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SANTA CRUZ

Some Aspects of Material Dynamics and Energy Flow

in a Kelp Forest in Monterey Bay, California

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Valrie Ann Gerard

December 1976

The dissertation of Valrie Ann
Gerard is approved:

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(Committee Chairperson)

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Dean of the Graduate Division

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INTRODUCTION

The high productivity and diversity of giant kelp forests have long attracted the attention of biologists. After observing the kelp forests of Tierra del Fuego, Charles Darwin (1860, p. 227-229) wrote:

> "There is one marine production, which from its importance is worthy of a particular history. It is the kelp, or _Macrocystis pyrifera_. . . The number of living creatures of all Orders, whose existence intimately depends on the kelp, is wonderful. . . I can only compare these great aquatic forests of the southern hemisphere, with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp."

Along the coast of California, forests of giant kelp also harbor rich and complex communities of marine plants and animals. The environmental conditions and species composition of these forests vary, but they all have one factor in common: the dominating presence of the giant kelp, _Macrocystis_ sp. In what ways are the organisms associated with this plant influenced by it and dependent on it?

Macrocystis plays a major role in determining the physical structure of the kelp forest community. It not only substantially increases the total substrate area (Clendenning, 1960, in North, 1971a), but also extends

that substrate vertically through the water column to the sea surface. The morphological heterogeneity of the plant itself provides a diversity of habitats (North, 1971a; Pearse and Gerard, in press). The influence of Macrocystis on the physical structure of the forest is comparable to that of the trees in a terrestrial forest and of the hermatypic corals in a tropical reef community.

Macrocystis also influences the trophic structure of the forest community as the dominant primary producer, outweighing and outproducing the other benthic algae and phytoplankton (Clendenning, 1971; North, 1971a). The magnitude and fate of the kelp production and its role as a food base within the forest community are the major concerns of this thesis.

In the first chapter, I investigate the dynamics of the attached kelp population, and examine the magnitude and mechanisms of drift kelp production and its importance, relative to grazing and detritus formation, as a pathway of primary production within and out of the kelp forest. The formation of drift kelp influences the availability of kelp production to and its utilization by members of the forest community. This trophic pathway is discussed in the second chapter, in which I consider benthic drift plant material as a resource within the forest. Finally, in the third chapter, I test my hypotheses on the role of benthic

drift algae and seagrasses as a trophic pathway by studying the feeding habits of the drift consumer, _Patiria miniata_. The dependence of this asteroid on the drift plant resource may provide insight into the dependence of other kelp forest inhabitants on the productivity of _Macrocystis_.

THE STUDY SITE

This study took place within the giant kelp forest of the Hopkins Marine Life Refuge off of Point Cabrillo in Pacific Grove, California (Figure 1). The study area was circumscribed by a circle with a 25 meter radius (approximately 2000 m^2 in area). Its center was 200 m offshore, marked on a permanent underwater cable, 100 m from the cable's southern point of entry into the kelp forest (Figure 2). The study area was located toward the southeastern end of the larger kelp forest of about 5 ha, in a relatively protected position from the dominant northwest swell. The majority of the area was 8 to 10 m in depth, although the entire depth range was 5 to 13 m. The substrate consisted of high relief granitic rock and boulders, interspersed with patches of sand and sand channels which comprised approximately 20-25% of the total area.

The kelp forest at Point Cabrillo supports a diverse association of plants and animals. Pearse and Lowry (1974) reported 77 species of red and brown algae and 292 species of invertebrate animals belonging to eight phyla; Miller and Geibel (1973) observed 59 species of fish in this forest. The giant kelp, Macrocystis pyrifera (L.) C. Agardh, dominates this association both visibly and in terms of biomass. The kelp forms a surface canopy which is typically

Figure 1. Location of the Point Cabrillo study site
in Monterey Bay, California.
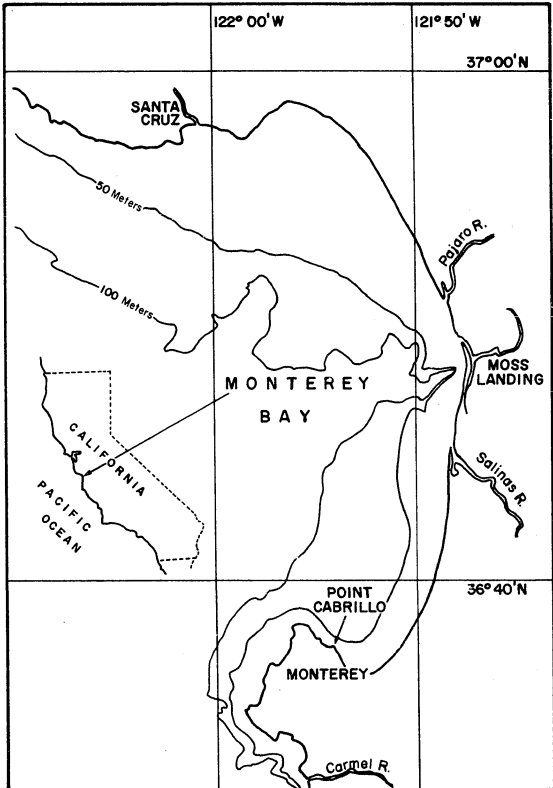
Figure 2. The location of the study area within the
Hopkins Marine Life Refuge at Point Cabrillo.
Crosshatching shows kelp forest areas.

POINT CABRILLO, PACIFIC GROVE, CALIFORNIA
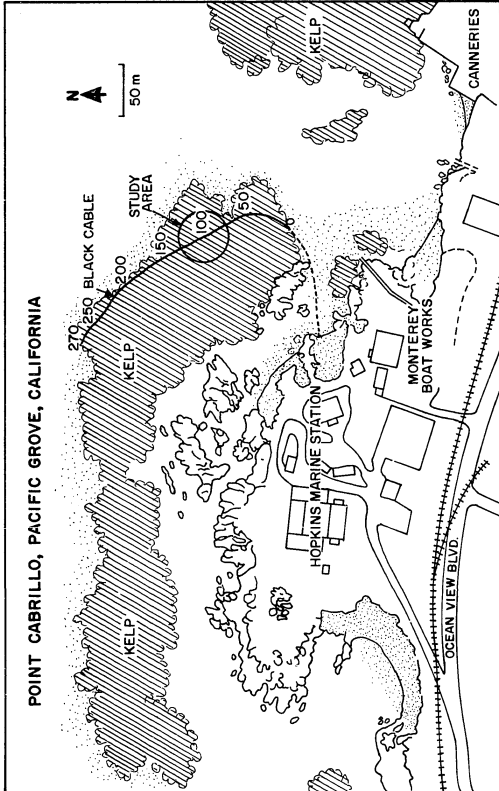
densest in the summer, but is present throughout the year. The dense summer canopy is further enhanced by the reproductive fronds of <u>Cystoseira</u> <u>osmundacea</u> (Menzies) C. Agardh and its epiphyte, <u>Coilodesme</u> <u>californica</u> (Ruprecht) Kjellman. The seaward edge of the entire kelp forest is limited by an extensive sand plain, faunally dominated by the tube-forming polychaetes, <u>Diopatra</u> <u>ornata</u> Moore and <u>Thelepus</u> <u>crispus</u> Johnson.

CHAPTER I

STANDING CROP, PRODUCTION, AND LOSS OF

MACROCYSTIS PYRIFERA

The giant kelps, Macrocystis spp., have enjoyed great popularity in scientific literature. Interest was originally focused on the commercial aspects of Macrocystis as a source of potash, and later, alginic acid. Recently, more attention has been given to its ecologic aspects. Standing crops of giant kelp have been measured by Aleem (1956, 1973), North (1957), McFarland and Prescott (1959), Grua (1964), Towle and Pearse (1973), and Barrales and Lobban (1975). Rates of growth or production of Macrocystis have been estimated by a variety of methods (Scagel, 1947; Sargent and Lantrip, 1952; Cribb, 1954; Aleem, 1956; McFarland and Prescott, 1959; Neushul and Haxo, 1963; Clendenning, 1964, 1971; North, 1971b, 1972; Miller and Geibel, 1973; Towle and Pearse, 1973; Littler and Murray, 1974; Jackson, 1975). These researchers have unanimously concluded that forests of Macrocystis are characterized by large standing crops, and by high rates of growth and production. Only a few studies have given attention to loss of kelp from the standing crop (North, 1961; Miller and Geibel, 1973; Rosenthal, Clarke, and Dayton, 1974; Barrales and Lobban,

1975), and these made no attempt to quantitatively relate loss to standing crop or production. The present study was designed to do just that: to investigate the relationships of and temporal fluctuations in standing crop, production, and loss of _Macrocystis pyrifera_ (L.) C. Agardh, and to evaluate the influences of various physical and biotic factors in a kelp forest in Monterey Bay, California.

THE STUDY ORGANISM

Macrocystis pyrifera belongs to the phylum Phaeophyta, order Laminariales, family Lessoniaceae. It has a hetero-morphic alternation of generations: the gametophyte stage is microscopic, and the plant known as "giant kelp" is the sporophyte. A giant kelp plant consists of a holdfast which anchors it to the substrate, and one or more fronds (Figure 3). Each frond is composed of a stem-like stipe and numerous blades. Each blade is comprised of a leaf-like lamina and a gas-filled bulb, or pneumatocyst, and is attached to the stipe by a short pedicel (North, 1971b). The pneumatocysts act as floats, keeping the fronds oriented vertically in the water column; the upper portions remain at or near the surface, where they often form a dense canopy. This allows the plant to receive a large amount of sunlight. The uppermost, or apical blade of an unbroken frond is the site of new blade formation. The sporophylls in California plants are typically the lowest blades on each frond, and consist of single or multiple laminae, with or without pneumatocysts.

Giant kelp plants are perennial, but individual fronds are relatively short-lived, and are continually being lost and replaced by new fronds. Broken off fronds, smaller kelp fragments, and whole plants that have been detached

Figure 3. Morphology of a giant kelp plant, <u>Macrocystis</u>
<u>pyrifera</u>: a) holdfast, b) primary stipe, c) sporo-
phyll, d) apical blade, e) pneumatocyst, f) lamina,
g) blade, h) stipe, i) frond, j) canopy.
(Adapted from Dawson with permission of Wm. C.
Brown Co. Publ.)
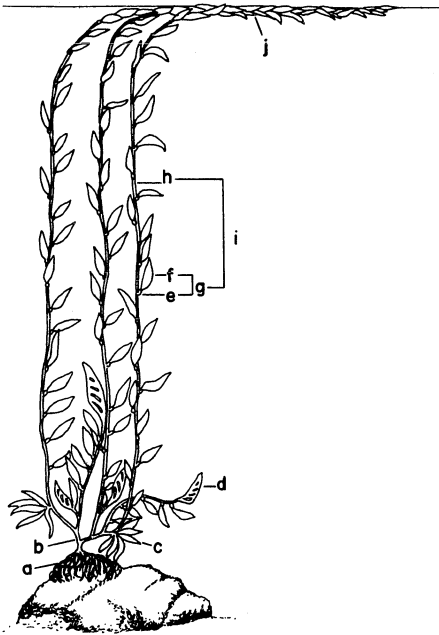
from the substrate form drift kelp. Drift kelp is differentiated from kelp detritus by size. Detritus particles are arbitrarily defined by some investigators as being a few millimeters or less in their largest dimension (Pearse, 1970; Heald, 1971; Lenz, 1972); drift kelp consists of any larger pieces detached from the substrate or parent plant. Drift kelp is often capable of photosynthesis, growth, and even reproduction (North, 1964a, 1972). Loss of attached kelp, or production of drift kelp, is closely linked to standing crop and production, but is an aspect of kelp forest dynamics that has been largely neglected in previous studies.

METHODS

Physical and Chemical Parameters

Twice daily throughout the 2.5 year study, the height of the highest wave occurring during a five minute interval was estimated to the nearest 0.5 m. These observations were always made on a particular nearshore channel, a short distance from the study area. Water movement intensity was then expressed as the frequency of various maximum wave heights observed during each monthly period of kelp tagging. Although these data were not direct measurements of the force of water motion within the kelp forest, they provided a means of assessing relative changes in water movement intensity from month to month.

Sea surface temperature was measured each morning from an intertidal water sample collected inshore from the study area. Solar radiation was recorded daily on a Belfort mechanical pyrheliograph located on the roof of the Loeb Building of Hopkins Marine Station.

At the beginning of every dive day, horizontal visibility was estimated in the study area by sighting along a particular section of transect line on the bottom. Averaged over seasonal intervals, these data provided a rough indication of changes in turbidity.

Measurements of the concentrations of dissolved
nutrients were available from semimonthly CalCoFI cruises
beginning in July, 1974 (Broenkow, Lasley, and Schrader,
1975, 1976). The data used were from station number 2201,
located approximately 1.5 km north of the study site.
Concentrations of phosphate and total nitrogen (nitrate +
nitrite + ammonia) were averaged from measurements made at
0, 5, and 10 m depths.

Standing Crop Measurements

Measurements of plant density, plant size, and frond
size were made during each season (once every three months)
from Fall, 1973 through Winter, 1976. Plant size was
measured as the number of fronds per plant; frond size was
expressed as a weight measurement. Plant density and plant
size data were collected before and after the first fall
storms in 1974 and 1975. Pre-storm frond size measurements
were made only in Fall, 1975.

Mean plant density was determined by counting adult
kelp plants in twenty-five circular 10 m^2 plots located by
simple random sampling within the study area. The plot
sites were chosen as random coordinates (x, y) and located
by compass heading and distance from permanent markers (see
Chapter II). A new set of random sites was used for each

data collection. Kelp plants within the plots were con-
sidered to be adult, if they had at least one frond greater
than 1 m long. In the same plots, plant size data were
collected by counting all fronds greater than 1 m in length
on each plant. Fronds less than 1 m long were not
enumerated. To determine the relative proportion of fronds
reaching the canopy, the fronds on each plant were also
counted at a depth of approximately 2 m below the zero tide
level.

During each season (twice in Fall, 1975), 100 fronds
were collected from 37 adult kelp plants. These plants were
chosen as the nearest to sites located by simple random
sampling within the study area; new locations were used
for each collection. Seventy-five of the collected fronds
were weighed to the nearest 0.2 kg using a spring scale,
scored for the presence or absence of an apical blade, and
discarded. The remaining 25 fronds were brought into the
laboratory for further measurement. The number of blades
present on each frond was recorded, as well as the number
of laminae and blades that were missing (indicated by a
pneumatocyst with no lamina, or a pedicel with no pneumato-
cyst or lamina). The sum of the blades present, and
missing laminae and blades was termed the "number of
possible blades" and was used in most calculations involving
frond size. Laminae that were only partially intact were

assumed to have been grazed or to have sloughed off the missing material and were included as present for the purpose of this study. The apical blade and all new blades not yet split completely off from it were counted as one blade. Each sporophyll or group of sporophylls connected to the stipe by a single pedicel was counted as one blade. The length of each of the 25 fronds was measured from the base of the stipe to the most recent split in the apical blade. The condition of the frond was subjectively judged to be good, fair, or poor from the physical state of the laminae on the upper half of the frond (Figure 4). Evidence of grazing and sloughing, and epiphyte concentration were the main criteria. Finally, each frond was separated into laminae and stipe components (pneumatocysts were included with the stipe), and these were weighed.

All weights not specified otherwise in this report are unblotted wet weights. Excess surface water was allowed to run off all frond material before weighing. Holdfast biomass was not included in any standing crop or production estimates.

Kelp Growth and Loss

To measure growth and loss rates of kelp, 25 individual plants and 100 fronds were tagged each month. Each tag

Figure 4. Sections of kelp fronds subjectively judged
to be in a) GOOD, b) FAIR, and c) POOR condition.
A meter stick is included for scale.
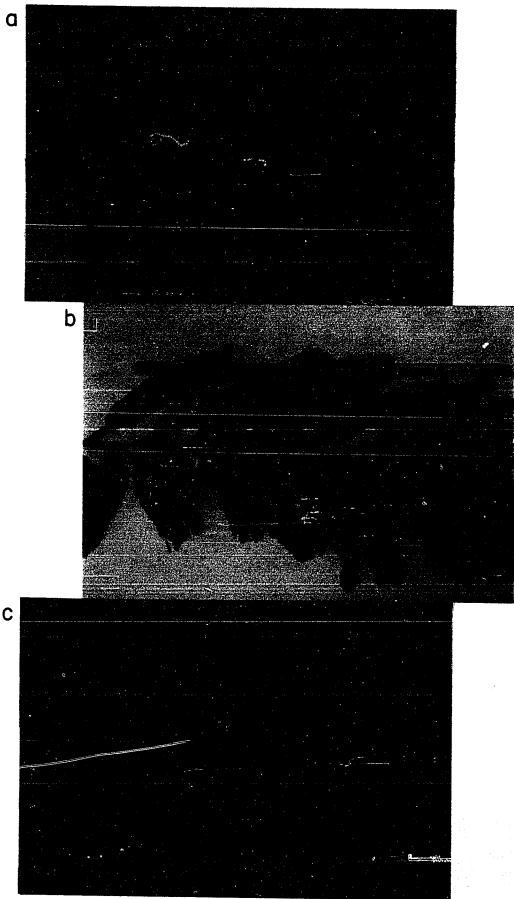
consisted of a 45 cm length of vinyl (bicycle handlebar) tape, numbered at one end with a marking pen. These tags could easily be tied around haptera, primary stipes, or frond stipes, and were visible at considerable distances underwater (white, yellow, and orange were found to be the most visible colors). Care was taken to make each tag firm enough on a stipe to prevent constant slippage and abrasion, but not tight enough to restrict growth. Even though each frond was tagged for only one month, a small number of stipes became pale under the tags. A few of the tags became loose or untied, especially during months with high water movement. At the end of the tagging period, the tags were easily removed with a small pair of scissors without damage to the plant.

