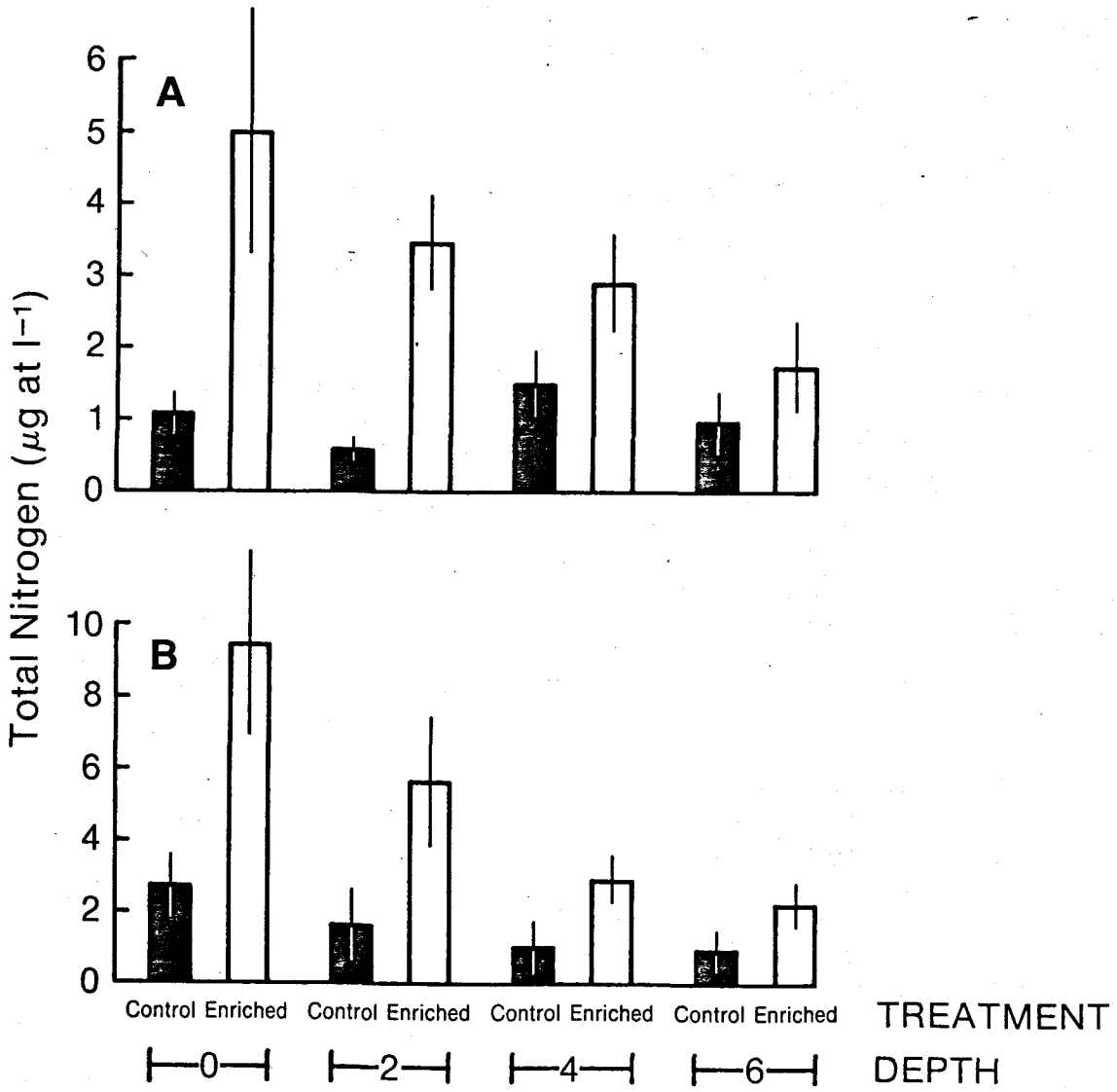
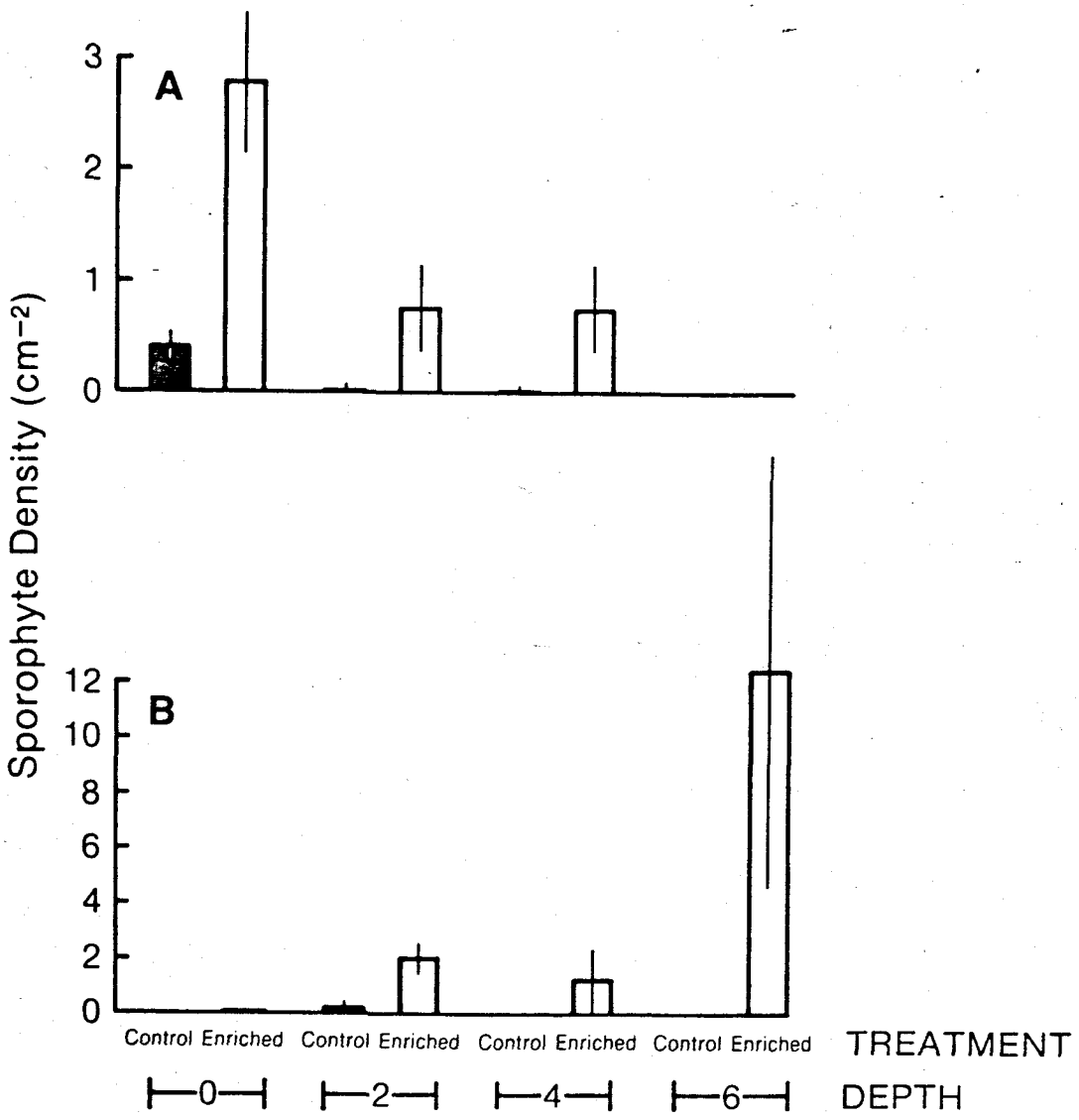

A
B
Total Nitrogen (μg at l−1)
0
1
2
3
4
5
6
0
2
4
6
8
10
Control Enriched Control Enriched Control Enriched Control Enriched
TREATMENT
0
2
4
6
DEPTH

Figure 6.13 Mean sporophyte densities on fertilized (enriched) and unfertilized (control) gametophyte outplant substrates at 0, 2, 4 and 6 m above the bottom in the two nutrient enrichment experiments. Sporophyte densities were determined at approximately 42 days after outplanting. These experiments were outplanted to SMK45 on 6 August (A) and 10 September (B) 1981. Vertical bars are ± 1 standard error of the mean.

Figure 6.13


Sporophyte Density (cm⁻²)
A
B
3
2
1
0
12
10
8
6
4
2
0
Control Enriched Control Enriched Control Enriched Control Enriched
TREATMENT
0
2
4
6
DEPTH

Appendix __. Comparison of densities (#/cm²) of sporophytes on inoculated and control substrates in the gametophyte outplant experiments. Classes are the percentages of gametophytes producing sporophytes on the inoculated slides.

Class	Treatment	N	Maximum	Mean
0 to 0.01%	Inoculated	168	4.19	0.59
	Control	162	0.60	0.04
0.01 to 0.1%	Inoculated	63	36.87	16.23
	Control	57	6.35	0.49
0.1 to 1%	Inoculated	48	415.41	124.89
	Control	47	51.57	3.72
> 1%	Inoculated	4	878.05	655.25
	Control	4	0.19	0.05

7.0 Growth and Survival of Microscopic Sporophytes

7.1 Introduction

The objective of our studies on the microscopic sporophyte stage of Macrocystis pyrifera has been to provide data to determine the potential effects of SONGS. We have done this by: 1) comparing the growth and survival of microscopic sporophytes at SOK, during both the pre-operational and operational periods, relative to a control station in SMK; 2) examining the differences in growth and survival at impact and control sites in relation to the presence of a turbid plume caused by the operation of SONGS; and 3) examining the relationships between growth and survival with physicochemical factors in order to provide a causative link between changes in biological processes and the physicochemical effects of SONGS. These results are presented elsewhere (Dean et al., 1987). Here we present background information on the quantitative relationships between physicochemical factors and the growth and survival of microsporophytes. This information is necessary to establish the mechanisms of potential SONGS impacts. These relationships are based primarily on field studies. We also present the results of laboratory studies that were used as a standard of comparison for relationships generated by the field data.

It is important to quantify these relationships for microscopic sporophytes because both the growth and mortality relationships with physicochemical factors appear to differ from those of older, larger sporophytes. The differences are related to the small size of the embryonic sporophyte and its position on the seafloor, both of which increase the probability of mortality from a host of factors. In addition, the monostromatic thallus of the microscopic sporophyte allows all cells to photosynthesize and absorb nutrients from the surrounding water. In older sporophytes there is a large amount of structural material that, on a biomass basis, reduces the efficiency of growth and photosynthesis.

Most studies on laminarian sporophytes have dealt exclusively with adult plants. There have been very few studies on embryonic sporophytes of laminarian algae (Kain, 1969; 1979) and the only previous study on embryonic sporophytes of Macrocystis (Murray and Fain, 1982) dealt with photosynthesis in laboratory culture. Our studies, therefore, are the first to quantify the relationships between both growth and mortality with various physicochemical factors in this species.

7.2 Methods

7.2.1 Inoculation and Culture Procedures

The microscopic sporophyte studies examined the effects of light on growth in the laboratory and the effects of light, temperature, seston flux, and nitrogen on growth and survival in the field. These studies, like the gametophyte outplant experiments (Section 6), utilized rope substrates inoculated with Macrocystis zoospores. The gametophytes were cultured, under optimal conditions for gametogenesis, for two weeks before being used in laboratory or field studies. This culture regime allowed for almost total recruitment from the gametophyte generation, thereby providing us with experimental sporophyte populations of approximately equal age, length, and density.

The rope substrates and inoculation procedures used in the microsporophyte experiments are identical to those used in the gametophyte outplant experiments (Section 6.5.2) with the exception of the concentration of zoospores used in the inoculation medium. The zoospore concentration used in the sporophyte substrate inoculation, 1×10^4 zoospores/ml, is one-tenth that used in gametophyte outplant experiments. This lower concentration was used to avoid the crowding of sporophytes recruited under optimal conditions in the laboratory. The higher concentration used in the gametophyte outplant experiments was necessary to offset the high rate of mortality of gametophytes under field conditions.

The inoculated substrates were cultured under a continuous irradiance regime (photon flux density = 45 $\mu E/m^2/s$) at 15°C in 25-liter plastic containers (35 x 20 x 45 cm) containing 10 liters of Provasoli's enriched seawater. One acrylic plate with attached ropes was suspended at mid-depth of the culture medium in each container by means of a PVC rack. An airstone was placed on the bottom of each culture vessel to provide circulation of the culture medium. The culture medium was changed once, halfway through the 14-day culture period.

7.2.2 Laboratory Studies on Microscopic Sporophyte Growth

At the end of the 2-week culture period, the substrates with attached sporophytes were transferred into new culture containers under predefined irradiation regimes ranging from 0.2 to 4.6 $E/m^2/d$. One plate containing seven ropes was placed into each container. Light levels were controlled with layers of screening and measured with a LI-COR 185 quantum irradiance meter. Culture medium was changed weekly during the course of the experiments. Length measurements were determined twice, when the sporophytes were transferred into the appropriate light regime and again after 21 days of culture. On each occasion, two ropes were chosen at random from each plate and estimates of sporophyte length were obtained for each rope by measuring the length of the 4 longest sporophytes (selected based on visual inspection) in each of 10 random 6.25 mm^2 quadrats.

Cultures for these experiments were started on 5 April and 22 May 1980, 19 December 1984, and 27 January 1985. All cultures were started from sporophylls obtained from adult sporophytes growing in the San Onofre kelp forest. The experiments conducted in 1980 had a 24-hr photoperiod and the later two experiments had a 12-hr photoperiod.

7.2.3 Field Studies

In the field studies, the substrates with attached sporophytes were outplanted to the same set of stations used in the gametophyte outplant experiments (see Figs. 3.1a & b). Immediately prior to outplanting, one rope from each plate was selected at random and removed for determination of initial densities and lengths. Estimates of initial sporophyte density were made by censusing seven random 6.25 mm^2 quadrats on each rope. Each quadrat was a 2.5 x 2.5 mm area on the top surface of the rope. The average density of recruited sporophytes at the end of the two-week culture period was 499 sporophytes/cm^2. Measurements of sporophyte length were made as described above for the laboratory experiments. The average sporophyte length was 0.52 mm.

Transport and attachment of substrates in the field were the same as described for the gametophyte outplant experiments. Two plates, each containing seven ropes, were placed at each station and depth. In outplants since 1981, substrate plates were placed on the seafloor at 6 field stations. During earlier experiments, substrates were also placed 2m above the seafloor.

Schedules for bringing the substrates in from the field varied between outplants. Since 1981, all substrates were brought back to the laboratory after approximately 21 days (range = 15 to 22 days), while in previous years the collection times varied from one to three weeks after outplanting. For the analysis presented here, we have used only the 21-day data. A complete listing of outplant schedules and stations is found in Appendix H.

Once in the laboratory, rope substrates were removed from the outplant plates and placed in plastic vials marked to indicate the proper station and depth.

Censusing of the ropes was completed within 3 days of collection to prevent any deterioration of the sporophytes while in storage. The ropes were stored in the dark at 2°C to prevent any continued growth of the sporophytes after collection. There was no evidence of grazing by herbivores while the ropes were in storage. Three of the seven ropes from each plate were sampled to determine densities of surviving sporophytes. The ropes with the densest cover of sporophytes (based on visual inspection of ropes after their return to lab) were chosen. We did this to minimize the effects of grazing and abrasion on our density estimates. On many occasions, one or more of the ropes were cleaned of almost all organisms while adjacent ropes on the same plate had luxuriant stands of sporophytes. This suggested that grazing by fish or invertebrates, or scouring by kelp fronds or other debris may have caused high mortality on some ropes. Since we were primarily interested in the effects of the physicochemical environment on sporophyte growth and survival, we attempted to minimize these other unmeasured effects when possible. Sporophytes were counted in seven randomly chosen 2.5 x 2.5 mm quadrats on each rope.

We measured the lengths of 40 sporophytes on two of the first three ropes sampled from each plate. The two ropes were chosen at random and the sporophytes were chosen by selecting the four largest individuals (estimated by visual inspection) in each of 10 random 2.5 x 2.5 mm quadrats. The use of the largest sporophytes on the ropes provided an estimate of maximum sporophyte growth rates.

Measurements of irradiation, temperature, seston flux, and nitrogen concentration were made at each of the stations during the times that the sporophyte outplant experiments were in place. These measurements were made in the same manner as in the gametophyte outplant experiments (Appendix C).

7.2.4 Analyses

Growth rates of microscopic sporophytes reared under different photoperiods in the laboratory were compared using an analysis of covariance (SAS, 1982). The covariate in these analyses was the daily irradiation under which the growth rate was determined. The homogeneity of slopes was tested by the interaction of the main effect (photoperiod) and the covariate ($\log_e$ irradiation). A similar ANCOVA was performed to test for differences in the relationships between growth and irradiation in the field and laboratory studies.

Regression analyses (SAS, 1982) were used to examine relationships between growth rate and irradiance in the laboratory experiments, and between growth rate and irradiance, temperature, seston flux, and nitrogen concentration ($NO_2^- + NO_3^- + NH_4^+$) in the field experiments. Preliminary analyses were performed to examine whether log-transformed or untransformed models provided the best fit to the data. In the laboratory studies, we also examined the growth vs irradiance relationship using the von Bertalanffy function (Ricker, 1975) using the SAS NLIN procedure (Goodnight, 1979).

Sporophyte growth was calculated both as an untransformed and $\log_e$ transformed rate:

$$\text{GRATE} = \frac{L_2 - L_1}{t_2 - t_1} \quad \text{and} \quad \text{LNGRATE} = \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1}$$

where L_1 and L_2 are the mean sporophyte lengths at times t_1 and t_2. The variables GRATE and LNGRATE are those used in all SAS analyses.

Sporophyte mortality was also calculated as an untransformed and $\log_e$ rate:

$$\text{DRATE} = \frac{d_1 - d_2}{t_2 - t_1} \quad \text{and} \quad \text{LNDRATE} = \frac{\log_e d_1 - \log_e(d_2 + 0.1)}{t_2 - t_1}$$

where d_1 and d_2 are the average densities at times t_1 and t_2, respectively.

Regression analyses for both growth and mortality rates in the field experiments were performed using the physicochemical variables measured at all stations in the period before SONGS Units 2 and 3 began operation (August 1979 to September 1983) and from the SMK45 station in the operational period (July 1984 to July 1986). Data from SOK in the operational period were omitted to avoid possible confounding effects of SONGS. Separate analyses were performed for each depth (0 m and 2 m above the seafloor) and for both depths combined. The variables that were not significant at $P < 0.10$ were eliminated and the analysis was rerun using only the significant factors as independent variables. A detailed description of the methods used for this selection procedure is given in Appendix D.

As in the gametophyte outplant experiments, there were cases when a full complement of daily means of temperature and irradiation was not available due to instrument failure and other causes. We eliminated all outplants from our analyses that had less than 11 days of temperature data or less than 10 days of irradiance data. Using a finite sampling distribution (Cochran, 1977), we calculated that given 11 days of temperature data, the true 21-day mean temperature could be estimated to within $\pm 0.2^{\circ}C$, 68% of the time or $\pm 0.4^{\circ}C$, 95% of the time. For irradiation, 10 days of data yielded estimates of 21-day means within ± 0.2 E/m²/d, 68% of the time or ± 0.4 E/m²/d, 95% of the time.

7.3 Results

7.3.1 Laboratory Growth Studies

The first step in defining the relationship between growth and irradiance was to find the function that provided the best fit to the laboratory data. We fit four linear least-squares regressions in which both the transformed (LNGRATE) and untransformed (GRATE) growth rates were regressed with both untransformed and $\log_e$ transformed values of daily irradiation. We also used a nonlinear function similar to the von Bertalanffy growth function. The von Bertalanffy model and the least-squares regression in which both growth and irradiation were $\log_e$ transformed fit the data equally well, as indicated by residual mean squares (Table 7.1). The least-squares regression was chosen as the model for further analyses because of its simplicity over the von Bertalanffy function.

The slopes of the growth vs irradiation relationships differed significantly between the 12 and 24-hr photoperiods (Table 7.2). Growth rates in the 12-hr photoperiod were slightly higher at lower daily irradiation levels, but then appeared to saturate at lower levels than those in the 24-hr photoperiod (Fig. 7.1). These differences may be related to the fact that instantaneous irradiances in the 12-hr photoperiod were twice as high as those in the 24-hr photoperiod at corresponding daily irradiations. At the higher daily irradiation levels, therefore, the sporophytes in the 12-hr photoperiod may have been experiencing saturating irradiance levels and therefore were using irradiance less efficiently. Growth appeared to saturate at about 1 $E/m^2/d$ in the 12-hr photoperiod and 2 $E/m^2/d$ or higher in the 24-hour photoperiod. The corresponding instantaneous irradiance levels were approximately 22 $\mu E/m^2/s$ in both cases, suggesting that the instantaneous saturation levels were the same in both photoperiods.

The compensation irradiation level estimated from the regression equation for the 12-hr photoperiod was 0.04 $E/m^2/d$ and 0.16 $E/m^2/d$ for the 24-hr photoperiod (Fig. 7.1). These values correspond to instantaneous irradiance levels of 0.9 and 1.8 $\mu E/m^2/s$ respectively (Fig. 7.2). Confidence intervals for the instantaneous irradiance levels for compensation overlapped, suggesting that our estimates of compensation did not differ significantly between photoperiods (Table 7.3).

7.3.2 Growth in the Field Outplant Experiments

A preliminary regression analysis was performed to examine whether $\log_e$ transformed or untransformed variables provided the best fit to the data. The $\log_e$ transformed model consistently provided the best fit (Table 7.4), as in the laboratory growth studies. The sporophyte length data used to generate the growth rates are found in Appendix I.

The final regression analyses, which used only the significant independent variables, showed that irradiation and seston flux explained a significant portion of the variance in growth of sporophytes on bottom substrates ($R^2 = 0.56$) and on bottom and 2m substrates combined ($R^2 = 0.52$) (Table 7.5). The initial analysis for the substrates at 2m above the bottom showed no significant independent variables for sporophyte growth. The relatively high R-square value for irradiation in this analysis, however, prompted further analyses which showed a significant positive relationship between irradiation and sporophyte growth when irradiation was the only independent variable used (Table 7.5). Irradiation explained 44% of the variance in growth in this analysis. In all of these analyses, irradiation was positively correlated with sporophyte growth and seston flux was negatively correlated.

The negative relationship between seston flux and growth may have been due to the covering of sporophytes with sediments or the selective removal of larger individuals from the population by sediment scour. Sediment deposits on the outplant plates would also result in the sporophytes being exposed to lower irradiance levels than actually recorded by our sensors. Seston flux was much lower at 2 m above the bottom than on the seafloor (Appendix I) and apparently did not affect growth on 2 m substrates.

The compensating irradiation level for outplanted sporophytes, as determined from the least-squares regression for substrates placed on the seafloor, was 0.3 $E/m^2/d$. Growth appeared to reach maximum levels at a saturating irradiation level of about 1.5 $E/m^2/d$. These values are higher than the corresponding values for compensation (0.08 $E/m^2/d$) and saturation (approximately 1 $E/m^2/d$) determined in the laboratory under a 12-hr photoperiod (Fig. 7.3). Also, the intercepts of the regression lines for field and laboratory populations differed significantly (Table 7.6). The function generated for the laboratory data appeared to form an envelope around the maximum growth rates observed in the field outplants (Fig. 7.3).

7.3.3 Mortality in the Field Outplant Experiments

The sporophyte density data used to generate the mortality rates are given in Appendix J. As in the sporophyte growth studies, a preliminary set of regression analyses was performed with all of the independent variables to show whether untransformed or $\log_e$ transformed variables provided the best fit to the data. Regression models with $\log_e$ transformations of mortality rate and the independent variables provided the greatest R^2 for 0 m data and data from all depths combined. Untransformed variables produced the highest R^2 for data from 2 m above the bottom (Table 7.7).

The only independent variable that showed a significant correlation with sporophyte mortality was seston flux. This variable was significant for substrates located on the bottom and for both depths combined (Table 7.8). However, in the analysis for the substrates located 2m above the bottom, seston flux was significant when all of the independent variables were analyzed together, but it was not significant when regressed separately with mortality rate. In the final analyses, seston flux explained only 6% of the variance in mortality rate for substrates located on the seafloor and and 7% for those at all depths combined. The correlation between seston flux and mortality was positive. The relatively small proportion of the variance explained, however, suggests that other factors, such as grazing by fish and invertebrates or abrasion by drift plants, are also important sources of mortality for microscopic sporophytes.

Sporophyte mortality rates ranged as high as 0.39 day^{-1} and averaged 0.09 day^{-1} on the bottom substrates (Appendix J). The latter rate indicates that the population size would be halved every 8 days. Even with our efforts to minimize the contributions to mortality made by grazing and abrasion, mortality rates were quite high, especially when compared with naturally-occurring adult sporophytes which have half-lives on the order of 1 year (Dean et al., 1987, Sections 9 and 11).

7.4 Discussion

The growth rate of microscopic sporophytes was largely dependent on irradiance levels. This was evident in both our field outplant experiments and our laboratory studies. There were some discrepancies in the results of field and laboratory studies with regard to compensating irradiation levels, saturating irradiation levels, and maximum growth rates. The reasons for the difference in the growth-irradiance relationships between the laboratory-reared sporophytes and field

outplants are not totally clear. The most likely contributing causes are: the optimal concentrations of nutrients available in laboratory culture, the potential for grazing fish and invertebrates in the field, and variability in the instantaneous irradiances in the field. The culture media for the laboratory studies included various micronutrients, such as trace metals and vitamins, as well as the macronutrients, nitrogen (as $NaNO_3$) and phosphorus (as glycerophosphate). These optimal nutrient conditions may have allowed higher growth rates at higher irradiances, while field growth may have been limited by the availability of one or more of these nutrients. In the field outplants, the larger sporophytes may have been subject to higher grazing pressure than the smaller ones. This selective grazing would have reduced the mean growth rate for the field populations.

The distribution of instantaneous irradiances in the field would tend to create lower growth rates for field sporophytes when compared to the growth rates of sporophytes receiving equal irradiation levels in the laboratory. Instantaneous irradiances vary as a sine function in the field (Section 6.0) compared to a square-wave function in the laboratory. As a result, field populations could be expected to receive some irradiances below the compensation level and some from above the saturation level. Even though irradiances at both of these levels would contribute to the integrated daily irradiation, they would not have had a proportional contribution to sporophyte growth.

It is clear, however, that the compensating irradiation level was extremely low (approximately 0.3 $E/m^2/d$) for field populations. Irradiation levels on the seafloor at San Onofre were seldom below 0.3 $E/m^2/d$ (ECOsystems' Final Report, Vol. VI, Chapter 3). Apparently, low irradiance seldom completely inhibited growth. In contrast, the saturating irradiation level of approximately 1.5 $E/m^2/d$ was well

within the range of irradiation levels at San Onofre. Of the 61 sporophyte outplants conducted on the bottom in the SONGS area kelp forests prior to SONGS operation, about 75% had irradiation levels below the saturation level. Thus, the growth rate of microscopic sporophytes was limited by light on most occasions.

The compensation irradiance levels for growth estimated from our laboratory experiments (0.9 $\mu E/m^2/s$ for the 12-hr photoperiod and 1.8 $\mu E/m^2/s$ for the 24-hr photoperiod) are approximately the same as the compensation irradiance for photosynthesis of embryonic sporophytes shown by Murray and Fain (1982) and Deysher (1984). Murray and Fain found a compensating irradiance for photosynthesis at 2.8 $\mu E/m^2/s$ (equivalent to 0.1 $E/m^2/d$ for a 12-hr photoperiod) and showed that this was unchanged at temperatures between 10 and 20°C. Deysher found a compensating irradiance level of 2.5 $\mu E/m^2/s$ (=0.1 $E/m^2/d$) that was constant for sporophytes between 6 and 25 mm in length.

The saturating irradiance level for photosynthesis, however, is higher than that for growth. In our laboratory studies, growth appeared to saturate at an irradiance of approximately 22 $\mu E/m^2/s$. The saturation level for photosynthesis found by both Murray and Fain (1982) and Deysher (1984) was 75 $\mu E/m^2/s$ (3.2 $E/m^2/d$ for a 12-hr photoperiod). It therefore appears that some process other than photosynthesis is limiting growth at high irradiance levels.

Growth of the microscopic sporophytes was generally high. Maximum doubling times observed in the field were less than four days, and even plants growing at irradiations of about 0.4 $E/m^2/d$ generally doubled in length in less than 10 days. A quantitative comparison of growth between microscopic sporophytes and juvenile sporophytes is difficult, and would need to be done on the basis of biomass. It is

clear, however, that at similar irradiance levels, microscopic sporophytes elongate more rapidly than juvenile sporophytes, which have maximum doubling times on the order of 3 weeks. The lower compensating irradiance levels and greater elongation rates of microscopic sporophytes probably result from the thin thallus of these small plants. Sporophytes less than 1.5 mm in length are only one or two cells thick. Therefore, the maximum photosynthetic capability of every cell can be reached at low irradiance levels because there is no self-shading among cells. Also, microscopic sporophytes may elongate faster than juveniles because they are growing in two dimensions instead of three.

The outplant experiments in 1984 were conducted during some of the highest water temperatures of the 1983-84 El Nino (Appendix J). Sporophyte growth rates were, however, generally higher than average at all stations and mean growth rates for these outplants had a good fit to the preoperational growth vs irradiation relationship (Fig. 7.3). These outplants reinforce the importance of light in the control of microscopic sporophyte growth even at temperatures up to 20°C and at below normal nutrient concentrations. This is in contrast to the growth of larger juvenile sporophytes that has been shown to be correlated with nitrogen levels in laboratory experiments (Wheeler and North, 1980), and which appeared to be nutrient limited during the El Nino period (Dean and Jacobsen, 1986). It appears that small sporophytes were able to sustain growth during the El Nino even though water temperatures were high and nutrients were low. This may have been due to their close proximity to the substrate where they could have utilized ammonia generated by various bacterial processes.

The mortality rate of microscopic sporophytes was determined to a significant extent by seston flux. While temperature and other physical factors may become

lethal at extreme values, they had no significant effect on mortality within the ranges observed in our outplant experiments. Laboratory experiments carried out by Schroeter et al. (1982) indicated that benthic invertebrates, especially the seastar Patiria miniata and the hermit crab Pagurus sp., can graze heavily on microscopic sporophytes. It seems likely that grazing pressures by these benthic invertebrates, as well as by fish, may further contribute to the high mortality rate of small sporophytes in the field. In addition, abrasion by drifting kelp and other algae appears to be a source of mortality. We have often observed drift algae entangled with and rubbing against our artificial substrates.

Table 7.1 Comparisons of various regression models and a von Bertalanffy growth function for the relationship between microscopic sporophyte growth and irradiation in laboratory studies.

LEAST-SQUARES REGRESSIONS

Dependent variable	Independent variable	R^2	Mean square error
GRATE	Irradiation	.30	0.073
LNGRATE	Irradiation	.75	0.001
LNGRATE	Log_e Irradiation	.77	0.001
GRATE	Log_e Irradiation	.41	0.062

VON BERTALANFFY FUNCTION

GRATE	Irradiation	-	0.001

Table 7.2 Results of ANCOVA testing for differences in sporophyte growth rates (LNGRATE) in 12- and 24-hr photoperiods in the laboratory studies. The covariate was $\log_e$ irradiation.