Each tagging period extended from the middle of one month to the middle of the next month, and was referred to by the month in which it ended. For example, growth or loss data cited in this report for November, 1974 were actually taken from mid-October, 1974 to mid-November, 1974.

The 25 plants tagged each month were selected as the adult plants nearest to 25 sites located by simple random sampling within the study area. New random sites were chosen each month. One tag was placed on the primary stipe of each plant and all fronds greater than one meter

long were counted. Four of the fronds on each plant were
arbitrarily chosen and tagged near the base of their stipes.
At the end of one month, the number of remaining tagged
plants and fronds was noted, and the total number of adult
fronds on each plant was recorded. These data were used
to calculate gross plant loss, and net and gross frond loss.
The percent of plants lost out of the 25 originally tagged
was equal to the gross percent loss of plants during that
tagging period. Similarly, the gross percent loss of fronds
was the number of fronds lost out of the 100 tagged. Net
frond loss or addition was equal to the difference in total
frond counts made at the beginning and end of the tagging
period, and was expressed as a percent of the original
total frond count. Gross frond addition was estimated as
the difference between net and gross frond losses, or as
the sum of net frond addition and gross frond loss.

All four fronds on each plant had the same tag number,
but one of the four fronds received an odd-colored tag.
This subsample of 25 fronds with odd-colored tags was used
to calculate frond growth rates, partial frond loss, and
lamina loss. The blades present, and missing laminae and
blades on each of these 25 fronds were counted at the start
of the tagging period. Each frond was scored for presence
or absence of an apical blade, its condition was judged,
and any morphological abnormalities or special conditions,

such as tangling, were noted. At the end of one month, the same data were collected for all remaining fronds of the 25 with odd-colored tags. Growth was expressed as an increase in the number of possible blades for those remaining fronds with intact apical blades. Partial frond loss was determined as the percent of the 25 fronds that lost the apical blade during the tagging period. Lamina loss was equal to the number of laminae and blades lost during the tagging period, out of the total number of blades present when tagged plus the new blades added by frond growth during the month of tagging.

Analysis of the Data

The significance of correlation between any two variables over time, for example, monthly percent loss of kelp plants and water movement intensity, was tested by calculating a product-moment coefficient of correlation (r). Relationships between variables, such as frond length and weight, were defined by linear regression analysis. The significance of the regression coefficients was determined by a t-test. The significance of the difference between the means of any two samples was also determined using a t-test, if the variances of the two samples could be assumed equal by the results of a variance ratio test

(F-test). If the variances were significantly different at the 95% confidence level, the means were compared by calculating the normal variable, d (Bailey, 1959).

All test results reported in this chapter as "significant" were found to be significant at the 95% confidence level ($p < 0.05$). Results reported as "highly significant" were found to be significant at the 99% confidence level ($p < 0.01$). The confidence intervals shown for means on all graphs and histograms or reported in the text are the 95% confidence limits.

RESULTS

Physical and Chemical Parameters

Water Movement Intensity. - The intensity of water movement during each interval of kelp tagging is shown in Figure 5a, expressed as the frequency of maximum wave heights greater than 0.5, 1.0, 1.5, and 2.5 m. The greatest wave height observed during the entire 21 months of the study was 5.0 m, which occurred during a storm in January, 1975. In general, maximum wave heights greater than 2.5 m indicate storm conditions. November was the time of highest water movement intensity during both years of the study. November, 1974 through April, 1975 was, overall, the period of highest water movement.

Sea Surface Temperature. - The water temperature at the surface of the study area ranged from 9.8 to 16.2°C during the 21 months of the study (Figure 5b). Temperature showed a repeated annual cycle, lowest between January and April and highest from August through October. The temperature at the bottom in the study area was typically 1-2°C lower than at the surface. Sharp thermoclines were noted sporadically year-round.

Figure 5. Physical parameters measured near the study
site during the monthly kelp tagging periods from
May, 1974 through January, 1976.

a) WATER MOVEMENT INTENSITY (OBSERVED 2X PER DAY)

b) SEA SURFACE TEMPERATURE

c) MEAN DAILY SOLAR RADIATION
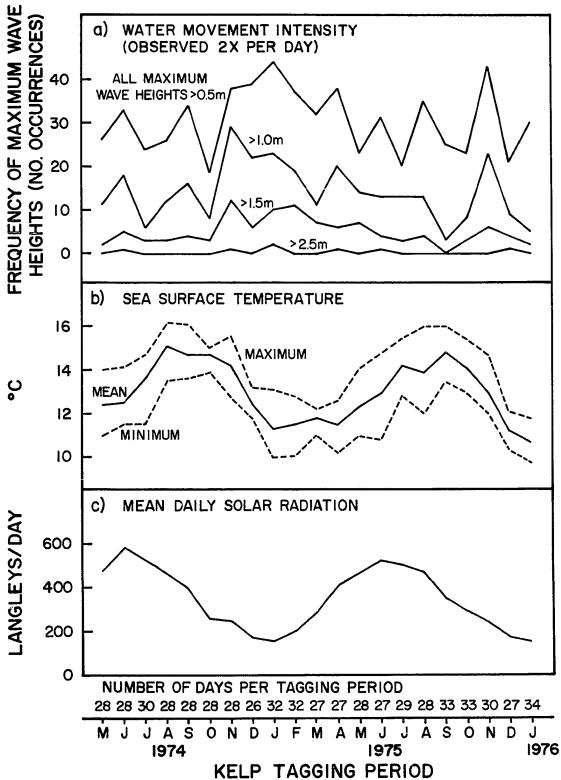
Solar Radiation. - Figure 5c shows the mean daily solar radiation for each tagging period. The repeated annual cycle reached a low in January and peaked in June and July.

Turbidity. - Horizontal visibility on the bottom ranged from 0 to 15 m, and averaged 5 m in the study area. Turbidity was generally lowest in winter and highest in spring, but varied widely on a daily basis during all seasons.

Nutrients. - Total dissolved nitrogen in the upper 10 m of the water column ranged from 0.4 to 18.3 μg-atoms/ liter (Figure 6). Nitrate was typically the largest component of total nitrogen, and the most variable. Nitrite was the smallest component, averaging less than 0.2 μg-atoms/liter. Ammonia was also low in comparison to nitrate. Ammonia averaged only 0.5 μg-atoms/liter, but did show one peak measurement of 4.1 μg-atoms/liter in mid-November, 1975. Dissolved phosphate was much less variable than total nitrogen, ranging from 0.3 to 1.4 μg-atoms/liter during the study. No trends or repeated seasonal changes were apparent in the concentrations of dissolved nutrients.

Figure 6. Nutrients measured near the study site at
    various times during the study. Values shown are
    averaged over the upper 10 m of the water column.
    (Data from Broenkow _et al_., 1975, 1976.)

a) TOTAL NITROGEN (NITRATE + NITRITE + AMMONIA)

b) PHOSPHATE

μg-atoms/liter

TIME (MONTHS)
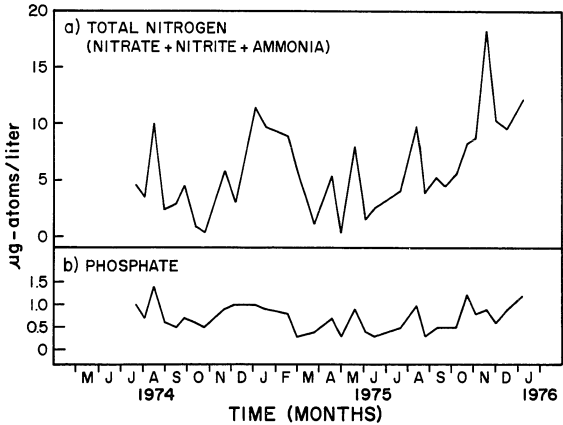
Standing Crop and Population Parameters

The standing crop estimates for each season (and for pre- and post-storm periods of Fall, 1974 and 1975) are shown in Figure 7a. These estimates are the products of the corresponding seasonal measurements of mean plant density, plant size, and frond size shown in Figures 7b, c, d.

The estimated standing crop of $\underline{M}$. $\underline{pyrifera}$ within the study area ranged from a high of 6.3 kg/m^2 in Spring, 1974 to a low of 0.7 kg/m^2 in Spring, 1975. There were no apparent seasonal trends in kelp standing crop; however, the observed fluctuations reflect long-term changes in plant density and plant size, and seasonal changes in frond size.

Plant Density. - The distribution of adult kelp plants per unit area in the kelp forest was very patchy throughout the duration of the study. This patchiness was partly due to substrate heterogeneity, especially to the existence of large permanent sand channels within the study area. In addition, areas dominated by larger kelp plants were generally less dense than areas where most of the plants were small. The resulting high variance in density measurements made it difficult to show statistically significant changes in mean plant density over time.

Figure 7. Standing crop and population parameters
(± 95% confidence limits) measured seasonally for
M. pyrifera. Pre- and post-storm measurements
are shown when available for Fall, 1974 and Fall,
1975. F = Fall, W = Winter, S = Spring, Z =
Summer, n = sample size.

a) STANDING CROP OF ATTACHED KELP

b) PLANT DENSITY
n=25

c) PLANT SIZE
$9 \leq n \leq 124$

d) FROND SIZE
(n)
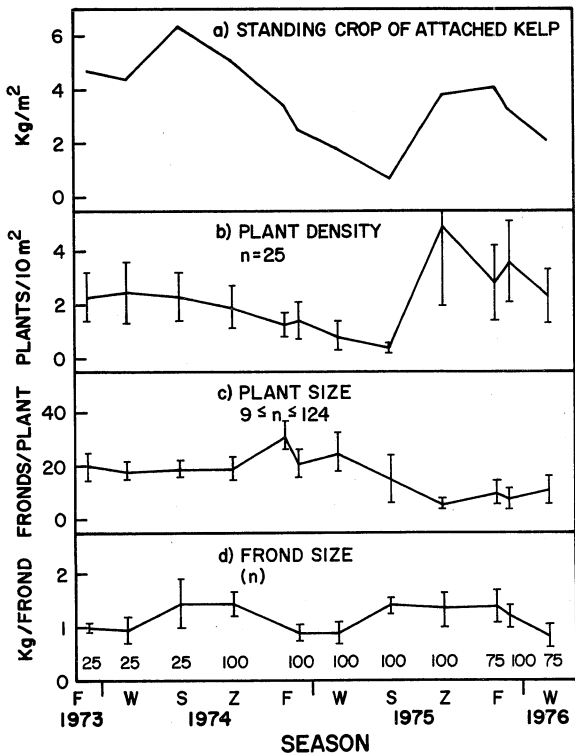
SEASON

The mean density of adult kelp plants in the study area showed a decreasing trend from 2.5 plants/10 m^2 in Winter, 1974 to 0.4 plants/10 m^2 in Spring, 1975. The mean density was significantly lower in Spring, 1975 than during any other season. This decrease was the result of the cumulative loss of approximately 80% of the plants during the preceding fall and winter. The decreasing density was visually obvious underwater and, as a severe canopy loss, from the surface.

The mean plant density increased significantly to 4.9 plants/10 m^2 in Summer, 1975. This increase was due to a large recruitment of juvenile sporophytes, first observed in March and April. The peak mean density of juveniles was 14.4 ± 7.8 plants/10 m^2, measured in May, 1975. Assuming that their growth rate was similar to that estimated by Neushul (1963) for juvenile sporophytes in the sea, these juveniles (15-50 cm in length) were approximately 4-6 months old at this time. Their density was at least 100 times greater than the highest density of juvenile plants measured in previous seasons, and was most likely a result of an increase in light reaching the bottom, due to the extremely low density of adult plants and reduced canopy shading during late Fall, Winter, and Spring. Kelp plants produce spores year-round (Anderson and North, 1967); microscopic gametophytes and sporophytes are probably always

present on the bottom, but may require some minimal light level for development and growth. Judged from the subsequent increase in adult plant density, approximately 20-30% of the juveniles present at their peak density grew into adult plants (with at least one frond greater than 1 m in length). Although some of the juvenile plants were destroyed by grazers or storms, their mean density was still high in Winter, 1976 (3.7 ± 2.2 plants/10 m^2). Therefore, approximately 25% of the peak density of recruited plants remained as juvenile plants nine months after the recruitment was first observed.

Plant Size. - In this study, plant size was measured as the number of fronds per plant. Adult _Macrocystis_ plants are continually losing fronds and adding new fronds, so the number of fronds on a plant is not a reliable indication of the age of the plant. Figure 7c shows the mean number of fronds per plant measured seasonally over 2.5 years. The variance was high during all seasons, because there was always a large range of plant sizes (from 1 to 166 fronds during the entire study); however, some significant changes are evident.

The mean plant size before the first fall storms in 1974, was 31.7 fronds, significantly higher than all previous seasons. Low water movement intensity during the

summer and the resulting reduced loss of fronds account
for this increase. Three weeks later, just after the
first storms, the mean plant size was significantly lower,
at 21.0 fronds.

The mean plant size in Summer, 1975 was significantly
lower than all previous seasons and remained low through
Winter, 1976. This decrease was due to the numerous small
plants recruited in the spring. The effect of these young
kelp plants on mean plant size can be more easily seen in
the seasonal plant size frequency histograms (Figure 8).
Through Spring, 1975, there was a relatively even distribu-
tion of plant sizes. Summer, 1975 showed a predominance of
plants with one to five fronds; most of these plants were
spring recruits. The growth of some of these plants to
6-10 and 11-15 fronds is shown by the Fall, 1975 and
Winter, 1976 distributions.

The increase in the estimated standing crop of $\underline{M}$.
$\underline{pyrifera}$ after the major recruitment of new plants was not
proportional to the increase in mean plant density, because
mean plant size decreased simultaneously.

Frond Size. - Mean frond size, expressed as a weight
measurement, showed repeated seasonal changes during the
2.5 year study (Figure 7d). Although the variance was
generally high because there were always large and small

Figure 8. Seasonal plant size frequency distributions
for Fall, 1973 through Winter, 1976. Fall
histograms include only post-storm data. Total
juvenile plant counts are shown for the 25 random
10 m^2 plots from Fall, 1974 through Winter, 1976.

FALL, 1973 n = 58
FALL, 1974 n = 34
2 JUVENILES/250 m²
FALL, 1975 n = 89
153 JUVENILES/250 m²
WINTER, 1974 n = 62
WINTER, 1975 n = 21
3 JUVENILES/250 m²
WINTER, 1976 n = 57
92 JUVENILES/250 m²
SPRING, 1974 n = 58
SPRING, 1975 n = 9
359 JUVENILES/250 m²
SUMMER, 1974 n = 47
SUMMER, 1975 n = 124
312 JUVENILES/250 m²

% OF PLANTS

PLANT SIZE (FRONDS/PLANT)
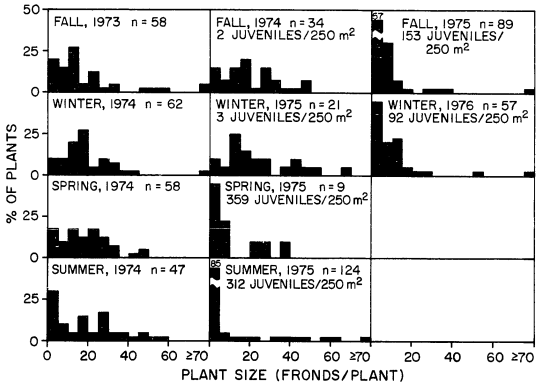
fronds present, the mean frond size was always less in
fall, after the first storms, and in winter than in spring
and summer. The seasonal frond size frequency distributions
(Figure 9) clarify the cause as a seasonal difference in
the range of frond sizes.

The maximum frond size in fall and winter was always
much less than in spring and summer. Large kelp fronds may
be more susceptible to increased water movement, because the
diameter and strength of their stipes do not increase in
proportion to the stress exerted on them by the buoyancy
and drag of an increased number of blades. Therefore,
large fronds are selectively removed during the periods of
high water movement in fall and winter. The maximum frond
weight measured in those seasons was 3-4 kg. Calmer
weather in spring and summer allowed the persistence of
much larger fronds, weighing up to 8.2 kg. These seasonal
changes in mean frond size did not impose an obvious re-
peated change on the estimates of kelp standing crop,
because they were usually exceeded by simultaneous changes
in plant density and plant size.

The seasonal differences in maximum frond size did,
however, influence changes in canopy cover and density. The
percent of fronds reaching the canopy in fall and winter
was lower (41-54%) than in spring and summer (55-64%) over
2.5 years. Furthermore, the very large fronds that are

Figure 9. Seasonal frond size frequency distributions
for Summer, 1974 through Winter, 1976. Sample size =
100 fronds for all seasons, except Winter, 1976
(n = 75).
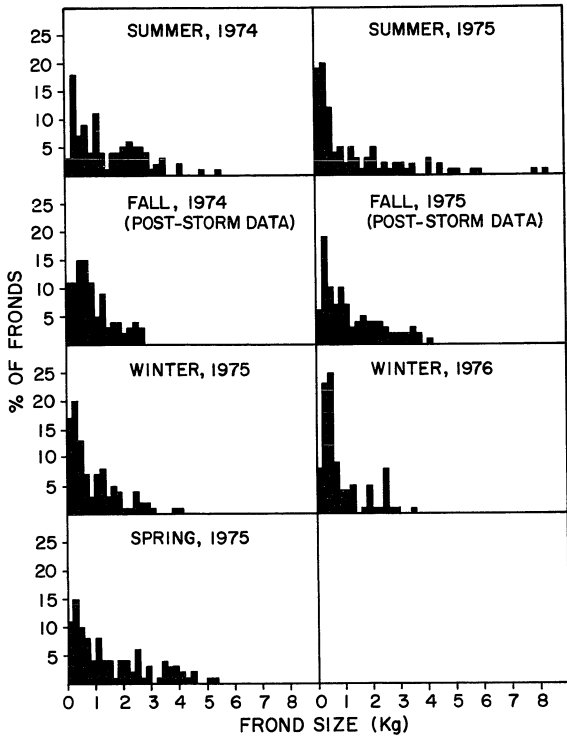
found in spring and summer have most of their biomass on the surface and contribute a disproportionately large amount to the canopy. It is primarily this small proportion of very large fronds that composes the dense kelp canopy in spring and summer.

Frond Condition. - Frond condition was subjectively judged on the presence of grazing damage, deterioration of laminae, and epiphyte concentration on the upper half of each frond (Figure 4). Figure 10 shows the percent by size class of all fronds that were found to be in good, fair, and poor condition. The physical condition of the kelp fronds varied with their size and age. Larger, older fronds sometimes become senescent and begin to decompose. These fronds also generally show more grazing damage; either they are more attractive to grazers and easier to consume, or they have accumulated more visible evidence of grazing through longer existence. However, even the largest frond size classes had less than 20% of their fronds in poor condition. Kelp fronds are subject to constant stress by water movement, and the most weakened material is rapidly removed, even in spring and summer. The tendency for larger fronds to be in poorer condition makes them even more susceptible to increased water movement in fall and winter.

Figure 10. Percent of fronds in GOOD, FAIR, and POOR
       condition for different frond size classes. Data
       combined from all monthly kelp tagging periods.

FROND CONDITION
(n = 879)
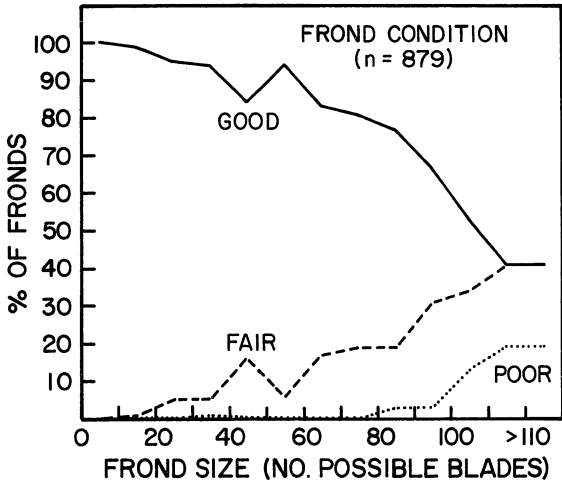
Standing Crop Composition. - Lamina weight always constituted at least half of the total kelp standing crop. The remaining portion consisted of stipes and pneumatocysts. There was a repeated annual cycle in the percent lamina weight which was highest in spring (62%) and lowest in fall (49-56%) (see Figure 17). Fronds with stronger, heavier stipes and less laminar drag may have been more successful in surviving periods of high water movement. Increased water movement probably also increased the sloughing off of senescent tips of the laminae (Pace, 1972) and, thus, reduced the percent lamina weight.

Frond Size Relationships. - Frond size was measured in terms of the number of possible blades per frond, frond length, and frond weight. The linear correlations of these parameters were all highly significant; the calculated regression coefficients are shown in Table 1.

The relationship between the number of possible blades per frond and frond length remained constant for the duration of the study. Very small fronds showed a slight lag in length per blade count. At the 10-15 blade stage (approximately 1-1.5 m), the number of elongating stipe internodes per frond reached a maximum. After this, the increase in length per added blade remained constant through the largest fronds measured (200 blades or 23 m in length).

Table 1. Frond size relationships. Based on linear regression analysis, where $Y = A + BX$, n = number of data pairs, r = coefficient of correlation.

FROND TYPE	MONTHLY DATA	X	Y	n	A	B	STANDARD ERROR OF B	r
Intact apical blade	All	Number of Possible Blades	Stipe Length (m)	129	1.14	0.109	2.76×10^{-3}	0.961
Intact apical blade	All	Number of Possible Blades	Frond Weight (gm)	176	-195	26.9	0.934	0.909
Intact apical blade and all laminae present	Low Growth Period	Number of Possible Blades	Frond Weight (gm)	28	-228	27.8	2.24	0.927
Intact apical blade and all laminae present	High Growth Period	Number of Possible Blades	Frond Weight (gm)	27	-224	33.7	1.29	0.982
Intact apical blade and all laminae present	Low Growth Period	Stipe Length (m)	Frond Weight (gm)	21	-109	158	22.9	0.846
Intact apical blade and all laminae present	High Growth Period	Stipe Length (m)	Frond Weight (gm)	27	-348	268	25.2	0.905

The regression of frond weight and the number of possible blades per frond was calculated for fronds with an intact apical blade and with no missing laminae, as well as for all fronds with an intact apical blade. Both of these analyses were necessary to estimate kelp production rates. The weight-blade count regression which included fronds with missing laminae was statistically constant during the entire study. This was probably due to a relatively high variance. However, the regression calculated for fronds with all laminae present was found to differ significantly during two time intervals which corresponded to periods of different frond growth rates. The relationship of frond weight to length also differed significantly during the two different growth periods.

Of the three parameters used to express frond size, blade counts were the most efficient and useful. The number of blades was quickly and easily determined by a single diver with no special equipment. Blade counts were especially useful in the growth studies, because blades on intact fronds could be counted in situ. Changes in blade count could be expressed as equivalent changes in frond length or weight by conversion with regression coefficients. Furthermore, frond length and weight both correlated more closely with blade count than with each other (Table 1).

Growth and Production

Estimates of _Macrocystis_ production during any period of time must include the recruitment of new plants, the addition of fronds by existing plants, and the growth of existing fronds. All of these processes were followed in this study. The recruitment of new kelp plants has been discussed in the previous section, and was included in the production calculations as an increase in frond density.

Addition of New Fronds. - _Macrocystis_ plants add new fronds by division of basal meristems located near the bottom of existing fronds. Figure 11 shows the mean number of new fronds added per month by different sizes of kelp plants. These means are based on measurements of 485 plants tagged for one month intervals between April, 1974 and January, 1976. Mean monthly frond addition increased from 2 to 14 fronds per plant with increasing plant size. This is an expected result, because plants with more fronds have more basal meristems. However, larger plants also lost more fronds on a monthly basis; therefore, the mean net addition rate of fronds was relatively constant for all plant sizes. Plants with up to 50 fronds had a net monthly increase of 1-2 fronds. Larger plants with up to 70 fronds increased by 3-5 fronds each month. Plants with more than

Figure 11. Monthly gross rates of frond addition and
loss for various plant size classes. Net change =
difference between the two gross rates. Data
combined from all monthly kelp tagging periods.
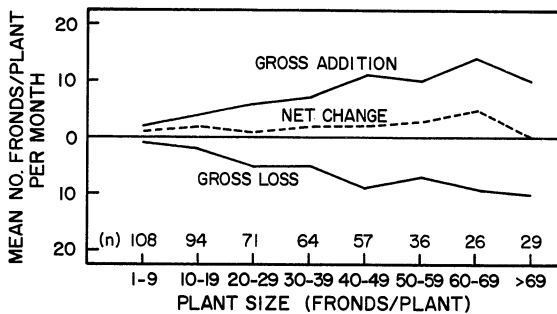
70 fronds showed no mean net increase of fronds, apparently due to a decrease in the addition rate of new fronds. This decrease may be the limiting factor which determined the maximum plant size in the study area.

Frond addition rates combined for all plant sizes and recalculated on a seasonal basis showed no repeated seasonal trends, although the mean size of the tagged plants remained relatively constant. However, from January through June, 1975, the monthly mean was higher (8-13 fronds/plant) than during the rest of the study (3-8 fronds/plant). This period of increased frond addition coincided with the first half of a period of increased frond growth rate.

Frond Growth. - Individual fronds of _Macrocystis_ grow by splitting off new blades acropetally (upward toward the apex) from a meristematic region of the apical blade. At first, these new blades are a part of and remain attached to the apical blade; eventually each new blade begins to form a pneumatocyst, and each in sequence splits completely from the apical blade. The stipe between blades increases in diameter and elongates, isolating each developing blade. Each pneumatocyst increases in size, and each lamina increases in area until its rate of sloughing at the tip equals or surpasses its rate of growth. In this study, frond growth was measured only as an increase in the number

of possible blades. Growth rates and production estimates could then be expressed as increases in frond length or weight by using the calculated relationships between those parameters (Table 1). The greatest monthly increase measured for any frond during the study was 120 blades (approximately 14 m in length, or a weight increase of 3.5 kg).

Figure 12 shows the generalized growth curve for a kelp frond. It was derived from measurements of 417 fronds of various sizes (3-200 possible blades when originally tagged), each tagged for one month between April, 1974 and January, 1976. To arrive at this curve, it was assumed that the minimum frond size tagged (1 m in length or about 5 blades) corresponded to a mean age of 2 months (North, 1971a). The mean increase in number of possible blades for this size class of fronds was then added to the original mean size to predict the mean frond size at 3 months. The calculation was repeated for that size class, and so on. The resulting growth curve shows that the mean rate of growth of a kelp frond increased with increasing frond size, until it reached a peak monthly growth rate which it maintained for about 1 month. The mean monthly growth rate then began to decrease. This decrease was at least partly due to the formation of a terminal blade in some of the large fronds; after a terminal blade was formed, no new blades

Figure 12. Growth curve showing increasing frond size
     with age for fronds with intact apical blades.
     Data combined for all monthly kelp tagging periods.
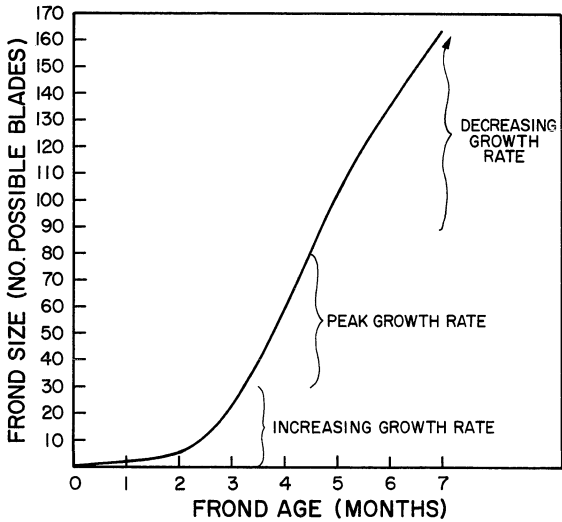
were added. The size at which a terminal blade was formed
varied from frond to frond and ranged from 80 to 200
possible blades.

The number of young blades attached to the apical blade
was expected to increase with an increasing rate of new
blade formation (Cribb, 1954; Pace, 1972). To test this,
the still-attached young blades were counted on 66 fronds
which were collected for size measurements in Spring,
Summer, and Fall, 1975, and which ranged in size from 4 to
200 possible blades. A highly significant correlation was
found between the mean number of young blades attached to
the apical blade and the mean growth rate of fronds in each
size class ($Y = 2.68 + 0.45X$, standard error of slope =
0.094, $r = 0.808$, where Y = number of attached young blades
and X = mean number of possible blades added/frond per
month). Although this relationship may vary temporally
and spatially, and may be affected by physical factors such
as water movement intensity (Pace, 1972), it should prove
to be a useful index of frond growth.

Variation in the measured growth rate from frond to
frond was extremely high throughout the study, even for
fronds of equal size measured during the same time interval.
This variation was probably due to differences in the
position of tagged plants within the study area, differences
in the condition of fronds nearest and most important in

translocation of photosynthate to the tagged fronds, differences in the physical and physiological condition of tagged plants and fronds, etc. Because the growth of only one frond was followed on each tagged plant, the variation within or between individual plants could not be analyzed. However, no difference in mean growth rate was found for similar-sized fronds on plants of different sizes.

The individual variation made it difficult to recognize temporal trends in the monthly mean frond growth rate. Analysis showed a significant increase in the mean frond growth rate in Winter, 1975 and a significant decrease in Fall, 1975. The rate remained high in the interval between these changes; therefore, February through October, 1975 was determined to be the period of high growth. Low growth periods included May, 1974 through January, 1975 and November, 1975 through January, 1976. Data from November, 1973 and February, 1974 indicated frond growth rates similar to the low growth periods.

Figure 13 shows the mean growth rates for each frond size during the high and low growth periods. Fronds always reached a maximum growth rate at a size of 30-40 possible blades. However, the mean growth rates for each size class up to 60 blades were significantly higher (t-tests, $p < 0.05$) during the high growth period. The cause or causes of increased growth rate during this 9 month interval

Figure 13. Monthly growth rates (mean ± 95% confidence
     limits; sample sizes shown at bottom of each bar)
     for various frond size classes. Data combined
     from monthly kelp tagging periods during the
     LOW GROWTH PERIOD (May, 1974 through January, 1975
     and November, 1975 through January, 1976) and
     during the HIGH GROWTH PERIOD (February through
     October, 1975).

FROND SIZE (NO. POSSIBLE BLADES)
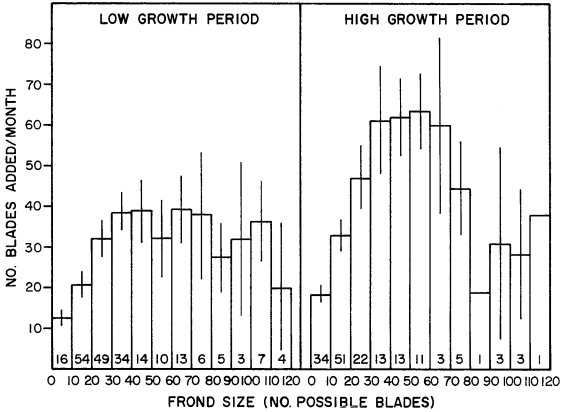
are not obvious.

The increase in the ratio of frond weight to length and blade count during this period appeared to be due to an increase in mean lamina weight which was 19.0 and 18.7 gm in Spring and Summer, 1975, respectively, and between 9.9 and 15.6 gm during all other seasons. This may have been a cause or an effect of the increase in growth rate. The fall decrease in growth rate corresponded to a decrease from the maximum surface temperature, but the winter increase occurred during the period of minimum temperature. The start of the high growth period corresponded to an increase from the minimum solar radiation and the fall decrease coincided with a decrease to the minimum monthly radiation. The winter increase coincided with a period of low turbidity, but the growth rate remained high through the spring period of high turbidity. It is important to note that no significant changes in the mean growth rate of kelp fronds occurred in the previous year, whereas similar seasonal changes in these physical parameters did occur. Furthermore, the high growth period did not correlate with a sustained increase in dissolved nitrogen or phosphate. High and low nutrient concentrations occurred during both the high and low growth periods.

Frond Lifespan. - The age of the oldest kelp fronds was estimated for each season from the maximum frond size and the mean frond growth rate. The mean growth rate calculated for the high growth period was used to estimate the age of the largest fronds found in Spring, Summer, and Fall, 1975. The low period growth rate was used for all other seasons. The maximum frond lifespan was greater in spring and summer (7-7.5 months) than in fall and winter (5.5-6.5 months). This seasonal difference was due to differences in water movement intensity during the later life of the fronds, at the time when the fronds were most susceptible to loss by water movement.

Estimation of Production. - Monthly production of kelp was estimated from standing crop and growth data (Table 2). Parameters measured on a seasonal basis were assumed constant for all three months of that season. The density of growing fronds was calculated by subtracting the density of fronds with no apical blade and the density of fronds lost during that month (see below) from the total frond density (mean plant density x mean plant size). The mean increase in frond weight was estimated by summing the products of the frequency of each frond size class and the mean growth rate for that size class. The rate measured during the high growth period was used in the calculations

Table 2. Production of attached kelp (kg wet weight/m²). Fronds lost during each month are assumed to have grown for half of the month.