Analysis of Covariance				
Source	d.f.	SS	F	PR > F
Log Irradiation	1	0.064	83.94	0.0001
Photoperiod	1	0.002	2.93	0.1039
Homogeneity of Slopes	1	0.003	4.58	0.0463
Error	18	0.014		
Total	21	0.083		

Table 7.3 Summary of the 95% confidence limits on the compensation irradiance levels in the 12 and 24 hour photoperiods in the laboratory experiments. These confidence limits were calculated from the regression between $\log_e$ growth (LNGRATE) and $\log_e$ Irradiance.

Photoperiod (hr)	Compensation irradiance ($\mu/E/m^2/s$)	Lower 95% boundary ($\mu E/m^2/s$)	Upper 95% boundary ($\mu E/m^2/s$)
12	0.9	0.3	1.5
24	1.8	0.6	3.3

Table 7.4 Summaries of initial regression models for sporophyte growth in the field outplant experiments. These models used untransformed growth (GRATE) and $\log_e$ transformed growth (LNGRATE) as the dependent variables and untransformed and $\log_e$ values for the various independent variables. Temp = temperature, Irr = irradiation, Ses = seston flux, and Nut = total nitrogen ($NO_3^- + NO_2^- + NH_4^+$).

0 meters above bottom

Dependent variable	Independent variables	R^2	Significant variables	d.f.
GRATE	Temp, Irr, Ses, Nut	.47	Irr, Ses	32
LNGRATE	Temp, Irr, Ses, Nut	.59	Irr, Ses	32
LNGRATE	Ln(Temp, Irr, Ses, Nut)	.63	LnIrr, LnSes	32
GRATE	Ln(Temp, Irr, Ses, Nut)	.52	LnIrr, LnSes	32

2 meters above bottom

Dependent variable	Independent variables	R^2	Significant variables	d.f.
GRATE	Temp, Irr, Ses	.27	none	13
LNGRATE	Temp, Irr, Ses	.30	none	13
LNGRATE	Ln(Temp, Irr, Ses)	.37	none	13
GRATE	Ln(Temp, Irr, Ses)	.34	LnIrr	13

Both depths combined

Dependent variable	Independent variables	R^2	Significant variables	d.f.
GRATE	Temp, Irr, Ses, Nut	.47	Irr, Ses	32
LNGRATE	Temp, Irr, Ses, Nut	.59	Irr, Ses	32
LNGRATE	Ln(Temp, Irr, Ses, Nut)	.63	LnIrr, LnSes	32
GRATE	Ln(Temp, Irr, Ses, Nut)	.52	LnIrr, LnSes	32

Table 7.5 Results of multiple regression analyses with $\log_e$ sporophyte growth as the dependent variable. The analyses included data from all stations during the SONGS pre-operational period, and from SMK45 during the operational period. Only the significant independent variables are presented in this table. All of the log transformations are to the base e.

0 m

Overall $R^2 = 0.56$
N = 63

Source	Parameter estimate	t	PR > T
Intercept	0.097	8.16	0.0001
Log Irradiation	0.028	3.54	0.0008
Log Seston flux	-0.030	-3.50	0.0009

2 m

Overall $R^2 = 0.44$
N = 18

Source	Parameter estimate	t	PR > T
Intercept	0.066	8.50	0.0001
Log Irradiation	0.056	3.69	0.0018

All Depths

Overall $R^2 = 0.52$
N = 63

Source	Parameter estimate	t	PR > T
Intercept	0.097	8.16	0.0001
Log Irradiation	0.028	3.54	0.0008
Log Seston flux	-0.030	-3.50	0.0009

Table 7.6 Results of ANCOVA testing for differences in sporophyte growth rates (LNGRATE) between the laboratory experiments and field outplants. The covariate was $\log_e$ irradiation.

Analysis of Covariance				
Source	d.f.	SS	F	PR > F
Log Irradiation	1	0.120	83.54	0.0001
Experiment Type	1	0.048	33.84	0.0001
Homogeneity of Slopes	1	0.001	0.70	0.4054
Error	89	0.127		
Total	92	0.297		

Table 7.7 Summaries of initial regression models for sporophyte mortality in the field outplant experiments. These models used untransformed mortality (DRATE) and $\log_e$ transformed mortality (LNDRATE) as the dependent variables and untransformed and $\log_e$ values for the various independent variables. Temp = temperature, Irr = irradiation, Ses = seston flux, and Nut = total nitrogen ($NO_3^- + NO_2^- + NH_4^+$).

0 meters above bottom

Dependent variable	Independent variables	R^2	Significant variables	d.f.
DRATE	Temp, Irr, Ses, Nut	.13	Ses	35
LNDRATE	Temp, Irr, Ses, Nut	.19	Ses, Nut	35
LNDRATE	Ln(Temp, Irr, Ses, Nut)	.28	Ln(Temp, Ses, Nut)	35
DRATE	Ln(Temp, Irr, Ses, Nut)	.13	LnSes	35

2 meters above bottom

Dependent variable	Independent variables	R^2	Significant variables	d.f.
DRATE	Temp, Irr, Ses	.54	Ses	13
LNDRATE	Temp, Irr, Ses	.29	none	13
LNDRATE	Ln(Temp, Irr, Ses)	.33	LnIrr	13
DRATE	Ln(Temp, Irr, Ses)	.47	LnSes	13

Both Depths Combined

Dependent variable	Independent variables	R^2	Significant variables	d.f.
DRATE	Temp, Irr, Ses, Nut	.13	Ses	35
LNDRATE	Temp, Irr, Ses, Nut	.19	Ses, Nut	35
LNDRATE	Ln(Temp, Irr, Ses, Nut)	.28	Ln(Temp, Ses, Nut)	35
DRATE	Ln(Temp, Irr, Ses, Nut)	.13	LnSes	35

Table 7.8 Results of multiple regression analyses with sporophyte mortality as the dependent variable. The analyses included data from all stations during the SONGS pre-operational period, and from SMK45 during the operational period. Only the significant independent variables are presented in this table. All of the log transformations are to the base e.

0 m

Dependent variable = LNDRATE
Overall R^2 = 0.06
N = 70

Source	Parameter estimate	t	PR > T
Intercept	0.056	2.74	0.0001
Log Seston flux	0.028	2.14	0.0359

2 m

Dependent Variable = DRATE
Overall R^2 = 0.09
N = 18

Source	Parameter estimate	t	PR > T
Intercept	11.01	2.50	0.023
Seston flux	9.25	1.32	0.203

All Depths

Dependent Variable = LNDRATE
Overall R^2 = 0.07
N = 89

Source	Parameter estimate	t	PR > T
Intercept	0.070	6.37	0.0001
Log Seston flux	0.020	2.54	0.0129

Figure 7.1 Growth rate of microscopic sporophytes (LNGRATE) plotted against daily irradiation levels in the 12-hr and 24-hr photoperiods.

Figure 7.1

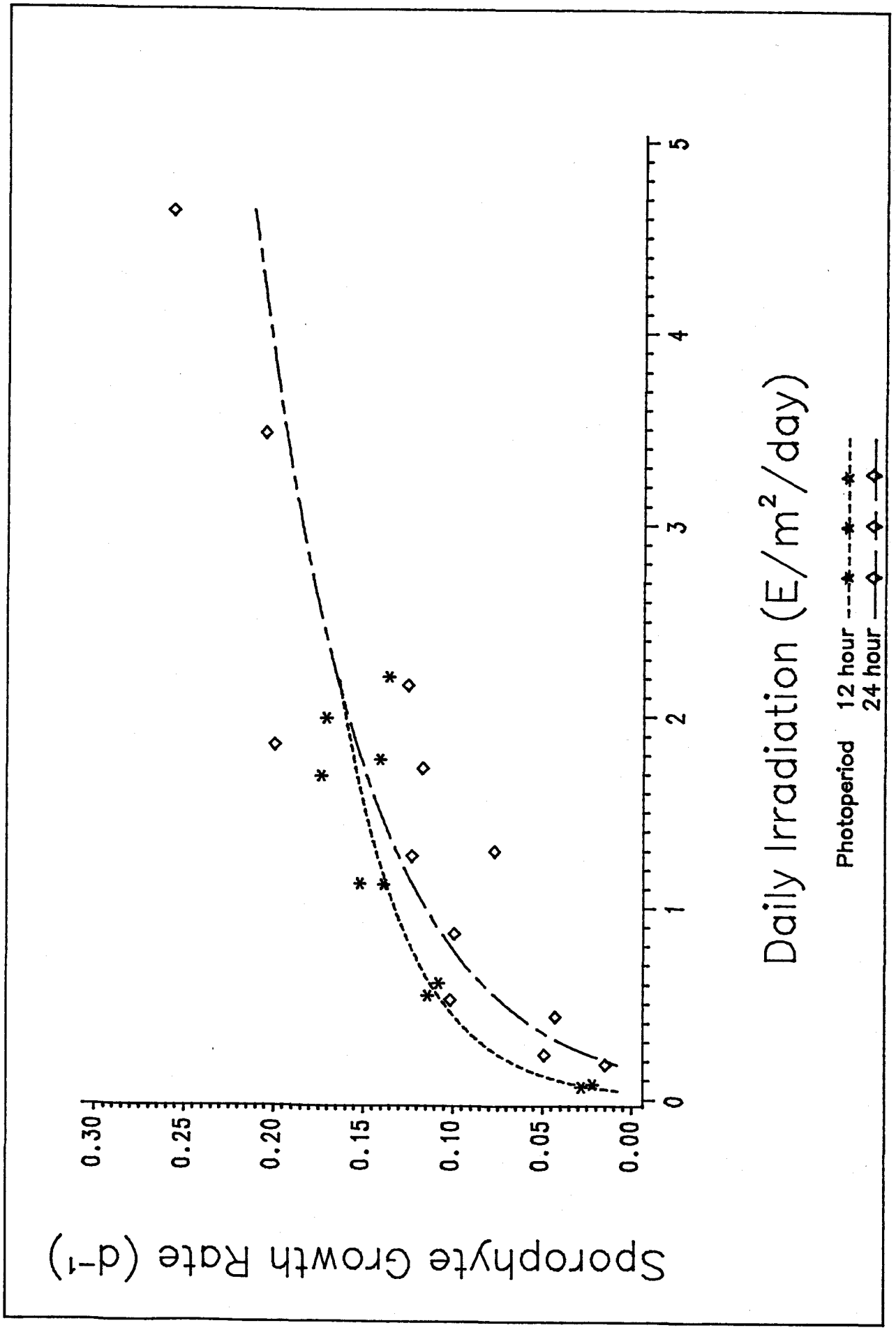

Sporophyte Growth Rate (d-1)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
1
2
3
4
5
Daily Irradiation (E/m2/day)
Photoperiod
12 hour
24 hour

Figure 7.2 Growth rate of microscopic sporophytes (LNGRATE) plotted against instantaneous irradiance in the 12-hr and 24-hr photoperiods.

Figure 7.2

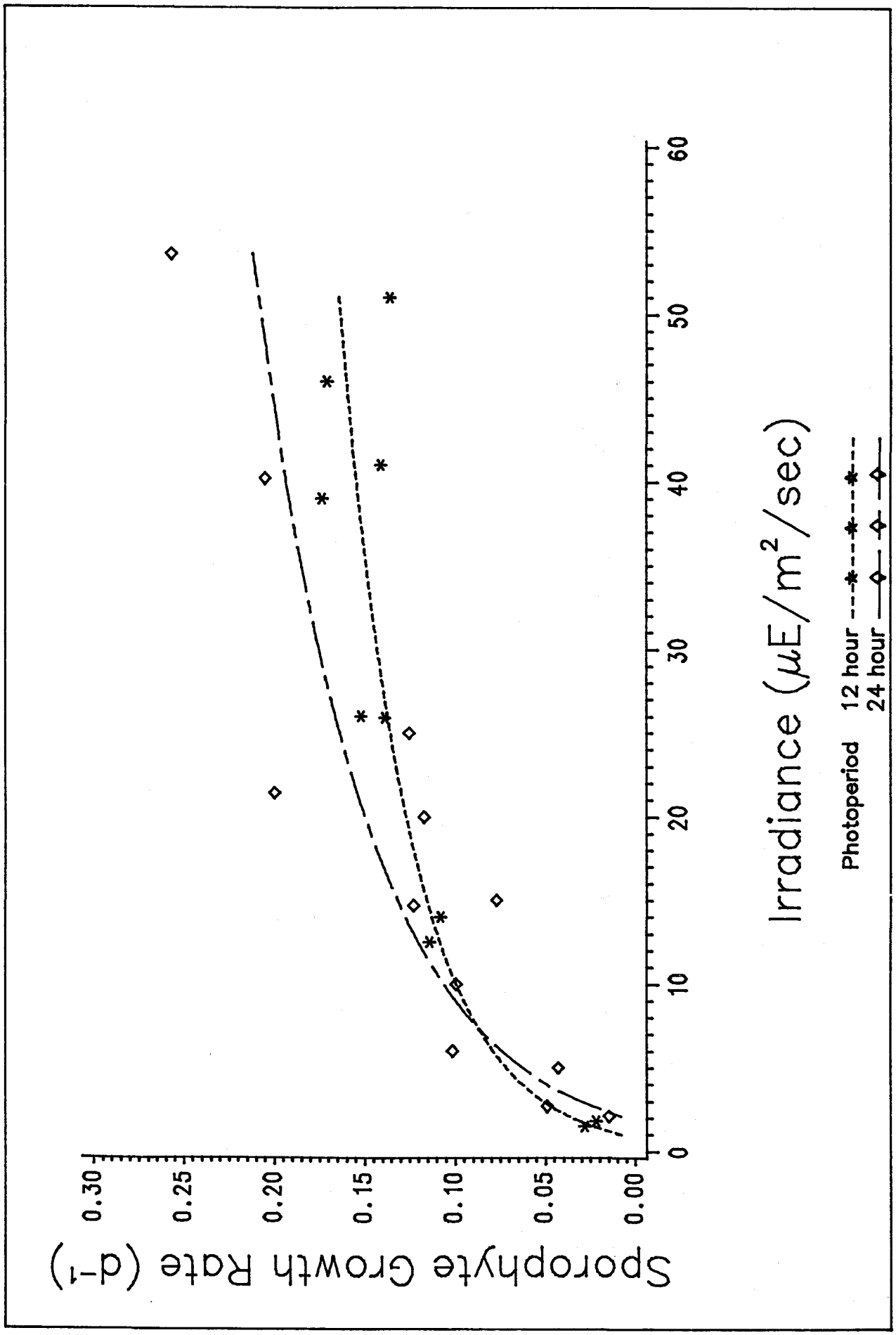
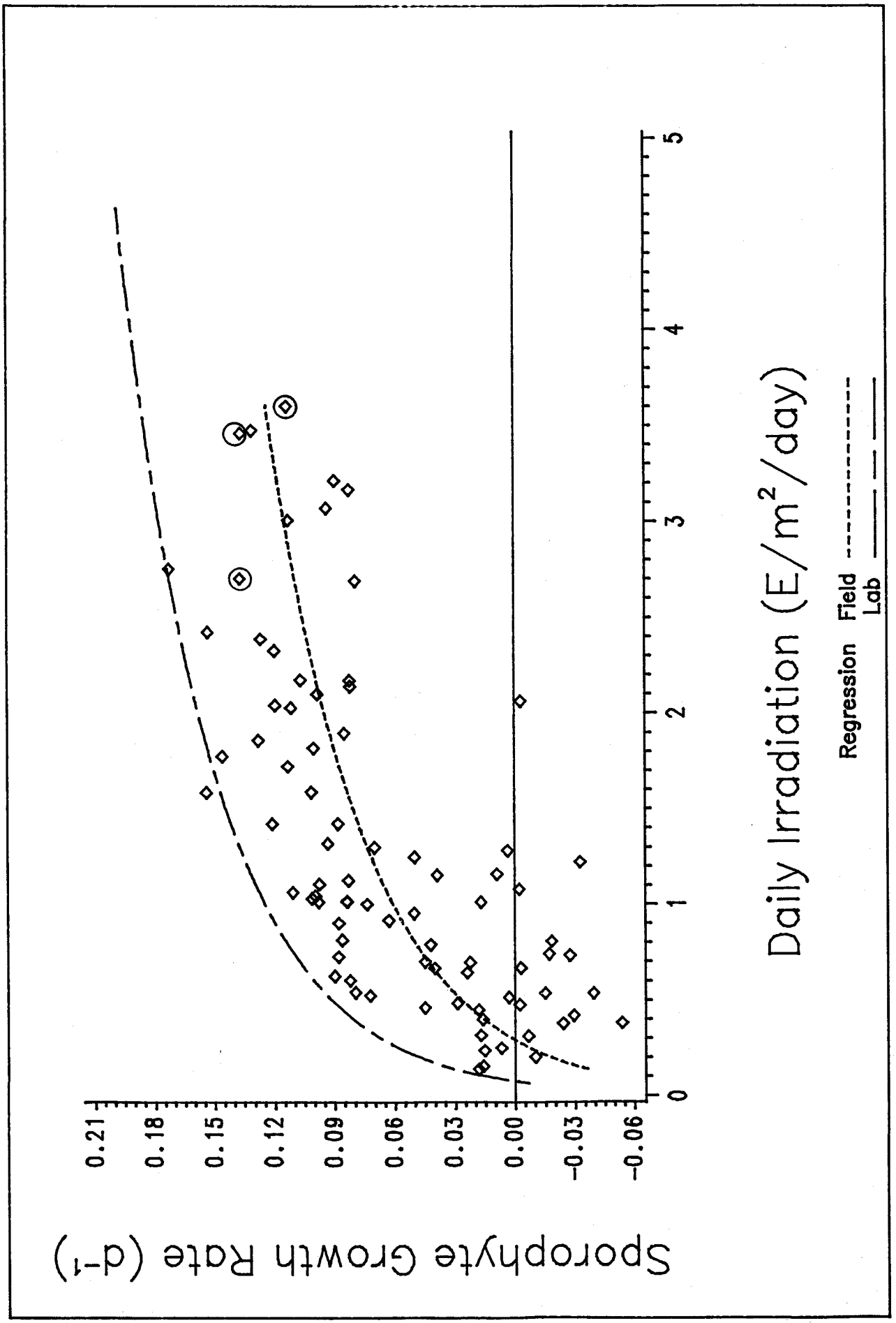

Sporophyte Growth Rate (d-1)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
10
20
30
40
50
60
Irradiance (μE/m2/sec)
Photoperiod
12 hour
24 hour

Figure 7.3 Growth rate of microscopic sporophytes (LNGRATE) in the field outplant experiments plotted against daily irradiation. The growth rate data is from all stations and depths in the SONGS pre-operation period and SMK45 in the operational period. The regression showing the relationship between the growth of microsporophytes and irradiation in the laboratory is also shown. Circled values indicate observations made during the El Nino that occurred from fall 1982 until fall 1984.

Figure 7.3


Sporophyte Growth Rate (d-1)
0.21
0.18
0.15
0.12
0.09
0.06
0.03
0.00
-0.03
-0.06
0
1
2
3
4
5
Daily Irradiation (E/m2/day)
Regression Field
Lab

8.0 GROWTH OF BLADE STAGE *MACROCYSTIS*

By:

Stephen C. Schroeter[1]

Thomas A. Dean[2]

John D. Dixon[1]

[1]Kelp Forest Invertebrate Ecology Project, U.S.C.

[2]Kelp Ecology Project, U.C.S.B.

8.0 Growth of Blade Stage Macrocystis

By Stephen C. Schroeter[1], Thomas A. Dean[2], and John D. Dixon[1]

8.1 Introduction

A primary goal of the Marine Review Committee, Inc. (MRC) has been to determine how the operation of the San Onofre Nuclear Generating Station's (SONGS) Units 2 and 3 affects the distribution and abundance of giant kelp, Macrocystis pyrifera. The life-cycle of Macrocystis consists of several objectively definable stages, each of which may be affected differently by biological and physicochemical factors in the environment. In our studies, we have adopted the strategy of examining each stage separately, hoping to integrate the information into a model of the effects of SONGS on the entire population.

We have excellent data on the temporal and spatial patterns of the distribution and abundance of blade stage kelp (plants with a single blade, generally less than 30 cm in height) in the field (Schroeter et al., 1987). However, most of the earlier mechanistic work on giant kelp concentrated on gametophytes, microsporophytes, juveniles (plants with two or more fronds), and adults (Neushul & Haxo, 1963; North, 1967, 1971, 1972; Devinny & Volse, 1978; Lobban, 1978; Neushul, 1978, 1981; Wheeler & North, 1981; Dean & Deysher, 1983; Zimmerman, 1983; Gerard, 1984; Dean & Jacobsen, 1984, 1986). The present report summarizes the results of two field experiments which examined the effects of light and temperature (a proxy for nutrient levels) on blade stage kelp. In these experiments there were two sources of variations in light levels: 1) light levels were experimentally manipulated by clearing kelp in one plot and leaving undisturbed canopy in a nearby plot, and 2) light and temperature regimes differed dramatically in the two years of the experiments.

[1]Kelp Forest Invertebrate Ecology Project, U.S.C.
[2]Kelp Ecology Project, U.C.S.B.

The first experiment was conducted in the late summer of 1983 during the 1982/84 El Nino event (Fiedler, 1984; Simpson, 1984). The other was in the late summer of 1986. Water clarity and light levels were two to three times higher in 1983 than in 1986. In addition, temperatures were higher and nutrient levels lower in 1983 than in 1986. These physicochemical differences allowed us to examine the effects of light (as affected by the canopy of adult plants) on the growth of blade stage kelp during periods of high and low nutrient conditions. This information, combined with knowledge of the effects of SONGS on light and nutrient levels, will aid our understanding of the mechanisms of the apparent effects of the plume of Units 2 and 3 on the recruitment of blade stage kelp in the San Onofre kelp bed (SOK) (Schroeter et al., 1987).

8.2 Methods

Two growth experiments with blade stage giant kelp were performed. In July 1983 two sites were established at a depth of approximately 13 meters in the San Mateo kelp bed (SMK) (Figure 8.1). One site was under a relatively dense stand of adult Macrocystis, and the other was about 50 meters away in an area without adult kelp. Six 10-m x 4-m transects were established at each site. The transects extended radially from a central point and were marked by steel spikes driven into the substrate at 1-meter intervals. Using the spikes as reference points, the positions of 100 blade stage plants ranging in size from 4 to 30 cm were mapped at each site. Numbered plastic tags were attached to the substrate next to each plant. To control for the possible effects of substrate size and blade stage density on survival and growth, only plants on stable boulders (greater than 30 cm in longest diameter) were used, and only one to three plants spaced 20 cm or more apart were selected on a boulder. Other Macrocystis were removed. Plants were tagged and first measured on July 13, 1983. Surviving individuals were censused and re-

measured on July 28, August 15, and September 13, 1983. At both sites the integral of daily irradiance was measured on the bottom with LI-182 quantum irradiance sensors (LI-COR, Inc., Lincoln, NB). Temperature was measured with YSI thermolinear thermisters (Yellow Springs Instruments, Yellow Springs, OH).

In 1983 the surface canopy sloughed off after July 28, about two weeks after the start of the experiment. This no doubt reduced the treatment effect, but light levels were still higher in the artificial clearing. The loss of canopy was associated with high temperature and low nutrient concentrations (see results below) associated with the strong 1982/84 El Nino (Fiedler, 1984; Simpson, 1984). Similar canopy die-offs have been observed elsewhere (Jackson, 1977; Tegner & Dayton, 1987), and are thought to be caused by prolonged periods of little or no upwelling (Jackson, 1977). We also noted a high incidence of black rot in the kelp canopy, a disease of unknown etiology that is also associated with high temperatures and low nutrient conditions (Scotten, 1971).

In 1986, transplants were performed about 400 meters from the sites used in the 1983 experiment, and at the same depth (Figure 8.1). As in 1983, one site was under a relatively dense stand of adult Macrocystis, and the other was about 50 meters away in an area from which adult kelp was cleared. Blades 10 to 15 cm in length attached to small cobbles were collected in situ in sealed plastic containers, covered with black plastic to seal out all light, and transported to the transplant sites. Sixteen blades were transplanted to the canopy site and 15 to the experimental clearing. The cobbles were secured with nylon cable ties to 10-meter lengths of chain, which were fastened to the substrate with steel reinforcing bars. The chains were spaced about 3 meters apart and laid in parallel arrays. Numbered plastic tags were attached to the chains next to the plants, which were spaced 20 cm

apart. Plants were first measured on August 8, 1986 and were subsequently censused and re-measured on August 21, September 19, and October 27, 1986. Irradiance and temperature were measured as in 1983, but were made at canopy and clearing sites about 100 meters away.

Relative growth rates were calculated for two approximately equal periods (from July 13 to September 13, 1983, and August 8 to October 27, 1986) as follows:

$$RGR = \{Log(L_2)-Log(L_1)\}/(t_2-t_1)$$

Where RGR = relative growth rate

L_1 = total frond length at time t_1

L_2 = total frond length at time t_2

The relationship between relative growth rate and irradiance was examined graphically. We first plotted the relative growth rates of blades against average daily irradiance. Two curves of growth rate versus irradiance for juvenile kelp were then superimposed on these plots. One curve was for data obtained during the 1982/84 El Nino; the other curve was fit to data from non-El Nino years. The curves were fit using the following modified form of the von Bertalanffy equation (Dean & Jacobsen, 1984, 1986).

$$G = G_{max}(1-\exp\{K(I-I_o)\})$$

where G = observed relative growth rate

G_{max} = upper asymptotic growth rate

K = constant describing rate of approach to asymptote

I = observed irradiance

I_o = compensating irradiance

G_{max} and I_o were estimated from the data.

Differences in nutrient regimes between 1983 and 1986 were examined by comparing the number of days in three temperature categories: <14°C, between 14°C and 17°C, and >17°C. These categories were based on work which showed that at temperatures less than 14°C, total nitrogen concentrations average about 3.0 micromolar, and increase rapidly as temperature decreases. Between 14°C and 17°C, total nitrogen concentrations are between 1 and 2 micromolar, and are 0.5 micromolar or less at temperatures greater than 17°C (Figure 8.2). This relationship is more precisely expressed as:

$$N(T) = b/2\{(T_B-T)(1 + \mathrm{erf}\{T_B-T/\theta\}) + \theta/(\Pi)^{1/2}\exp\{-(T_B-T)^2/\theta^2)\}$$

Where: N = concentration of NO_3^- (µmol)

T = temperature (°C)

T_B = average temperature at base of photic zone

θ = parameter describing sharpness of bend at inflection point

b = straight-line slope below T_B

erf = normal error function

(from Reitzel et al., 1987b). This relationship was used to estimate nitrate concentrations in 1983 and 1986.

The effects of adult kelp canopy and the year of the experiment on irradiance and temperature were examined by analysis of the paired differences between canopy and clearing treatments. Since daily temperature and light measurements (and differences of those measurements between sites) often exhibit serial correlation (Reitzel et al., 1987a), the analysis used was PROC AUTOREG, which estimates auto-

correlated errors (Freund & Littell, 1986). The effect of year was modelled as an indicator variable, with a value of 0 for 1983 and 1 for 1986. The resulting model is:

$$Y_{ij} = \beta_o + \beta_1 T_i + E_{ij}$$

Y_{ij} = jth difference between canopy and clearing sites in year i

T_i = 0 for 1983, 1 for 1986

β_o = canopy-clearing in 1983

$\beta_o - \beta_1$ = canopy-clearing in 1986

β_1 = differences between 1983 and 1986 differences

Differences between canopy and clearing treatments in each year, and the differences of these differences, were thus estimated as linear combinations of the autoregressive coefficients (Draper & Smith, 1981).

The effect of adult canopy and year on relative growth rates was examined with a fixed-effects, two-way analysis of variance. Main effects and interactions were tested over the residual, or error mean square (Winer, 1971). A two-way, fixed effects analysis of variance was also done to compare total lengths of plants in canopy and clearing treatments at the beginning and end of the 1983 experiment.

Finally, a categorical analysis (PROC CATMOD, SAS, 1985) was done to estimate the effects of treatment and year on the proportion of single and double frond plants at the end of each experiment.

8.3 Results

Oceanographic conditions varied markedly between 1983 and 1986. Average irradiance levels in 1983 were about three times higher than for a similar time

period in 1986 (Table 8.1a). Irradiance was 20% to 30% lower under the canopy than in the clearings in both years (Table 8.1a & b). The reduction in irradiance in 1983 was somewhat surprising in view of the disappearance of the surface canopy, and was most likely due to shading by subsurface fronds.

Overall temperatures were about 2.5 degrees higher in 1983 than in 1986 (Table 8.2a & b). This difference reflected the fact that in 1983, temperatures exceeded 17° two-thirds of the time, and there were no days on which temperatures were below 14°. In contrast, in 1986 temperatures were less than 14° about 40 percent of the time, and exceeded 17° only about 9 percent of the time (Table 8.3). Using the temperature/nutrient relationship provided by Reitzel et al., (1987b) (Figure 8.2), this difference in temperature regimes translates into two to three order of magnitude higher nutrient concentrations in 1986 compared to 1983 (Table 8.3).

There were significant effects of treatment and treatment-by-year interactions on the growth of blades (Table 8.4a & b). Growth was higher (but the difference was not statistically significant) at the clearing than the canopy site in 1983, and significantly higher (about four times as high) at the clearing site in 1986 (Table 8.4a; Figure 8.3). Despite the lack of significant differences in the analysis of relative growth rates, analysis of changes in total frond lengths in canopy and clearing treatments in 1983 indicate a significant treatment x time interaction (Table 8.5a & b), arguing that there was a real, though smaller difference between treatments.

There was a significant positive correlation between relative growth rate and irradiance (slope = 0.006, R^2 = 0.04, p = .017) (Figure 8.3). The small R^2 reflects a poor fit resulting from the non-linear relationship between relative growth rate

and irradiance. The apparent fit is much better with a modified form of the von Bertalanffy equation which was used to describe the relationship between irradiance and the growth of juvenile kelp (Figure 8.3; Dean & Jacobsen, 1984, 1986).

The relationship between relative growth and irradiance for blades was similar to that for juveniles during the non-El Nino conditions, but was very different in 1983 during the oceanographic conditions associated with the 1982/84 El Nino (Figure 8.3). In 1983 the relationship between light and blade growth more closely resembled the relationship between light and juvenile growth during non-El Nino conditions (Figure 8.3; Dean & Jacobsen, 1986).

In addition to differences in growth rate, there were differences in the form of growth between years. The proportion of one-frond blades was higher at the end of the experiment in 1986 (77% to 87%) than in 1983 (0% to 22%) (Table 8.6a & b). The lower rates of transformation to two-frond plants in 1986 were associated with lower average lengths at the end of the experiment.

8.4 Discussion

The results of the present study indicate that the growth of blade stage kelp is limited by light in kelp forests. In both 1983, during the 1982/84 El Nino, and 1986, after the El Nino, irradiance and blade growth were reduced by the surface canopy of adult kelp. A similar effect of canopy has been noted for blade stage kelp during non-El Nino conditions (Neushul, 1981).