KELP TAGGING PERIOD	CONTRIBUTION OF INTACT FRONDS			CONTRIBUTION OF LOST FRONDS			CONTRIBUTION OF NEW FRONDS			TOTAL
	Number of growing fronds/m²	Produced kg/frond	Produced kg/m²	Number of lost fronds/m²	Produced kg/frond	Produced kg/m²	Number of new fronds/m²	Produced kg/frond	Produced kg/m²	Produced kg/m²
1974										
May	3.5	0.75	2.6	0.5	0.38	0.2	0.8	0.2	0.2	3.0
June	3.0	0.75	2.2	1.0	0.38	0.4	1.1	0.2	0.2	2.8
July	2.5	0.79	2.0	0.5	0.40	0.2	0.4	0.2	0.1	2.3
Aug.	2.3	0.79	1.8	0.7	0.40	0.3	0.8	0.2	0.2	2.3
Sept.	2.0	0.79	1.6	1.0	0.40	0.4	0.7	0.2	0.1	2.1
Oct.	2.0	0.83	1.7	1.0	0.42	0.4	0.6	0.2	0.1	2.2
Nov.	0.6	0.83	0.5	2.4	0.42	1.0	0.7	0.2	0.1	1.6
Dec.	1.3	0.83	1.1	0.9	0.42	0.4	0.1	0.2	0.0	1.5
1975										
Jan.	0.7	0.74	0.5	0.9	0.37	0.3	0.5	0.2	0.1	1.9
Feb.	1.1	1.36	1.5	0.5	0.68	0.3	0.8	0.2	0.2	2.0
March	1.2	1.36	1.6	0.4	0.68	0.3	0.4	0.2	0.1	2.0
April	0.2	1.22	0.2	0.3	0.61	0.2	0.1	0.2	0.0	0.4
May	0.4	1.22	0.5	0.1	0.61	0.1	0.1	0.2	0.0	0.6
June	0.4	1.22	0.5	0.1	0.61	0.1	0.5	0.2	0.1	0.7
July	2.2	1.12	2.5	0.5	0.56	0.3	0.7	0.2	0.1	2.9
Aug.	2.2	1.12	2.5	0.5	0.56	0.3	0.8	0.2	0.2	3.0
Sept.	2.5	1.12	2.8	0.2	0.56	0.1	0.3	0.2	0.1	3.0
Oct.	1.8	1.29	2.3	0.5	0.65	0.3	0.6	0.2	0.1	2.7
Nov.	1.6	0.73	1.2	0.7	0.37	0.3	0.4	0.2	0.1	1.6
Dec.	1.7	0.79	1.3	0.6	0.40	0.2	0.9	0.2	0.2	1.7
1976										
Jan.	1.5	0.79	1.2	0.5	0.40	0.2	0.6	0.2	0.1	1.5
Mean kg/m² per month			1.5			0.3			0.1	1.9
kg/m² per year			18.3			3.6			1.4	23

for February through October, 1975; the low growth rate was assumed for all other months. Production (kg wet weight/m^2 per month) was then equal to the density of growing fronds times the mean monthly weight increase per frond. The recruitment of new plants was included in this calculation as an increase in frond density.

Fronds lost during the month contributed to the total production of kelp until the time of their loss. Therefore, it was assumed that an average lost frond grew for half a month before being lost. The contribution of these fronds to total kelp production was determined by multiplying the density of lost fronds with apical blades by half of the monthly mean increase in frond weight (calculated as above).

The monthly addition of new fronds was also added to the estimate of total kelp production. The mean size of the newly added fronds (newly added to the frond count; actually about 2 months old) was estimated to be 0.2 kg.

The total wet weight production of M. pyrifera per month ranged from 0.4 to 3.0 kg/m^2 (Table 2). The average monthly production of attached kelp measured over 21 months was 1.9 kg/m^2. Annual production was 23 kg/m^2, almost 50 metric tons within the entire 2000 m^2 study area. This is an estimate of the net production of wet weight of M. pyrifera. Because it is based on the weight of fronds that have been grazed, have sloughed off senescent material,

and have leaked photosynthetic products, this estimate
does not include the part of production that was lost to
grazers, or as detritus and dissolved organic material
(DOM). It does include produced kelp biomass that was
lost as drift kelp during the same month.

Loss of Attached Kelp and Production of Drift Kelp

Laminae, fronds, and whole plants lost from the stand-
ing crop of attached kelp become drift kelp. The amount of
drift kelp produced during any time interval depends partly
on the magnitude of the source, i.e., the standing crop of
attached kelp. The proportion of kelp that is lost from
the standing crop depends primarily on water movement
intensity. Figures 14b, c, d, e show the gross monthly
percent losses of whole kelp plants, fronds, frond fragments,
and laminae (including lost blades) measured over 21 months.
Figure 14a shows the water movement intensity during that
time, expressed as the frequency of maximum wave heights
greater than 1 m.

Loss of Whole Plants. - Of 525 kelp plants tagged for
1 month intervals during this study, 40 were lost. There
was no apparent influence of plant size on the probability
of loss: the lost plants ranged in size from 4 to 93 fronds,

Figure 14. Water movement intensity (from Figure 5a) and percent losses of whole plants, fronds, frond fragments, and laminae measured during the monthly kelp tagging periods from May, 1974 through January, 1976.

Figure with five stacked panels plotted against KELP TAGGING PERIOD (months M J J A S O N D J F M A M J J A S O N D J for 1974, 1975, 1976). Y-axis label: NO. OCCURRENCES / % LOSS/TAGGING PERIOD.

a) WATER MOVEMENT INTENSITY - MAXIMUM WAVE HEIGHTS > 1.0 m (o INCLUDES WAVE HEIGHTS > 2.5 m)

b) PLANT LOSS n = 25

c) FROND LOSS 64 ≤ n ≤ 100

d) PARTIAL FROND LOSS 16 ≤ n ≤ 25

e) LAMINA LOSS 1000 < n < 2000

KELP TAGGING PERIOD
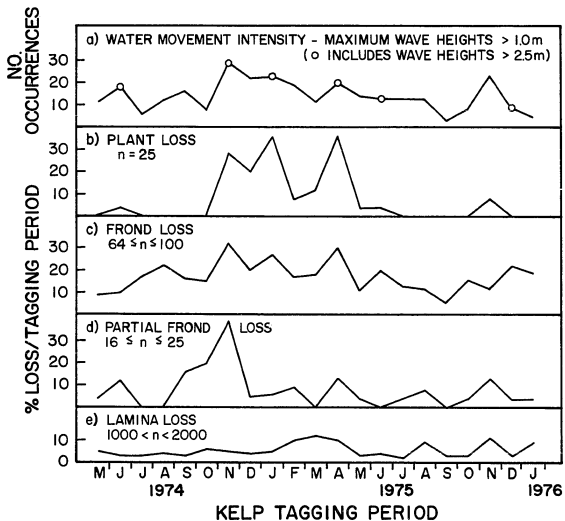
and the size distribution of the lost plants was similar to that of all plants tagged. More than two thirds of the plants were lost with the holdfast intact on the plant; the others were broken at the primary stipe above the holdfast which was left on the bottom.

Monthly plant loss had a strong positive correlation with water movement intensity for the 21 months measured ($r = 0.73$, $p < 0.01$). Figure 14b shows that most of the plants were lost between November, 1974 and April, 1975, during a period of high water movement intensity. However, several other factors besides water movement are involved in determining losses of whole plants. Kelp plants that accumulate very large frond masses in relation to their holdfast size during calm summer weather are probably the first to be torn loose by fall storms. These become tangled with other plants, increasing the drag on the still attached plants and the probability of these also being lost. Therefore, tangling often causes a disproportionately large increase in plant loss with respect to the increase in water movement intensity, and enhances the tendency for plant loss to be patchily distributed in time and space. This is especially true when plant density is high.

Loss of Fronds and Frond Fragments. - Figure 14c shows the monthly percent loss of fronds (not including fronds

lost as whole plants). Frond loss per month ranged from 6 to 32% of the attached standing crop, and showed a significant positive correlation with water movement intensity over time ($r = 0.48$, $p < 0.05$). However, the effect of increased water movement on frond loss was less dramatic than on the loss of whole plants. Fronds were lost during even the calmest months; perhaps the influence of senescence and grazing damage on frond loss was relatively greater during those periods.

Similarly to plant loss, frond loss was influenced by tangling. In some instances, tangling increased frond loss; for example, tangling with detached plants could cause the loss of a large number of fronds from an attached plant, rather than the loss of the whole plant. Young fronds entwined with large, old fronds on the same plant were sometimes ripped out by water movement that the young fronds alone could have withstood. By means of the same entangling, large fronds were sometimes able to survive periods of high water movement intensity.

The probability of any frond being lost increased only slightly with increasing frond size (measured when originally tagged). During the 21 month study, 7% of the tagged fronds with up to 40 possible blades were lost, and 12% of fronds with between 40 and 90 blades. None of the fronds with greater than 90 possible blades were lost completely, but

over 50% of these very large fronds were partially lost, compared to only 5% of the smaller fronds. This high frequency of fragmentation in very large fronds explains the observed peak in partial frond loss in Fall, 1974 (Figure 14d). The November, 1974 sample was tagged before the first fall storms, when a relatively high proportion of large fronds remained from the summer. The first storms occurred during that month, and almost all of the large fronds were broken. The absence of a corresponding peak in Fall, 1975 was due to a lower proportion of large fronds in the randomly selected sample. In spite of this, partial frond loss had a strong positive correlation with water movement intensity during the 21 months ($r = 0.72$, $p < 0.01$).

Loss of Laminae. - The monthly percent loss of laminae (including blade loss) ranged from 2 to 12% during the study (Figure 14e), but did not show any positive correlation with water movement intensity or any seasonal trends. Most of the laminae lost were the oldest on large fronds. These laminae were generally in poor condition, and their loss was at least partially due to age and senescence, and perhaps also to their location in the surge zone (Neushul, 1972). Breakage occurred more commonly where the lamina joined the pneumatocyst than between the pneumatocyst and stipe.

Estimated Production of Drift Kelp. - The amount of kelp
lost from the attached standing crop each month was esti-
mated from standing crop measurements and percent losses
(Table 3). As in the calculations of attached kelp produc-
tion, parameters measured on a seasonal basis were assumed
constant for all three months of that season. Because
standing crop was determined from fronds with previous
leakage, sloughing, and grazing damage, the estimates of
kelp loss do not include losses due to DOM and detritus
formation, or to grazing. The estimates of kelp loss are
equivalent to the production of drift kelp.

Total drift kelp production was taken as the sum of
the kelp lost as fronds, frond fragments, and laminae. For
these calculations, percent frond loss included fronds lost
as whole plants. The average lost frond was assumed to
have grown for half the month before being lost. Therefore,
the estimated growth of these fronds which was calculated
as part of attached kelp production (Table 2) was also
added to each month's drift production estimate.

The monthly production of drift kelp as whole fronds
(and plants) was determined as the monthly percent loss of
the attached kelp standing crop. The amount of drift kelp
produced by partial frond loss was calculated as the monthly
percent loss times the mean frond density times the mean
fragment size. The mean frond fragment lost was approximately

Table 3. Production of drift kelp (kg wet weight/m²). Whole fronds and plants lost during each month are assumed to have grown for half of the month (see Table 2). All lost frond fragments are assumed to equal the mean size of 1.1 kg.

KELP TRACKING PERIOD	CONTRIBUTION OF WHOLE PLANTS AND FRONDS				CONTRIBUTION OF FROND FRAGMENTS			CONTRIBUTION OF BLADES AND LAMINAE			TOTAL
	Kelp standing crop (kg/m²)	% frond loss	Half month of growth (kg/m²)	Produced kg/m²	Number of fronds /m²	% partial frond loss	Produced kg/m²	Lamina standing crop₂ (kg/m²)	% lamina loss	Produced kg/m²	Produced kg/m²
1974											
May	6.3	9	0.2	0.8	4.4	4	0.2	3.9	5	0.2	1.2
June	6.3	14	0.4	1.3	4.4	12	0.6	3.9	3	0.1	2.0
July	5.1	17	0.2	1.1	3.6	0	0.0	2.9	3	0.1	1.2
Aug.	5.1	22	0.3	1.4	3.6	0	0.0	2.9	4	0.1	1.5
Sept.	5.1	16	0.4	1.2	3.6	16	0.6	2.9	3	0.1	1.9
Oct.	3.4	15	0.4	0.9	3.9	20	0.9	1.7	6	0.1	1.9
Nov.	3.4	51	1.0	2.7	3.9	28	1.2	1.7	5	0.1	4.0
Dec.	2.5	36	0.4	1.3	2.9	4	0.1	1.2	4	0.1	1.5
1975											
Jan.	1.8	53	0.3	1.3	2.1	4	0.1	1.0	5	0.1	1.4
Feb.	1.8	24	0.3	0.7	2.1	8	0.2	1.0	10	0.1	1.0
March	1.8	28	0.3	0.8	2.1	0	0.0	1.0	12	0.1	0.8
April	0.7	55	0.2	0.6	0.5	8	0.0	0.4	10	0.0	0.6
May	0.7	14	0.1	0.2	0.5	4	0.0	0.4	0	0.0	0.3
June	0.7	24	0.1	0.3	0.5	0	0.0	0.4	4	0.0	0.3
July	3.8	13	0.3	0.8	2.9	4	0.1	2.3	2	0.1	1.0
Aug.	3.8	12	0.3	0.8	2.9	8	0.3	2.3	9	0.2	1.3
Sept.	3.8	6	0.1	0.3	2.9	0	0.0	2.3	3	0.1	0.4
Oct.	4.1	16	0.3	1.0	2.9	4	0.1	2.3	3	0.1	1.2
Nov.	4.1	19	0.3	1.1	2.9	12	0.4	2.3	11	0.2	1.8
Dec.	3.3	22	0.2	0.9	2.8	4	0.1	1.8	3	0.1	1.1
1976											
Jan.	2.1	19	0.2	0.6	2.6	4	0.1	1.2	9	0.1	0.8
Mean kg/m² per month				1.0			0.2			0.1	1.3
kg/m² per year				11.5			2.9			1.2	16

50 blades or 1.1 kg wet weight. The contribution of partial frond loss to total drift production was primarily from very large fronds. Many of these fronds have formed terminal blades, so a half-month growth estimate was not included for them. The contribution of lamina loss to total monthly drift production was computed as the percent loss of the standing crop of laminae.

The estimated total monthly production of drift kelp ranged from 0.3 to 4.0 kg/m^2 (Table 3). The average for the 21 months measured was 1.3 kg/m^2. Annual production of drift kelp was estimated to be 16 kg/m^2, approximately 32 metric tons within the entire 2000 m^2 study area.

DISCUSSION AND CONCLUSIONS

The standing crop, production, and loss of <u>Macrocystis</u> in any kelp forest are interdependent. Standing crop is determined by the balance of the rates of production and loss. Production is a function of standing crop and the rate of growth. Loss of attached kelp or drift production depends on the standing crop of attached kelp and the rate of loss from that source. Consideration of all three together provides more information than the sum of separate examinations of each.

The standing crop of <u>M. pyrifera</u> at Point Cabrillo averaged 3.5 kg/m^2 over a 2.5 year period. This estimate falls in the lower end of the range cited by North (1971a) for Southern California and Baja California (3-22 kg/m^2). The lowest standing crop measured in this study area (0.7 kg/m^2 in Spring, 1975) is appreciably lower than all others reported in the literature for California (Aleem, 1956, 1973; North, 1957, 1971a; McFarland and Prescott, 1959; Towle and Pearse, 1973). At the time that this low standing crop was measured, <u>M. pyrifera</u> was present at Point Cabrillo, but hardly formed a "forest". The surface canopy was almost nonexistent and the distribution of adult plants was visibly sparse underwater. As noted above, this low density was due to an 80% cumulative loss of plants by

detachment and tangling in the storms of Fall, 1974 and Winter, 1975.

The mean density of adult plants at Point Cabrillo in Spring, 1975 was comparable to that found by Rosenthal, Clarke, and Dayton (1974) in the kelp forest at Del Mar, California in Spring, 1970. They also cited plant losses, due primarily to increased water movement and tangling with detached plants, as the cause of the low density. A large recruitment of young kelp plants, similar to the recruitment that occurred in the Point Cabrillo study area after the reduction in standing crop, was also reported by Rosenthal et al. (1974). By Summer, 1971, the adult plant density in the Del Mar study area was the highest measured since the beginning of that study in 1967. An analogous increase in density was seen at Point Cabrillo in Summer, 1975.

This pattern of change in plant density, a decrease due to loss by storms and tangling followed by a large recruitment and an increase to the maximum density, has also been noted by North (1971a) and is characteristic of giant kelp forests in California. Between the times of recruitment and extreme loss, plant density slowly decreases as single plants or small patches of plants are lost. Recruitment occurs in the resulting open spaces, but is low overall in the forest. Mean plant size is slowly increased by the net addition of fronds to surviving plants. If no extremely

stormy years occur, the population of kelp plants reaches a state of equilibrium with a mean density, plant size, standing crop, and frond turnover rate determined by characteristics of the plants and the physical environment. The Point Cabrillo kelp forest may have been in a state of equilibrium when this study was initiated in Fall, 1973. The average plant density and size had not changed significantly during the previous two years (Davis, 1971; J. S. Pearse, unpublished data).

A variation of this long-term pattern of loss and recruitment of _Macrocystis_ plants has been described for the kelp forests at Chubut, Argentina. Barrales and Lobban (1975) predicted a complete turnover of kelp populations every 3 or 4 years, and proposed that the cause was a combination of severe winter storms and holdfast damage by the grazing gribble (isopod), _Phycolimnoria_ sp. The regular periodicity of the cycle was attributed to the preference of these grazers for old haptera; holdfast weakening was not effective in plants only a year or two old. In contrast, holdfast damage due to grazing was not an obvious factor determining plant loss in the kelp forests at Del Mar and Point Cabrillo. In these areas, the period of the cycle is primarily determined by the occurrence of exceptionally stormy years, and is much less regular.

The kelp forests at Chubut, Argentina were all composed of a high density of small plants. Their mean plant densities and plant sizes were most similar to the Point Cabrillo forest as it was found in Summer, 1975, in the early stages of a new cycle. None of the forests described by Barrales and Lobban were comparable to the later stages of a California kelp forest, characterized by a relatively low density of large plants. The Argentine forests never attain these characteristics, because their cycles of loss and renewal are regular and frequent.

In contrast to the rapid turnover of kelp plants occurring in Argentina, the _Macrocystis_ forests between Santa Barbara and Point Conception, California have been noted for their lack of plant turnover (North, 1971a). These kelp forests are composed of low densities of very large _Macrocystis_ plants which may belong to a _Macrocystis_ species other than _M. pyrifera_ (Neushul, 1971). North (1971a) found no juvenile plants during almost two years of periodic observation in this area, and concluded that the kelp standing crop was maintained by vegetative growth. He did suggest, however, that a cataclysmic event could destroy the established plants and allow recruitment. The relative stability of the kelp populations in this area may be due to their protected position from prevailing northwest winds and swell, and to characteristics of the plants themselves.

Study of these forests over a long time interval would probably show a similar cyclical pattern in standing crop, plant size, and plant density to that found at Del Mar and Point Cabrillo, but with a much longer period.

In the terminology of Reichle, O'Neill, and Harris (1975), the magnitude of the equilibrium standing crop, or maximum persistent biomass, of an ecosystem will always be lower than its maximum potential biomass. The more severe or more frequent the environmental fluctuations, the lower the maximum persistent biomass will be. Thus, the long-term mean standing crops of $M.$ pyrifera are expected to be lowest in the forests at Chubut, Argentina, intermediate at Point Cabrillo and Del Mar, and greatest at Santa Barbara. Forests of Macrocystis are often able to reestablish a high biomass very rapidly after an environmental catastrophe: the kelp standing crop at Point Cabrillo was not significantly lower 3 months after its lowest point in Spring, 1975 than its estimated maximum during this study; the maximum adult plant density at Del Mar was regained within a year of the time of its minimum level (Rosenthal et al., 1974); the kelp canopy at the site of the wreck of the "Tampico Maru" in Baja California reached its maximum cover in the first year after the oil spill (North, Neushul, and Clendenning, 1964). These examples suggest that Macrocystis forests rapidly regain their maximum persistent

biomass after catastrophic events. However, it is apparent from differences in plant density and size between the kelp forests at Chubut, Argentina and Santa Barbara, California, and from differences in the mean plant density and size measured in the Point Cabrillo forest in Spring, 1974 and Summer, 1975, that these parameters of kelp populations continue to change over a longer recovery interval.

The frequency and extent of the turnover cycle of plants, thus, influences the population structure of kelp forests. The period and amplitude of each cycle have been shown to be influenced locally by the regularity and severity of storms, and in some areas by the action of grazers. Exposure and substrate type must also affect the turnover rate of a kelp population (Barnes and Topinka, 1969). In addition, characteristics of the population, such as plant density and plant size, can determine the effectiveness of increased water movement and tangling. The population structure of any kelp forest must, therefore, be affected by numerous physical and biotic factors.

Mean plant size (number of fronds per plant) in a kelp forest is influenced by the age of the population, especially in the early stages after a large recruitment. In older populations, the rates of frond addition and loss become more important factors determining plant size. The kelp plants at Point Cabrillo showed an overall net increase

in size because the rate of frond addition was greater than the rate of frond loss during the 21 months of the study. However, the net change in plant size varied from month to month. Frond loss was more variable than frond addition and, therefore, had a greater effect on plant size. For example, the increase in mean plant size between Summer and Fall, 1974 was primarily due to a low rate of frond loss during that time. Frond loss doubled in late Fall, 1974, and the mean plant size subsequently decreased. Miller and Geibel (1973) found a similar pattern of change in the Point Cabrillo kelp population from July through October, 1971.

The distribution of frond sizes in a kelp forest is influenced, similarly to plant size, by a balance of frond addition and loss. Because small new fronds are continually being added and larger older fronds lost, the distribution of frond sizes is always skewed toward the lower end of the size range (Figure 9). The turnover rate of kelp fronds is much higher than that of whole plants, and more constant over time. During the 21 months of this study, frond loss and addition averaged approximately 20% per month; therefore, the turnover time of the frond population was approximately 5 months. The seasonal changes in the maximum lifespan of fronds noted in this study were primarily due to seasonal differences in water movement

intensity. The maximum lifespan of kelp fronds in different populations is surprisingly constant. The age of the largest fronds in the Point Cabrillo kelp forest was estimated to be between 5.5 and 7.5 months. Estimates of maximum frond lifespan made for other _Macrocystis_ populations in California (Brandt, 1923; North, 1961), western Canada (for _M. integrifolia_; Lobban, in Barrales and Lobban, 1975), and Tasmania (Cribb, 1954) were all similar to this.

The distribution of frond sizes in a kelp population is influenced by the frond turnover rate. The actual size of the fronds is determined by their lifespan and rate of growth. The growth rate of the kelp fronds in the Point Cabrillo forest varied with the size of the fronds: from small to large fronds, the rate of growth increased, reached and was maintained at a maximum level, and decreased (Figure 12). Similar growth patterns have been described for _M. pyrifera_ in other studies (Cribb, 1954; North, 1971b, 1972; Miller and Geibel, 1973). In the present study, the peak frond growth rate averaged approximately 40 blades per month (5.5 m in length, 0.9 kg) during the low growth periods and 60 blades per month (7.5 m in length, 1.5 kg) during the high growth period. A comparison of these growth rates with those reported by other researchers is complicated by the variety of techniques used. In general,

the results reported here fall in the center of the range of growth rates of M. pyrifera measured in other areas (Scagel, 1947; Sargent and Lantrip, 1952; North, 1971b, 1972) and closely agree with limited measurements made at Point Cabrillo by Miller and Geibel (1973).

The causes of the differences measured during the periods of high and low frond growth rates are unclear. The simultaneous increase in the rate of frond addition at the beginning of the high growth period indicated that there was an overall enhancement of plant growth. The increased ratio of frond weight to length and blade number, and the corresponding increase in mean lamina size, may have been a cause or an effect of the higher growth rate. Greater laminar area for photosynthesis could have influenced the growth rate, but the increase in mean lamina size was not found until Spring, 1975, three or four months after the beginning of the high growth period. As discussed above, the beginning and end of the high growth period corresponded to various changes in sea surface temperature, solar radiation, and turbidity. However, these physical factors fluctuate regularly on an annual basis, and the increased growth rate was observed for only one nine month period out of 21 months. Pace (1972) found a direct relationship between water movement intensity and frond growth rate in M. integrifolia. However, the high growth period defined

by the present study included months of both relatively
high and low water movement intensity. Nutrients have
been considered as important factors limiting kelp produc-
tion (Jackson, 1975), but no correlations were found
between nutrient concentrations and growth rates in this
study. If nutrients are ever limiting to kelp growth at
Point Cabrillo, the effects are probably short-term and
would not be seen in monthly growth measurements.

The most obvious factor corresponding to the start of
the high growth period was the reduced standing crop of
kelp in the study area. The low standing crop could have
influenced growth by allowing greater light penetration
or increased water flow through the forest. Although
North (1971b) found no influence of frond density on growth
rate, these standing crop changes at Point Cabrillo may
have had a synergistic effect with the changes in physical
conditions and, thus, caused the increase in growth rate.
This hypothesis is weakened by the fact that, even though
the rate of frond addition decreased in June, 1975 after
the summer increase in kelp standing crop, the high frond
growth rate was maintained. This continuance was not due
to the vigorous growth of the young plants; no difference
in growth rate was found for fronds on plants of various
sizes (contrary to North's findings (1971b) that fronds on
young plants have lower elongation rates). Finally, the

subsequent fall decrease in growth rate may have been due to a combination of changes in physical factors and a possible increase in energy going to reproductive activity by the kelp. Whatever the determining factors were, the increased rate of growth contributed to the production of kelp at Point Cabrillo.

The rate of production of $\underline{M. \text{ pyrifera}}$ is dependent on its standing crop and rate of growth. During the 21 months of this study, the trends in monthly production of attached kelp (Figure 15) showed a strong positive correlation ($r = 0.77$, $p < 0.01$) with the fluctuations in standing crop (Figure 7a). The differences in growth rate between the high and low growth periods were much less than the changes in standing crop, and, therefore, had less impact on production rates. The lowest estimated monthly kelp production (0.4 kg/m^2) coincided with the lowest standing crop measurement in Spring, 1975, even though the growth rate was high at this time. The highest monthly production (3.0 kg/m^2) occurred during both the high and low growth periods, and corresponded to the highest standing crop measurements. The extreme increase in monthly production in Summer, 1975 was the result of the recruitment of new kelp plants and the subsequent increase in standing crop.

Figure 15. Monthly estimates of net production of attached
kelp, and loss of attached kelp or production of drift
kelp from May, 1974 through January, 1976 (data from
Tables 2 and 3).

Figure showing Production of Drift Kelp and Production of Attached Kelp, with y-axis "Kg/m² PER MONTH" and x-axis "KELP TAGGING PERIOD" spanning 1974, 1975, 1976.
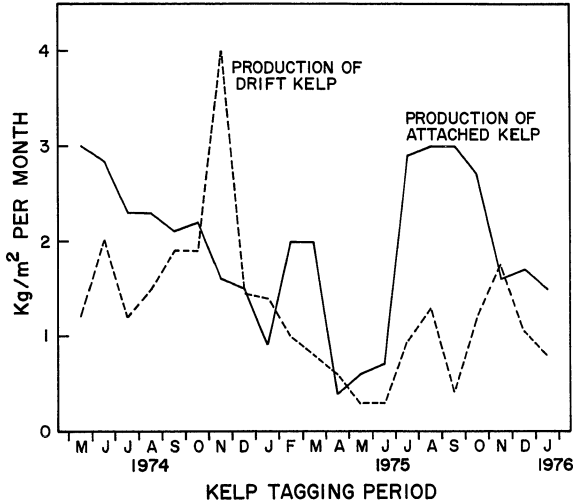
All of the biotic and physical factors that have been shown to influence the standing crop and growth of M. pyrifera also influence production. From the results of this study, water movement intensity must be acknowledged as the single most important physical factor limiting the rate of kelp production: monthly production closely follows standing crop, and standing crop fluctuations are primarily determined by monthly losses which are in turn determined by water movement intensity. Severe storms generally cause the rate of production to decrease, and periods of calm weather allow the production rate to increase. Therefore, the long-term cycles of loss and renewal that are characteristic of kelp forests, and that are so greatly influenced by storms, are not only manifested as changes in population structure, but also as changes in production rate.

The estimated annual production of kelp was 23 kg wet weight/m^2 or 2.2 kg dry weight/m^2 (M. pyrifera is approximately 9.4% dry matter by weight; V. A. Gerard, unpublished data). This is an estimate of net production which does not include losses as dissolved organic matter (DOM), detrital particles, or grazed material. The proportion of photosynthetic products released by marine macrophytes as DOM may be as low as 4% or as high as 40% (Mann, 1972a, 1973). A quantitative measurement of DOM

production by Macrocystis has never been published, however it has been reported to be considerable (Oguri, in Bakus, 1969). Estimating production lost as detritus presents a similar problem. Although this has been studied for the Atlantic kelps, Laminaria and Agarum (Mann, 1972b, 1973; Webster, Paranjape, and Mann, 1975), no estimates have been made for Macrocystis. Macrocystis pyrifera forms detritus by sloughing off the senescent tips of old blades. But detritus production never accounts for the high proportion of total net production at Point Cabrillo that it does in North Atlantic kelps, because a much larger portion of M. pyrifera biomass is lost as drift kelp (K. H. Mann, 1972a, personal communication).

The common grazers of attached kelp in the Point Cabrillo forest include three species of turban snails, Tegula brunnea, T. montereyi, and T. pulligo (Lowry, McElroy, and Pearse, 1974); the isopod, Idothea resecata; the kelp crab, Pugettia producta; and a few fish species, such as the señorita, Oxyjulis californica, which ingest M. pyrifera while picking off epiphytic invertebrates. Preliminary studies of population density and feeding rates at Point Cabrillo have been conducted only on Tegula spp. (J. D. Trent, unpublished data). The results indicate that these three species of snails together ingest between 0.6 and 1.5 kg/m^2 of attached kelp annually. This is only

3-6% of the 23 kg/m^2 annual non-grazed production estimated
in this study. The role of grazers in the production of
drift kelp is unclear. Although North (1964b) described
the severance of kelp laminae from pneumatocysts by
grazing Idothea resecata, the plants at Point Cabrillo
showed no evidence of this, even during peak isopod density
in summer and fall. Furthermore, a Point Cabrillo kelp
plant that was experimentally subjected to a ten-fold
increase in density of Tegula spp. lost no fronds or
laminae, and showed no visible signs of damage due to
grazing after one week (V. A. Gerard, unpublished data).

Because the amount of kelp production lost as DOM,
detritus, and grazed material is unknown, the total net
production of M. pyrifera at Point Cabrillo cannot be
calculated. However, the partial net production of kelp
reported here exceeds the total net production estimates
for M. pyrifera reported by Aleem (1956), Clendenning (1971),
and Littler and Murray (1974) (based on assumptions for
unit conversion according to Towle and Pearse, 1973). The
annual production of kelp at Point Cabrillo is comparable
to the worldwide mean of 2.0-2.5 dry kg/m^2 per year esti-
mated for marine algae beds and reefs (Lieth, 1975;
Whittaker, 1975). It is greater than the total net produc-
tion estimated for most terrestrial forests in temperate
areas (Lieth, 1975; Olson, 1975; Whittaker, 1975). The

partial net annual production (23 kg/m^2) and the average
standing crop at Point Cabrillo (3.5 kg/m^2) indicate a
biomass turnover rate of 6-8 times per year. The addition
of the leaked, sloughed, and grazed portions of kelp
production would raise this estimate; however, it is
closely comparable to the turnover rate of 4-10 times
per year estimated by Mann (1972b) for Atlantic kelps.
These kelp forest turnover rates are two orders of magnitude
greater than the average turnover rates of tropical,
temperate, and boreal terrestrial forests, all of which
approximate 0.04 times per year (Whittaker, 1975). This
difference can be at least partly explained by the great
proportion of long-lasting structural materials that make
up the biomass of terrestrial forests, where primarily
leaves, twigs, and small branches are regularly lost and
replaced. In Macrocystis forests, perennial biomass
consists only of holdfasts and primary stipes.

The 23 kg/m^2 of M. pyrifera produced annually at Point
Cabrillo should ultimately have been measured during this
study as an increase in standing crop or as part of the
drift kelp production. However, the standing crop actually
showed a small net decrease over the 21 months of measure-
ment, and the total annual production of drift kelp was
estimated as only 16 kg/m^2. This imbalance of results is
probably the result of an underestimation of losses. Loss

of kelp plants has been shown to be patchily distributed
in space, due to the role of tangling. Measurements made
by the tagging of individual randomly selected plants may
have underestimated total kelp loss or drift production.
Nevertheless, the trends seen in drift production are valid.

The temporal fluctuations in drift kelp production
(Figure 15) are primarily the result of changes in standing
crop of attached kelp and water movement intensity. The
extreme peak in November, 1974 marked the initial loss of
kelp during the first fall storms. These storms were
particularly effective in producing drift kelp, because
the plants had accumulated large numbers of fronds and a
large proportion of old, senescent fronds during the calm
summer weather. The high initial loss resulted in a
decreased standing crop of attached kelp and a much smaller
proportion of plants and fronds that were susceptible to
increased water movement. Monthly drift production subse-
quently decreased, although high water movement intensity
and tangling maintained high percent losses. An analogous,
but smaller peak in drift production occurred in November,
1975. Percent losses were much lower than during the
previous year, due to calmer weather. At Point Cabrillo,
it is essentially the magnitude of the fall storms which
determines whether the standing crop will be reduced enough
for a new cycle of renewal and loss to be initiated in the

kelp forest that year.