We could find no evidence that the growth of blade stage kelp was nutrient limited, as plants in the clearings grew at about the same rate in 1983 (when nutrient levels were low) and 1986 (when nutrient levels were high). This is in

contrast to results from laboratory studies (Wheeler & North, 1980) which indicated that the growth of blade stage kelp was directly correlated with ambient levels of nitrogen. It also contrasts with both experimental evidence (Dean & Jacobsen, 1986) and anecdotal observations (Dayton & Tegner, 1984) indicating that the growth of slightly larger juveniles was nutrient limited during the El Nino.

The lack of evidence for nutrient limitation may have been the result of confounding effects of light and nutrients. Even though nitrogen levels were lower in 1983, light levels were substantially higher and may have compensated for differences in nutrient availability. Since we did not manipulate light and nutrients factorially in our experiments, such a possibility cannot be ruled out.

Alternatively, blade stages may have been able to obtain more nutrients than larger kelp and avoid nutrient limitation because of their proximity to the substrate and their proportionally large amount of tissue that is capable of uptake. Relatively large amounts of ammonia can be generated from the sediment near the blades (Hartwig, 1974), and these amounts may be more available to blade stage kelp that have more absorptive tissue near the bottom.

How do these results relate to the possible effects of SONGS on the growth and recruitment of blades? Detectable reductions in growth occurred in both years as the result of reductions in irradiance between 20% and 30%. Recent studies of the plume of Units 2 and 3 suggest that such reductions will occur routinely, due to the operation of SONGS (Reitzel et al., 1987b). Thus, we can expect the growth of blades to be negatively affected by reductions in irradiance due to the operation of SONGS. The effects will be most extreme during non-El Nino conditions when light levels are lower.

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Table 8.1a. Average daily irradiance ($E/m^2/day$) at canopy and clearing sites in 1983 (July 13 to September 28) and 1986 (August 8 to October 27).

	Average Daily Irradiance		
Year	Canopy	Clearing	% Reduction Under Canopy
1983	3.36	4.74	29%
1986	0.97	1.23	21%

8.1b. Results of analysis of variance using dummy variables and PROC AUTOREG to test for differences in irradiance ($E/m^2/day$) between canopy and clearing sites in 1983 and 1986, and the differences of the differences between years. The error term in the analysis is an auto-correlated error with a lag of two days.

Comparison	df	T-value	P>T
1: Canopy-Clearing 1983	1	5.96	<.001
2: Canopy-Clearing 1986	1	13.21	<0.0001
3: 1 - 2	1	-4.25	0.0001

MSE = 0.32 df = 104

Table 8.2a. Average daily temperature (^{o}C) in canopy and clearing treatments of blade transplants in 1983 (July 13 to September 28) and 1986 (August 8 to October 27).

	Average Daily Temperature ^{o}C		
Year	Canopy	Clearing	Difference
1983	17.5	17.4	0.1
1986	14.0	14.1	0.1

8.2b. Results of analysis of variance using dummy variables and PROC AUTOREG to test for differences in temperature between clearing and canopy treatments of blade transplants in 1983 and 1986, and the differences of the differences between years. The error term in the analysis is auto-correlated with a lag of two days.

Comparison	df	T-value	P>T
1: Canopy-Clearing 1983	1	-1.24	0.20
2: Canopy-Clearing 1986	1	0.30	.59
3: 1 - 2	1	1.59	0.11

MSE = 0.04 df = 105

Table 8.3. Distribution of daily temperatures into three ranges (<14°C, 14°C to 17°C, and >17°C) in 1983 and 1986, and estimated nitrate concentrations.

	Number of Days	
Range	1983	1986
<14°	0	87
14°-17°	24	48
>17°	48	13
Estimated NO_3^- Concentration (μmol)	0.01	4.8

Table 8.4a. Average relative growth rates of blades in canopy and clearing treatments in 1983 (July 13 to September 13) and 1986 (August 8 to October 27).

	Treatment			
Year	Canopy	Clearing	% Reduction Under Canopy	P-value For Difference
1983	0.018	0.021	14.3%	0.20
1986	0.005	0.022	77.3%	<0.01

8.4b. Results of analysis of variance of relative growth rates of blades at canopy and clearing treatments in 1983 and 1986.

Source	df	Mean Square	F-value	P>F
Year	1	0.0006	3.19	0.076
Treatment	1	0.0017	8.80	0.004
Year * Treatment	1	0.0008	4.03	0.047
Error	134	--	--	

Table 8.5a. Average total lengths (cm) of individually marked blades in canopy and clearing treatments at the beginning and end of the growth experiment in 1983.

Time	Canopy	Clearing
Beginning	14.6	16.6
End	29.5	38.3

8.5b. Results of analysis of variance of total lengths of blades in canopy and clearing treatments in 1983. Time has two levels: beginning and end of experiment.

Source	df	Mean Square	F-value	P>F
Treatment	1	2137.1	17.2	<0.0001
Time	1	24888.5	200.7	<0.0001
Treatment x Time	1	875.5	7.1	0.0083
Error	315	--	--	--

Table 8.6a. Percentage of blades (one-frond plants) at canopy and clearing treatments at the end of transplant experiments in 1983 and 1986. All plants were single blades at the beginning of the experiments.

		Number of One-frond Plants (%)	
Year	Time	Canopy	Clearing
1983	Beginning	100 (100)	100 (100)
	End	15 (15)	7 (7)
1986	Beginning	16 (100)	15 (100)
	End	13 (81)	7 (47)

8.6b. Results of X^2 tests of main effects (Year, Survey, and Treatment), and selected interactions. The tests were made using PROC CATMOD.

Source	df	Chi-square	P-value
Year	1	28.3	0.0001
Survey	1	52.8	0.0001
Year * Survey	1	23.0	0.0001
Treatment	1	3.5	0.0662
Year * Treatment	1	0.0	0.9736
Survey * Treatment	1	3.7	0.0662

Figure 8.1. Location of canopy and clearing sites for 1983 (CAN83 and CLR83) and 1986 (CAN86 and CLR86) blade transplants. In 1986, irradiance and temperature were monitored at canopy (PCAN86) and clearing (PCLR86) sites about 100 meters away from the transplant sites. Hard substrate is outlined in inset.

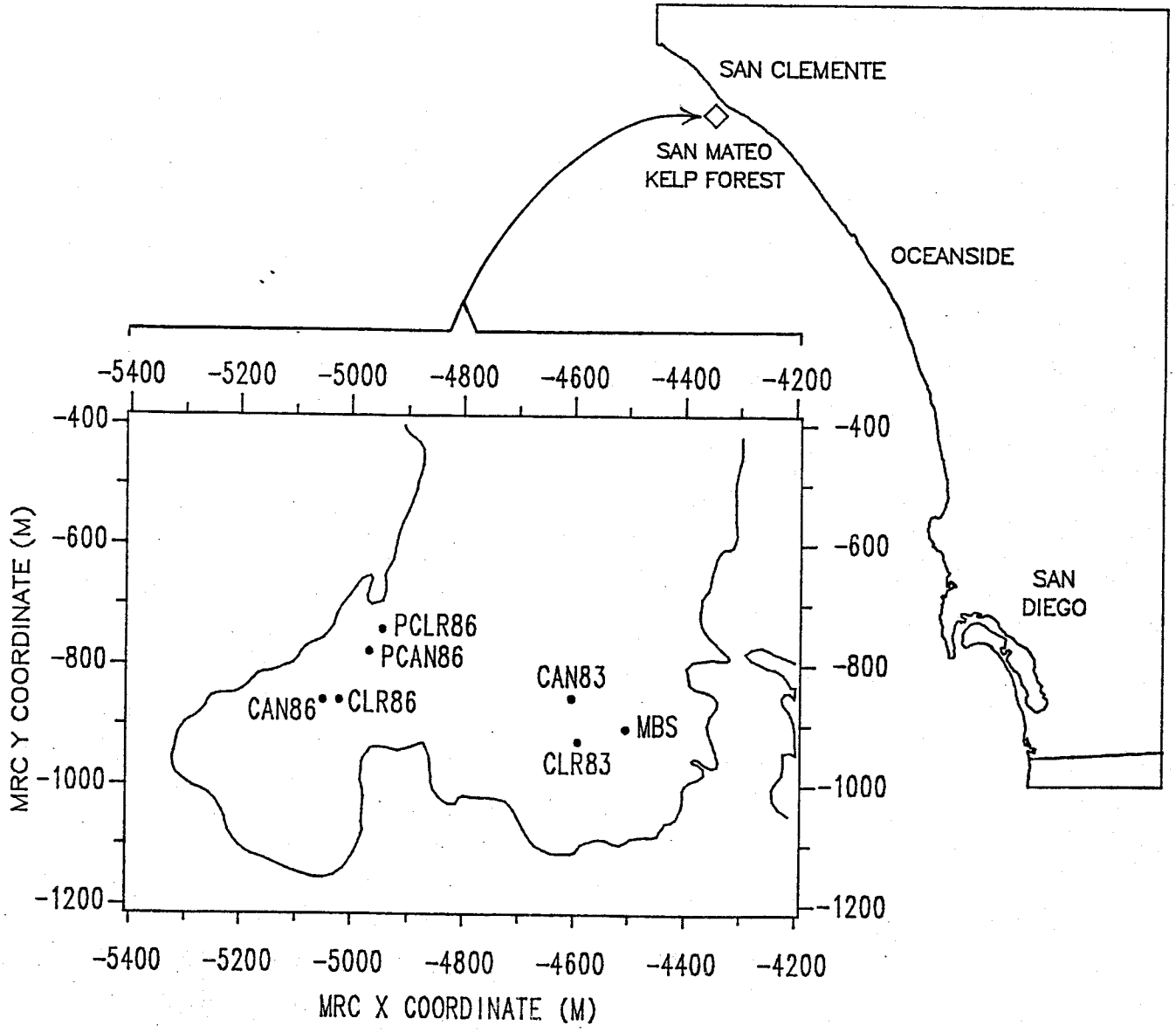

SAN CLEMENTE
SAN MATEO
KELP FOREST
OCEANSIDE
SAN
DIEGO
PCLR86
PCAN86
CAN86
CLR86
CAN83
MBS
CLR83
-5400
-5200
-5000
-4800
-4600
-4400
-4200
-400
-600
-800
-1000
-1200
MRC Y COORDINATE (M)
MRC X COORDINATE (M)

Figure 8.2. Plot of nutrient concentration (μmol NO_3^-) versus temperature (^oC), using data from all years (1978-1986) and water depths. Predicted values from non-linear fit are indicated by solid line.

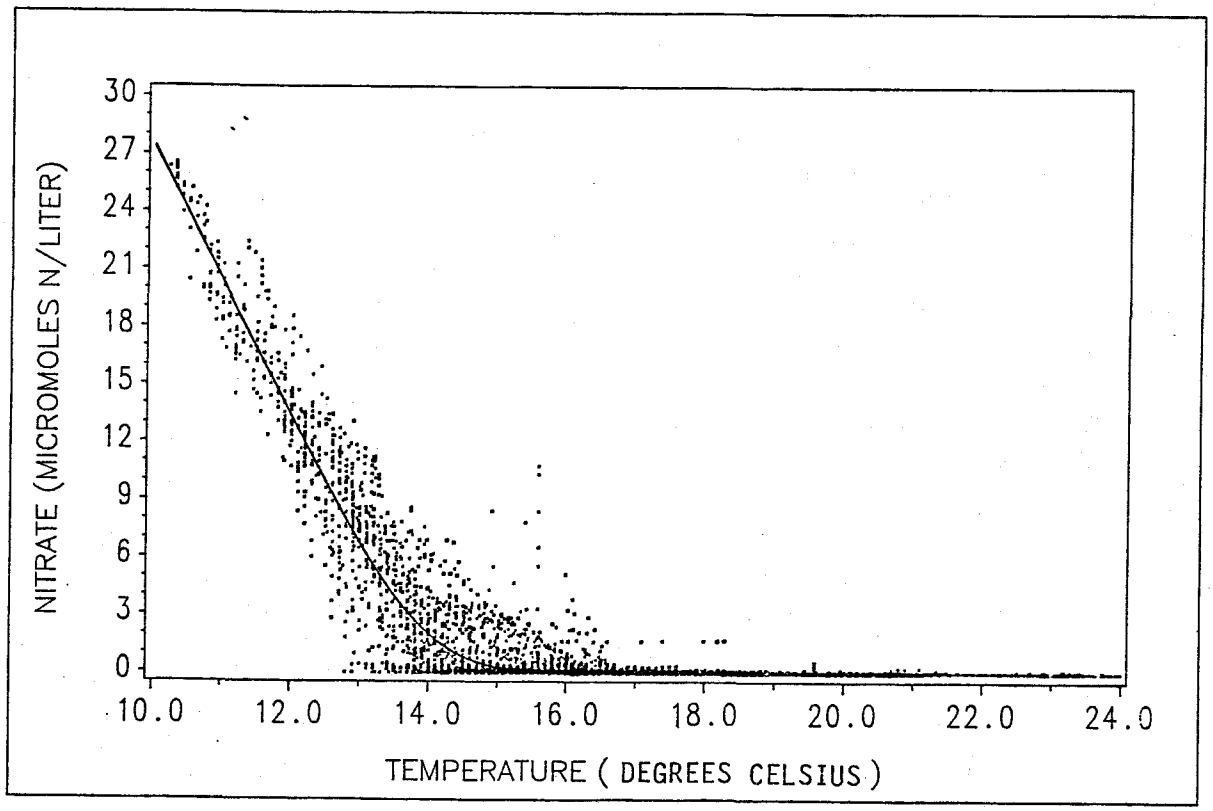
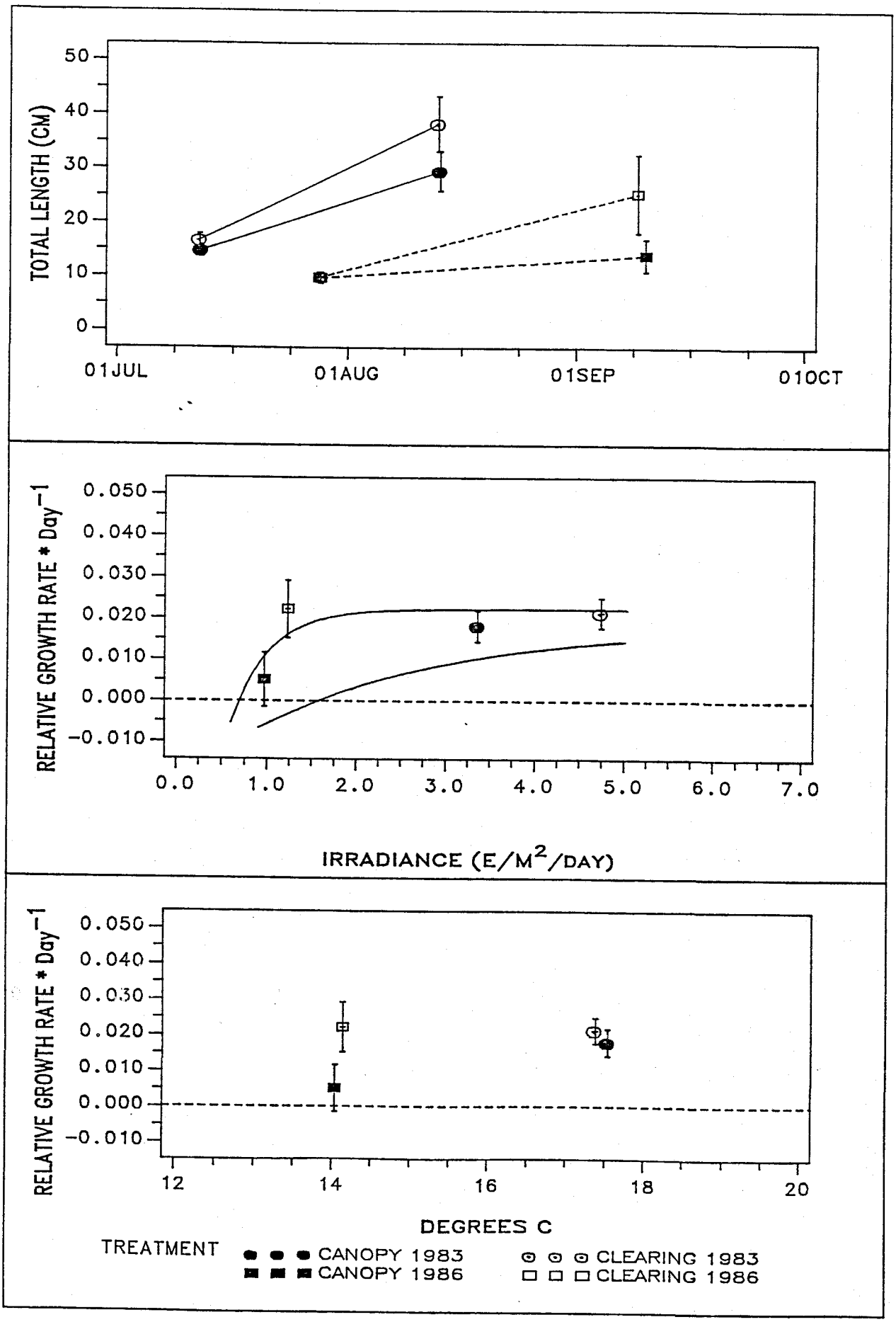

NITRATE (MICROMOLES N/LITER)
30
27
24
21
18
15
12
9
6
3
0
10.0
12.0
14.0
16.0
18.0
20.0
22.0
24.0
TEMPERATURE (DEGREES CELSIUS)

Figure 8.3a. Average total frond lengths (+/-2se) of blades in canopy and clearing treatments in 1983 and 1986.

8.3b. Average relative growth rates (+/-2se) of blades versus irradiance at canopy and clearing sites in 1983 and 1986. Smooth lines are fit to relative growth rate versus irradiance curves for juvenile kelp before 1982 (upper line) and in 1984, during the 1982/84 El Nino (lower curve).

8.3c. Average relative growth rates (+/-2se) of blades versus temperature at canopy and clearing sites in 1983 and 1986.


TOTAL LENGTH (CM)
50
40
30
20
10
0
01JUL
01AUG
01SEP
01OCT
RELATIVE GROWTH RATE * Day^{-1}
0.050
0.040
0.030
0.020
0.010
0.000
-0.010
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
IRRADIANCE (E/M^2/DAY)
RELATIVE GROWTH RATE * Day^{-1}
0.050
0.040
0.030
0.020
0.010
0.000
-0.010
12
14
16
18
20
DEGREES C
TREATMENT
CANOPY 1983
CANOPY 1986
CLEARING 1983
CLEARING 1986

9.0 Survival of Juvenile Macrocystis

9.1 Introduction

In this chapter we examine factors that determine the survival of juvenile Macrocystis following recruitment, with emphasis on the causes of spatial variability in survival. Factors examined include grazing by sea urchins, presence of canopy-forming adults, time of recruitment, and density of recruits. The data analyzed are from observations of survival of juveniles at permanent transects in the San Onofre Kelp forest (SOK) following the recruitment of juveniles in 1978 and 1979. The results will not be used to directly assess the impact of the operation of SONGS because these studies were conducted in the period prior to the operation of SONGS Units 2 and 3. However, they are important for interpreting the population consequences of the demonstrated effects of SONGS on recruitment (Schroeter et al., 1987). The importance of density dependence, the mechanisms of density-dependent survival, and the effects of the presence of adult canopy on survival are of particular significance because losses in the number of recruits due to the adverse effects of SONGS may be partially compensated by the positive effects of reduced density on survival.

9.2 Methods

In summer 1978, we established 12 transects within the San Onofre kelp forest (Fig. 9.1). Eleven transects were set up in June and the twelfth (Transect #8) was established in August 1978. Each transect was permanently marked with steel reinforcement bars driven into the bottom and measured 6 m wide by 50 m long (Fig. 9.2). At the start of our study in 1978, the kelp forest consisted of 3 patches: the southwest, northwest, and southeast. Two transects each were positioned in the centers of the southeast and southwest patches under heavy canopy. All other

transects were positioned along the edges of the kelp forest such that half the transect was outside the forest but on areas of hard substratum. For the purposes of the analyses presented in this chapter, we divided each transect into two 25 x 6 m segments so that each area sampled would represent a relatively homogeneous environment (with respect to initial adult abundance) and would be equal to every other sampling area in size.

We tagged all kelp plants that were of juvenile size or larger (see definition below), on each transect by driving a steel spike with a numbered plastic tag into the seafloor next to each plant. In addition, we mapped the position of each plant by noting the distance of the plant from the center line, and also from the head of the transect. Mapping allowed us to identify individual plants in cases where tags were lost and also allowed for evaluation of the dispersion patterns of plants within each transect.

The plants were divided into 3 size categories: juveniles, subadults, and adults, according to the following arbitrary criteria. Those plants which had split into at least two fronds, but were less than 1 m in height were juveniles. Subadults were those plants taller than 1 m, that did not have haptera protruding above the primary basal dichotomy of the stipe (see Lobban, 1978, for a description of plant morphology). Plants that had haptera above the primary dichotomy were adults. Size categories were based primarily on morphologies because of the difficulty in measuring adult plants underwater. Preliminary observations indicated that adult plants generally had from 6 to 8 fronds, with at least one frond reaching to, or near, the water's surface (i.e., from 12 to 15 m long).

Surveys of Macrocystis were conducted at approximately monthly intervals in 1978, and quarterly thereafter, through December 1980 (Appendix M). In each survey, we determined the presence/absence of each plant tagged in previous surveys, determined the size class of survivors, and tagged and mapped any newly recruited plants. Occasionally, surveys were postponed or cancelled because of poor underwater visibility. Densities of the white sea urchin, Lytechinus anamesus, and two dominant understory algae, Pterygophora californica, and Cystoseira osmundacea, were also determined in each survey. These were censused in each of 10 contiguous 2 x 5 m quadrats along the center line of each transect.

The composition of the substrata within on each transect was determined once in December 1979. Substratum types were classified in the following categories: sand, cobbles $\leq$ 20 cm in the longest dimension, and cobbles >20 cm. The occurrence of each type was noted at 25 cm intervals along the center line of each transect.

9.3 Analyses

The effects of time of initial recruitment and time of year on survival were examined using Chi-square statistics. We tested the hypothesis that the proportion of plants surviving was independent of initial time of recruitment (i.e., cohort) by comparing survival of different-aged plants over a given observation interval. The hypothesis that survival was independent of time of year was tested by comparing the proportion of plants surviving over different time intervals, within each cohort. Each of the overall comparisons was followed by single degree of freedom Chi-square tests (Snedecor and Cochran, 1967). These tests were used to identify groups of cohorts or times of year among which rates of survival did not differ significantly.

The effects of age and size of plants on survival were tested using linear categorical analyses (Grizzle et al., 1969). The analyses were performed using the CAMOD procedure of the SAS statistical package (SAS, 1982). We tested the hypothesis that the probability of survival over a given time interval did not differ among plants of different ages (i.e., when they were initially tagged) or sizes. We also examined possible interactions among age and size. Two separate analyses were performed, one for survival over the period from August 1979 to November 1979, and the other from November 1979 to June 1980. In the first analysis, we compared survival among juvenile, subadult, and adult size classes from three cohorts (tagged October 1978, December 1978, and March 1979). The second compared survival among 5 cohorts initially tagged between October 1978 and November 1979. These intervals and cohorts were selected because they were the only times when all 3 size classes of plants were present.

The possible effect of grazing by Lytechinus on the survival of juvenile kelp was examined by comparing the proportions of plants that survived in areas of high vs low densities of white urchins on Transects 6, 7, and 8. We could not analyze these data using a categorical analysis (as described above) because there were no survivors in two cases, thereby, violating an assumption of the test.

The effect of the presence of adult canopy on the survival of juvenile Macrocystis was tested by comparing the proportions of recruits that survived at canopy, edge, and out-of-bed transects using a linear categorical analysis as described above. Transects with high densities of urchins (i.e., those portions of Transects 6, 7, and 8 that were outside of the kelp forest) were eliminated from the analysis. Survival was determined as the proportion of juveniles, recruited between August 1978 to November 1979, that survived in June 1980.

In order to examine other possible causes of the observed spatial variability in survival, we performed a regression analysis on the proportion of plants surviving on each transect half in June 1980 versus the number of juveniles recruited between August 1978 and November 1979, the densities of two potential competitors (Pterygophora californica and Cystoseira osmundacea), and the proportion of hard substrata on each transect that were cobbles >20 cm in diameter. Canopy transects (9, 10, 11, and 12) and transects with high densities of Lytechinus (out-of-bed portions of Transects 6, 7, and 8) were eliminated from the analysis. Densities of Pterygophora and Cystoseira are mean values of the number of plants (greater than 30 cm in height) on each transect obtained from surveys conducted between August 1978 and November 1979. A multiple regression analysis (Belsley et al., 1980) was performed using the PROC REG Procedure of SAS (SAS 1982). Mean values for densities of Pterygophora, Cystoseira and Macrocystis recruits, were log transformed while percent survival and percent large cobbles values were arcsin transformed.

Dispersion patterns for juvenile plants in each survey and on each half transect were determined using the Clark-Evans index of non-randomness based on nearest neighbor distances, with a toroidal edge correction (Ripley, 1981). It was determined whether dispersion patterns deviated significantly from random using the Chi-square statistic, as described by Ripley (1981).

The relationship between density and size was examined by regressing the proportion of survivors in a given size class in November 1979 vs the number of plants originally recruited. Separate regression analyses were performed of juvenile and adult plants, and for cohorts recruited in 1978 and 1979.

9.4 Results

9.4.1 Patterns of Recruitment and Survival

In spring 1978, there were virtually no juvenile Macrocystis in the San Onofre Kelp forest. By July, large numbers of small, single-bladed plants began to appear with densities reaching several hundred/m² on some transects. We did not make regular quantitative estimates of the density of blade stages because of the difficulty in discriminating Macrocystis from other laminarian algae when plants are small.

By August 1978, many of these plants had grown to juvenile size (~40 cm). Newly recruited plants continued to appear through November 1979 (Fig. 9.3). It is impossible to determine when these plants were initially produced from gametophytes, since gametophyte and early sporophyte stages cannot be identified in situ. We suspect that juveniles tagged between August and December 1978 were produced from gametophytes during a several-week period in April-May 1978. A second peak in juvenile recruitment occurred in the March 1979 survey; most of these plants were probably produced from gametophytes in fall 1978. The lack of small blade stage plants (single blades measuring 2 to 3 cm), in fall 1978, helped confirm that juveniles tagged in spring 1979 were not slow growing individuals that had recruited in the previous spring. We operationally define "cohorts" of plants as those initially tagged during a given survey. Hereafter, in this chapter, we refer to "recruitment" as the initial appearance of juvenile stage plants, recognizing that the actual production of sporophytes from gametophytes occurred at some previous time and that the production of juveniles requires the survival of microscopic sporophytes and visible blade stage plants.

There was considerable variability in the numbers of juveniles recruited among transects (Table 9.1) and among cohorts (Table 9.2). The highest densities of juveniles (greater than $2.4/m^2$) were observed on Transects 11 and 12 in October 1978. Little recruitment was observed on Transects 9 and 10, and on the out-of-bed portions of Transects 7 and 8 where the densities of recruits never exceeded $0.1/m^2$. Causes of temporal and spatial patterns in recruitment are examined elsewhere (Schroeter et al., 1987).

In the months following our initial observations of recruitment, abundance patterns and size distributions of Macrocystis within the kelp forest changed dramatically (Fig. 9.3). These changes were the result of growth, survival, and continued recruitment of juveniles. Occasionally, we found adult or subadult plants that had not been tagged in previous surveys. These were mostly plants that were attached to small cobbles and had apparently recruited elsewhere and had drifted onto transects and become lodged there. After November 1979, adult abundances began to decline as mortality of adults outpaced their rate of replacement (Fig. 9.3). By June 1980, almost all plants recruited in 1978 and 1979 had either died or grown to adult size.

Only a small fraction of those plants initially recruited survived for 2 years (Fig. 9.4). Of the over 8,000 juveniles tagged in 1978 and 1979, only 145 (~2%) survived until June 1980 (Table 9.1). There were significant differences in survival among times within each cohort, and among cohorts within each time (Table 9.2, $P<0.05$, Chi-square). All cohorts showed an increase in survival after June 1980 when most plants reached adult size. In all cohorts except two (August and September 1978), survival was significantly higher from June 1980 through December 1980, than in all other time intervals ($P<0.05$, single df Chi-square).

For all cohorts initially tagged after October 1978, survival was significantly lower from November 1979 to June 1980 than during all other time intervals (Table 9.2, $P<0.05$, Chi-square). This was a particularly stormy period, especially compared with the mild winter of 1978-79, and the high mortality was probably the result of plants being dislodged from the substratum by heavy surge. There was a general tendency for earlier cohorts to exhibit higher survival than later cohorts during the stormy period of November 1979 to June 1980. The oldest plants (the August and September 1979 cohorts) had higher rates of survival than all other cohorts over this time interval ($P<0.05$, single df Chi-square).

9.4.2 Effects of Age and Size on Survival

The average size of plants increased with age, but the relationship between size and age was a rather loose one. Individual plants of the same age were often quite different sizes. Some plants reached adult size within 6 mo while others remained juveniles (<1 m in height) for over a year (Fig. 9.4).

Size was more important than age in determining survival. Survival was much higher in the period from August to November 1979 than from November 1979 to June 1980, but in both instances, the survival of adult plants was greater than for juveniles and subadults (Table 9.3).

There was no significant effect of age on survival when ages were summed over all size classes (Table 9.3). However, the significant interactions between age and size suggested that there were differences in survival among ages within particular size classes and that, in some cases, small plants that were old may have had a lower probability of surviving than small plants that were young. For the period from August to November 1979, younger plants within juvenile and subadult size classes

tended to have higher survival than older plants. There were no obvious orderings within a size class with respect to the effects of age on survival in the period from November 1979 to June 1980.

9.4.3 Causes of Spatial Variability in Survival

We also noted considerable spatial variability in survival. The proportion of plants recruited in 1978 and 1979, that survived through June 1980 ranged from 0% to 24% on the various transects (Table 9.1). Variability in survival was attributable to grazing by white sea urchins, shading by the canopy of adults, and effects of neighboring juveniles. White sea urchins were abundant (greater than $10/m^2$) on the portions of Transects 6, 7, and 8 that were outside of the kelp forest. There were no survivors on the outside portions of Transects 7 and 8, and the only survivors observed on the portion of Transect 6 outside of the kelp forest were in patches where there were few urchins (T.A. Dean, personal observations). Although the proportion of plants surviving on the halves of transects in the kelp forest did not differ significantly from portions of the outside transects where urchins were more abundant (Table 9.4), our observations as well as experiments reported elsewhere (Leighton, 1971; Dean et al., 1984) leave little doubt that survival was reduced by the grazing activity of Lytechinus.

Survival was significantly lower on transects under a canopy of adults than on transects that were positioned either on the edge of the kelp forest or outside of the kelp forest (Table 9.5). Urchin densities were low in all locations used in this analysis ($<10/m^2$), and on at least 2 of the transects (9 and 10) densities of recruits were low, suggesting that the observed effect of canopy cover was unrelated to possible confounding effects of these other factors. Densities of adults did not differ significantly on edge and canopy transects ($t = 0.34$, $df = 14$, $P = 0.74$),

suggesting that canopy effects were due to shading and were not related to the effects of density per se. Even though densities of adults were high, transects on the edge of the kelp forest received considerably more light than those in the center of the kelp forest because of irradiance that entered the forest obliquely.