The physical condition of the attached kelp affects the amount of drift kelp produced, and the form and fate of the drift kelp as well. A large proportion of the kelp lost during the fall and winter storms consists of whole plants and fronds with enough intact pneumatocysts to float. This drift kelp may be transported great distances by surface currents. Rafts of reproductively mature kelp plants are an important means of dispersal of all species of Macrocystis (North, 1972). They also provide a unique habitat, food source, and means of dispersal for associated raft animals (Mitchell and Hunter, 1970). These drift kelps are frequently washed up on beaches, where they provide food and shelter for a variable association of wrack organisms. Zobell (1971) found that the highest wrack standing crops on Southern California beaches occurred in the fall and winter, particularly in November. According to the results of the present study, this corresponds to the time of peak losses from the kelp forests. During Zobell's 12-year study, Macrocystis made up 60% of the total beach wrack.

During the summer, a greater proportion of drift kelp is produced as fragments of senescent fronds or as individual laminae which have too few intact pneumatocysts to float, and which sink to the bottom within the kelp forest.

This benthic drift kelp makes up a large proportion of the total benthic drift algae within the forest (see Chapter II). It is utilized as a habitat and food source by many different animals, including sea urchins and abalones (Lowry and Pearse, 1973), several species of benthic crabs (J. S. Pearse, unpublished data), and the batstar, _Patiria miniata_ (see Chapter III). Benthic drift kelp which is not eaten or decomposed is transported out of the kelp forest by tides and currents, and may be an important allocthonous source of energy for other subtidal communities, especially those with low intrinsic rates of primary production. For example, drift _Macrocystis_ has been cited as a major food source for sea urchin-dominated areas (Leighton, Jones, and North, 1966), and for sand-bottom communities dominated by the tube-worm, _Diopatra ornata_ (Emerson, 1975); dense populations of both sea urchins and tube-worms are often found adjacent to California kelp forests. Drift algae have also been reported to be important to benthic communities in the deep sea (Shepard and Dill, 1966; Grassle _et al_., 1975). Thus, the fluctuations in drift kelp production in the Point Cabrillo kelp forest and in all other kelp forests may have far-reaching effects.

Figure 15 shows the monthly production of attached and drift kelp measured at Point Cabrillo. Their peaks

do not coincide, because these two production rates are related through the fluctuating standing crop of M. pyrifera. For example, during Fall, 1974 and Winter, 1975, the monthly production of drift kelp was equal to or exceeded the production of attached kelp, and the standing crop of attached kelp decreased (Figure 7a). In Summer, 1975, the production of attached kelp was much greater than the losses, and the standing crop increased. Thus, production and loss are determined, in part, by standing crop, and standing crop is determined by the balance of production and loss.

In summary, the kelp forest at Point Cabrillo has been shown to be an extremely productive system, characterized by a high standing crop and rapid turnover of M. pyrifera. Standing crop, production, and loss are interdependent, and are greatly influenced by water movement intensity. The production of drift kelp accounts for a large part of the total net production of M. pyrifera. It is probable that the majority of this drift kelp is exported from the forest and provides an important allocthonous source of energy to other marine communities.

CHAPTER II

THE ROLE OF BENTHIC DRIFT ALGAE AND SEAGRASSES

The rates of production and turnover of the giant
kelp, Macrocystis pyrifera (L.) C. Agardh, are among the
highest measured in forest ecosystems (see Chapter I).
As in terrestrial forests, only a small proportion of the
produced kelp biomass is consumed directly by grazers;
most becomes drift kelp. Drift Macrocystis with enough
intact pneumatocysts remains at or near the sea surface
and is often transported out of the kelp forest by water
movement. Detached kelp with too few pneumatocysts sinks
to the forest floor. This benthic drift kelp, along with
other species of drift algae and seagrasses, may decompose
or be consumed by herbivores within the forest, or may be
exported from the forest by water movement.

Subtidal aggregations of "loose-lying" benthic algae
have been described from various parts of the globe
(Burrows, 1958; Austin, 1959; Conover, 1964). These
algae grow from spores which settle on sand or shell
fragments, and they show characteristics specific to
existence on soft substrates. In contrast, the benthic
drift algae and seagrasses considered in the present study
are produced by detachment or fragmentation of attached

plants, and are not specifically adapted to a drifting existence.

Benthic drift algae and seagrasses have been considered in previous studies as a food source utilized by various subtidal herbivores, such as abalones, sea urchins and tubeworms (Leighton, Jones, and North, 1966; Poore, 1972; Lowry and Pearse, 1973; Shepherd, 1973, 1975; Emerson, 1975). Smith (1968) examined the role of drift algae in the littoral phosphate cycle. However, the magnitude and dynamics of the drift plant association within a kelp forest have not been quantitatively investigated by any previous researchers. Therefore, the purpose of the present study was to collect quantitative information on the standing crop, composition, export, and decomposition of benthic drift algae and seagrasses within the kelp forest at Point Cabrillo; to define the influences of various physical and biotic factors on these parameters; and to examine the role of benthic drift plant material as a resource of nutrients and energy within the kelp forest.

METHODS AND MATERIALS

Standing Crop and Composition of Benthic Drift Material. - In Summer, 1973, twelve permanent plot locations were selected by simple random sampling within the Point Cabrillo study area. These sites were marked with 1 m lengths of garden hose attached to stainless steel posts which were cemented into holes drilled in the granite substrate. All benthic drift algae and seagrasses were collected from circular 10 m^2 plots at these sites twice each season (twice every 3 months) from Fall, 1973 through Fall, 1975. Each second seasonal collection was made at least two weeks, but no more than one month, after the first collection. The drift material was collected by hand into 5 mm mesh bags, brought to the laboratory, and sorted into predetermined categories: <u>Macrocystis pyrifera</u>, other brown algae, red algae, green algae, and seagrasses. <u>Macrocystis pyrifera</u> was further separated into laminae and stipes (pneumatocysts were included with stipes); <u>Cystoseira osmundacea</u> (Menzies) C. Agardh was separated from the other brown algae, and divided into vegetative and reproductive portions; and the rhodophytes were split into <u>Gigartina</u> spp., coralline algae, and other red algae. Excess surface water was drained, and the drift material in each category was weighed for each plot. All weights

reported here are unblotted wet weights. Holdfast
material of M. pyrifera and all material of terrestrial
origin were discarded. All living, motile animals
collected with the drift were preserved.

Export of Benthic Drift Algae. - Drifters were used to
study seasonal differences in the export rate of benthic
drift algae. The drifters consisted of 10 x 15 cm pieces
cut from sheets of white corrugated vinyl material and
numbered with a waterproof marking pen. They were
designed to mimic individual kelp laminae in size, shape,
surface texture, density (1.1-1.2 gm/cc), and transport
by water movement. Two replicate sets of 50 drifters each
were released at 25 sites selected by simple random samp-
ling within the 2000 m^2 study area at the beginning of
each seasonal sampling period. New random release sites
were selected each season. After 4 weeks, all drifters
remaining within the study area were collected and counted.
The efficiency of collection was affected by physical
conditions, especially turbidity. To estimate this effi-
ciency, two replicate sets of 50 drifters each were
randomly released within the study area one hour before
each collection. The percentage of these drifters that
was found during the collection was equivalent to the
collection efficiency. The actual number of originally

released drifters remaining in the study area was then
calculated as 100 × No. of Original Drifters Collected/
Percent Collection Efficiency. Because no data were
available to estimate relative changes in local currents,
relative differences in seasonal water movement intensity
were measured as described in Chapter I.

Decomposition of Benthic Drift Kelp. - The loss of
unblotted wet weight over time was determined for
Macrocystis pyrifera during Winter, 1976. Kelp fronds were
arbitrarily selected within the study area, brought to the
surface, and separated into laminae and stipes (pneumato-
cysts were included with stipes). Approximately 3 kg of
lamina or stipe material was placed in each of six pre-
weighed, 5 mm mesh litter bags. Excess surface water was
allowed to drain off, and each bag was weighed to the
nearest 0.1 kg. The bags were then placed in a sand
channel within the study area, and tied to an anchored
trotline so that they could be moved back and forth along
the bottom by surge. After two days, and then at weekly
intervals, the bags were brought to the surface, drained,
and weighed. The mean weights minus the empty bag weights
were used to calculate percent wet weight of kelp
remaining.

RESULTS

Standing Crop and Composition. - Figure 16a shows the
mean seasonal standing crops of benthic drift algae and
seagrasses in the permanent plots. The total amount of
drift material in each collection was expressed in gm/m^2,
and the mean of each seasonal pair of collections was taken
as the seasonal mean (the variance between the two collec-
tions is expressed in Figure 16a as ± 1 standard error).
The mean seasonal standing crops ranged from 32 to 340
gm/m^2, and were always higher in summer and fall than in
winter and spring. Despite the order of magnitude variance
between seasonal measurements, the variance between two
collections made during any one season was generally small.
The fall measurements showed the greatest differences
between collections, because the first fall storms
occurred in the interval between those collections. The
influence of these storms on the drift standing crop is
discussed below. The variances between the summer collec-
tions were also relatively high, because the drift biomass
removed by the first collection was not completely replaced
in the interval between collections, due to low summer
turnover rates. During the entire study, the smallest
amount of drift material collected from a single 10 m^2 plot
was 31 gm, the greatest amount was 16,041 gm.

Figure 16. Seasonal mean standing crop measurements of
total benthic drift algae and seagrasses (n = 2
semiseasonal collections; ± 1 standard error) and
various types of drift plant material from Fall,
1973 through Fall, 1975. Dashed lines show the
percent of each drift category in the total drift
standing crop.
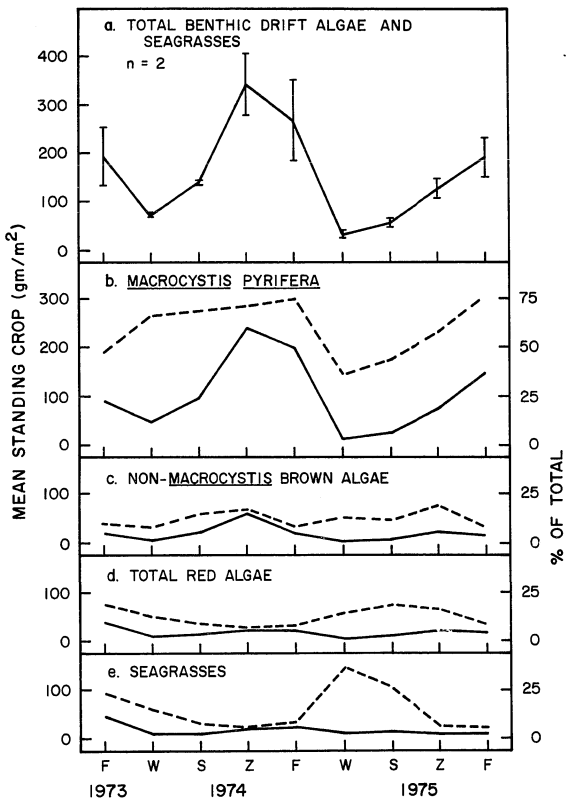
Macrocystis pyrifera, which dominated the attached
algae in the study area in terms of biomass, typically
made up 50% or more of the total drift standing crop, and
averaged 11-240 gm/m^2 within the permanent plots (Figure
16b). The lowest standing crops and percentages of drift
M. pyrifera occurred in Winter and Spring, 1975, during the
period of lowest standing crop and loss of attached kelp
in the forest (see Chapter I). Juvenile plants were found
in the drift collections in Spring, 1975, after a large
recruitment of attached juvenile kelp plants in the study
area (see Chapter I). The benthic drift kelp consisted of
pieces of various sizes, from small fragments of laminae
to whole adult plants. Although small fragments were
always most numerous, large frond fragments and whole fronds
sometimes made up a greater proportion of the benthic drift
kelp, especially in summer. The proportion of drift kelp
that consisted of laminae varied seasonally, and was
generally highest in summer and lowest in winter (Figure 17).
This cycle did not correspond to the proportion of lamina
weight in the standing crop of attached kelp in the study
area.

A number of species of brown algae other than Macro-
cystis were collected as drift algae. These included
Coilodesme californica (Ruprecht) Kjellman, Cystoseira
osmundacea, Desmarestia ligulata var. ligulata (Lightfoot)

Figure 17. Proportion of lamina weight in the standing
       crops of attached and benthic drift M. pyrifera,
       measured seasonally from Fall, 1973 through
       Fall, 1975.
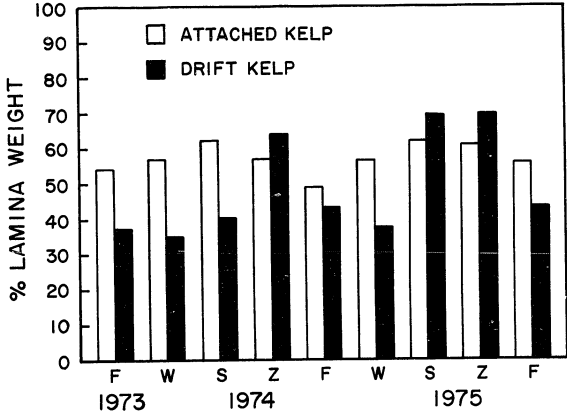
Lamouroux, _Dictyoneuropsis reticulata_ (Saunders) Smith,
Dictyoneurum californicum Ruprecht, _Egregia menziesii_
(Turner) Areschoug, _Laminaria setchellii_ Silva, and
Nereocystis luetkeana (Mertens) Postels and Ruprecht.
The mean seasonal standing crops of these phaeophytes
ranged from 4 to 59 gm/m^2, and made up 8-19% of the total
drift material (Figure 16c). All of these species had
attached populations within the Point Cabrillo forest,
except _N. luetkeana_. Bull kelp was undoubtedly trans-
ported from other kelp forests as floating plants which
became tangled in the _Macrocystis_ canopy and sank.
Nereocystis luetkeana never comprised a large proportion
of the total drift standing crop. _Cystoseira osmundacea_,
the most abundant attached non-_Macrocystis_ brown alga in
the Point Cabrillo forest (Lowry, 1971), was also most
abundant in the drift material, forming 17-62% of the
non-_Macrocystis_ brown drift algae. The composition by
weight of _C. osmundacea_ showed a repeated annual cycle:
100% vegetative fronds in winter, over 90% reproductive
material in spring, 65-83% reproductive material in summer,
and only 14-24% reproductive material in fall. This cycle
followed a similar pattern observed in the composition of
attached _C. osmundacea_ in the study area. _Desmarestia
ligulata_ also showed a distinct seasonal distribution; it
was absent from both the attached and drift floras in winter.

Between 7 and 19% of the drift standing crop during any season consisted of rhodophytes (Figure 16d). The species composition of this red fraction of the drift algae was always extensive. The most common species included *Callophyllis flabellulata* Harvey, *Gigartina californica* J. Agardh, *G. corymbifera* (Kutzing) J. Agardh, *Prionitis lanceolata* Harvey, and *Rhodymenia californica* Kylin. *Gigartina* spp. comprised between 16 and 60% of the red algal drift biomass in any seasonal collection. Articulated coralline algae, including *Bossiella californica* (Decaisne) Silva, *Calliarthron cheilosporoides* Manza, and *Corallina officinalis* var. *chilensis* Decaisne, were always present in the drift collections. They formed a small proportion (5-12%) of the drift rhodophytes, except in Winter, 1975, when the standing crop of the drift rhodophytes was lowest and 38% consisted of coralline algae. Species which exist as attached algae only in the intertidal zone, such as *Endocladia muricata* (Postels and Ruprecht) J. Agardh, were often present as subtidal drift algae, but were generally less abundant than species with attached populations within the forest.

Figure 16e shows the seasonal standing crops of drift seagrasses (9-45 gm/m^2). *Phyllospadix scouleri* Hooker, which has attached populations at Point Cabrillo inshore from the kelp forest, was the most abundant species.

Phyllospadix torreyi Watson and Zostera marina Linnaeus were uncommon. These seagrasses formed the largest non-Macrocystis component of the total drift standing crop during 5 of the 9 seasons (6-36%).

Green algae, including Cladophora sp. and Ulva sp., were present in 5 of the 18 collections. They totalled only 14 gm of the 340 kg of drift algae collected and sorted during this study.

The significance of spatial and temporal effects on the standing crop of benthic drift algae and seagrasses was tested by two-way analysis of variance. The spatial effect was represented by the variation between the 12 permanent plots, and the temporal effect by the 9 seasons. The two collections made in each plot every season provided replicate data. The results of the significance tests are shown in Table 4.

The standing crops of all categories of drift material varied significantly in space. Bottom substrate and topography greatly influenced the distribution of drift material which tended to accumulate in sand channels and rock crevices where water movement was lowest or where physical barriers blocked further transport, and only settled on extensive sand plains or flat rock surfaces during the calmest weather.

Table 4. Significance of variation in the standing crop of
benthic drift material in space (12 plots) and time
(9 seasons). Results of two-way ANOVA with two observa-
tions per cell (temporal replicates). ** denotes
significance at the 99% confidence level. NS denotes
no significance at the 95% confidence level.