In portions of the kelp forest where densities of white urchins were low and where there was not a dense overlying canopy, 65% of the variability in survival among transects could be explained by the density of juveniles (Table 9.6). There was a significant negative relationship between the density of recruits and the proportion of plants which survived (Fig. 9.5). There were no significant effects of either density of competitors or substrate composition on survival (Table 9.6).

Density-dependent survival was also indicated by patterns of dispersion within each transect over time (Fig. 9.6). Prior to the appearance of large numbers of juveniles on transects in September 1979, plants were generally distributed randomly within transects. Following recruitment, the dispersions patterns were strongly clumped. As plants were thinned, the degree of clumping decreased, and by June 1980 (when most remaining plants were adults) the dispersion patterns had returned to random on most transects. We infer from this that mortalities were not random and that plants located within dense patches were more likely to die than those that were more sparsely distributed.

9.4.4 Correlation Between Size Distributions and Spatial Patterns of Survival

Density-dependent survival was correlated with the size distributions of plants prior to the winter storms of 1979. Transects with high initial densities of recruits (and low subsequent rates of survival) had proportionally fewer adult plants prior to the 1979 storms than transects with low levels of recruitment,

suggesting that density was negatively correlated with average growth rates. (Fig. 9.7). For plants recruited in 1978, there was a significant negative correlation between the proportion of surviving adult plants on a given transect in November 1979 and the initial density of recruits, and a significant positive correlation between the proportion of juveniles and the initial density of recruits. Trends were similar for the 1979 cohorts, but were not significant. The lack of significance in the latter case was due to the small proportion of plants that had grown beyond the juvenile size-class. As further evidence of the effect of size on survival, there was a significant positive correlation between the number of adults on transects in November 1979 and the total number of survivors in June 1980 (Fig. 9.7).

9.5 Discussion

Spatial patterns of survival of juvenile kelp in the San Onofre kelp forest were primarily determined by intra-specific interactions, both between juveniles and between juveniles and adults. Results from canopy-thinning experiments conducted in the nearby Point Loma Kelp forest (Dayton et al., 1984), in central California (Pearse and Hines, 1979; Reed and Foster, 1984) and in Chile (Santelices and Ojeda, 1984) suggest that adult-juvenile interactions are predominant factors determining the patterns of survival in most Macrocystis populations. Intra-cohort density-dependent mortality has been less widely studied in Macrocystis populations, but some observational evidence (Santelices and Ojeda, 1984) suggests it too may be a common feature in kelp forests over a wide geographical area.

The probable mechanism for both inter- and intra-cohort, density dependence appears to be competition for light. The growth of juvenile Macrocystis is generally light limited (Dean and Jacobsen, 1984) and significant reductions in light can be

attributed to both surface canopies formed by adults and understories formed by dense assemblages of juveniles. Underwater irradiance measurements indicate that dense canopies of adults reduce light on the seafloor by about 50% at San Onofre (Dean, 1985) and up to 90% in other kelp forests (Neushul, 1971; Gerard, 1984; Reed and Foster, 1984; Santelices and Ojeda, 1984). Subadult kelp can also provide significant shading of nearby juveniles. In a dense, even-aged stand of juvenile and subadult Macrocystis (densities = $18/m^2$), trimming plants larger than 1 m the increased irradiance available to smaller plants by 50% (T.A. Dean, unpublished data). Reduced irradiance results in reduced growth rate which, in turn, leads to higher mortality. The smaller, slower growing individuals suffered higher mortality than larger, faster growing individuals, probably because they had poorly developed holdfast structures and were more easily torn loose by waves. Further manipulative experiments, similar to those proposed by Schiel and Foster (1986), are needed to test this hypothesis. Regardless of the mechanism, it is clear that the effect of inter-cohort, density-dependent survival was to reduce the differences among transects, with regard to initial densities of recruits such that all transects eventually produced more similar numbers of adults than expected, based on a simple ratio of recruits to survivors.

In portions of the kelp forest where white urchins were abundant, both recruitment (Dean et al., 1984; Schroeter et al., 1987) and survival of juvenile Macrocystis was inhibited. However, Lytechinus were not widely distributed and were restricted to the offshore edges of the kelp forest. Red urchins, which were also abundant, can form moving aggregations or "fronts" that have resulted in the formation of extensive barren grounds (Leighton, 1971; Pearse and Hines, 1979; Dean et al., 1984; Ebeling et al., 1985; Harrold and Reed, 1985). However, during this study, red urchins at San Onofre remained in stationary aggregations and did not actively graze kelps (Dean et al., 1984).

Interspecific interactions between understory algae and Macrocystis appeared to be less important in determining the spatial patterns of Macrocystis survival at San Onofre than elsewhere. We observed no significant negative effects of Pterygophora or Cystoseira on the survival of juvenile Macrocystis. This stands in contrast to results from manipulative experiments conducted in the nearby Point Loma kelp forest in San Diego (Dayton et al., 1984), and in kelp forests in Carmel, central California (Reed and Foster, 1984) which indicated that understory algae had significant negative impacts on survival of young Macrocystis. This difference between kelp forests may have been due to differences in both densities and sizes of competitors. Densities of Pterygophora at Point Loma (Dayton et al., 1984) and Carmel (D. Reed, personal communication) were nearly twice those at San Onofre (where we observed a maximum density of $4/m^2$) and the plants were nearly twice as large elsewhere as compared to San Onofre (Dayton et al., 1984, Reed and Foster, 1984, and T.A. Dean, personal observation). These biological differences may ultimately relate to the different substrata present at the various sites. At San Onofre, the primary substratum is cobble as opposed to more consolidated rock reefs elsewhere. The lack of a stable substratum at San Onofre might have led to a higher rate of disturbance and a less stable assemblage of understory algae. In this respect, the San Onofre kelp forest appears similar to disturbance-dominated systems in central California such as Piedras Blancas (Dayton et al., 1984) and Sandhill Bluff near Santa Cruz (Cowen et al., 1982; Foster, 1983), which are less influenced by competitive interactions among species.

One would ideally like to compare rates of survival in the San Onofre kelp forest with published records from other kelp forests (Rosenthal et al., 1974; Coyer and Zaugg-Haglund, 1982; Dayton et al., 1984). However, quantitative comparisons are difficult and because of the lack of replication in most studies and because

each study began to follow survivorship at different point in the plant's life history. The lack of replication is especially problematic since we have demonstrated high spatial and temporal variability within the San Onofre Kelp forest, depending, in part, on the number of plants recruited, the timing of recruitment with respect to storms, the density of grazers, and the degree of shading by overlying canopy. Qualitative comparisons of survival in various kelp forests indicate that the survival of juvenile sporophytes, through the adult stage (a period of 1 to 1.5 years, on average), are generally on the order of 1% to 10%. This corresponds to a half-life of about 2 to 6 months (Rosenthal et al., 1974; Dayton et al., 1984, this study). Survivorship curves for visible sporophytes of Macrocystis (Rosenthal et al., 1974; Dayton et al., 1984, this study) are generally type III, with older (and generally larger) plants having lower mortalities than juvenile plants.

The observed density-dependent survival of juvenile kelp at San Onofre suggests that a possible reduction in recruitment due to SONGS could be compensated for by increased survival of juveniles, such that there would be no net change in the number of adults produced from a given cohort. However, this need not be the case, especially if the mechanism of impact is the same as the limiting resource (i.e., irradiance). A reduction in irradiance due to SONGS would be analogous to the presence of a "permanent canopy" and may reduce growth and decrease survival regardless of the density of juveniles. A reduction in initial density of recruits due to SONGS may provide more light allowing for better growth and survival of remaining recruits. However, a continued reduction in irradiance due to SONGS may be sufficient to offset these gains in irradiance, growth,and survival.

Results presented elsewhere (Schroeter et al., 1987; Reitzel et al., 1987) indicate that the reduction in irradiance caused by SONGS (on the order of 15%) is less than reduction in irradiance caused by an overlying canopy of adults (on the order of 50%). As a result, some compensation may be expected. At present, the population consequences of a reduction in irradiance due to SONGS can best be evaluated using population models that incorporate the mechanisms of density dependence described herein (e.g., Nisbet and Bence, 1987).

Table 9.1 Total number of juvenile Macrocystis recruited per half transect from August 1978 through November 1979. Also given are the number of those recruits that survived in June 1980 and the percent survival.

Transect	Half	Number Recruited	Number Surviving	% Survival
1	1	38	3	8
1	2	76	11	14
2	1	107	5	5
2	2	624	15	2
3	1	133	10	8
3	2	90	4	4
4	1	66	16	24
4	2	7	2	29
5	1	560	14	3
5	2	311	4	1
6	1	41	4	8
6	2	45	6	13
7	1	23	0	0
7	2	250	6	2
8	1	33	0	0
8	2	864	12	1
9	1	13	0	0
9	2	31	0	0
10	1	16	0	0
10	2	2	0	0
11	1	932	15	2
11	2	1344	13	1
12	1	1120	3	<1
12	2	1327	2	<1
Total =		8040	145	1.8*
Mean =		335.0	6.0	
C.V. =		134.1	93.3	

*Total surviving/total recruited

Table 9.2 Percent survival of juvenile *Macrocystis pyrifera* from different cohorts (i.e., plants recruited at different times) calculated over 5 to 7 mo intervals between September 1978 and December 1980. Total numbers of individuals at risk in each period are given in parentheses.

Time interval	Cohort (Time of Recruitment)						
	Aug78	Sep78	Oct78	Dec78	Mar79	Jul79	Nov79
Sep78-Mar79	36 (33)	51 (243)	-	-	-	-	-
Mar79-Nov79	17 (12)	22 (124)	19 (2109)	20 (1447)	50 (2419)	-	-
Nov79-Jun80	100 (2)	44 (27)	10 (411)	8 (295)	3 (1219)	4(424)	5 (220)
Jun80-Dec80	100 (2)	67 (12)	93 (41)	74 (23)	73 (40)	73 (15)	60 (10)

Table 9.3 Percent survival of newly recruited *Macrocystis pyrifera* by age (i.e., cohort) and size; from the periods August 1979 to November 1979 and from November 1979 to June 1980. Also shown are results of categorical analyses testing the equality of survival among ages and size-classes.

	Adult					
	Aug79 to Nov79			Nov79 to Jun80		
Cohort	Living	Dead	% Survival	Living	Dead	% Survival
Oct78	42	5	89	33	19	63
Dec78	13	1	93	11	10	52
Mar79	10	7	59	20	13	61
Jul79	8	0	-	3	6	33
Nov79	-	-	-	6	4	60
			Mean = 83%			Mean = 65%

	Subadult					
	Aug79 to Nov79			Nov79 to Jun80		
Cohort	Living	Dead	% Survival	Living	Dead	% Survival
Oct78	107	139	43	7	123	5
Dec78	41	38	52	10	53	16
Mar79	110	50	69	15	200	7
Jul79	40	6	87	12	61	14
Nov79	-	-	-	1	41	2
			Mean = 63%			Mean = 9%

Table 9.3 continued

	Juvenile					
	Aug79 to Nov79			Nov79 to Jun80		
Cohort	Living	Dead	% Survival	Living	Dead	% Survival
Oct78	262	356	42	1	228	0.4
Dec78	241	282	46	2	209	0.9
Mar79	1099	592	65	5	966	0.5
Jul79	376	60	86	1	341	0.3
Nov79	-	-	-	4	164	2.4
			Mean = 60%			Mean = 0.7%

Source	df	X^2	P	Source	df	X^2	P
Intercept	1	20.36	<0.01	Intercept	1	20.36	<0.01
Age	2	0.62	0.73	Age	4	2.11	0.72
Size	2	16.73	<0.01	Size	2	165.91	<0.01
Age X Size	4	18.21	<0.01	Age X Size	8	18.50	0.02

Table 9.4 Percent survival of juvenile *Macrocystis* on transects with and without high densities of *Lytechinus*.

	No. surviving		% surviving	
Transect #	with urchins	without urchins	with urchins	without urchins
6	4	6	8	13
7	0	6	0	2
8	0	12	0	1

Paired t-test on survival

$t = 2.22$, $P = 0.16$

Table 9.5 Percent survival of juvenile Macrocystis on transects located under a canopy of adult Macrocystis in the center of the kelp forest, at the edge of the kelp forest, and outside of the kelp forest. Mean adult densities are given for August 1978.

Location relative to kelp forest	Mean adult density (no./100 m2)	Mean % survival
CANOPY	10.2	0.4
EDGE	10.1	8.5
OUTSIDE	0.5	9.3

Categorical Analysis - Survival

Source	df	Chi-square	P
Intercept	1	1880.27	<0.01
Location	2	82.74	<0.01
Contrasts			
Canopy vs Edge	1	8.57	<0.01
Canopy vs Outside	1	13.98	<0.01
Edge vs Outside	1	0.01	0.93

Table 9.6 Summary of regression analyses of the proportion of plants surviving on each transect in June 1980 vs the number of plants recruited, the proportion of hard substrata that was cobbles greater than 20 cm diameter, and the densities of Pterygophora and Cystoseira on each respective transect. Independent variables (with the exception of percent large cobbles) were $\log_e$ transformed. The angular transformation was applied to both the proportion of plants surviving and the proportion of large cobbles. Transects that were under a canopy of adult kelp or had high densities of Lytechinus were not included in this analysis.

Variable	Parameter Estimate	P>T	Partial Coefficient of Determination
Intercept	27.49	0.18	-
Log No. recruited	-4.57	<0.01	0.65
Arcsin percent cover large rocks	0.17	0.15	0.24
Log Pterygophora density	2.72	0.36	0.10
Log Cystoseira density	0.83	0.39	0.09

Overall R^2=0.81 N=13

Figure 9.1 Map of the San Onofre kelp forest as it appeared in summer 1978 and the position of permanent transects within the kelp forest. Shaded areas are locations of kelp canopy. SONGS is the San Onofre Nuclear Generating Station. Depth contours (in meters) are indicated.

Figure 9.1

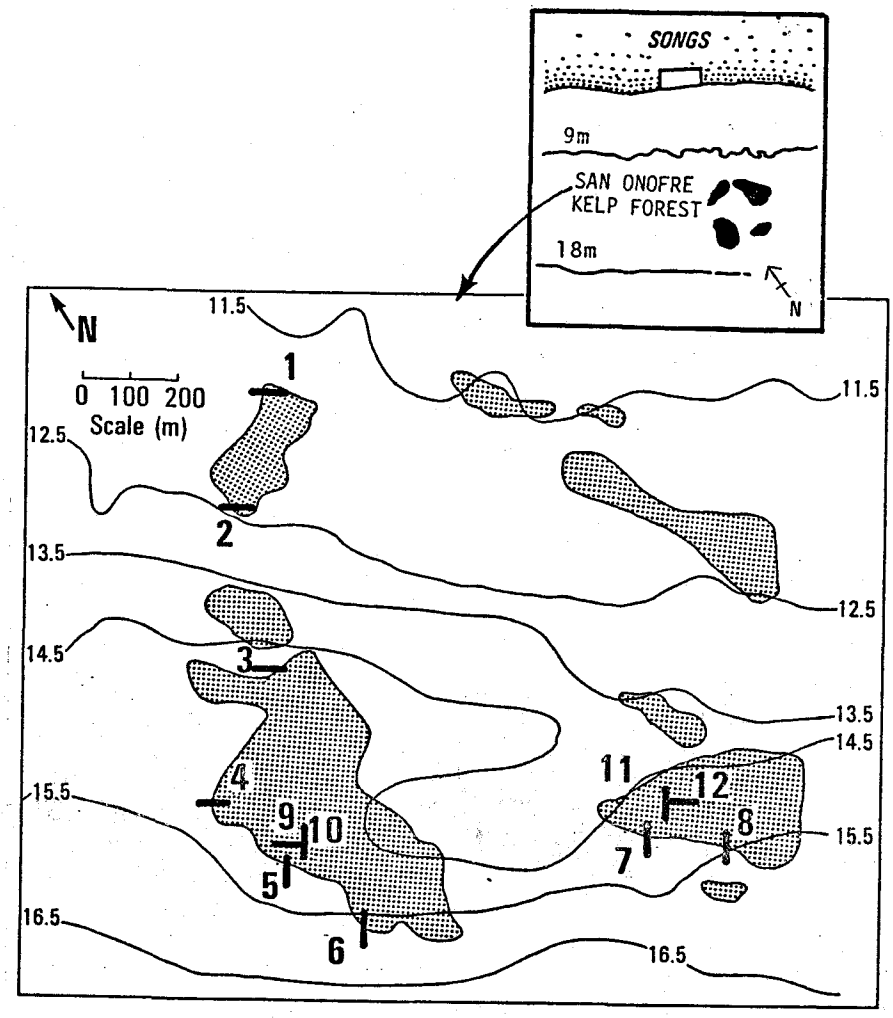

SONGS
9m
SAN ONOFRE
KELP FOREST
18m
N
N
0 100 200
Scale (m)
11.5
12.5
13.5
14.5
15.5
16.5
1
2
3
4
5
6
7
8
9
10
11
12

Figure 9.2 Schematic drawing of stations used to sample kelp and sea urchins at 6-m wide by 50-m long transects in SOK and SMK.

Figure 9.2

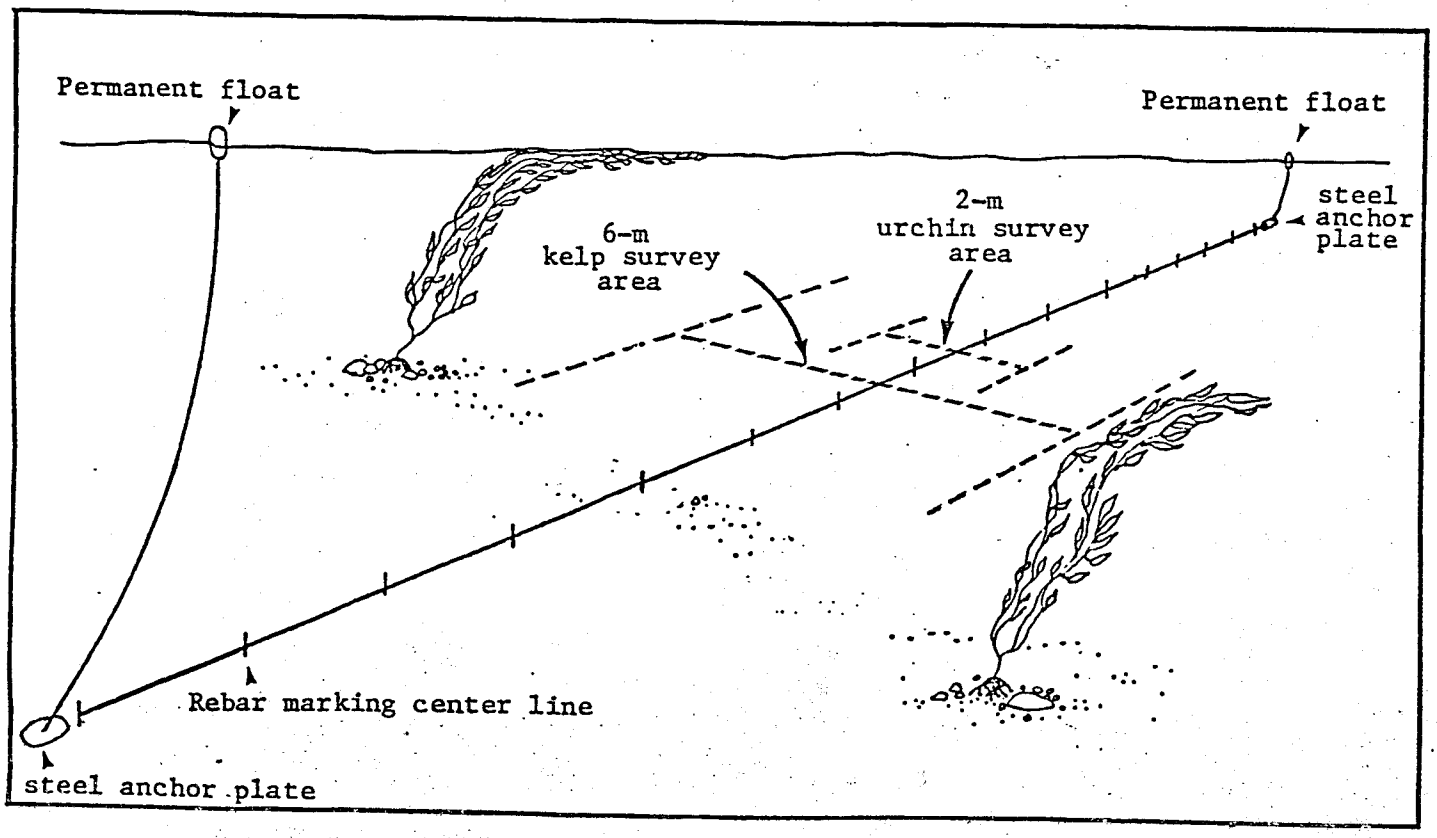

Permanent float
Permanent float
steel anchor plate
2-m urchin survey area
6-m kelp survey area
Rebar marking center line
steel anchor plate

Figure 9.3 Mean abundances of juvenile, subadult, and adult Macrocystis from 24 transects within the San Onofre kelp forest from 1978 through 1980. Also shown are the numbers of those plants that (a) recruited over the previous survey interval, (b) grew from a smaller size-class in the previous survey interval and, (c) survived from the previous survey interval without growing into the next size-class.

Figure 9.3

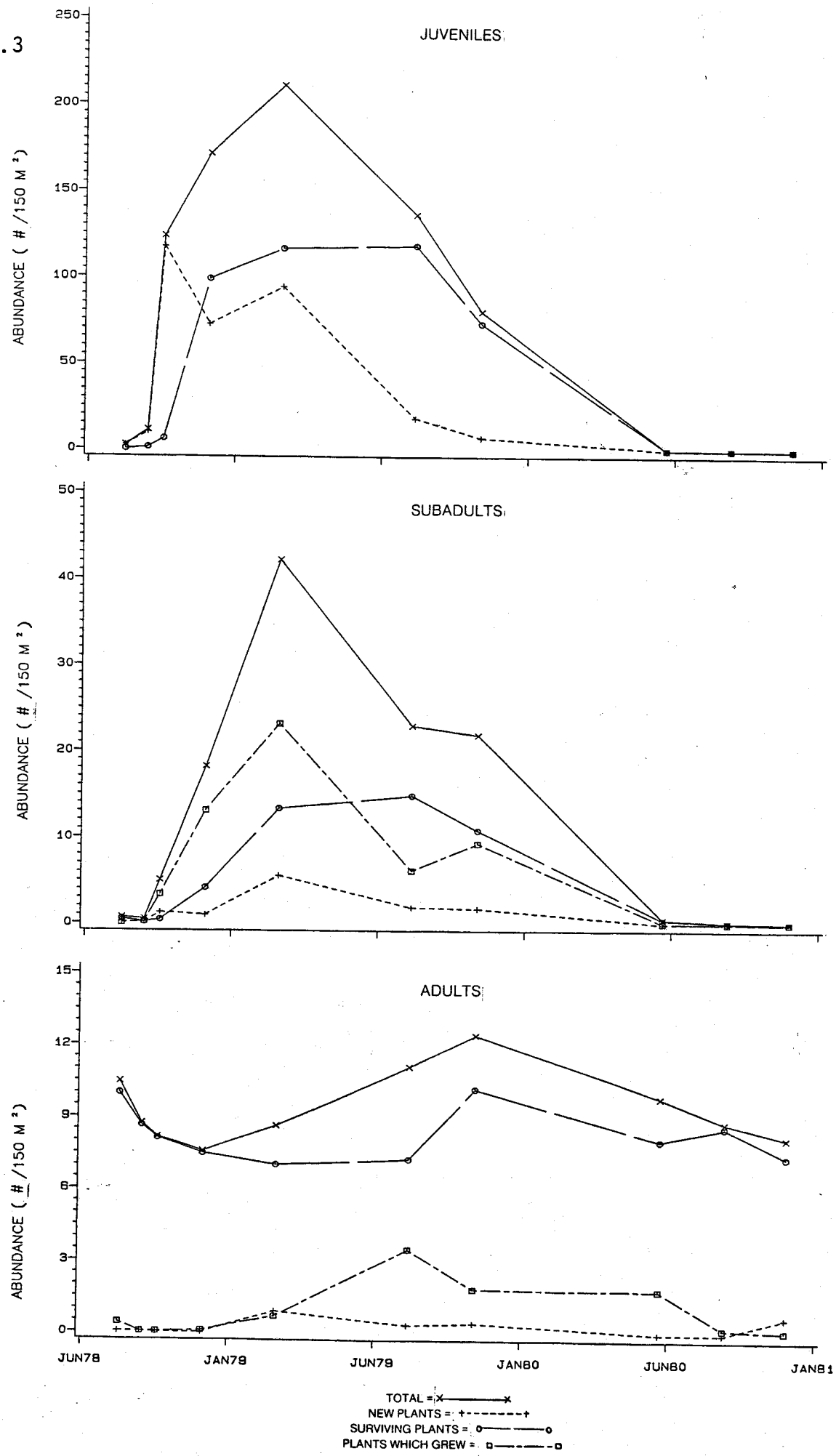

JUVENILES
SUBADULTS
ADULTS
ABUNDANCE (# /150 M ²)
250
200
150
100
50
0
40
30
20
10
15
12
9
6
3
JUN78
JAN79
JUN79
JAN80
JUN80
JAN81
TOTAL =
NEW PLANTS =
SURVIVING PLANTS =
PLANTS WHICH GREW =

Figure 9.4 Average survivorship (±1 SE) and size distribution of 6 cohorts of Macrocystis recruited on 24 transect halves in the San Onofre kelp forest from September 1978 through December 1980. Size categories are given as juvenile (open circles), subadult (filled circles) and adult (triangles). Survivorship data were scaled to produce a hypothetical cohort of 1000 individuals. Actual numbers of plants initially tagged in each cohort are also given.

Figure 9.4

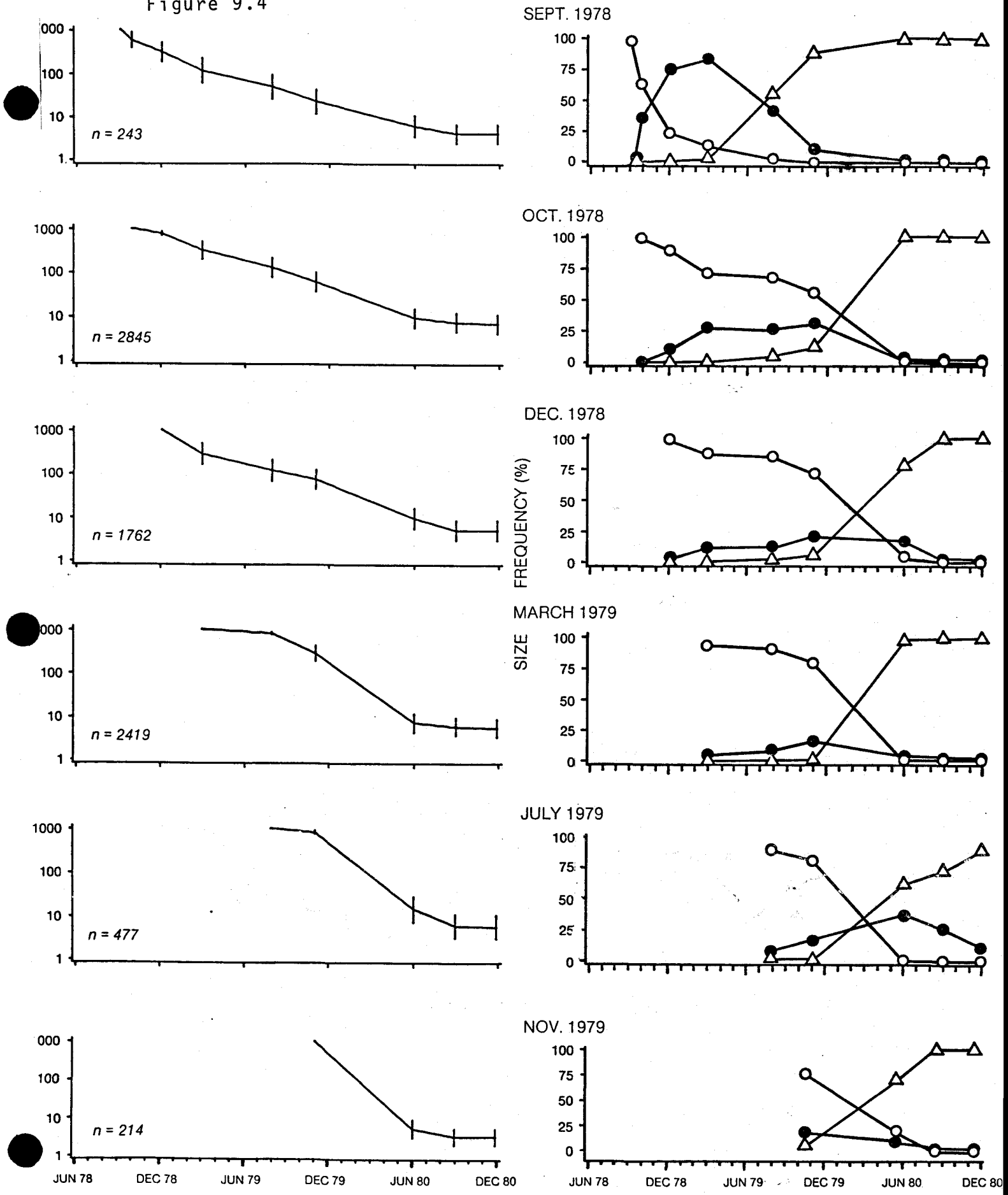

SEPT. 1978
OCT. 1978
DEC. 1978
MARCH 1979
JULY 1979
NOV. 1979
n = 243
n = 2845
n = 1762
n = 2419
n = 477
n = 214
FREQUENCY (%)
SIZE
JUN 78
DEC 78
JUN 79
DEC 79
JUN 80
DEC 80

Figure 9.5 Percent survival of plants in June 1980 vs the total number of recruits on each transect half over the period from August 1978 to November 1979. The curve was fit using a least squares regression of log y with log x.

Figure 9.5

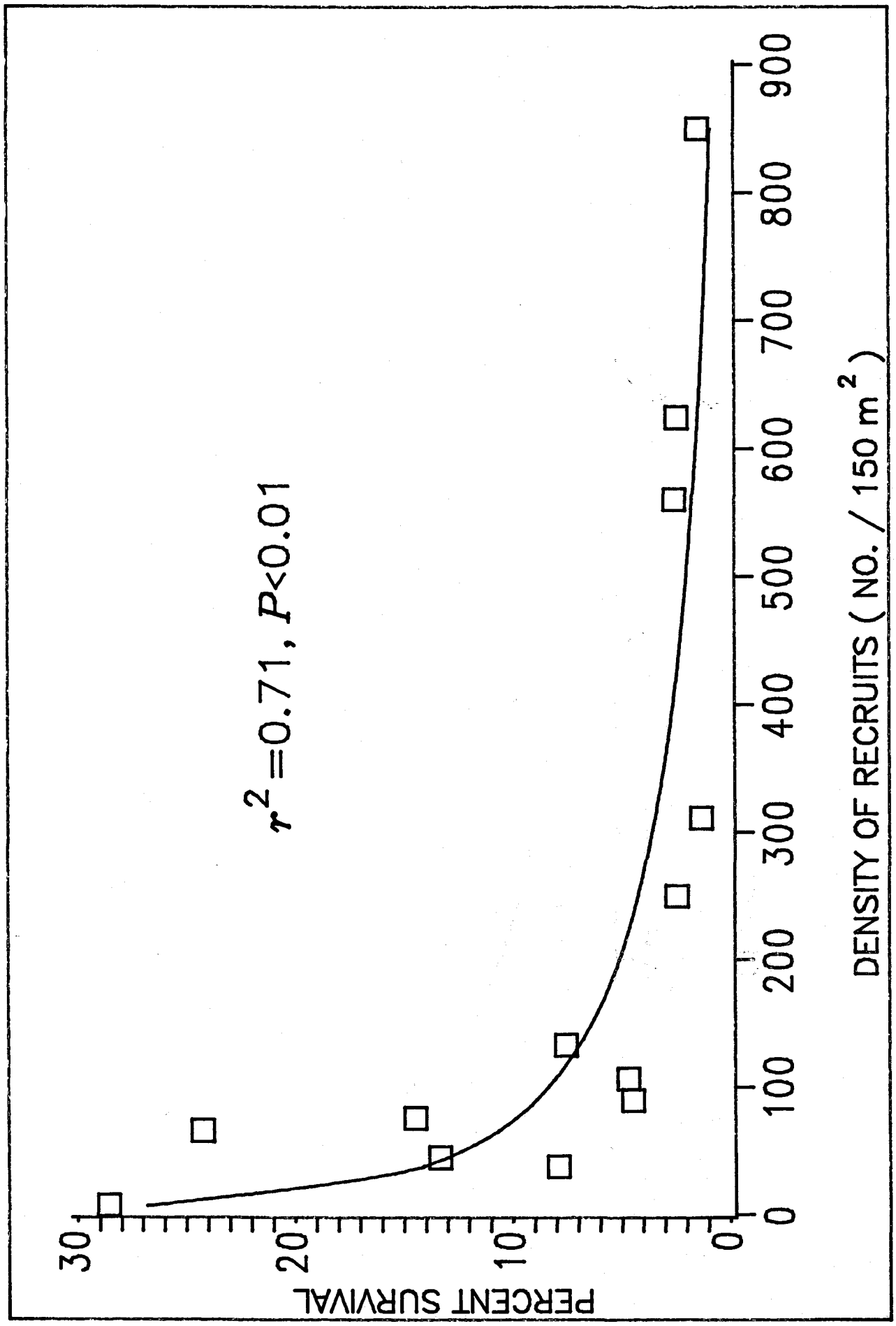

r^2=0.71, P<0.01
PERCENT SURVIVAL
30
20
10
0
0
100
200
300
400
500
600
700
800
900
DENSITY OF RECRUITS (NO. / 150 m^2)

Figure 9.6 Changes in dispersion pattern of Macrocytis as indicated by the Clark-Evans index, R, over time. Values given are means ± 1 S.E. from transect halves where numbers of recruits was ≥ 6. R values of 1 indicate a random distribution, while values greater than 1 are uniform, and values of less than 1 are clumped. Also shown are the number of transect halves with uniform (U), random (R), or clumped (C), distributions before recruitment (when only adults were present) after recruitment, and after recruits had either died or grown to adult size. "IN" indicates that there were insufficient numbers of plants (<6) on transects to compute meaningful nearest neighbor relationships.

Figure 9.6

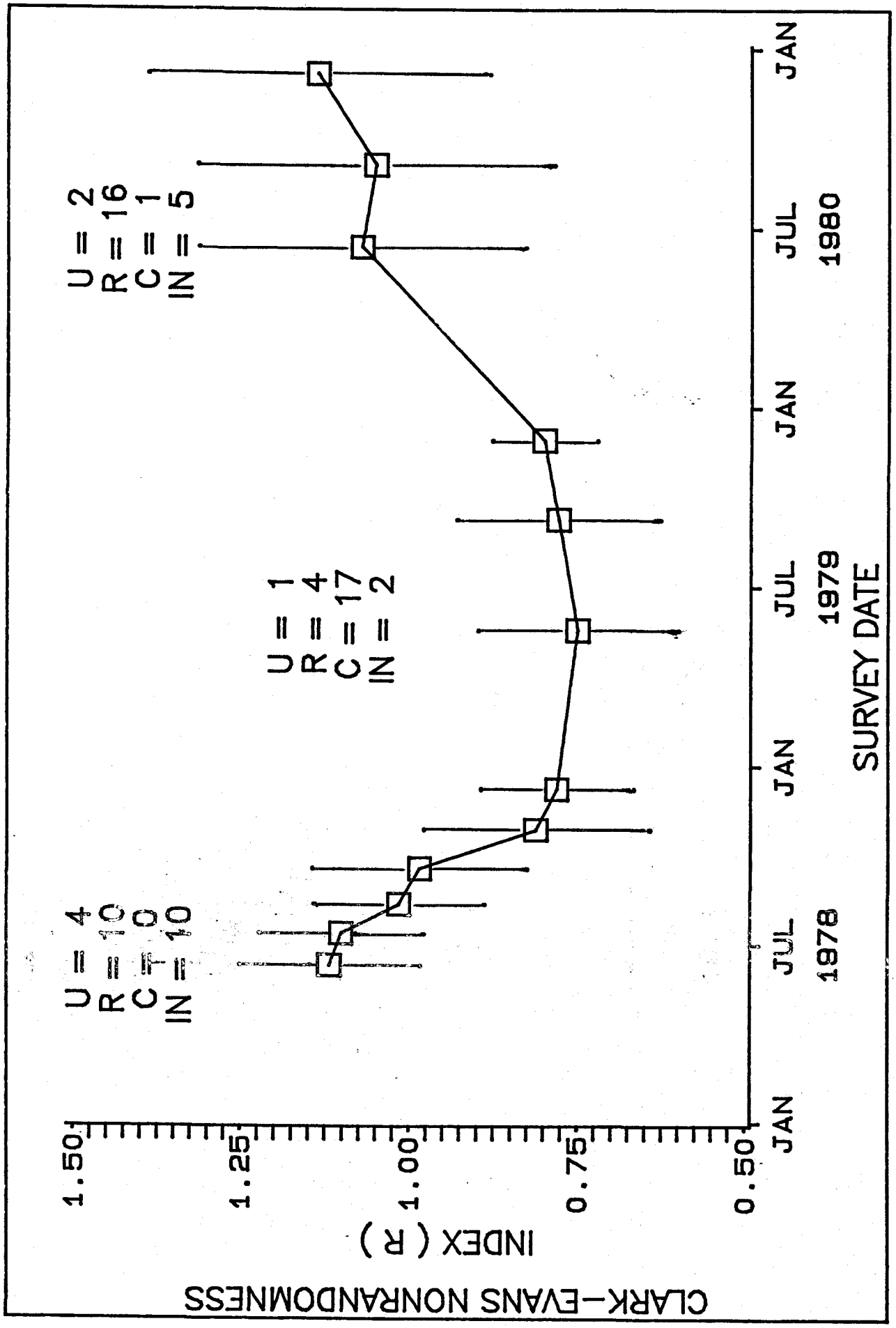

CLARK–EVANS NONRANDOMNESS
INDEX (R)
1.50
1.25
1.00
0.75
0.50
JAN
JUL
1978
JAN
JUL
1979
JAN
JUL
1980
JAN
SURVEY DATE
U = 4
R = 10
C = 10
IN = 10
U = 1
R = 4
C = 17
IN = 2
U = 2
R = 16
C = 1
IN = 5

Figure 9.7 Relationship between the proportion of surviving plants that were juveniles (top) or adults (bottom) in November 1979 and the number of plants initially recruited on each transect half. The squares are for plants recruited between August 1978 and December 1978; the circles are for plants recruited between March 1979 and November 1979.

Figure 9.7

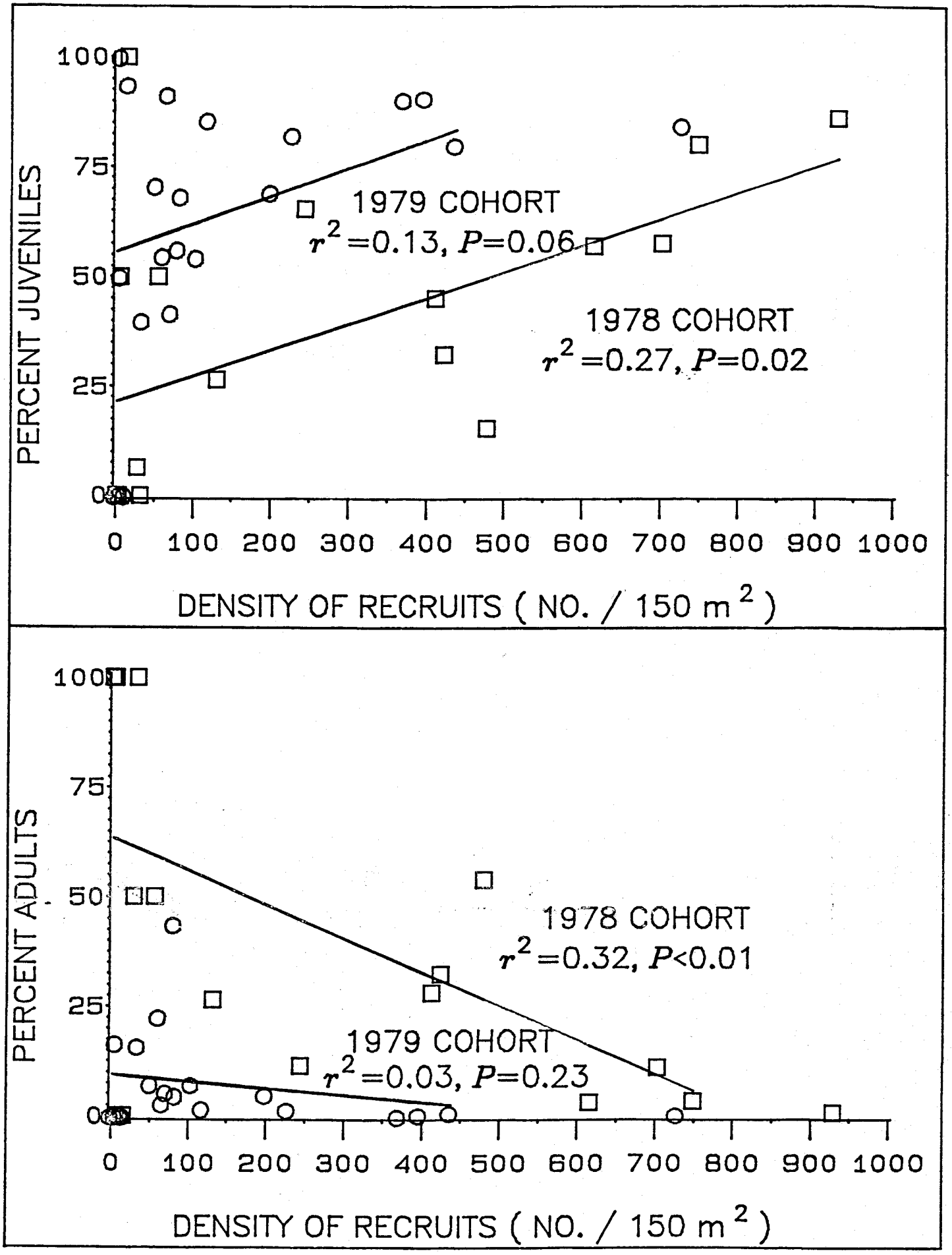
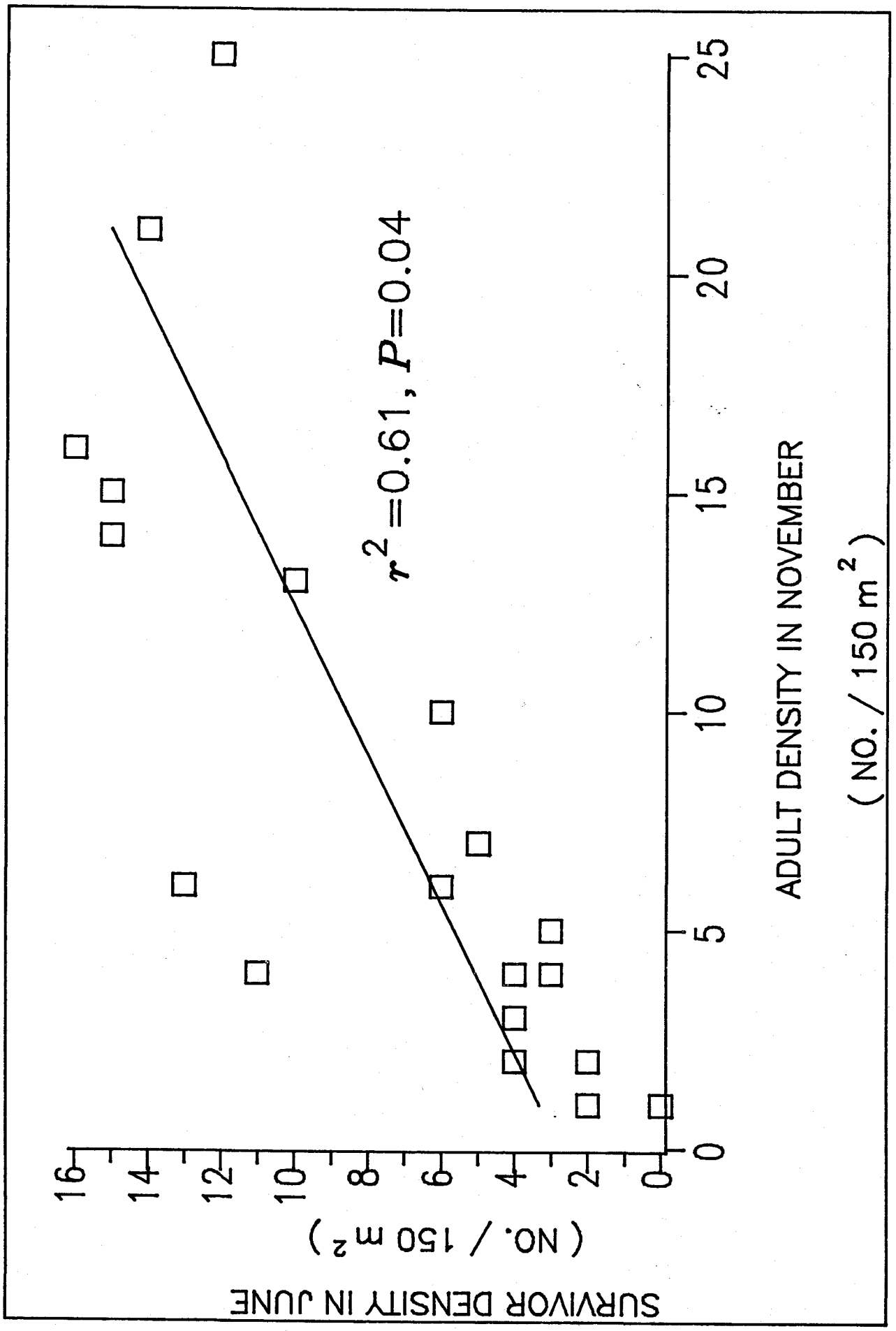

PERCENT JUVENILES
100
75
50
25
0
1979 COHORT
r^2=0.13, P=0.06
1978 COHORT
r^2=0.27, P=0.02
0 100 200 300 400 500 600 700 800 900 1000
DENSITY OF RECRUITS (NO. / 150 m^2)
PERCENT ADULTS
100
75
50
25
0
1978 COHORT
r^2=0.32, P<0.01
1979 COHORT
r^2=0.03, P=0.23
0 100 200 300 400 500 600 700 800 900 1000
DENSITY OF RECRUITS (NO. / 150 m^2)

Figure 9.8 Relationship between the number of plants recruited on each transect half in 1978 and 1979 that had reached adult size by November 1979 and the total number of survivors from those cohorts in June 1980.

Figure 9.8


SURVIVOR DENSITY IN JUNE
(NO. / 150 m²)
16
14
12
10
8
6
4
2
0
0
5
10
15
20
25
ADULT DENSITY IN NOVEMBER
(NO. / 150 m²)
r²=0.61, P=0.04

10.0 Growth of Juvenile Sporophytes

10.1 Introduction

In this chapter, we examine the factors which may limit the growth of juvenile kelp *in situ* as part of our effort to understand the factors controlling the distribution of *Macrocystis pyrifera*. We examine the effects of irradiance, nitrogen availability, temperature, and fouling on the growth of juvenile sporophytes, and attempt to establish the levels of these factors which are limiting to growth. In addition, we test the hypothesis that growth of juvenile kelp during periods of high temperature is nutrient-limited. These relationships will be used to establish possible mechanisms of impact of SONGS Units 2 and 3 on the growth rate of juvenile sporophytes which is presented in a separate document.

Studies of factors which may influence growth and abundance of *M. pyrifera* have focused primarily on the adult sporophyte. Particular attention has been given to the effects of temperature and nutrient availability on adult survivorship (North and Schaeffer, 1964; Jackson, 1977) and on adult frond growth (North, 1971; Wheeler and North, 1981; Gerard, 1982a, 1982b; and Zimmerman, 1983) and to the effects of urchin grazing (Leighton, 1971, Dean *et al*., 1983) storms, (Rosenthal *et al*., 1974), or a combination of all of the above factors (Foster, 1982; Cowen *et. al*., 1982), on adult survivorship. However, the distribution of *M. pyrifera* may be largely determined by growth and survival of gametophyte or small sporophyte stages (Foster, 1975; Devinny and Volse, 1978; Neushul, 1978, 1981; Dean and Deysher, 1983; Dayton *et al*., 1984).

Non-manipulative ecological studies have indicated light intensity, water temperature, and nutrient availability as important factors affecting the growth of mature *Macrocystis pyrifera* (North, 1967, 1971, 1972; Lobban, 1978a). More recent

experimental studies by North and Zimmerman (1984) and Zimmerman and Kremer (1984) have shown that the fertilizing of adult plants under high temperature and low nutrient conditions enhances growth. The growth of adult sporophytes during the recent El Nino was slowed because of nitrogen starvation and possibly temperature stress (Gerard, 1984; Zimmerman and Robertson, 1985). Fouling of kelp blades by sessile invertebrates may also affect growth of adult plants (Lobban, 1978b).

The growth and survival of juvenile kelp are presumably determined by the same environmental factors that influence the adult sporophytes. Neushul (1981) found that juveniles located under a canopy of adult kelp had poorer survivorship than juveniles in more open (i.e., higher light) environments. Dayton and Tegner (1984) and Zimmerman and Robertson (1985) observed poor growth of juveniles during an El Nino event. The El Nino caused a shift in current regimes and an intrusion of offshore surface waters into coastal southern California (Fiedler, 1984; Simpson, 1984). This water mass was characterized by high temperatures and low nutrients (Fiedler, 1984; Simpson, 1984). The poor growth of juveniles during the El Nino was associated with the increased temperature and reduced nutrient levels. However, it was unclear whether the high temperatures, low nutrients or other factors actually caused the slower growth. Juvenile plants held in a high light, high temperature and low nutrient environment on an offshore platform grew better when fertilized with nitrogen and phosphorus, thereby indicating nutrient limitation under El Nino-like conditions (North et al., 1982). Laboratory studies have also suggested that irradiance (Neushul and Haxo, 1963) and nitrogen availability (Wheeler and North, 1981; Shivji, 1985) may limit the growth of juvenile sporophytes. The relative importance of these physical factors in determining the growth rates of juveniles in natural populations may be quite different than that governing the growth of adults; simply because the physical and chemical environment near the bottom (where

juveniles reside) is different from that of the surface water (where most adult tissue is located).

10.2 Methods

10.2.1 General Methods

We examined the relationship between the growth of Macrocystis pyrifera and environmental factors by transplanting juvenile kelp to various locations in SOK and SMK and concurrently measuring physical and chemical variables. Plants used in these experiments were taken from a number of sources (Table 10.1). Laboratory-recruited populations were used when possible. These plants were cultured on 0.6 cm diameter nylon rope. Two 2-m lengths of rope were looped across the surface of 30 x 10 x 0.6 cm plexiglass plates and secured with small plastic cable ties. The inoculation procedures used were identical to those used in the gametophyte survival and outplant experiments (Sections 3.2 and 6.2) with one exception; the zoospore concentration used in the sporophyte substrate inoculation was 1×10^4 zoospores/ml, an order of magnitude lower than that used in the gametophyte outplant inoculation. This lower concentration was used in order to avoid severe crowding of sporophytes.

Substrates used in the sporophyte experiments were cultured for 14 days in the laboratory before being outplanted to the field. The plates were cultured under a continuous irradiance regime (photon flux density = 45 $\mu E/m^2/s$) at 15^oC in 25ℓ plastic containers (35 x 20 x 45 cm) containing 10ℓ of Provasoli's enriched seawater (Appendix ___). One plate was suspended in each container at mid-depth of the culture medium by means of a PVC rack. The culture medium was changed midway through the 14-day culture period. Cultured substrates were transported to the field stations in the same manner as plates in the gametophyte outplant experiments (Section 6.2).

Ropes were outplanted to either SOKD45, or after Units 2 and 3 became operational in 1983, to SMK45. Both of these sites were cleared of Macrocystis and large understory algae. Rows of steel reinforcement bars (rebar) were driven into the seafloor with 1 m of each bar left standing about 1 m above the seafloor. The rebar were set about 1 m apart with equivalent spacing between rows. Divers removed the 2 m sections of rope from the plates while on the bottom. Each rope was spread between 3 rebar and secured with platic cable ties. The small sporophytes were then allowed to grow to a height of 40 cm before being used in experiments.

10.2.2 The Effects of Transplanting on Growth

In 1978, a preliminary study was conducted to determine how the transplanting procedures affected the growth rates of Macrocystis pyrifera. Growth rates of naturally-occurring juveniles at a site in the San Onofre Kelp forest were compared with growth rates of juveniles which were transplanted from the same site onto artificial substrates positioned adjacent to the "natural" (i.e. undisturbed) plants. The artificial substrates consisting of L-shaped pieces of steel reinforcement bar anchored by cement bags. The holdfast of each juvenile was secured to the L-rebar with plastic cable ties. Juveniles in the control plot were thinned and were tagged for future identification. All other macroalgae, including large adult M. pyrifera, were cleared from around both the natural and transplanted individuals.

Each plant was measured at the beginning of the experiment and at 2-wk intervals throughout. Each frond was measured from the primary basal dichotomy of the stipe to the tip of the apical scimitar blade (see Lobban, 1978a and Section 1.0 for a description of plant morphology). Secondary- and higher-order fronds were measured when they began to form visible pneumatocysts. At the completion of the experiment, surviving plants were collected and measured again.

10.2.3 Comparison of Growth Rates of Naturally-Recruited Juveniles and Juveniles Grown from Outplanted Stock

Another preliminary experiment was performed on 2 separate occasions in order to examine possible differences in the growth of juvenile Macrocystis pyrifera grown from outplanted sporophytes vs those that had recruited on natural substrates. On 18 December 1980, we collected 26 juvenile plants from ropes harboring sporophytes recruited and reared in the laboratory. These plants were attached to sawhorse-like racks using plastic cable ties (Fig. 10.2) at the SOKD45 site. The racks were arranged in 2 parallel rows. The rows, as well as the racks within each row, were spaced 2 m apart. Five days later (on 23 Dec 1980), 15 juveniles were collected from the Carlsbad kelp forest, about 21 km to the south of San Onofre, and transplanted to the same SOKD45 station in the manner just described. Immediately after transplanting, each frond on both transplanted and natural plants was measured as described in the previous section. Approximately 1 month after transplanting (on 19 January 1981), we collected all remaining plants and again measured the fronds.

We conducted a similar experiment in 1982. On 19 January 1982, we transplanted 24 laboratory-recruited plants along with 26 naturally-occurring juveniles taken from the eastern portion of SOK forest to racks at the SOKD45 site. These plants were similarly measured immediately after transplanting and again on 2 March 1982.

10.2.4 The Effects of Physicochemical Factors on Growth and Mortality

We conducted 16 transplant experiments from 1979 through 1986 in order to examine the effects of environmental variables on the growth and mortality of juvenile kelp. Six stations located in the San Onofre and San Mateo kelp forests were used at various times throughout our study (Fig. 10.1). A complete tabulation of the dates for each transplant and the stations used are given in Table 10.1. All

stations were located within 50 m of adult kelp populations that persisted for the length of the study, and all were at a depth range of 13.2 to 14.4 m. At the canopy stations (SMK-CAN, SOKD-CAN, SOKU-CAN) transplants were placed under a stand of adult Macrocystis pyrifera. At the other stations (SOKD45, SOKU45, and SMK45), all adult plants located within approximately 10 m of the transplant racks were cleared so that they would not shade the transplanted individuals. At each site, we transplanted 25 to 40 juveniles onto racks, as described previously, for a period of between 6 and 10 weeks.

During the course of each experiment, integrated quantum irradiation and temperature were measured at 2 m above the bottom at each site. Methods used to measure temperature and irradiance are given in Appendix C. Mean values for given experimental periods were calculated from irradiation and temperature values recorded at 1 to 2-hr intervals.

Nitrogen data were obtained from Marine Ecological Consultants (MEC), and Ecosystems Management Associates. We used their values for total nitrogen (NO_2 + NO_3 + NH_4). Samples were taken at various frequencies ranging from weekly to bi-monthly. Water samples collected for nitrogen analysis were not always taken from exactly the same locations as our stations. In these instances, we used data collected from within 100 m of our stations in a given kelp forest. This was justified based on the relative lack of longshore variability in nutrients within these kelp forests (Reitzel, et al., future MRC report).

After plants were collected at the end of an experiment, a bottom blade from each plant (or a subset of 5 randomly selected plants in 1979 experiments) was removed for a determination of the abundance of fouling organisms. A grid of points

spaced 1 cm apart, was laid over the blade, and the number of points contacting fouling organisms was recorded. For both the fouling study and the tissue carbon/nitrogen analyses described below, a bottom blade refers to the first intact blade encountered when moving up each frond from the primary dichotomy.

Beginning in 1981, we also sampled juvenile plants to determine tissue carbon (C) and nitrogen (N) levels. At the beginning of each transplant experiment, one blade from each of the 10 to 20 plants left over from the pool of plants collected for transplanting was sampled bottom to determine initial levels of C and N. Each blade was cleaned of any fouling organisms, frozen, and subsequently analyzed with a Hewlett-Packard CHN analyzer. From 1981 to 1984, we sampled a bottom blade at the end of each experiment from each surviving plant to determine the final levels of C and N in the plants. During 1985 and 1986, we sampled bottom blades from a subset of 5 randomly selected plants from each station at the end of the transplant experiments. Levels of C and N were determined by averaging the initial measurements and those taken from each station at the end of the transplant period.

10.2.5 Comparison of Growth Rates of Fertilized vs Unfertilized Juveniles

The effect of nutrient availability on growth was examined by fertilizing transplanted juveniles at the SMK45 station, and comparing the growth of these fertilized plants to unfertilized controls placed on racks about 15 m away. Muslin mesh bags, measuring 30 cm long x 4 cm in diameter, were filled with 200 g of Osmocote fertilizer (Sierra Chemical Co., Milpitas, California). This fertilizer is a blend of ammonium nitrate and phosphate salts (26% N and 11% P) which is pelletized and coated with a semipermeable polymer film. The bags of fertilizer were attached to the racks and were arranged so that one bag surrounded the holdfast of each plant. Bags of fertilizer were replaced by new bags every 7 to 10 days.

We did not measure nitrogen and phosphorus levels in the seawater within the vicinity of the fertilizer during this experiment. However, studies at SOKD in 1981 showed that during a period when ambient nitrogen levels (NO_3 + NO_2 + NH_4) were approximately 1 to 3 µM, total nitrogen levels within several cm of the fertilizer were 10 to 18 times higher than ambient after 2 days, and were 7 to 8 times higher than ambient after 7 to 10 days (Table 10.2). No increase in nitrogen level over ambient could be detected at 10 m from the fertilizer. Phosphorus levels were not measured in 1981 either, but since both nitrogen and phosphorus were coated with the same semipermeable film, we presume that the release rates for phosphorus were similar to that of nitrogen, and that phosphorus levels were also elevated in the vicinity of the fertilizer.

Two nutrient addition experiments were conducted from 5 July to 24 July 1984, and from 24 July to 4 September 1984. In the first experiment, 20 plants were transplanted to the SMK45 site. Ten plants (5 on each of two racks) were fertilized and 10 plants (placed on another two racks) were unfertilized. In the second experiment, we transplanted 35 plants to SMK45. Ten plants were fertilized and the other 25 were unfertilized. In both experiments, fertilized racks and control racks were spaced 15 m apart to prevent drift of fertilizer from the fertilized to the control plants. During the second experiment, 25 unfertilized plants were also transplanted to SOKU45 and SOKD45 stations (as part of our ongoing BACI-P and physiochemical studies). Tissue nitrogen was measured as described previously.

10.2.6 Growth Rate and Mortality Rate Calculations and Statistical Analyses

Relative growth rates (RGR) were calculated as:

$$RGR = \frac{\ln(L_2) - \ln(L_1)}{t_2 - t_1}$$

where L_2 and L_1 are the final and initial lengths summed over all fronds on the plant, and $(t_2 - t_1)$ is the number of days between measurements. Data on all plants with missing fronds or damaged scimitar blades were eliminated from the analyses of growth rate. This function was appropriate for measuring the growth of juvenile Macrocystis because plants in this size range display a geometric pattern of growth (Lobban, 1978a and results below).

Instantaneous mortality rates were calculated using an equation similar to that described above:

$$\text{Mortality rate} = \frac{\ln(N_2) - \ln(N_1)}{t_2 - t_1}$$

where N_2 and N_1 are the number of plants surviving at times t_2 and t_1, respectively.

Differences in mean growth rates among transplanted vs control plants and among naturally-recruited vs laboratory-recruited sporophytes in our preliminary experiments were tested with the Student's t-statistic (Sokal and Rohlf, 1969).

The relationships between growth rates and environmental variables, and mortality rates and environmental variables, were determined by a multiple regression analysis (Belsley et al., 1980) using a Statistical Analysis System (SAS) package (SAS, 1982). For these analyses, the independent variables were log-

transformed. Preliminary analyses indicated that the log transformed model yielded a better fit to the data (higher R^2) than untransformed models in most cases.

We used mean growth rates in our models rather than the growth for individual plants for two reasons. First, the number of plants which survived undamaged at each station through each experiment varied. Using growth rates for individual plants would have weighed more heavily those stations with higher numbers of useable growth rates. Second, the irradiation, temperature, and nutrient data were collected from a single site near the transplant racks. Therefore, each plant did not have its own unique set of data for independent variables. Using mean growth rates in the regression models over-estimates the R^2 because between-plant variability is ignored. However, this source of variability is relatively unimportant in our evaluation of the effects of physical/chemical factors on growth.

Data that were collected from sites in SOK after the beginning of operation of SONGS Units 2 and 3, were eliminated from the analyses. Also, we only used data from depths of approximately 13 to 14 m. Data from earlier experiments near the Unit 1 discharge (depth = 8 m) and from the inshore portions of SOK and SMK (depth = 10 m) were eliminated. We did not use these data because the morphometrics of plants changes with depth, making it impossible to compare growth rates based on frond length measured at different depths.