TYPE OF DRIFT MATERIAL	BETWEEN PLOTS	BETWEEN SEASONS	INTERACTION
(degrees of freedom)	(11)	(8)	(88)
		F-Ratios	
Total Drift Algae and Seagrasses	21.74 **	13.36 **	2.48 **
Macrocystis pyrifera	17.61 **	15.13 **	2.64 **
Non-Macrocystis Brown Algae	9.56 **	9.83 **	1.58 **
Cystoseira osmundacea	4.85 **	9.38 **	1.29 NS
Total Red Algae	8.61 **	3.11 **	1.22 NS
Gigartina spp.	17.12 **	5.76 **	1.90 **
Coralline Algae	8.80 **	1.63 NS	0.96 NS
Seagrasses	3.83 **	1.75 NS	0.91 NS

The seasonal differences in standing crop were significant for most of the drift categories. Only coralline algae and seagrasses did not vary significantly over time. The seasonal differences were primarily due to temporal fluctuations in the production and accumulation of drift material; however, one biotic factor also appeared to be influential. As large masses of drift material accumulated in late summer and early fall, the material became tangled and was cemented together by the tube-building worms, _Platynereis agassizi_ Ehlers. These densely consolidated bundles of drift material were probably less susceptible to transport by low intensity water movement than smaller drift fragments, and were not exported from the forest until the first fall storms. Thus, the action of the worms may have enhanced the accumulation of drift algae and seagrasses in the kelp forest.

Export. - The monthly export of benthic drifters from the study area was lowest in summer (15-20%), greatest in fall (87-88%), and intermediate in winter and spring (51-53%), as shown in Figure 18. These estimates have been corrected for varying collection efficiencies which ranged from 82 to 96%. The seasonal differences in export rate were primarily due to differences in water movement intensity, which is expressed as the frequency of observed maximum

Figure 18. Monthly export rates of benthic drifters
from the study area (n = 2 replicate sets of 50
drifters each; ± 1 standard error), and water
movement intensity measured during the drifter
experiments (see Figure 5a) from Summer, 1974
through Fall, 1975.

a. EXPORT OF DRIFTERS
n = 2

b. WATER MOVEMENT INTENSITY –
MAXIMUM WAVE HEIGHTS > 1.0 m
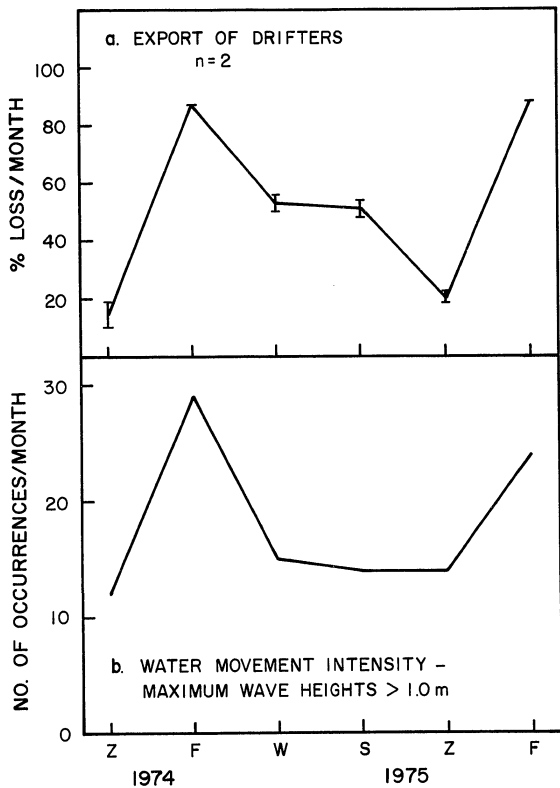
wave heights greater than 1.0 m. Increased water movement
in fall caused an increase in the rate of benthic drift
transport and export. The incorporation of the drifters
and drift plant material into large masses and consolidated
bundles in summer probably caused the disproportionately
low percent export in relation to water movement during
that season.

Decomposition. - Figure 19 shows the wet weight loss
over time of laminae and stipes of M. pyrifera that were
removed from attached plants and held in litter bags as
drift kelp. The laminae showed an average initial weight
loss of 21% in the first two days, but the stipes lost only
6%. Aside from this initial difference, the weight of the
laminae and stipes decreased at similar rates and, at the
end of the first month, only about 33% of the original
lamina biomass and 45% of the stipe biomass remained.

Figure 19. Decomposition of laminae and stipes of

M. pyrifera expressed as the percent of the

original wet weight remaining over time. Each

point represents one litter bag (○ = laminae,

+ = stipes).
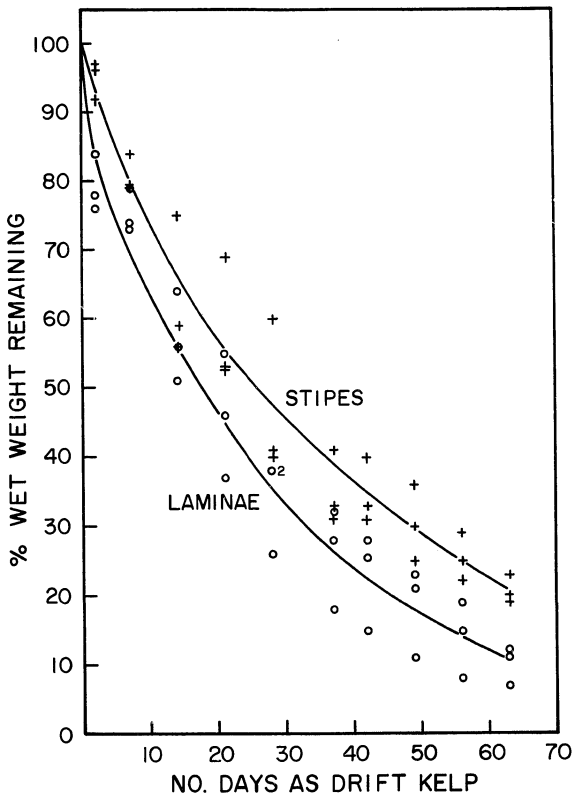
DISCUSSION AND CONCLUSIONS

The role of benthic drift algae and seagrasses in the flow of materials and energy in the kelp forest is twofold: they form a resource within the forest community, and they serve as a pathway of export to other communities. The present study is primarily concerned with the former aspect.

Drift plant material provides a potential food source for herbivores within the forest. The importance of this source of primary production relative to other sources, i.e., attached algae, must depend on its abundance, turnover, and availability to consumers. In terms of biomass, benthic drift material is not a major plant component of the kelp forest community at Point Cabrillo. The greatest proportion of macrophyte biomass in the study area was comprised of attached <u>Macrocystis pyrifera</u>, which averaged 3.5 kg/m^2 from Fall, 1973 through Winter, 1976 (see Chapter I). The mean standing crop of all other attached macro-algae (including juvenile plants of <u>M</u>. <u>pyrifera</u>) in an adjacent and partially overlapping area was estimated to be 0.1-0.15 kg/m^2 in Fall, 1973 (D. L. Garrison, unpublished data). The standing crop of benthic drift algae and sea-grasses measured during the present study averaged 0.15 kg/m^2. Thus, on the average, benthic drift plant material made up less than 5% of the total macrophyte biomass in

the forest.

The standing crop of benthic drift algae and sea-grasses fluctuated greatly from season to season. This variation was primarily due to seasonal variation in the standing crop of benthic drift _Macrocystis_, the major component of the drift plant material (Figure 16). In Chapter I, the total production of drift kelp was shown to be dependent on the standing crop of attached kelp and the rate of loss from that source. Loss was found to be primarily determined by water movement intensity. Figure 20 shows the standing crop of attached kelp, the estimated total monthly production of drift kelp, and the standing crop of benthic drift kelp in the Point Cabrillo study area. The temporal fluctuations in the two standing crops did not correspond, nor was there a significant correlation ($p > 0.05$) between the total production of drift kelp and the standing crop of benthic drift kelp. This lack of correlation was partly due to temporal variation in the proportion of the total drift kelp which sank to the forest floor, and the proportion which was exported as floating drift kelp.

The standing crop of benthic drift kelp was highest in summer and early fall, and lowest in winter. The standing crop of most of the non-_Macrocystis_ drift algae at Point Cabrillo showed similar patterns (Figure 16). These

Figure 20. Standing crop of attached $\underline{M}$. pyrifera (from
Figure 7a), total production of drift $\underline{M}$. pyrifera
(from Figure 15), and standing crop of benthic
drift $\underline{M}$. pyrifera (from Figure 16b) measured in the
study area from Fall, 1973 through Fall, 1975.

a. STANDING CROP OF ATTACHED KELP

b. PRODUCTION OF DRIFT KELP

c. STANDING CROP OF BENTHIC DRIFT KELP
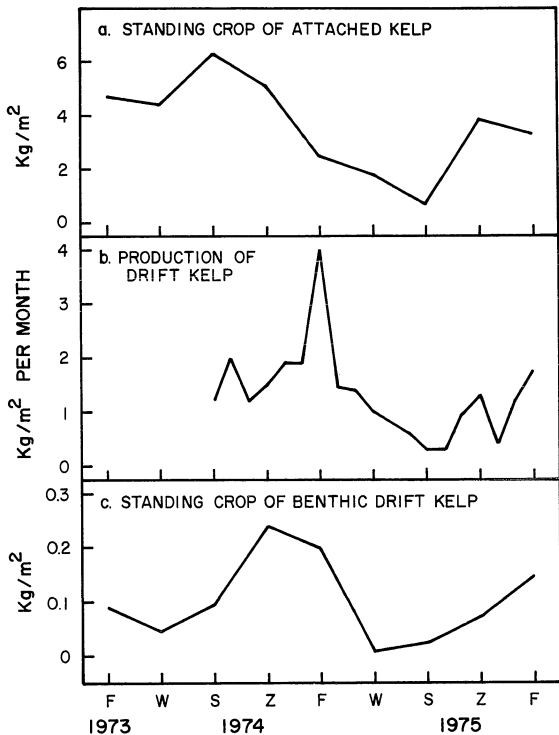
seasonal changes were primarily attributable to the influence of water movement intensity. Water movement influences the standing crop of benthic drift material by affecting the rate of loss of attached algae and seagrasses; greater water movement causes greater drift production and should augment the standing crop of benthic drift material. However, greater water movement also causes an increased export rate (Figure 18), and a decrease in the drift standing crop. The actual standing crop of benthic drift material observed in the study area at any time was a product of the interaction of these opposed effects. During the calm weather in summer, the rates of production and export were low. The drift algae produced in the kelp forest accumulated and, by early fall, the maximum standing crop had been reached. This accumulation was probably enhanced by the cementing activities of _Platynereis agassizi_. The first fall storms caused a great increase in both drift production and export, and the accumulated, as well as the freshly produced drift material was rapidly transported out of the forest. The lowest standing crops, but highest production and turnover rates of drift material occurred in late fall and winter. Therefore, low standing crops did not necessitate reduced supply to drift consumers.

Decomposition of benthic drift algae and seagrasses also influences their rate of turnover within the kelp forest. The decomposing M. pyrifera in the Point Cabrillo study area lost approximately 40% of its wet weight each month in winter (Figure 19). This loss rate may have been affected by physical factors which vary seasonally and spatially: temperature, light, water movement, and abrasion. However, it was similar to the decomposition rate found by Zobell (1971) for chopped seaweeds held in seawater at $10^{\circ}C$ in the laboratory. The high initial weight loss of the kelp laminae observed in the present study (21% in 2 days) appeared to be due to the loss of a large quantity of mucus, and may have been an artifact of the experimental procedure which included a 30 minute exposure to air and fragmentation of the fronds. Further weight loss during the course of the experiment was probably due to physical abrasion on the substrate, sand scouring, breakdown by bacteria and/or fungi, and the action of small consumers. In addition to ingesting drift material, consumers may increase the rate of decomposition by decreasing the sizes and increasing the surface area of the individual pieces of drift material (Fenchel, 1970; Zobell, 1971; Harrison and Mann, 1975). Thus, decomposition of drift kelp produces detritus which may be utilized by filter and deposit feeders within the kelp forest community.

During decomposition, the remaining drift material undergoes changes in its physical characteristics, chemical composition, and associated microflora. These changes appear to affect its nutritional value, at least to _Patiria miniata_ (see Chapter III). The utilization of drift material by consumers may also be affected by these changes. For example, in a Y-maze experiment, the sea urchin, _Strongylocentrotus dröbachiensis_ Müller showed a strong preference for freshly detached laminae of _Nereocystis luetkeana_ over aged laminae (V. A. Gerard, unpublished data), presumably due to differences in the dissolved organic material released by the laminae. However, when provided with both fresh and aged laminae in equal amounts, these urchins ingested a greater amount of the aged material, perhaps due to its greater flaccidity.

Drift consumers show preferences for different species of drift plants (Vadas, 1968), as well as for different decompositional states of the same species. Leighton (1966, 1971) tested the preferences of a variety of kelp forest herbivores, including sea urchins and abalones, for various food species. His results indicated a generally high preference for _Macrocystis pyrifera_, which is the most abundant drift component at Point Cabrillo and probably in many other California kelp forests. In contrast, coralline algae and seagrasses were poorly preferred. Low

consumption rates of these drift plants could partially account for their lack of seasonal standing crop fluctuations. Both coralline algae and seagrasses may also have low decomposition rates, due to the presence of calcium carbonate or cellulose. Furthermore, their export rates may be low, because coralline algae have a high specific gravity, and the filiform seagrasses tend to tangle in attached algae. Thus, differential rates of consumption, decomposition, and export may influence the composition of the benthic drift material.

Differential export rates also influenced the composition of the benthic drift Macrocystis at Point Cabrillo, especially during periods of high water movement intensity. The detached kelp laminae seemed to be more readily transported by water movement than drift stipes, due to differences in shape, surface area, and the tendency to tangle with attached algae. Therefore, the proportion of lamina weight in the standing crop of drift kelp was considerably lower in winter than in summer, although the percent lamina weight in the standing crop of attached kelp was similar during those two seasons (Figure 17). This compositional change could affect drift consumers, which show a general feeding preference for kelp laminae over stipes (Leighton, 1971).

Although differential turnover rates influenced the composition of the drift standing crop, the major determining factor was the composition of the local attached flora, the source of the drift material. The most abundant species of attached macrophytes, such as M. pyrifera and Cystoseira osmundacea, dominated the drift material in terms of biomass. Species, such as Nereocystis luetkeana and Zostera marina, with attached populations some distance from Point Cabrillo were generally less abundant as drift than attached species occurring within the forest. Temporal changes in the attached flora were reflected in the drift material, as evidenced by the seasonality of the reproductive fronds of C. osmundacea, juvenile M. pyrifera plants, and Desmarestia ligulata in both associations. During the present study, the observed overall stability of the attached flora within the forest was evident in the relative stability of the composition of drift algae and seagrasses, despite large fluctuations in the drift standing crop.

The influence of temporal variation in the composition, standing crop, and turnover rate of benthic drift algae and seagrasses on their utilization by benthic herbivores was not determined during this study; however, some conclusions can be drawn from previous work. The sea urchins, Strongylocentrotus purpuratus Stimpson and S. franciscanus Agassiz,

and the abalones, <u>Haliotis</u> <u>rufescens</u> Swainson and <u>H</u>. <u>walallensis</u> Stearns, are common herbivores occurring primarily in crevices at Point Cabrillo (Lowry and Pearse, 1973). They have all been found to feed primarily on drift algae when it is available (Cox, 1962; North et <u>al</u>., 1963; Leighton, Jones and North, 1966; Ebert, 1968; Olsen, 1968; Vadas, 1968; Leighton, 1971). In Fall, 1972, the densities of urchins and abalones at Point Cabrillo averaged 0.22 and 0.21 m^2, respectively (Lowry and Pearse, 1973). Their feeding rates are on the order of 2 and 12 gm of algae/animal per day, respectively (Leighton, 1971). Therefore, these herbivores consumed an estimated total of 3 gm/m^2 per day, or between 1 and 10% daily of the standing crop of benthic drift material in the study area. It is unlikely that this food source was ever limiting to these grazers during the present study, because the highest turnover rates coincided with the lowest benthic drift standing crops, and vice versa. The supply of benthic drift algae and seagrasses to these consumers must be less variable than the standing crop of drift material. Furthermore, the urchins and abalones inhabit crevices where drift material tends to accumulate.

Benthic drift material is also a major food source for other kelp forest inhabitants. For example, more than half of the food items of the batstar, <u>Patiria</u> <u>miniata</u>

Brandt, at Point Cabrillo consisted of drift algae and
seagrasses (see Chapter III). A wide variety of motile
organisms was associated with the drift material collected
during the present study. Many of these animals utilize
drift as a habitat, as well as a food source. Their
densities varied directly with the drift standing crop,
and were highest in the consolidated bundles present in
late summer and early fall (C. R. Agegian and V. A. Gerard,
unpublished data). A number of these animals must have been
exported from the forest along with the drift material
during the fall storms. Among the most abundant species
of this benthic drift association were the grazing snail,
Tegula _pulligo_ Martyn, and the crab, _Pugettia_ _richii_ Dana.