We determined the compensating irradiation level (I_o, the irradiation level below which no growth occurs) and the maximum growth rate (G_{max}) by fitting a function similar to the von Bertalanffy growth equation (Ricker, 1975):

$$G = G_{max} (1-e^{k(I - I_o)})$$

where G is the relative growth rate (d^{-1}), G_{max} is the maximum growth rate or asymptote of the growth curve, I is the irradiation level in $E/m^2/d$ and I_o is the compensating irradiation level.

10.3 Results

10.3.1 Preliminary Experiments: Patterns of Growth and the Effect of Transplanting on Growth

In preliminary experiments of September 1978, there were no significant differences in the average growth rates among transplanted and control plants (Table 10.3) indicating that our transplant procedure had no effect on the growth rate of Macrocystis pyrifera.

Both transplanted and control plants showed similar patterns of exponential growth (Fig. 10.3). The actual rate of growth varied depending on the physicochemical conditions during the transplant period. The growth of plants in the 0.5 to 4 m size-range remained on the exponential part of the growth curve and there was no indication of growth rate approaching an asymptote.

Experiments comparing laboratory-recruited vs naturally-recruited plants indicated that there were no significant differences among the two groups with respect to growth rate, variance in growth, or survival (Tables 10.4 and 10.5). However, the growth rate of laboratory-recruited plants was somewhat lower than for naturally-recruited plants (doubling times of 18 and 24 days, respectively),

suggesting that differences in sources may have contributed to the variance in the growth rate.

10.3.2 Factors Affecting Growth

We examined the following factors which could have influenced the growth rate of juvenile plants and may have been responsible for both temporal and spatial differences in growth: (1) irradiation, (2) temperature, (3) total inorganic nitrogen, and (4) fouling of blades (Appendix _). A regression of the mean of growth rates of plants at each station during each experiment vs their associated environmental variables indicated that irradiation and temperature (at the 0.1 level) explained a significant portion of the variance in growth rate with an R^2 = 0.50 (Table 10.6). There was a positive relationship between growth and irradiation, while growth was inversely related to temperature. Irradiation explained the largest portion of the variance, while the relationship of temperature with growth was weak.

In order to examine the possible effects of stored carbon and nitrogen on growth, we added tissue carbon and nitrogen as independent variables and ran the regression again. This analysis used a slightly different data set. Tissue C and N data were not collected in 1979 or 1980. Data collected prior to 1981, therefore, were not included in the regression. Irradiation and temperature were the most significant contributors to the explained variance in growth rate. Tissue nitrogen was significant only at the 0.1 level and tissue carbon was not significant (Table 10.7). The analysis yielded an R^2 of 0.72.

The relationship of growth rate with irradiation and temperature is given in Figure 10.4. Growth rate at a given irradiation level was lower at temperatures

above about 16.5°C. However, there is some question as to whether growth was actually limited by high temperatures or by low nutrient levels that are associated with high temperature. Studies conducted by ECOsystems Management Assoc. (Section 6.0, Fig. 6.5) indicate that there is a strong negative correlation of nitrate and nitrite nitrogen with tempeature and that nitrate and nitrite levels in sea water are seldom above 1 μM at temperatures greater than 16.5°C.

We tested the hypothesis that growth was nutrient-limited in two nutrient addition experiments conducted in summer 1984. This was during the El Nino period when temperatures were high (averaging 16.5° and 17.7°C near the bottom during the two experiments) and nitrogen concentrations were low. The fertilized plants grew significantly better than the unfertilized plants in both experiments (Table 10.8). The relative growth rates of the fertilized plants were similar to the maximum growth rates observed in our study when light levels were high, temperatures were below 16.5°C and nitrogen levels were high (Fig. 10.5).

Mean tissue nitrogen levels were slightly higher for fertilized plants than for unfertilized ones. However, differences in tissue nitrogen levels at the end of the experiments were not significant (Table 10.9).

10.3.3 Compensating Irradiation and Maximum Growth Rates

The compensating irradiation level, under non-limiting nutrient conditions, was estimated first by using an equation derived from the regression of growth vs irradiance for all cases when temperatures were below 16.5°C (Table 10.10). This yielded an estimate for the compensation point of 0.23 $E/m^2/d$.

We also determined the compensating irradiation level and the maximum growth rate by fitting a function similar to the von Bertalanffy growth equation (Ricker, 1975). This function appeared to fit the available data better than the simple logarithmic one used in the regression analysis. We again eliminated data with temperatures greater than 16.5°C. This curve fitting procedure yielded a compensation value of 0.69 $E/m^2/d$ and a maximum growth rate of 0.022 d^{-1} (Table 10.10). The latter value corresponds to a doubling time of 31 days. The maximum growth rate occurred when irradiation levels were above the apparent saturation level of between 2 and 3 $E/m^2/d$ (Fig. 10.5).

10.3.4 Factors Affecting Mortality

We examined the same set of environmental factors as was previously used in the growth rate analysis to determine what influence they had on mortality rates of the transplants. Regression of mortality rates with these environmental variables indicated that none of the variables explained a significant portion of the variance in mortality rates of the juvenile transplants (Table 10.11 and 10.12).

10.4 Discussion

The growth of juvenile Macrocystis pyrifera in the San Onofre and San Mateo kelp forests was determined primarily by irradiation and nutrient levels. In most instances, growth appeared to be irradiance limited. We estimated the compensating irradiation level at 0.7 $E/m^2/d$ and the saturation level at between 2 and 3 $E/m^2/d$. Irradiation at 2 m above the bottom in the kelp forests generally fall between the compensation and saturation points. Nutrient limitation was most prevalent during the El Nino from fall 1982 through fall 1984, when temperatures were high and nutrient levels were low. Of the 9 instances when mean temperatures during our experiments were above 16.5°C (indicating low nutrient levels), 6 occurred during the El Nino.

Regression analyses indicated that temperature was negatively correlated with growth rate. However, nutrient addition experiments demonstrated that given sufficient nitrogen and phosphorus, maximum growth could be maintained at temperatures of up to 18°C. Temperature appeared to act as an indicator nutrient availability because of the correlation between temperature and nutrients (Reitzel, et al., future publications). Hourly temperatures, as measured in our study, probably gave an even better estimate of nutrient availability than nitrate and nitrite concentrations measured on a weekly basis. This is because of the high degree of short-term temporal variability in nutrients that is observed in shallow coastal waters in southern California (Zimmerman and Kremer, 1984).

Tissue nitrogen was only weakly correlated with growth rates of juveniles. Gerard (1982) indicated that tissue nitrogen levels become limiting for growth when they fall below 1.1% N. However, supplies of tissue nitrogen can vary considerably from week to week. Unlike other laminarian species, Macrocystis has relatively limited supplies of tissue nitrogen and depletes them rapidly (Wheeler and North, 1981; Gerard, 1984). Our sampling of tissue nitrogen at only the beginning and end of our experiments probably gave a poor estimate of the tissue nitrogen levels in plants over the 6-week period.

We cannot completely rule out the possibility that growth may at times be limited by some other factors. Gerard (1984) suggested that high temperatures (>18°) may limit the growth of small fronds on adult Macrocystis. We did not conduct nutrient addition experiments at such high temperatures and therefore cannot address the possibility of direct effects of temperature. It may also be that there is some interactive effect of temperature and nutrients as was reported by Lapointe et al. (1984). Fouling of kelp blades by sessile invertebrates may also affect growth

(Lobban, 1978b). We found no significant effect of fouling on the growth of the juvenile kelp in our experiments, however, Dixon et al. (1981) found that very heavy cover of kelp by fouling organisms could cause reduced growth.

It is probable that irradiation and nutrient availability interacted to control growth. Although we do not have sufficient nutrient data to allow us to develop a model of interactive effects, it appears that both the compensating and saturating irradiation levels increased during the period when nutrients were limiting (Fig. 10.5). Nutrients and irradiance have been shown to have an interactive effect on juvenile Macrocystis grown in laboratory culture (Shivji, 1985) and other algae as well (Lapointe and Tenore, 1981; Rhee and Gotham, 1981).

Regression analyses explained approximately 50% to 70% of the variance in mean growth rate on a given station and date. The unexplained variance can likely be attributed to several causes, including measuring error in both dependent and independent variables and possible effects of history or conditioning of plants prior to transplanting. However, we suspect that a large portion of the unexplained variance was due to variability in the nitrogen-temperature relationship. Nitrate and nitrite levels in seawater are uniformly low at temperatures above 16.5°C and are uniformly high at temperatures below 13°C, but there is considerable variability at temperatures between 13° and 16.5°C (see Section 6.0, Fig. 6.5). Temperatures on the seafloor at the San Onofre and San Mateo kelp forests generally fall within this range making the use of temperature as an indicator of nitrogen crude.

Analyses of the juvenile transplant mortality data showed no significant correlations with environmental variables. This is not surprising and certainly does not mean that environmental factors are not influencing juvenile kelp

mortality. The transplant experiments were designed to minimize mortality in order to avoid the confounding effects of mortality on our estimation of growth rate. This was done transplanting juveniles onto racks and by raising the juveniles up off the seafloor. This reduced the potential for competition with other plants, predation by benthic grazers (such as sea urchins), and effects of sediment/sand movement. In addition, the length of the experiments, 6 weeks, was selected to minimize mortality. Plants which were stressed would likely be able to survive for 6 weeks but would not be able to survive much longer time periods.

Table 10.1 Dates, sources of juvenile kelp, and stations for each of 16 transplant experiments.

Date Transplanted	Source	Stations
22 Aug 79	La Jolla	SOKD45, SOKU45
15 Nov 79	Laboratory	SOKD45, SOKU45
18 Sep 80	Carlsbad	SOKD45, SOKU45, SOKD-Can
25 Nov 80	Laboratory	SOKD45, SOKU45, SOKD-Can, SOKU-Can
16 Jul 81	SOK	SOKD45, SOKU45, SMK-Can, SMK45
28 Aug 81	Laboratory	SOKD45, SOKU45, SMK-Can, SMK45
02 Dec 81	SOK	SOKD45, SOKU45, SMK-Can, SMK45
09 Sep 82	Laboratory	SOKD45, SOKU45, SMK-Can, SMK45
24 Jul 84	SOK	SOKD45, SOKU45, SMK45
13 Sep 84	Laboratory	SOKD45, SOKU45, SMK45
09 Jul 85	Laboratory	SOKD45, SOKU45, SMK45
05 Sep 85	Laboratory	SOKD45, SOKU45, SMK45
22 Oct 85	Laboratory	SOKD45, SOKU45, SMK45
18 Dec 85	Encinitas	SOKD45, SOKU45, SMK45
24 Jun 86	Laboratory	SOKD45, SOKU45, SMK45
07 Aug 86	SMK	SOKD45, SOKU45, SMK45

Table 10.2 Nitrogen concentrations of seawater sampled within several centimeters of bags of fertilizer and at control sites 10 m away. Both sites were in SOK; nd = no data.

No. of days after initial placement	Replicate #	Total nitrogen concentration µM	
		Control	Fertilized
Experiment #1 13 July 1981			
7	1	0.6	5.1
	2	0.7	nd
	3	0.6	nd
Experiment #2 29 July 1981			
2	1	1.9	28.0
	2	2.9	35.0
10	1	0.8	6.0
	2	0.7	5.7

Table 10.3 T-test comparing growth of transplanted vs undisturbed plants. An F-test indicated that variances at the two sites did not differ significantly (P = 0.88).

Treatment	N	Mean relative growth rate (/d)	T	DF	PR > T
Transplanted	19	0.024	-0.729	28	0.47
Control	11	0.025			

Table 10.4 T-test comparing mean growth rate (/d) of laboratory vs naturally-recruited plants. F-tests indicated that variances at the two sites did not differ significantly (P = 0.07 and P = 0.55, respectively, for the two experiments).

Experiment of 18 December 1980 to 19 January 1981

Plants	N	Mean growth rate (/d)	T	DF	PR > T
Naturally recruited	23	0.038	2.02	35	0.051
Laboratory reared	12	0.029			

Experiment of 19 January 1982 to 01 March 1982

Plants	N	Mean growth rate (/d)	T	DF	PR > T
Naturally recruited	20	0.013	1.89	36	0.067
Laboratory reared	18	0.011			

Table 10.5 Survival of juveniles that were grown from laboratory-recruited sporophytes vs survival of naturally-recruited juveniles. Alive and dead refer to the number of plants alive or dead at the end of the experiment.

18 December 1980 to 19 January 1981

Source	Alive	Dead
Naturally-recruited	13	2
Laboratory-recruited	24	1

$x^2 = 1.22$, $0.10 < P < 0.20$

19 January 1982 to 2 March 1982

Source	Alive	Dead
Naturally-recruited	23	3
Laboratory-recruited	24	0

$x^2 = 2.80$, $0.05 < P < 0.10$

Table 10.6 Regression of mean growth rates vs log-transformed irradiance and temperature. A preliminary analysis indicated that nitrogen in seawater and percent cover fouling were not significant at $P < 0.10$.

R-square = 0.498
n = 24

Variable	df	Parameter estimate	T	PR > T
Intercept	1	0.184	2.08	0.050
Log irradiation	1	0.012	4.44	<0.001
Log temperature	1	-0.064	-1.96	0.063

Table 10.7 Regression of mean growth rates vs log-transformed irradiance, temperature, and tissue nitrogen. Data collected prior to 1981 were omitted since no tissue nitrogen data were available. A preliminary analysis indicated that nitrogen in seawater and percent cover fouling were not significant at $P < 0.10$.

R-square = 0.723
n = 22

Variable	df	Parameter estimate	T	PR > T
Intercept	1	0.228	6.003	<0.001
Log temperature	1	-0.062	-4.003	0.001
Log irradiation	1	0.013	4.869	<0.001
Log tissue nitrogen	1	0.013	1.940	0.068

Table 10.8 T-tests comparing growth rates (/d) of fertilized vs control plants. In both experiments, variances in growth rates of fertilized and control plants did not differ significantly (F = 0.16 and F = 0.18).

Experiment of 05 July 1984 to 24 July 1984

Plants	N	Mean growth rate (/d)	T	DF	PR > T
Fertilized	8	0.026	-3.96	15	0.001
Control	9	0.012			

Experiment of 24 July 1984 to 04 Sept 1984

Plants	N	Mean growth rate (/d)	T	DF	PR > T
Fertilized	5	0.029	-6.60	19	<0.001
Control	16	0.009			

Table 10.9 T-tests comparing arcsin-transformed tissue nitrogen values (%N) for fertilized vs control plants. Values for damaged plants were eliminated from the analysis. Means are for untransformed data.

Experiment of 05 July 1984 to 24 July 1985

Plants	N	Mean	T	DF	PR > T
Fertilized	8	0.099	-1.46	15	0.164
Control	9	0.092			

Experiment of 24 July 1984 to 04 Sept 1984

Plants	N	Mean	T	DF	PR > T
Fertilized	4	0.092	-1.90	18	0.074
Control	16	0.083			

Table 10.10 Regression of mean growth rates vs log-transformed irradiance during times when water temperatures were less than 16.5°C.

R-square = 0.384
n = 26

Variable	df	Parameter estimate	T	PR > T
Intercept	1	0.011	4.500	<0.001
Log irradiation	1	0.011	3.871	0.001

Table 10.11 Regression of mortality rates vs log-transformed irradiation, temperature, nitrogen and fouling.

R-square = 0.156
n = 19

Variable	df	Parameter estimate	T	PR > T
Intercept	1	-0.018	-0.403	0.693
Log irradiance	1	-0.002	-0.978	0.345
Log nitrogen	1	-0.002	-0.917	0.375
Log temperature	1	0.009	0.558	0.585
Log fouling	1	-0.000	-0.201	0.843

Table 10.12 Regression of mortality rates vs log-transformed irradiation, temperature, nitrogen, fouling, tissue nitrogen and tissue carbon. Data collected prior to 1981 are not included in this analysis because tissue nitrogen and carbon were not analyzed.

R-square = 0.169
n = 19

Variable	df	Parameter estimate	T	PR > T
Intercept	1	-0.028	-0.528	0.607
Log irradiation	1	-0.027	-0.940	0.366
Log nitrogen	1	-0.002	-0.648	0.529
Log temperature	1	0.004	0.171	0.867
Log fouling	1	-0.000	-0.321	0.754
Log tissue nitrogen	1	-0.027	-0.307	0.764
Log tissue carbon	1	-0.011	-0.437	0.670

Figure 10.1 a & b. Maps of the study area and location of stations used in juvenile transplant experiments.

Figure 10.1 a

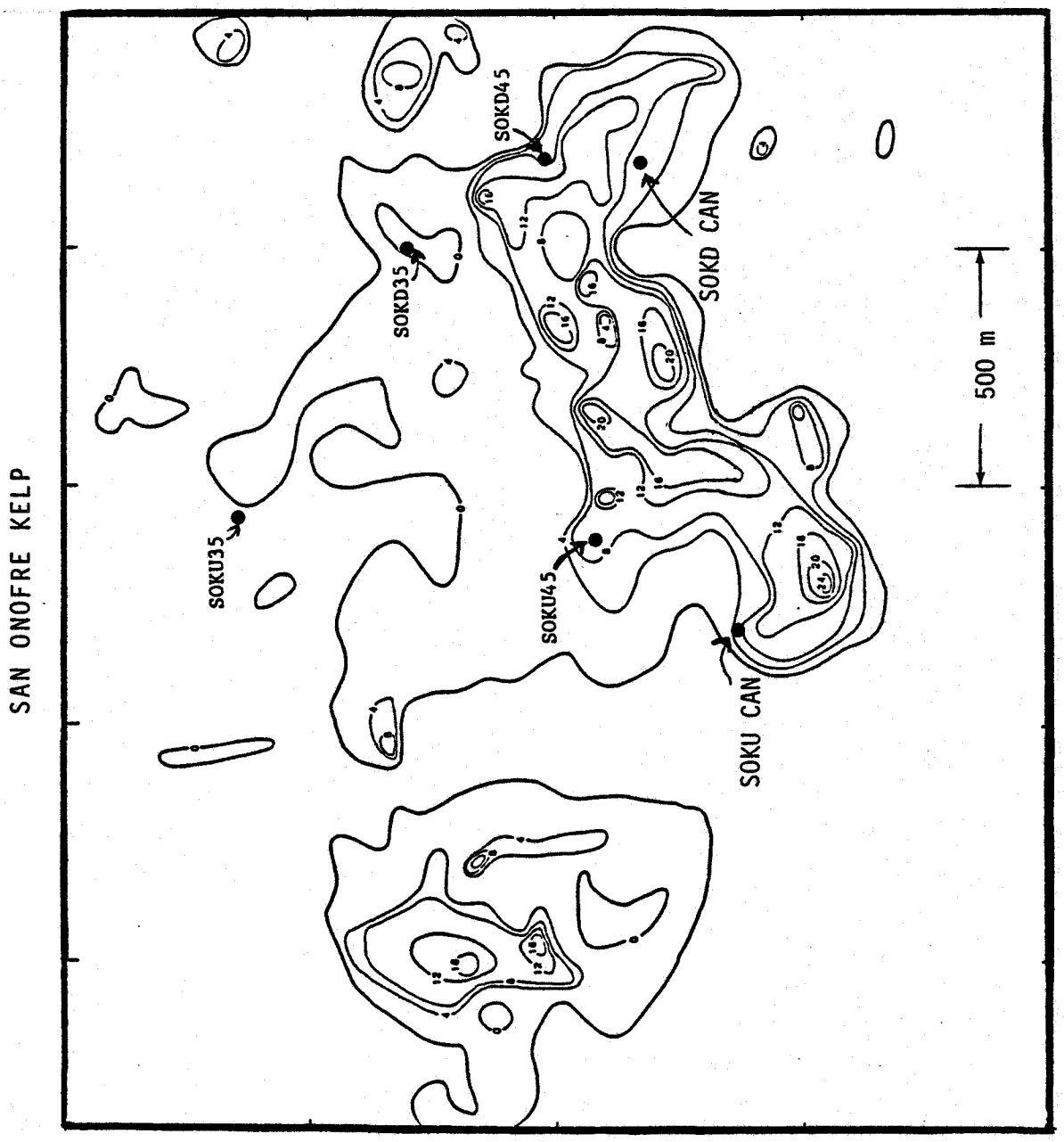

SAN ONOFRE KELP
SOKU35
SOKD35
SOKD45
SOKU45
SOKU CAN
SOKD CAN
500 m

Figure 10.1 b

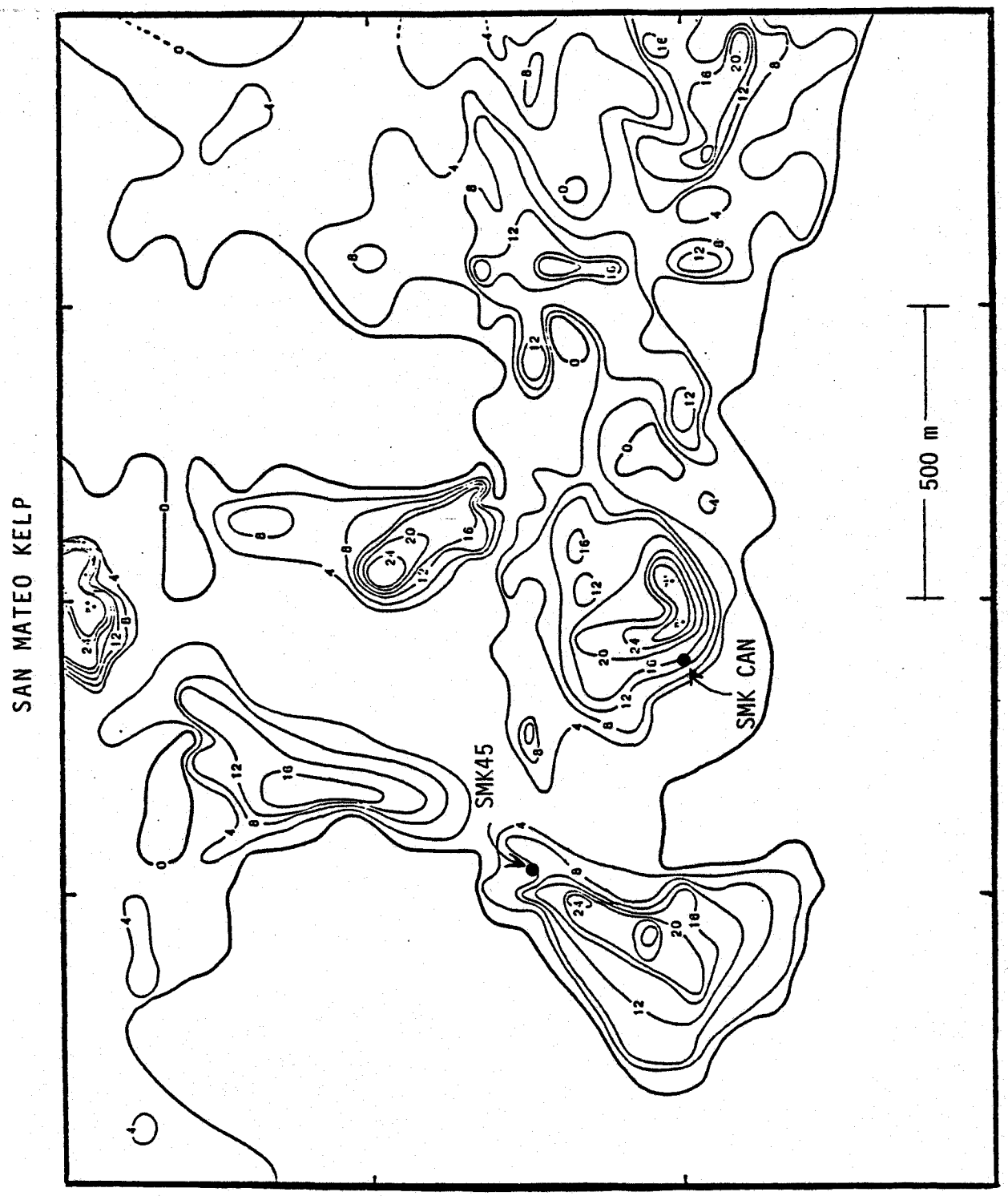


Fig. 10.2 A diagram of the juvenile transplant racks, showing method of attachment for juvenile Macrocystis plants.

Figure 10.2

JUVENILE TRANSPLANT RACKS

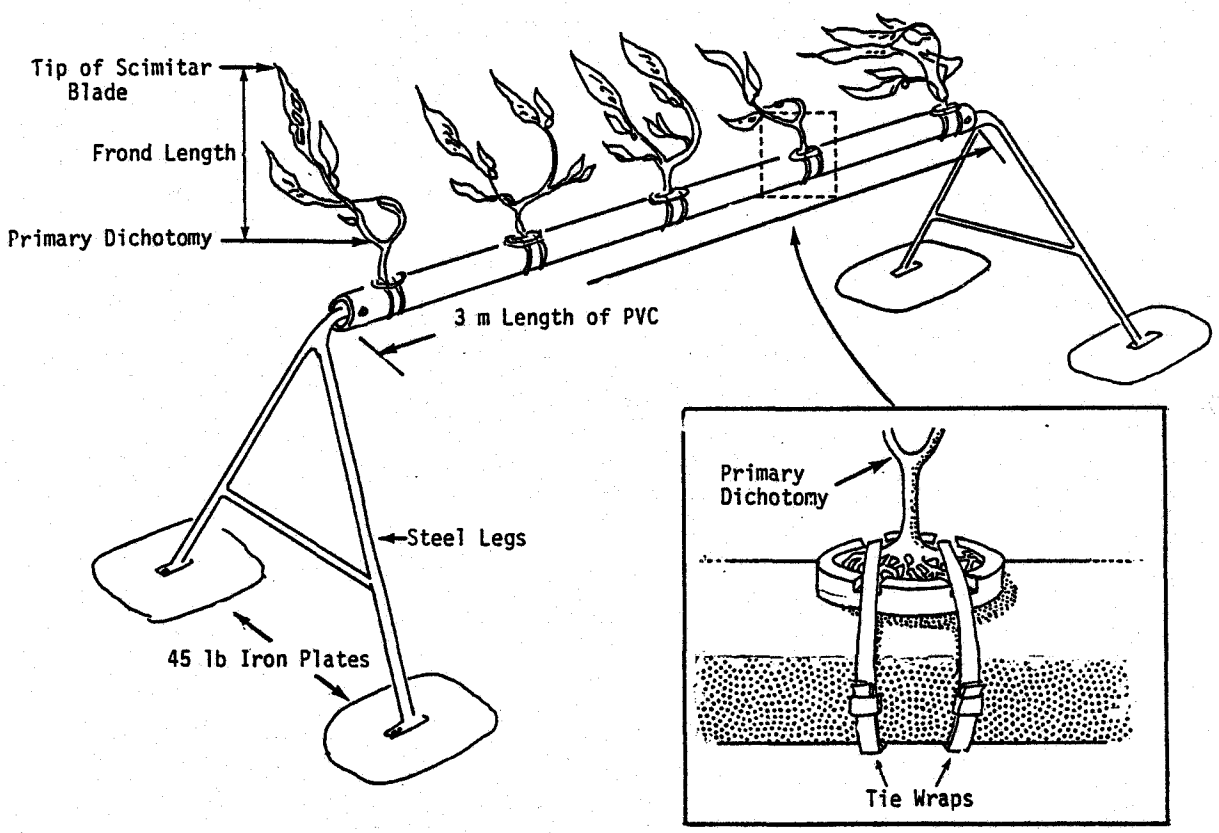


Figure 10.3 Mean log-total frond length (±95% CI) vs. time for juveniles that were transplanted and for control plants that were left undisturbed.

Figure 10.3

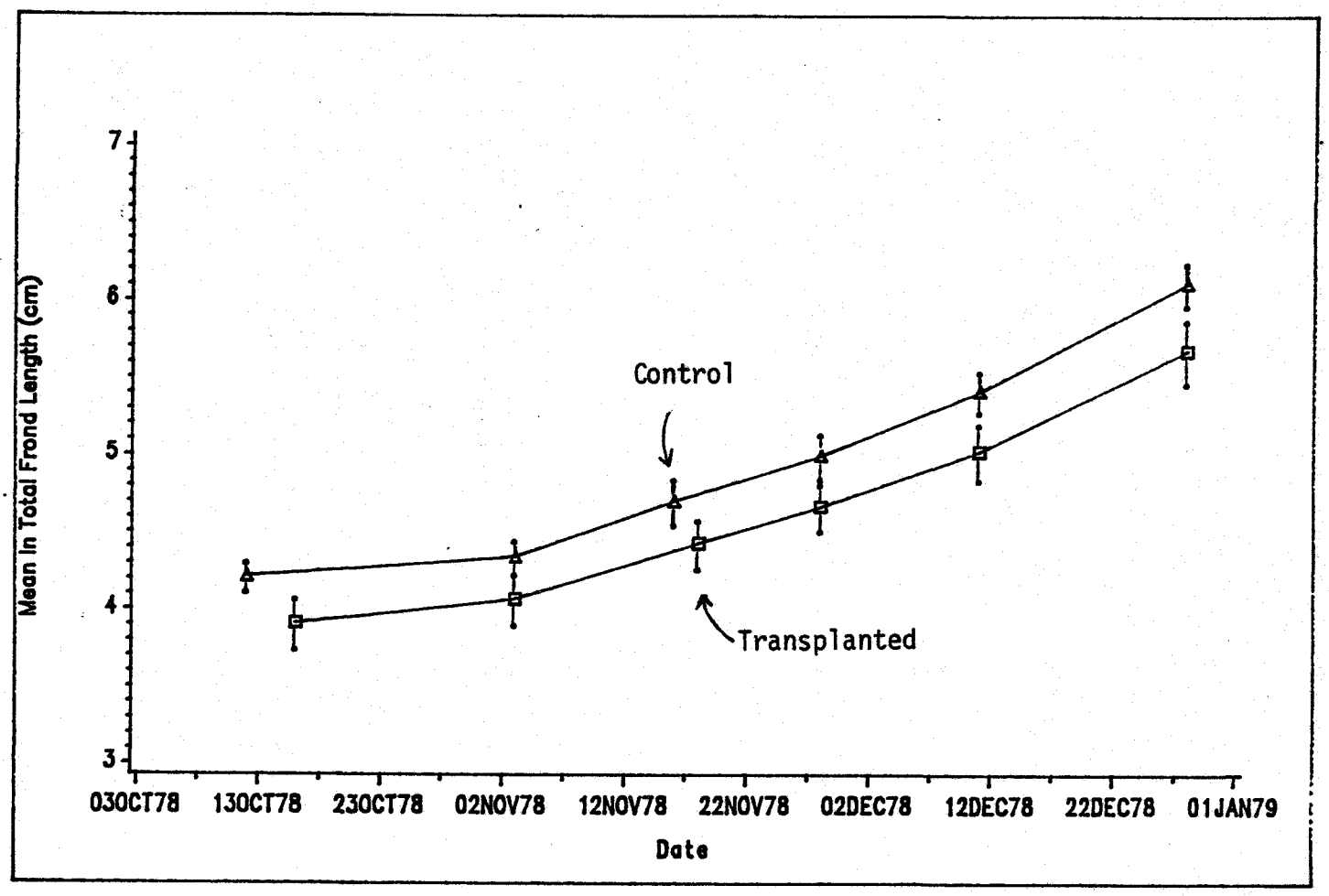

Mean ln Total Frond Length (cm)
7
6
5
4
3
Control
Transplanted
03OCT78
13OCT78
23OCT78
02NOV78
12NOV78
22NOV78
02DEC78
12DEC78
22DEC78
01JAN79
Date

Figure 10.4 A three-dimentional plot of growth rate vs irradiation and temperature.

Figure 10.4

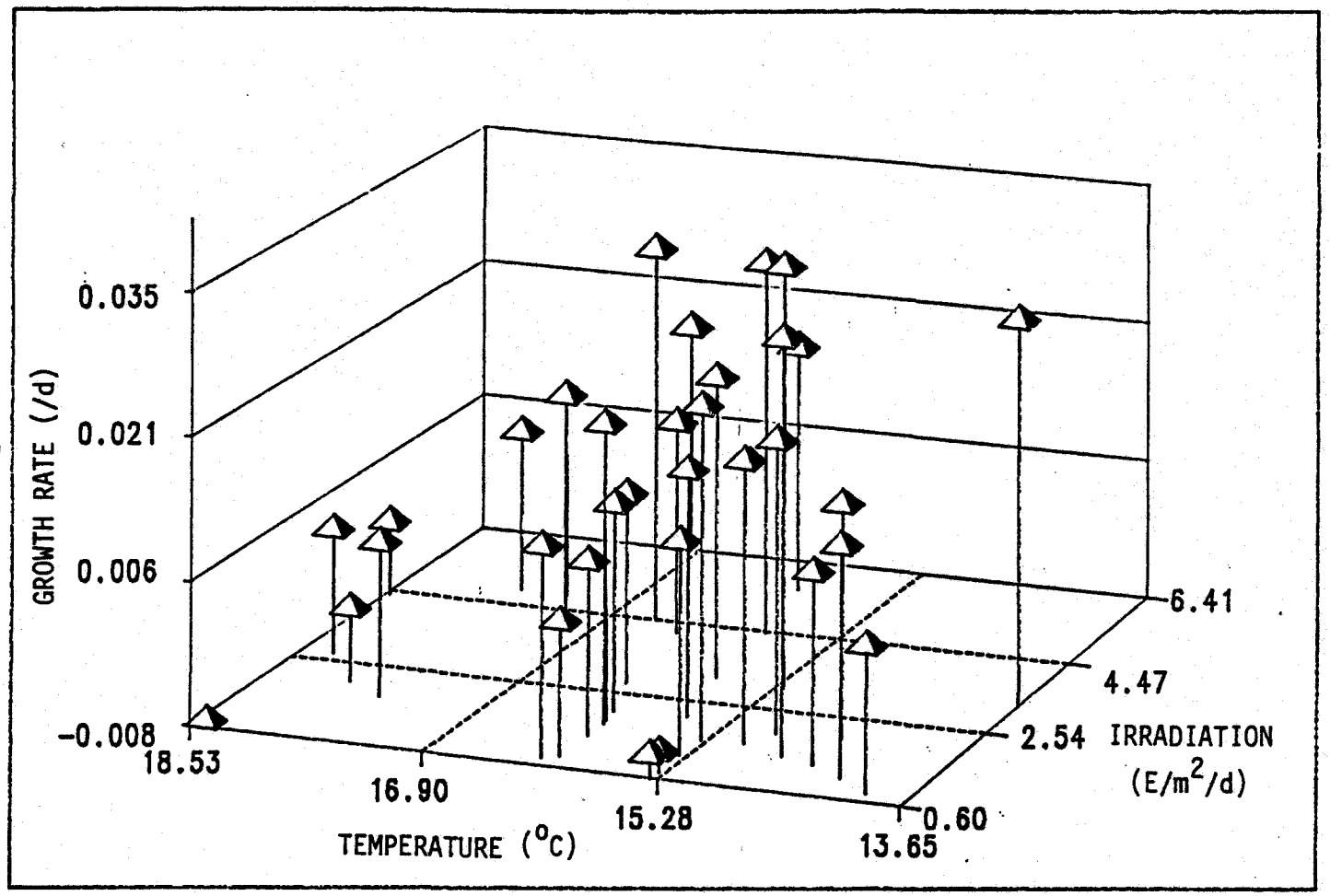
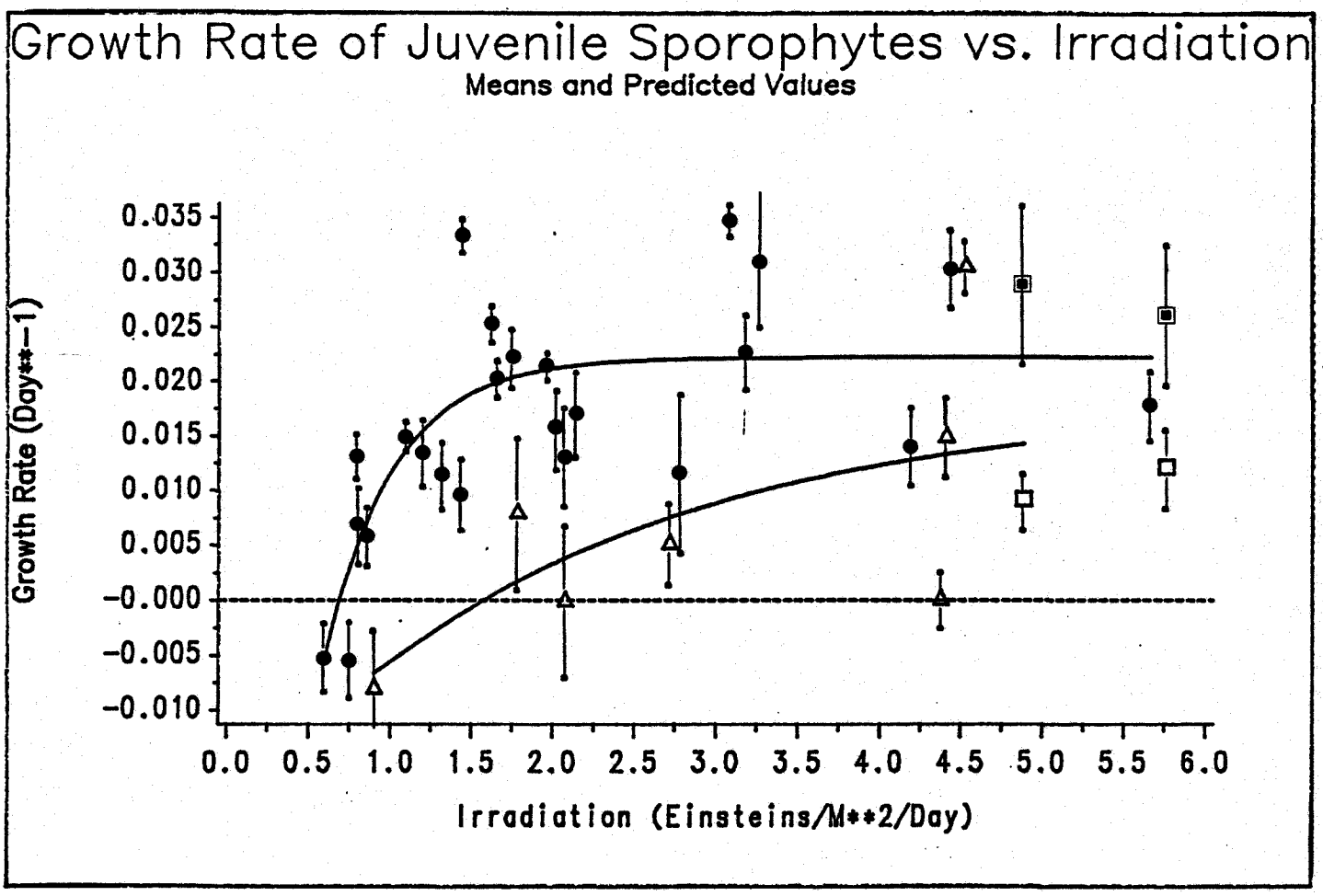

0.035
0.021
0.006
-0.008
GROWTH RATE (/d)
18.53
16.90
15.28
13.65
TEMPERATURE (°C)
0.60
2.54
4.47
6.41
IRRADIATION
(E/m²/d)

Figure 10.5 Mean relative growth rates (±95% CI) for juveniles transplanted to various stations in the San Onofre and San Mateo kelp forests vs. mean daily irradiation levels during the transplant period. The upper curve was fit to all data obtained when temperatures were less than 16.5°C (symbol = ●). The lower curve was fit to data obtained when temperatures were greater than 16.5° (symbol = Δ). Data for plants in the fertilizer experiments is also plotted. A "□" represents unfertilized control plants while a "▣" represents fertilized plants. Lines were fit by a non-linear fitting procedure using the von Bertalanffy equation (see text for details).

Figure 10.5


Growth Rate of Juvenile Sporophytes vs. Irradiation
Means and Predicted Values
Growth Rate (Day**-1)
0.035
0.030
0.025
0.020
0.015
0.010
0.005
-0.000
-0.005
-0.010
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
Irradiation (Einsteins/M**2/Day)

10.0 Survival of Adult Sporophytes

10.1 Introduction

The purpose of this section is twofold. First, we will examine the effects of age and density on the survival of adult Macrocystis. Recently proposed stage-based models of kelp population dynamics (Nisbet and Bence, 1987) have assumed that age and density do not affect the survival of adults. However, previous studies (Dayton et al., 1984; Rosenthal et al., 1974) indicated that mutual entanglement of adults occurred during storms, and we hypothesize that this might result in density-dependent mortality. Also, we hypothesize that older, larger adults may be less susceptible to being torn loose from the substratum by waves, which may lead to age-dependent mortality. We will test these hypotheses using observations of marked adult plants located along permanent transects within the San Onofre kelp forest. We will also examine the relative influence of age and density on variability in survival compared with other sources of temporal variability (e.g., storms, grazing). Testing the assumptions of the aforementioned models is important because these models are intended to be used as additional tools for evaluating the effects of SONGS on kelp.

The second purpose of this section is to examine the relative importance of recruitment vs survival of adult kelp in determining spatial and temporal patterns of abundance within the San Onofre and San Mateo kelp forests. Abundance patterns of adult kelp in Southern California kelp forests tend to be cyclical, with peaks occurring every 2 to 3 years on average (North, 1971; Rosenthal et al., 1974; Dayton, et al. 1984). Previous studies of kelp bed dynamics have stressed the importance of mortality events, such as storms, grazing by sea urchins, or warm, nutrient-poor waters associated with El Nino events, in determining these temporal

patterns as well as large-scale spatial patterns of abundance (North, 1974; Dayton, et al., 1984; Ebeling, et al., 1985). An alternative view is that adult abundance patterns are largely determined by the frequency and intensity of episodic recruitment events. Recruitment occurs infrequently in Southern California kelp forests, and cyclical abundance patterns may result from periodic recruitment coupled with relatively high, but constant rates of adult mortality. Similarly, the lack of recruitment in one kelp forest may cause its decline relative to other kelp forests, even though mortality rates in the two forests are similar.

A third possibility is that a closely coupled association exists between recruitment and catastrophic disturbances such that recruitment is triggered by the large-scale die-offs of adults (Ebeling et al., 1985; Dayton et al., 1984). Disturbances reduce the cover of adult canopy and thereby increase the light levels available to smaller life stages on the bottom. Additionally, these disturbances (e.g., storms) may enhance the dispersal of propagules, reduce the densities of both potential grazers (e.g., sea urchins) and competitors (e.g., Pterygophora or other subcanopy algae), and clear substrate necessary for zoospore settlement.

We will test the above hypotheses using data on the recruitment and survival of adult Macrocystis in the San Onofre and San Mateo kelp forests. The relative importance of recruitment vs survival is critical to our evaluation of the effects of SONGS on kelp, since SONGS inhibits recruitment (Schroeter, 1987) but has little effect on the survival of adults (Dixon et al., 1987).

10.2 Methods

We examined patterns of abundance, recruitment, and survival of adult Macrocystis pyrifera at a series of permanent transects located within the San

Onofre and San Mateo kelp forests. Each transect was 50 m long by 6 m wide and was marked with steel reinforcement bars driven into the seafloor at 1-m intervals (see Section 9.0, Fig. 9.2). For the purposes of these analyses, we examined data from 13 transects in SOK and 4 in SMK (Fig. 10.1). Transects 1 through 12 were established in summer 1978 (Appendix L) and an additional transect (number 13) was added in March 1979 to expand our coverage of the San Onofre kelp forest following recruitment in 1978-79. Two transects (numbers 14 and 15) were established in the San Mateo kelp forest in June 1981, and two more (numbers 16 and 17) were added in December 1982. Although additional transects were added in SOK in 1982 and 1985, we limited our analyses of SOK to Transects 1-13. We did this to avoid introducing spatial variability as an artifiact of our experimental design.

Nine of the 13 transects in SOK, and 2 of the 4 transects in SMK were initially established perpendicular to various edges of the kelp forest, with half of each transect located on cobble substrate outside of the kelp forest and half extending under the kelp canopy. These were chosen to represent the most dynamic portions of the kelp forest. The other transects (numbers 9-12 in SOK, 14 and 15 in SMK) were established within dense patches of kelp.

Surveys were conducted at approximately monthly intervals in 1978 and at quarterly intervals thereafter through December 1986 (Appendix L). Occasionally, surveys were either missed or postponed because of poor underwater visibility. During each survey conducted between June 1978 and May 1981, we counted, noted the size, and marked all of the Macrocystis that were juveniles or larger (see below for definitions of size categories). Thereafter, only adult plants were tagged and counted. We marked plants by driving steel spikes with numbered acetate tags into the seafloor next to them. Positions of plants were also noted by measuring

distances from the end of the transect, and from the center line of the transect, to each plant.

Size categories were defined as follows: Plants with at least 2 fronds (usually about 40 cm in height), but less than 1 m were classified as juveniles. Plants greater than 1 m, and lacking haptera above the primary basal dichotomy, were termed subadults. Plants with haptera above the primary basal dichotomy were classified as adults. This method of categorizing "adults" based on holdfast morphology was necessary because it was impractical for divers to measure frond lengths of large plants. A preliminary survey indicated that plants which we termed adults generally had 6 or more fronds with the longest fronds reaching the surface from depths of 13 to 14 m.

10.3 Analyses

10.3.1 Age Effects

The effects of age on survival and possible interactions between age and location within the kelp forest were examined by testing for differences in the proportion of survivors among age groups and locations using a linear categorical analysis (Grizzle et al., 1969). In order to avoid confounding the effects of age with temporal variability resulting from other factors, such as wave surge or urchin grazing, we examined survival over specific time intervals in which two distinct age classes were present: from May 1979 to June 1980, from June 1980 to July 1981, from July 1981 to July 1982, and from July 1982 to May 1983.

The ages of adult plants (time from initial recruitment of sporophytes) were determined based on our observations of initial appearance visible blade stages and on an estimated 60-day lag between the recruitment of sporophytes and the production

of visible blades. This 60-day period is based on average growth rates of microscopic sporophytes as determined in our outplant experiments (Section 7.0). The estimated times of recruitment for plants initially tagged in different surveys are given in Table 10.1. We assumed that adult plants tagged during our initial surveys were at least 2 years old. This seems a reasonable assumption based on the size of these plants, which generally had 20 or more fronds (T.A. Dean, pers. obs.). After assigning ages, plants were placed into age categories. Categories were divided into 1-year intervals, e.g., age class 1 = plants $\geq$ 0.5 and < 1.5 years old, age class 2 = plants $\geq$ 1.5 and < 2.5 years old, etc. The use of relatively large age classes allowed for the categorization of sufficient numbers of plants for statistical evaluation.

For the purpose of the analysis, we divided the San Onofre kelp forest into 3 quadrants: the inshore-upcoast (Transects 1, 2, and 3), the offshore-upcoast (Transects 4, 5, 6, 9, 10, and 13), and the offshore-downcoast (Transects 7, 8, 11, and 12) quadrants.

Age effects were examined in relation to other possible sources of temporal variability in survival by comparing the survival of adults between years in which 1-year-old plants predominated (1982 and 1985) and years when older adults were most abundant. A linear categorical analysis was used for this comparison.

10.3.2 Density Effects

We examined the possible effect of density on survival using 3 methods, each of which expressed density on a different spatial scale. First, we examined the relationship between probability of survival and distance to nearest neighbor. Nearest neighbor distances were computed for each transect half (25 x 6 m segment)

using a toroidal edge correction (Ripley, 1981). The nearest neighbor distance was determined for each adult plant, and plants were then divided into 6 categories based on 0.5-m increments of distance to nearest neighbor: $\leq$ 0.5 m, > 0.5 m and $\leq$ 1.0 m, etc., up to > 2.5 m.

The effects of density over a somewhat larger spatial scale were examined by computing the average density on each transect half and correlating it with the proportion of plants surviving.

We also examined whether the survival of adult plants living in the center of large patches of adults differed from that of plants located on the edges of the kelp forest. Survival of adults on canopy transects (9, 10, 11, and 12) was compared with survival of adults on the in-bed portions of the edge-of-kelp forest transects (1, 2, 3, 4, 6, 7, 8, and 13) using chi-square statistics. Transect 5, originally established on the edge of the kelp forest was classified as a "canopy" transect after 1979 because of recruitment and subsequent expansion of the kelp forest in 1978-79.

For each spatial scale examined, we conducted separate analyses for each of 3 time intervals: August to September 1978, December 1982 to May 1983, and January to April 1986. During these periods, the kelp population was comprised mostly of adults, and there were large, intense storms occurring. We selected such periods in order to test our hypothesis that storms were a potential source of density-dependent survival.

10.3.3 The Relative Importance of Recruitment and Survival

Changes in mean densities of adult kelp within the San Onofre kelp forest over the period from June 1978 to December 1986 were examined in relation to patterns of recruitment and survival of adults. Mortality rates were computed as:

$$MR = \frac{\ln(N_i) - \ln(N_{i+1})}{(t_{i+1} - t_i)}$$

where:

MR = mortality rate

N_i and N_{i+1} = the number of individuals present at time i and the number of those plants that survived to time i + 1. These are sums of the number of adults present on Transects 1 through 13.

Abundances of adult plants recruited in each survey were obtained either from plants that were tagged as juveniles or subadults in prior surveys and grew to adult size (for surveys conducted from 1978 to June 1981) or from plants which were tagged upon reaching adult size (surveys conducted after June 1981). Data on the abundances of blade-stage and juvenile kelp were obtained from either transects (for surveys conducted prior to 1982) or from nearby quadrats (from 1982 to 1986).

A description of sampling procedures for juveniles and blades are given in Schroeter et al., 1987. Using a Student's t-test, we tested the hypothesis that temporal changes in abundance were independent of mortality rate, or remained constant, by comparing mortality rates averaged over surveys in which abundances increased vs those in which abundances decreased. A description of sampling procedures for juveniles and blades are given in Schroeter et al., 1987. We also

tested the hypothesis that recruitment events were independent of adult mortality by comparing survival over approximately 6-month periods (generally December to June) prior to recruitment events vs survival over similar periods during years when there was no recruitment. Recruitment of blade-stage kelp occurred in the spring or early summer of 1981, 1983, 1984, and 1986. We excluded the 1984 recruitment period from our analysis because this recruitment may have been influenced by shading from recruits of the previous year as well from adults. No recruitment was observed in 1980, 1982, or 1985. The proportion of plants surviving in recruitment vs nonrecruitment periods were compared using a categorical analysis, with years nested within periods (recruitment or nonrecruitment).

The relative importance of recruitment and survival in determining large-scale spatial patterns (among kelp beds) was determined by examining abundances, recruitment rates, and mortality rates of adults in the San Onofre and San Mateo kelp forests over the period from June 1981 to December 1986. Patterns in abundance were similar in the kelp forest through 1982, but thereafter, abundances decreased at San Onofre and increased at San Mateo Kelp. We tested the hypothesis that differences in abundance that occurred after 1982 were independent of survival by comparing mortality rates of adults in the two kelp forests using a paired t-test.

10.4 Results

10.4.1 The Effects of Age on Survival

Densities of adult kelp within the San Onofre kelp forest displayed a cyclical pattern over time, with peaks occurring every 1.5 to 3 years (Fig. 10.2). The peaks coincided with periods of recruitment by adults, which lagged recruitment by blade-stage plants by about one year. As a result of periodic recruitment, the age distribution of the adult population at any point in time tended to be dominated by a

single year class (Fig. 10.3). However, over the period from 1979 through 1983, there were sufficient numbers in two-year classes present to allow us to examine the possible effects of age on survival.

The survival of adult plants was dependent on age, with highest survival rates among plants 2 to 3 years old. Plants younger than 2 or older than 3 years of age tended to have higher mortality rates. From May 1979 to June 1980, the proportions of 1-year-old plants surviving were significantly less than those for 3-year-old plants (Table 10.2). The following year, the 2-year-old plants survived better than the 4-year-old plants, at least in the inshore-upcoast and offshore-downcoast quadrants of the kelp forest. No significant differences were noted between 3- vs 5-year-olds or between 1- and 4-year-olds in subsequent years, but the trend was for mean survival to decrease with age.

The low survival rate of 1-year-old plants apparently had a relatively large impact on temporal patterns of adult mortality. Survival in 1982 and 1985, when 1-year-old plants predominated, was lower than for all other years but one (Table 10.3). Both 1982 and 1985 were relatively "normal" years in terms of weather, sea conditions, and activities of sea urchins, and that the high mortality rates were difficult to account for based on external events. The higher mortality rates of plants older than 3 years of age had little apparent effect on temporal patterns in survival, primarily because very few plants ever reached this age.

10.4.2 The Effects of Density on Survival

We examined the effects of density during 3 periods of particularly stormy weather, in the fall of 1978 and the winters of 1982-83 and 1986, when mortality rates of adults were high (Fig. 10.2). During these times, we could find no evidence of a negative effect of density on survival.

There was no particular relationship between distance to the nearest neighbor and survival. In both 1978 and 1982, the survival of plants that were different distances from one another did not differ significantly (Table 10.4). In 1986, we noted differences among groups of plants with differing nearest neighbor distances, but the highest survival rates were for those plants at intermediate distances or very close to one another (Table 10.4). Also, the correlations between density of plants on a given transect half and survival rate were not significant in 1982 and 1986 (Fig. 10.4) and showed a significant positive relationship in 1978.

On an even larger spatial scale, there were no negative effects of density on adult survival, and at times, positive effects were observed. In 1982, there were no significant differences in survival among plants located in the center of the kelp forest vs those at the edge (Table 10.5), and during the periods high mortality in 1978 and 1986, plants in the center survived better than those on the edge. This may have been caused by greater grazing pressure on the edges where sea urchins tended to be more abundant, or by a more severe effect of wave action on the edges of the kelp forest.

10.4.3 The Relative Importance of Recruitment and Survival in Determining Patterns of Abundance

As indicated above, temporal patterns in abundance of kelp in the San Onofre kelp forest were cyclical, with peaks in abundance coinciding with periods of recruitment. While mortality rates tended to be slightly higher following recruitment (because of the aforementioned effects of age), temporal patterns of abundance were largely unaffected by patterns in adult survival (Fig. 10.2). Mortality rates during times of increasing abundances did not differ significantly from those observed during periods of declining abundances (Table 10.6).

Recruitment events in 1983 and 1986 followed large storms, and in 1986, the storms resulted in high adult mortality. However, recruitment events were not necessarily preceded by storms or periods of high adult mortality. Survival during the 6 months prior to recruitment did not differ significantly from survival other times (Table 10.7) and in at least one instance (1981), recruitment followed a period of particularly high adult survival in which there was little storm activity.

Large-scale spatial patterns of abundance also appeared to be primarily determined by differences in recruitment rather than differences in survival. Over the period from 1982 through 1986, abundances of adult kelp in the San Onofre and San Mateo kelp forests diverged widely (Fig. 10.5). Following strong recruitment of blade-stage kelp in 1983 and 1984, densities of adult plants in the San Mateo kelp forest increased from 14.8 plants/100 m^2 in October 1982 to a peak of almost 50 plants/100 m^2 in late winter 1984-85. By December 1986, the densities had thinned to near previous levels (8/100 m^2). During this same time, there was little recruitment at San Onofre and densities fell from 8.6/100 m^2 in October 1982 to less than 0.5/100 m^2 in December 1986. Over this period, mortality rates were slightly higher at SOK than at SMK, but did not differ significantly at the two locations (Table 10.8) and could not account for the observed differences in density in the two kelp forests. Mortality rates at both locations were sufficiently high so that none of the plants that recruited prior to 1983 were surviving in December 1986. If we assume that recruitment rates of adults were similar in both beds in 1983 and 1984, then differences in subsequent survival could account for only a two-fold difference in abundance in December 1986. This is compared with the nearly twenty-fold difference that we observed.

10.5 Discussion

Models of kelp bed dynamics have been based, in part, on the assumption that mortality rates of adult plants are unrelated to age distributions. Our data suggest that these assumptions are sometimes violated. After recruitment events, populations tend to be dominated by young plants that have a lower probability of survival. This effect needs to be incorporated into refinements of the models.

While it is impossible to compare survival age classes in the different years (because of temporal variability in storms, grazing, etc.), the relative rankings of survival among different age classes within a given year suggest that the probability of survival increases between 0.5 and 2.5 years of age and then decreases thereafter (Fig. 10.6). We hypothesize that 2- to 3-year-old plants survive better than younger individuals because they have the ability to develop larger holdfasts that can attach the fronds more securely to the substrate. In a cobble-bottom kelp forest such as San Onofre, adults routinely incorporate cobbles in their holdfasts as they grow, such that older plants with larger holdfasts are better anchored. We also suspect that the probability of survival decreases after 3 years because holdfasts tend to get hollowed out by sea urchins and other grazers, thereby providing a less secure anchorage.

The assumption of density-independent mortality among adults was also violated. While we found no evidence for negative effects of density among adults, positive effects of density were evident in some instances. We suspect that plants in less dense patches along the edges of the kelp forest were more susceptible to storm waves or grazing. Also, plants that were located extremely close to one another (< 1 m) sometimes had haptera that grew together forming what appeared to be a single holdfast, and without our long-term mapping records these would not have been recognizable as more than 1 individual. Such "fusing" of holdfasts may have provided some advantage in terms of anchorage and survival.

Both Rosenthal et al. (1974) and Dayton et al. (1984) have indicated that mutual entanglement of adults during storms may cause spatial patchiness in survival. We too have observed masses of drifting plants entangled with one another, and with anchored plants, but our data suggest that the probability of an individual being torn up by other drifting plants does not increase with density. While entanglement may well result in nonrandom mortality of adults within the population, this does not necessarily imply density dependence.

Spatial variability in the mortality of adult kelp, caused by either storms or grazing by sea urchins, can result changes in the abundance patterns of kelp within a kelp forest (Dean et al., 1984; Dayton et al., 1984; Dayton and Tegner, 1984). However, in the San Onofre and San Mateo kelp forests, large scale patterns of abundance, i.e., changes in average abundance within the kelp forests over time and differences in average abundance between kelp forests, were largely determined by differences in recruitment. Within the San Onofre Kelp forest, changes in density over time showed little relation to patterns of mortality. Mortality rates were relatively constant, and peaks in abundance corresponded with periodic peaks in recruitment. Also, differences in average adult kelp density between the San Onofre and San Mateo kelp forests were largely attributable to differences in recruitment, as mortality rates were similar for the two kelp forests.

We found no evidence that recruitment events were necessarily preceded by catastrophic declines in adult density. While there is sometimes a clear correspondence between storms, high adult mortality, and subsequent recruitment events, both at San Onofre (present study) and elsewhere (Ebeling et al., 1985; Tegner and Dayton, 1987), we also observed recruitment in years in which the mortality of adults was abnormally low. We hypothesize that recruitment is

triggered in part by a thinning of the adult canopy which increases the light levels necessary for sporophyte production and for survival of small sporophytes (Luning and Neushul, 1978; Deysher and Dean, 1984; Dean et al., 1987, Sections 7 and 8). However, a thinning of the canopy is not necessarily linked to higher-than-normal adult mortality. During the 1983-84 El Nino, for example, we observed near total loss of surface canopy at the San Onofre and San Mateo kelp forests. This loss was primarily due to "blackrot," a disease of unknown etiology (Scotten, 1971) that is associated with warm, nutrient-poor waters. Unlike many other kelp forests in Southern California, however, the San Onofre and San Mateo kelp forests did not suffer severe storm damage in the winter of 1982-83, and adult mortality rates were not significantly higher during the El Nino than in other years.

Alternatively, canopy thinning can result from a failure of recruitment over several years, coupled with a steady and normal rate of adult mortality. We estimated that the average half-life of adults in the San Onofre kelp forest was less than 1 year, indicating that adult densities could be reduced by almost 90% over 3 years without recruitment.

We suspect that recruitment rather than adult survival may also be responsible for large-scale changes in the abundance of kelp in other Southern California kelp forests. An examination of other published records of the survival and recruitment of Macrocystis pyrifera revealed many of the same patterns that we observed at San Onofre and San Mateo. While an adult Macrocystis may live for 7 years or more (Rosenthal et al., 1974), average half-lives are generally on the order of 10 mos. to 1.3 years (Table 10.9). Also, mortality rates of adults appear to be relatively constant over time, as indicated by survival curves given for kelp populations at Point Loma (Dayton et al., 1984), Catalina Island (Dayton et al., 1984) and Del Mar

(Rosenthal et al., 1974). Finally, in all other reported cases, it is clear that peaks in abundance follow peaks in recruitment (Dayton et al., 1984; Rosenthal et al., 1974).

We also hypothesize that the historic decline in kelp abundance in Southern California, that occurred following the 1957-58 El Nino (North and Schaefer, 1964; Dayton et al., 1984), may have been largely caused by a lack of recruitment rather than by abnormally high adult mortality. While there is little direct demographic evidence for this, estimates of kelp canopy in the literature suggest that the decline in kelp abundance occurred over a period of several years. Losses did not appear appreciably higher than would be expected by "normal" adult mortality accompanied by a lack of recruitment. El Nino events in Southern California are characterized by warm, nutrient-poor waters (Tegner and Dayton, 1987) that are generally unfavorable for kelp recruitment (Deysher and Dean, 1984). It seems likely that without a hiatus in the El Nino conditions (as occurred in spring 1983) recruitment would not have occurred. While the decline in kelp abundance in the late 1950s and early 1960s was clearly hastened by extensive grazing by sea urchins (North and Pearse, 1970), this may have been an indirect effect of recruitment failure. In times of declining supplies of drift algae, urchins become more active as grazers (Dean et al., 1984; Harrold and Reed, 1985), and there is a direct relationship between drift "kelp" abundance and kelp recruitment (Harrold and Reed, 1985).

The analyses presented here and elsewhere (Schroeter et al., 1987; Dixon et al., 1987a) clearly indicate that the failure of recruitment in the San Onofre kelp forest in 1983 had a demonstrable effect on the abundance of adult kelp. While there has been little apparent effect of SONGS on the mortality rates of adult plants

within SOK (Dixon et al., 1987), the probable effect of SONGS on the recruitment processes (Schroeter et al., 1987) may, in itself, be sufficient to cause long-lasting changes in the patterns of adult abundance in the San Onofre Kelp forest.

Table 10.1 Estimated times of recruitment for plants initially tagged as either juveniles or adults during surveys in which new plants were tagged.

Survey date	Plants tagged as juveniles or adults	Estimated time of recruitment
Jun78*	Adults	Jun76
Jul78 to Dec78**	Juveniles	May78
May79 to Nov79	Juveniles	Dec78
Dec78 to Oct82	Adults	Jul81
Oct84	Adults	Apr83
Jul85 to Jan86	Adults	Feb84

* Includes Transect 6, surveyed Jul78 and Transect 8, surveyed Aug78.

**Includes Transect 6, surveyed from Jul78 to Dec78 and Transect 8, surveyed from Aug78 to Dec78.

Table 10.2 Results of categorical analyses of age and location effects on the survival of adult kelp plants. Individual chi-square analyses performed for each location for the June 1980 to July 1981 period are also given.

May 1979 to June 1980

Area	Age	Live	Dead	Total	Percent surviving
Inshore	1	2	8	10	20.0
Inshore	≥ 3	13	7	20	65.0
SOKD	1	2	11	13	15.4
SOKD	≥ 3	29	36	65	44.6
SOKU	1	17	30	47	36.2
SOKU	≥ 3	66	17	83	79.5

Source	df	chi-square	PROB
Intercept	1	2.17	0.141
Area	2	10.00	0.007
Age	1	17.64	<0.001
Area*Age	2	0.26	0.878

June 1980 to July 1981

Area	Age	Live	Dead	Total	Percent Surviving
Inshore	2	28	12	40	70.0
Inshore	4	2	11	13	15.4
SOKD	2	34	13	47	72.3
SOKD	4	14	15	29	48.3
SOKU	2	36	33	69	52.2
SOKU	4	41	25	66	62.1

Source	df	chi-square	PROB
Intercept	1	0.35	0.552
Area	2	3.27	0.195
Age	1	9.36	0.002
Area*Age	2	13.40	0.001

	Single df chi-square		
Area	df	chi-square	PROB
Inshore	1	11.91	< 0.01
SOKD	1	4.46	< 0.05
SOKU	1	1.36	> 0.10

Table 10.2, continued

JULY 1981 to JULY 1982

Area	Age	Live	Dead	Total	Percent surviving
Inshore	3	6	26	32	18.8
Inshore	5	0	2	2	0.0
SOKD	3	18	16	34	52.9
SOKD	5	5	9	14	35.7
SOKU	3	17	20	37	45.9
SOKU	5	13	28	41	31.7

Source	df	chi-square	PROB
Intercept	1	3.01	0.083
Area	1	0.32	0.569
Age	1	2.64	0.104
Area*Age	1	0.02	0.901

July 1982 to May 1983

Area	Age	Live	Dead	Total	Percent surviving
Inshore	1	9	31	40	22.5
Inshore	4	0	6	6	0.0
Inshore	6	0	0	0	-
SOKD	1	23	40	63	36.5
SOKD	4	5	13	18	27.8
SOKD	6	0	5	5	0.0
SOKU	1	61	61	122	50.0
SOKU	4	6	11	17	35.3
SOKU	6	3	10	13	23.1

Source	df	chi-square	PROB
Intercept	1	7.04	0.008
Area	1	1.28	0.258
Age	1	1.60	0.206
Area*Age	1	0.07	0.798

Table 10.3 Results of a categorical analysis examining differences in percent survival of adult *Macrocystis pyrifera* in different years. Letters indicate groups of means that did not differ significantly at the $P<0.05$ level using single df chi-square tests. Also shown are the dominant age classes in each year. The survival values are for periods of approximately 1 year, generally from June of the year indicated to June of the following year.

Year	Total	Dominant age class	Percent survival	Group
1984	62	3	4.8	A
1985	137	1	11.7	A
1982	285	1	37.5	B
1981	92	3	44.6	B C
1983	122	2	50.8	C D
1979	238	3	54.2	C D
1980	229	2	57.6	D
1978	195	2	77.4	E

Table 10.4 Chi-squared tests of differences in survival of adult *Macrocystis pyrifera* grouped according to distances from their nearest neighbor. Separate analyses were performed for each of 3 periods. Letters indicate groups that did not differ significantly at the P<0.05 level using single df chi-square tests.

August 1978 to September 1978

Distance to nearest neighbor (m)	Percent survival	Group
1.0 to 1.5	89	A
0.5 ot 1.0	87	A
1.5 to 2.0	84	A
0.0 to 0.5	77	A
>2.5	76	A
2.0 to 2.5	74	A

chi-square = 6.31, df = 5, P > 0.20

December 1982 to May 1983

Distance to nearest neighbor (m)	Percent survival	Group
0.0 to 0.5	69	A
0.5 to 1.0	69	A
2.0 to 2.5	65	A
1.5 to 2.0	64	A
>2.5	56	A
1.0 to 1.5	47	A

chi-square = 5.27, df = 5, P < 0.3

January 1986 to April 1986

Distance to nearest neighbor (m)	Percent survival	Group
2.0 to 2.5	56	A
0.5 to 1.0	44	A
0.0 to 0.5	23	A
1.0 to 1.5	15	B
>2.5	14	B
1.5 to 2.0	7	B

chi-square = 15.27, df = 5, P < 0.01

Table 10.5 Comparisons of survival of adult *Macrocystis pyrifera* located within the center portion of the San Onofre Kelp forest vs those on the edge. Separate analyses were performed for the 3 indicated.

August 1978 to September 1978

Location	N	Percent survival
Canopy	122	89
Edge	129	78

chi-square = 5.35, df = 1, $P > 0.05$

December 1982 to May 1983

Location	N	Percent survival
Canopy	95	61
Edge	92	68

chi-square = 1.13, df = 1, $P > 0.10$

January 1986 to April 1986

Location	N	Percent survival
Canopy	60	42
Edge	60	8

chi-square = 17.78, df = 1, $P < 0.01$

Table 10.6 T-test comparing mortality rates of adult *Macrocystis pyrifera* in periods of increasing vs decreasing abundances.

	Mean	N	SE	t	P
Increasing	0.0020	9	0.0005	1.75	0.09
Decreasing	0.0037	23	0.0008		

Table 10.8 A comparison of mortality rates of adult *Macrocystis pyrifera* in the San Onofre and San Mateo Kelp forests from October 1982 through December 1986.

Kelp forest	Half-life	Mortality rate				
		Mean	N	SE	t	P
SOK	173	0.0040	16	0.0009	2.04	0.06
SMK	246	0.0028	16	0.0006		

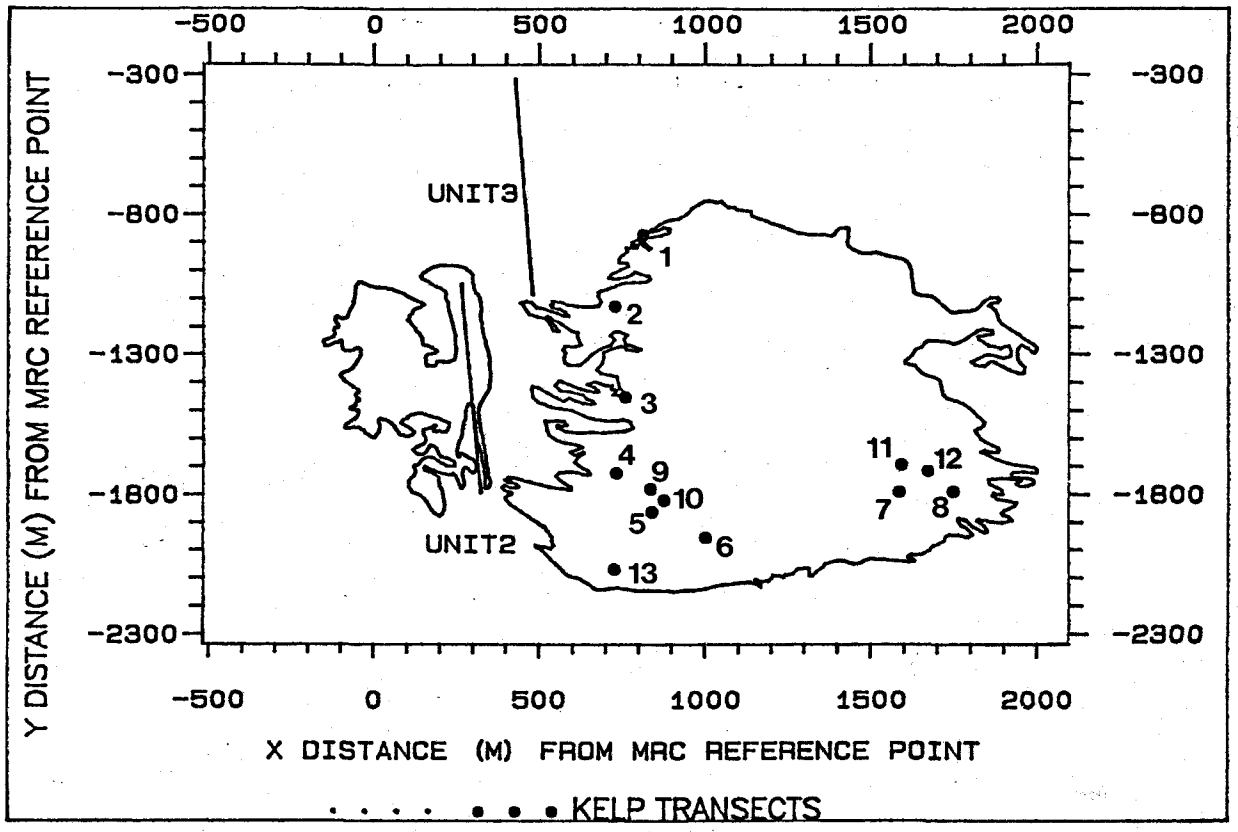
Table 10.9 Half-lives of populations of adult *Macrocystis pyrifera* in Southern California kelp forests.

Kelp forest	Source	Years observed	Half-life
Pt. Loma	Dayton et al., 1984	1974-79	10 to 11 mo
Catalina	Dayton et al., 1984	1974-75	4 to 6 mo
Del Mar	Rosenthal et al., 1974	1967-72	9 to 12 mo
SOK	Present study	1978-83	10 to 16 mo
Turtle Bay (Mexico)	North, 1964*	1961	7 mo
La Jolla	North, 1964*	1959-61	10 to 16 mo

*Other data given by North are excluded because data collection periods were too short (<4 mos).

Figure 10.1 Map of the San Onofre (TOP) and San Mateo (BOTTOM) kelp forests showing the locations of transects used in the analyses of adult mortality.

Figure 10.1


-500
0
500
1000
1500
2000
-300
-800
-1300
-1800
-2300
UNIT3
UNIT2
1
2
3
4
5
6
7
8
9
10
11
12
13
Y DISTANCE (M) FROM MRC REFERENCE POINT
X DISTANCE (M) FROM MRC REFERENCE POINT
KELP TRANSECTS

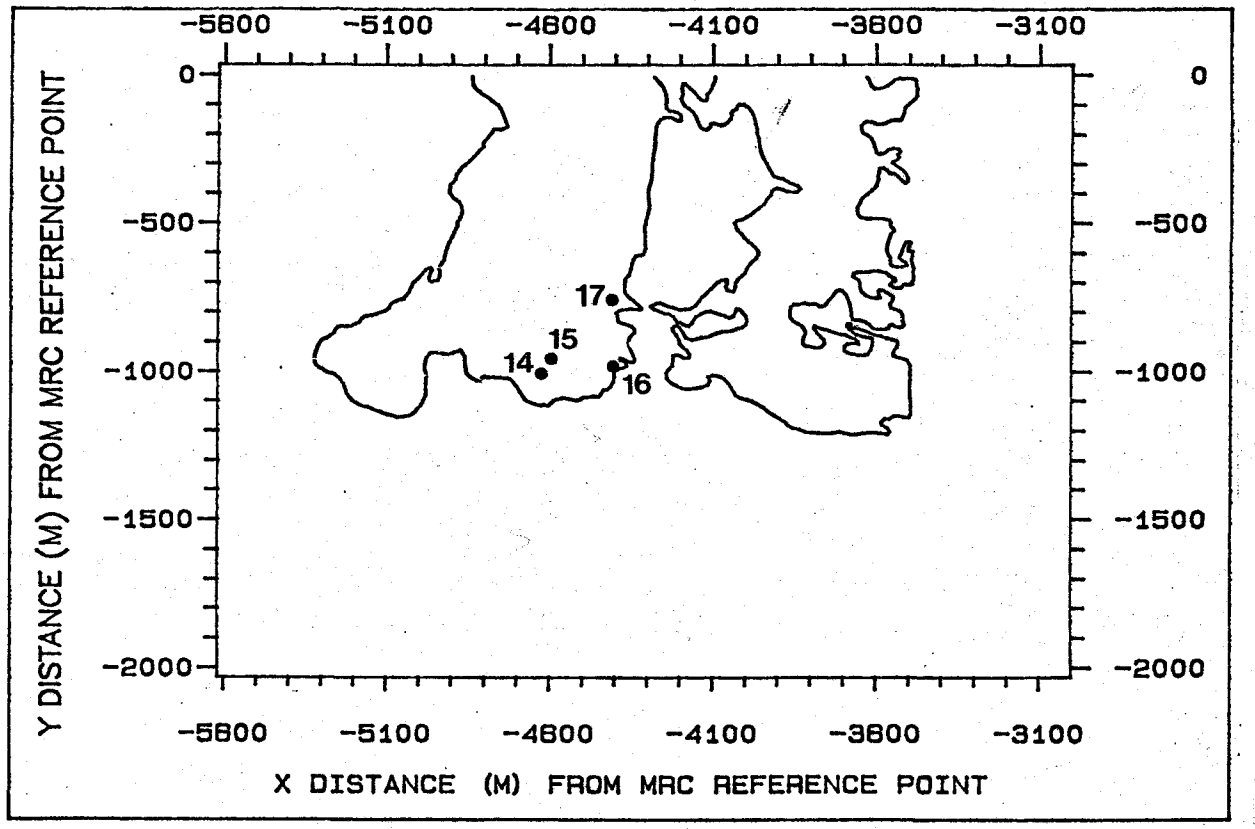

-5600
-5100
-4600
-4100
-3600
-3100
0
-500
-1000
-1500
-2000
14
15
16
17
Y DISTANCE (M) FROM MRC REFERENCE POINT
X DISTANCE (M) FROM MRC REFERENCE POINT

Figure 10.2 Abundances of blade stage, juvenile, and adult Macrocystis pyrifera; the number of new adult recruits; and the mortality rate of adults within the San Onofre Kelp forest from June 1978 through December 1986. Mean values (± 1 SE) are given for all but the mortality rate data. Mortality rates were computed, based on the sums of the number of plants present at all transects sampled at any given time.

Figure 10.2

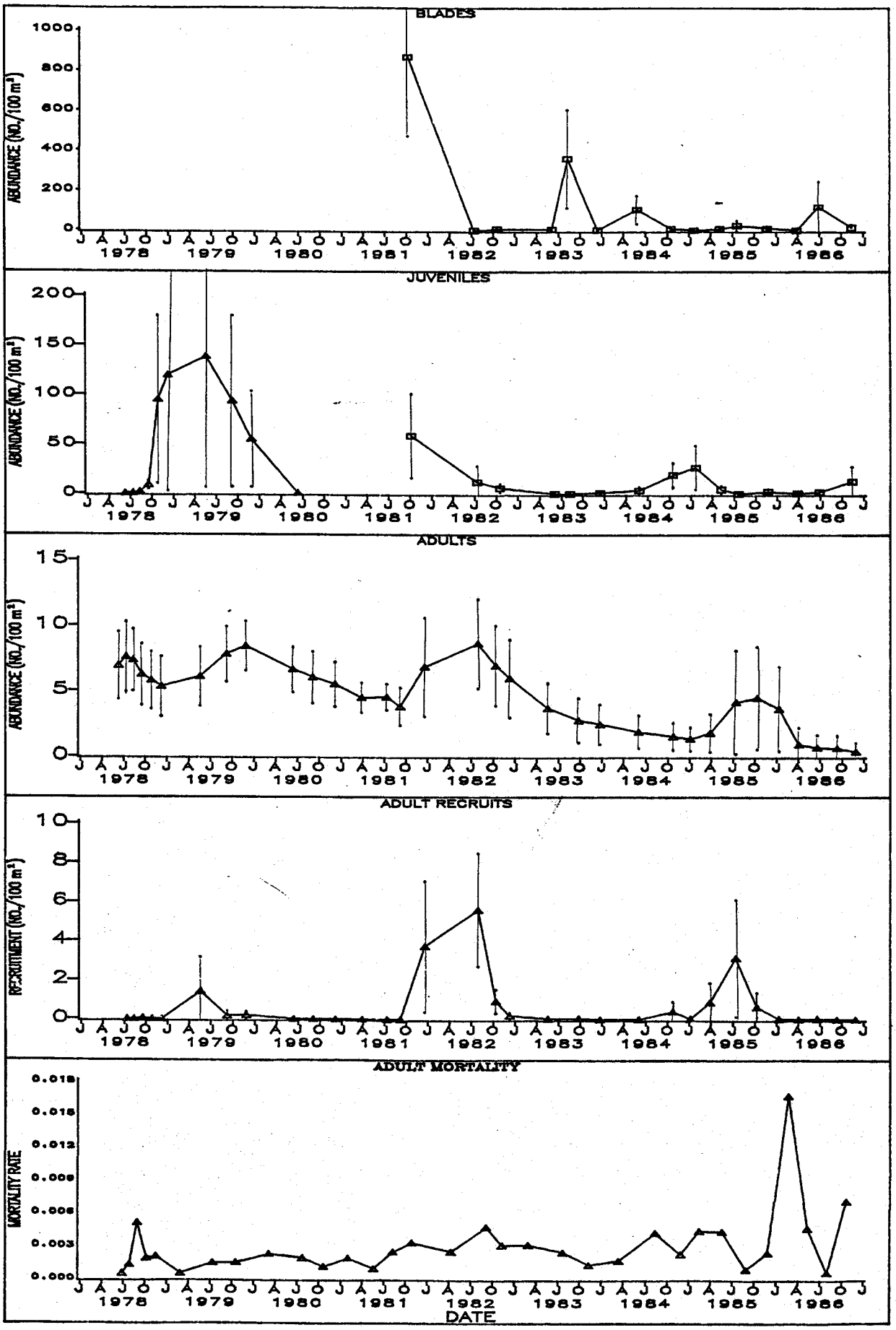

BLADES
ABUNDANCE (NO./100 m²)
JUVENILES
ABUNDANCE (NO./100 m²)
ADULTS
ABUNDANCE (NO./100 m²)
ADULT RECRUITS
RECRUITMENT (NO./100 m²)
ADULT MORTALITY
MORTALITY RATE
J A J O J A J O J A J O J A J O J A J O J A J O J A J O J A J O J A J O J A J O J A J O J A J O J
1978 1979 1980 1981 1982 1983 1984 1985 1986
DATE

Figure 10.3 Age distributions of adult Macrocystis pyrifera within the San Onofre Kelp forest for each year from 1978 through 1986. Each age class is represented by the indicated value ±0.5 years.

Figure 10.3

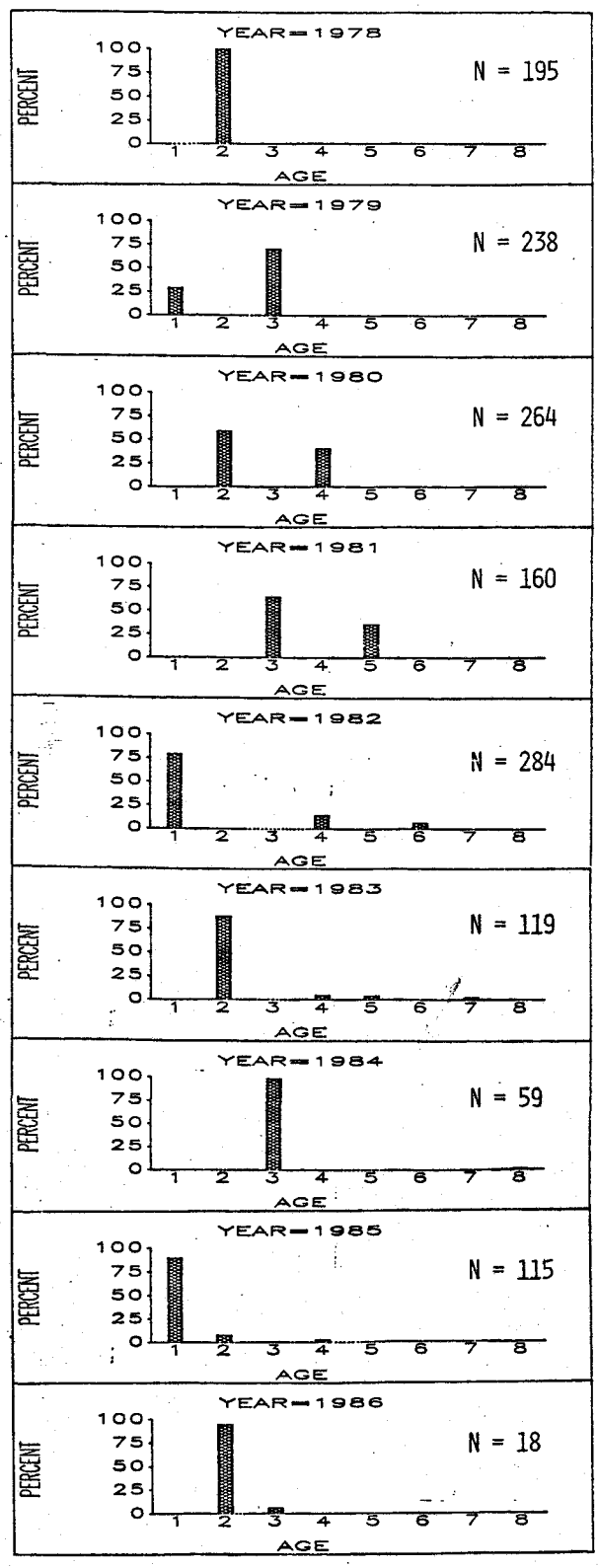

YEAR=1978
N = 195
YEAR=1979
N = 238
YEAR=1980
N = 264
YEAR=1981
N = 160
YEAR=1982
N = 284
YEAR=1983
N = 119
YEAR=1984
N = 59
YEAR=1985
N = 115
YEAR=1986
N = 18
PERCENT
100
75
50
25
0
1 2 3 4 5 6 7 8
AGE

Figure 10.4 The relationship between the density of adult Macrocystis pyrifera in the San Onofre Kelp forest and the proportion of plants surviving. Separate plots are given for survival over each period examined.

Figure 10.4

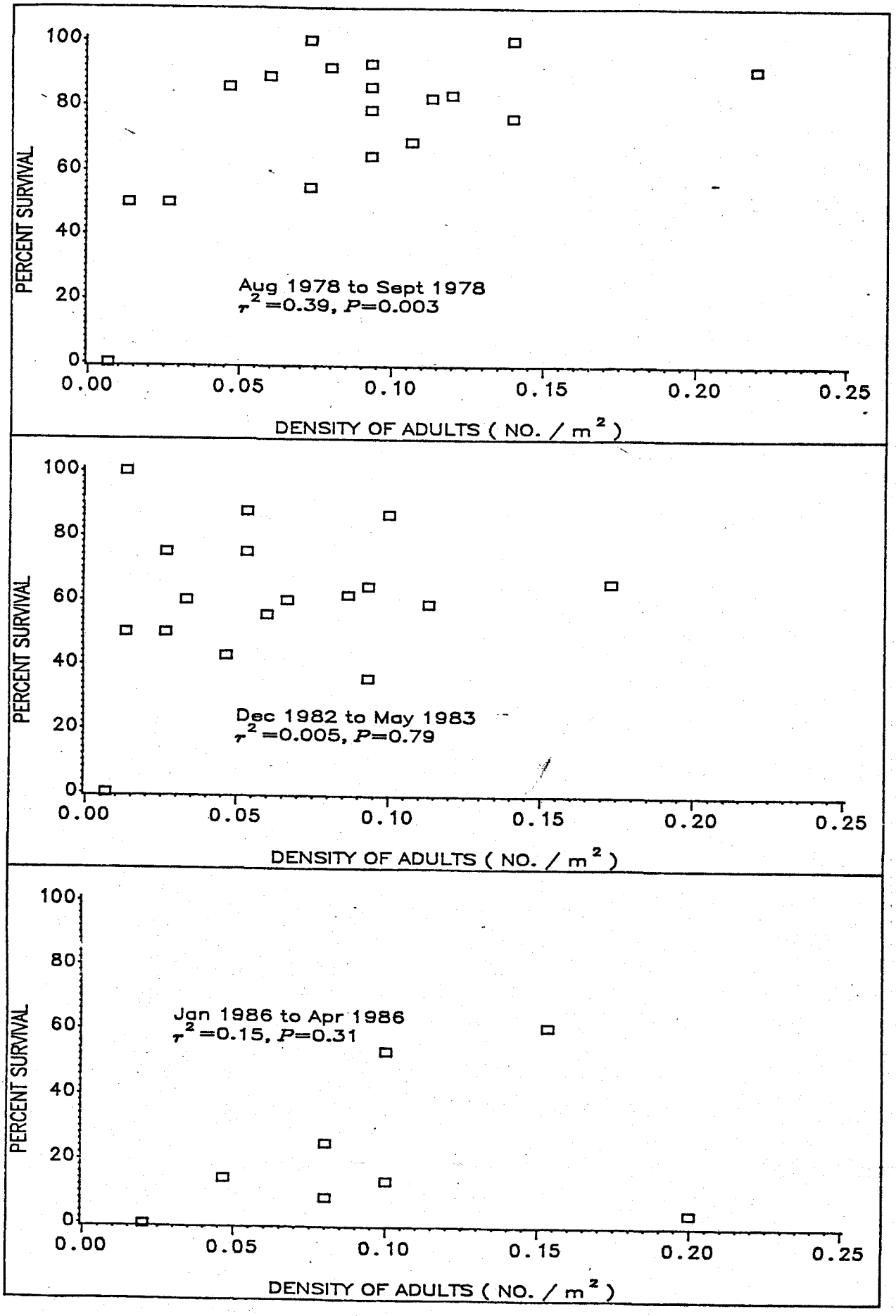

PERCENT SURVIVAL
100
80
60
40
20
0
Aug 1978 to Sept 1978
r^2=0.39, P=0.003
0.00
0.05
0.10
0.15
0.20
0.25
DENSITY OF ADULTS (NO. / m^2)
PERCENT SURVIVAL
Dec 1982 to May 1983
r^2=0.005, P=0.79
DENSITY OF ADULTS (NO. / m^2)
PERCENT SURVIVAL
Jan 1986 to Apr 1986
r^2=0.15, P=0.31
DENSITY OF ADULTS (NO. / m^2)

Figure 10.5 Recruitment, mortality, and abundances of adult Macrocystis pyrifera within the San Onofre (□) and San Mateo Kelp (Δ) forests from June 1981 through December 1986. Mean values (±1 SE) are given for all but the mortality rate data. Mortality rates were computed based on the sums of the numbers of plants present at all transects sampled at a given time.

Figure 10.5

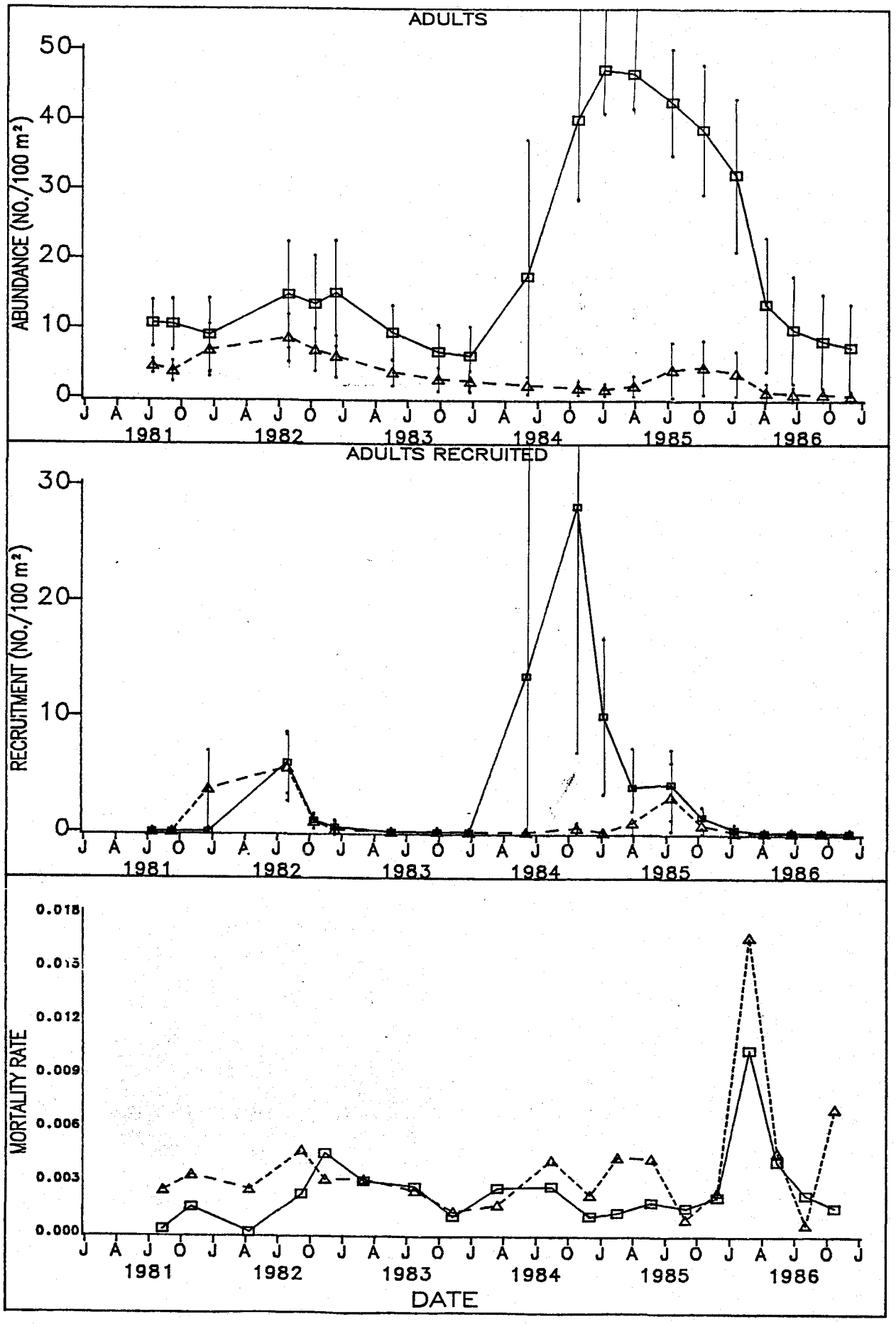

ADULTS
ABUNDANCE (NO./100 m²)
50
40
30
20
10
0
J A J O J A J O J A J O J A J O J A J O J A J O J
1981
1982
1983
1984
1985
1986
ADULTS RECRUITED
RECRUITMENT (NO./100 m²)
30
20
10
0
J A J O J A J O J A J O J A J O J A J O J A J O J
1981
1982
1983
1984
1985
1986
MORTALITY RATE
0.018
0.015
0.012
0.009
0.006
0.003
0.000
J A J O J A J O J A J O J A J O J A J O J A J O J
1981
1982
1983
1984
1985
1986
DATE

Figure 10.6 A model of the relationship between probability of survival of adult *Macrocystis pyrifera* and age of the plants.

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