From the estimated rates of consumption, decomposition,
and export, it is possible to arrive at a rough estimate
of the turnover rate of benthic drift algae and seagrasses
in the Point Cabrillo kelp forest. The drift standing crop
averaged 150 gm/m^2. Assuming that all drift material de-
composes at a similar rate to that of _M._ _pyrifera_, 40% or
60 gm/m^2 was lost each month through decomposition. On
the average, 50% or 75 gm/m^2 was transported out of the
forest monthly. At least 90 gm/m^2 must have been consumed
by grazers each month, if this estimated amount went to
sea urchins and abalones alone. Therefore, the total loss
and replacement of benthic drift material averaged 225 gm/m^2

per month or 2700 gm/m^2 per year, and the turnover rate of benthic drift algae and seagrasses within the kelp forest was approximately 18 times per year.

Although benthic drift algae and seagrasses comprise only a small proportion of the total macrophyte biomass in the Point Cabrillo kelp forest, this resource is important to many members of the forest community, primarily due to its spatial distribution and rapid turnover. Attached Macrocystis pyrifera, the major component of the plant biomass and the major primary producer within the forest, mainly occupies the water column and is spatially unavailable to many of the bottom-dwelling herbivores. The production of benthic drift kelp literally puts this energy source within their reach. Other attached benthic algae are within the reach of benthic consumers, but the rates of production and turnover of these algae are undoubtedly much lower than that of the drift material. It is especially significant to consumers that the highest turnover rates of benthic drift material coincide with the lowest drift standing crops. Finally, the drift resource is unique in that consumers can utilize benthic drift algae and seagrasses without directly affecting their source and supply.

To summarize the role of benthic drift algae and seagrasses in the flow of materials and energy within the

kelp forest, it is instructive to consider this resource as forest litter, and to compare it to litter in terrestrial forests. Table 5 shows the average dry plant biomass, annual net primary production, and litter mass for the kelp forest at Point Cabrillo and for five types of terrestrial forests (Whittaker, 1975). The standing crop and annual production cited for the kelp forest include only attached _Macrocystis pyrifera_ (see Chapter I) which is by far the dominant producer of this system. The marine litter was assumed to average 10% dry matter by weight, the measured mean value for drift _Macrocystis pyrifera_ (V. A. Gerard, unpublished data). The differences between the terrestrial and marine forests are striking: giant kelp forests have a similar annual net production, but an attached plant biomass and litter mass one to two orders of magnitude lower than those of terrestrial forests. Only a small proportion of the primary production, perhaps 5-10%, is consumed directly by grazers in both types of forests (Reiners, 1973; Chaper I). In terrestrial forests, a large part of the produced biomass accumulates and persists as part of the producer standing crop or as litter on the forest floor. In contrast, most of the production in giant kelp forests is exported as floating drift kelp, or becomes benthic drift material which is rapidly consumed, decomposed, or exported.

Table 5. Average standing crop, production, and litter
mass in six different forest types. Terrestrial
data from Whittaker (1975).

FOREST TYPE	PRODUCER BIOMASS (dry kg/m^2)	ANNUAL NET PRODUCTION (dry kg/m^2/yr)	LITTER MASS (dry kg/m^2)
Tropical rain forest	45	2.2	0.2
Tropical seasonal forest	35	1.6	0.5
Temperate evergreen forest	35	1.3	3.0
Temperate deciduous forest	30	1.2	2.0
Boreal forest	20	0.8	4.0
Giant kelp forest	0.35	2.2	0.015

The litter formed in terrestrial forests becomes part of the large mass of decomposing and detrital material which serves as a reservoir of nutrients and energy within the forest community (Reichle, O'Neill, and Harris, 1975). The carbon component of this litter may have a residence time of up to 200 years (Reichle et al., 1973). Kelp forests do not depend on such a reservoir. They receive a constant supply of dissolved nutrients from flowing water, and their energy base is characterized by a relatively small standing crop and rapid turnover. Kelp forest litter provides an alternate pathway from primary producers to consumers; it is available to benthic consumers and, through decomposition, to filter and deposit feeders. Thus, benthic drift algae and seagrasses provide a means of retaining nutrients and energy within the kelp forest community without forming a large and persistent biomass.

CHAPTER III

UTILIZATION OF BENTHIC DRIFT ALGAE AND
SEAGRASSES AS A FOOD SOURCE BY THE
BATSTAR, PATIRIA MINIATA

   Benthic drift algae and seagrasses provide a source
of food for a variety of kelp forest inhabitants. The
spatial availability and rapid turnover of drift material
have been suggested as the particular advantages of this
as a food source for benthic consumers, in contrast to
the attached algae that comprise a much greater proportion
of the plant biomass in the forest community (see Chapter
II). Information on drift composition, abundance, and
utilization by a consumer are all necessary to test this
hypothesis. Shepherd (1973), studying the feeding habits of
Australian abalones, concluded that drift consumption was
advantageous because no energy was expended in searching
for food, feeding could be continuous without exposure to
predators, and a greater diversity of algae was available
as drift material than as attached plants. However, Shepherd
presented no quantitative data on the abundance and
composition of drift material. Poore (1972) compared the
composition of attached and drift floras and used this
information to examine selectivity in two species of

New Zealand abalones, but did not measure the absolute
abundance of drift material.

The composition and abundance of benthic drift algae
and seagrasses were determined semiseasonally in the Point
Cabrillo kelp forest from Fall, 1973 through Fall, 1975
(see Chapter II). In conjunction with that study, quanti-
tative information was collected on the population density,
feeding frequency, diet, and nutritional state of the
batstar, _Patiria miniata_ Brandt. _Patiria miniata_ was chosen
as the study animal because it was the most common asteroid
in the Point Cabrillo kelp forest (Pearse and Lowry, 1974),
and was known to utilize algae, including a large proportion
of drift material, as a food source (Araki, 1964; Gerard,
1971). The present study was, therefore, designed to
determine the extent of this utilization, the effects of
temporal changes in drift composition and abundance, and
the advantages of benthic drift algae and seagrasses as a
food source for _P. miniata_.

METHODS

Population Density. - The population density of
Patiria _miniata_ was determined twice during each seasonal
sampling period, except in Winter, 1974. All batstars were
counted within ten circular 5 m^2 plots selected by simple
random sampling within the study area. The sample sites
were selected as random coordinates (x, y) and located by
distance and compass heading from a permanent marker at
the center of the study area. New random locations were
selected for each density determination, and each sampling
day was scheduled within a few days of a collection of
benthic drift algae and seagrasses (see Chapter II).

Feeding and Food Preference. - To determine feeding
frequency and food sources, each batstar counted in the
density samples was turned over and examined. If its
cardiac stomach was extruded, the star was considered to
be feeding, and its source or sources of food were deter-
mined as the items or substrate directly in contact with
its stomach. Drift algae and seagrasses were differentiated
according to the categories used in the study of benthic
drift material (see Chapter II); the non-drift food items
were qualitatively noted, and were enumerated in a single
non-drift category. Each item or food source was recorded

as one feeding observation; two or more observations were
often scored for a single feeding batstar. Stars feeding
on both laminae and stipes of Macrocystis pyrifera were
scored in a separate category, rather than as two indi-
vidual feeding observations. The drift material held by
the feeding batstars was collected in 5 mm mesh bags and
brought back to the laboratory where it was sorted and
weighed according to the procedures described in Chapter II.
Large pieces of drift material, such as whole kelp fronds,
were broken off within 5 cm on either side of the feeding
batstar. Preference for various types of drift algae and
seagrasses could then be determined by comparing their
proportions in the drift standing crop (see Chapter II)
with their proportions in the feeding observations and in
the drift material held by feeding batstars.

Pyloric Caecal and Gonadal Indices. - Organ indices
were determined for the P. miniata population each season
in order to follow relative changes in the nutritional
and reproductive states. Twelve batstars were arbitrarily
collected from the study area and dissected in the labora-
tory. The pyloric caeca and gonads were removed, and were
blotted dry and weighed separately from the eviscerated
body. The total body weights were determined as the sum
of these three components; the perivisceral fluid was not

included, although it comprises approximately 23% of the animal's wet weight (Giese, 1966). The organ indices for each star were calculated as, Organ Index = 100 x Organ Weight/Eviscerated Body Weight.

To determine the nutritive value of the drift material, 58 small P. miniata were collected, divided into three groups, and held in aquaria with running sea water at ambient temperature for 4 months. One group was not supplied with any drift material; the second group was supplied with 10 "fresh" laminae of M. pyrifera which had been removed from an attached frond the same day; the third group was supplied with 10 "aged" kelp laminae which had been previously collected from an attached frond, and held for two weeks in an aquarium with running seawater at ambient temperature. All laminae were cut in half lengthwise before being given to the batstars; the fresh laminae were replaced twice each week, and the aged laminae once every two weeks. Growth of the stars in the three groups was measured by blotted and submerged weights taken every two weeks. At the end of 4 months, the stars were dissected, and organ indices were determined for the three groups.

Statistical Analysis of the Data. - The significance of differences between the means of any two samples was

determined by a t-test. A product-moment coefficient of correlation (r) was calculated to determine the significance of correlation between any two parameters. All results reported as "significant" were found to be statistically significant at the 95% confidence level ($p < 0.05$); "highly significant" denotes significance at the 99% confidence level ($p < 0.01$).

RESULTS

Population Density. - The mean density of $\underline{P}$. $\underline{miniata}$ in the Point Cabrillo kelp forest was 20.6 batstars/5 m^2 for the entire study, and the seasonal means ranged from 16.9 to 25.8 batstars/5 m^2 (Figure 21). There were no statistically significant differences between the density measurements made in sequential seasons, and no evidence of cyclical patterns or long-term trends. The variation between seasonal samples can be attributed to random sampling of the clumped $\underline{P}$. $\underline{miniata}$ in the study area. Batstars were generally most abundant in areas with sand and rock interspersed; the lowest densities occurred on broad sand plains and on rock surfaces which had a heavy cover of attached algae. Every random 5 m^2 plot of the 170 totalled over all seasons contained at least one batstar. The greatest number of batstars found in a single 5 m^2 plot was 71.

Feeding and Food Preference. - Figure 22 shows the percent of the $\underline{P}$. $\underline{miniata}$ population that was found to be feeding, the proportion of total feeding observations that consisted of benthic drift material, the mean wet weight of drift material held by the feeding batstars, and the standing crop of total benthic drift algae and seagrasses,

Figure 21. Population density of *P. miniata* (mean ± 1
standard error) measured seasonally in the study
area from Fall, 1973 through Fall, 1975.

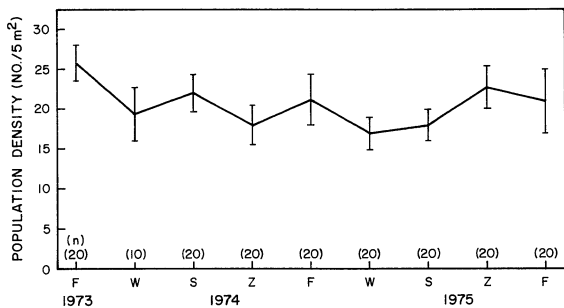Figure 22. Semiseasonal measurements of the proportion
of the _P. miniata_ population feeding, the proportion
of the total feeding observations consisting of
benthic drift algae and seagrasses, the mean wet
weight of drift material held per feeding batstar,
and the mean standing crop of benthic drift
material collected from 12 permanent plots in the
study area (see Figure 16a) from Fall, 1973
through Fall, 1975.

140

a. PROPORTION OF POPULATION FEEDING
   $155 \leq n \leq 258$

b. PROPORTION OF FEEDING OBSERVATIONS
   CONSISTING OF DRIFT MATERIAL
   $134 \leq n \leq 290$

c. AMOUNT OF DRIFT MATERIAL HELD

d. STANDING CROP OF TOTAL DRIFT ALGAE AND
   SEAGRASSES
   n = 12
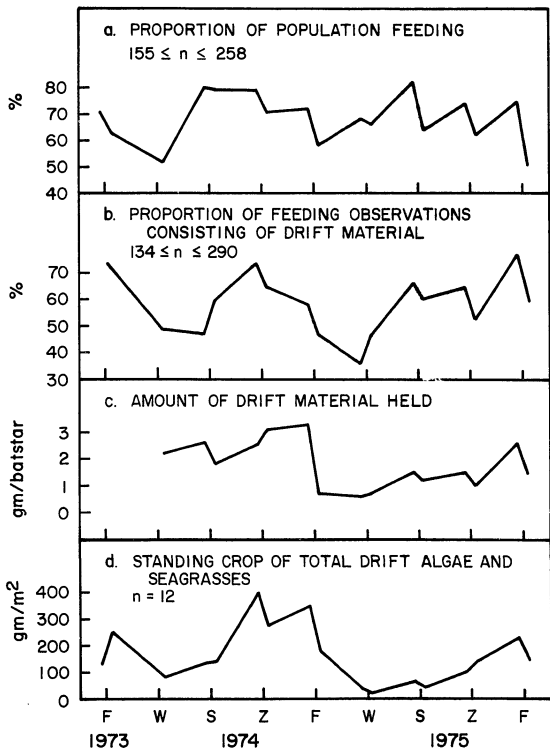
all measured twice each season in the study area. Out of
a total of 3504 stars examined during the entire study,
68% were found to be feeding. The percent feeding in
individual samples ranged from 51 to 82% (Figure 22a), and
did not show a significant positive correlation (p > 0.05)
with the standing crop of drift material (Figure 22d). No
seasonal trends were apparent in the proportion of the
population feeding, nor were significant correlations found
with sea surface temperature or water movement intensity
measured on the morning of each sampling day or averaged
for the entire seasonal sampling period (see Chapter I).
The percent of batstars feeding varied in individual plots
sampled on the same day; however, no correlation was
found between the number of batstars per plot and the
percent feeding.

Between 36 and 77% of the feeding observations in the
individual samples consisted of benthic drift algae and
seagrasses (Figure 22b). This proportion correlated
significantly over time with the standing crop of benthic
drift material in the study area (r = 0.57, p < 0.05).
Of 3271 total feeding observations made during the study,
60% consisted of benthic drift plant material. Dead
animals and animal remains, as well as living animals,
attached algae, and bottom substrates, were included in
the non-drift feeding observations. Dead fish and

scyphozoans, and other animal macrodetritus were typically found buried under dozens of feeding batstars, and appeared to be preferred foods of P. miniata. Living, motile animals were rarely observed as food sources, but sessile invertebrates, such as sponges, bryozoans, and ascidians, were relatively common food items. Batstars were never found feeding on attached algae, unless the algal surfaces were covered by epiphytic invertebrates. Approximately half of the non-drift feeding observations consisted of visually barren rock and sand surfaces.

The drift algae and seagrasses collected from 2051 feeding batstars during the entire study averaged 1.8 gm wet weight/batstar. The mean drift weight held per feeding batstar ranged from 0.6 to 3.3 gm in the individual samples (Figure 22c), and showed a positive correlation with the standing crop of benthic drift material ($r = 0.71$, $p < 0.01$).

Preference of P. miniata for various types of drift algae and seagrasses was determined by comparing the proportions of each category in the total benthic drift standing crop, drift feeding observations, and drift material held by feeding batstars. Table 6 shows these percentages for each drift category averaged over the 15 semiseasonal samples. As evidenced by the low standard error values in all drift categories, the three compositional measurements showed little temporal variation.

Table 6. Proportions of different types of benthic drift
algae and seagrasses in the drift feeding observations,
drift standing crop, and drift material held by feeding
batstars. Each percent shown is the mean of 15 semi-
seasonal samples (± 1 standard error).

DRIFT CATEGORY	% OF TOTAL DRIFT FEEDING OBSERVATIONS	% OF TOTAL DRIFT STANDING CROP	% OF TOTAL DRIFT MATERIAL HELD BY FEEDING BATSTARS
Total *Macrocystis pyrifera*	44 ± 3	61 ± 4	77 ± 3
Laminae	39 ± 2	31 ± 3	40 ± 3
Stipes	13 ± 2	30 ± 3	37 ± 3
Total Non-*Macrocystis* Brown Algae	6 ± 2	13 ± 1	4 ± 1
Cystoseira osmundacea	4 ± 1	4 ± 1	3 ± 1
Other Brown Algae	2 ± 1	9 ± 1	1 ± 1
Total Red Algae	13 ± 2	12 ± 1	8 ± 1
Gigartina spp.	1 ± 0.3	4 ± 0.4	3 ± 1
Coralline Algae	2 ± 0.5	2 ± 1	1 ± 0.4
Other Red Algae	10 ± 2	6 ± 1	4 ± 1
Seagrasses	36 ± 3	14 ± 3	12 ± 2

Therefore, only the results of correlational analyses for the mean values will be reported here. Highly significant positive correlations (p < 0.01) were found between the weight proportions of different drift types (both total and subtotal categories) in the drift standing crop and in the drift material held by feeding batstars. No significant correlation (p > 0.05) was found between the proportions in the drift standing crop and of the feeding observations; however, when the seagrass category was omitted and the proportions were recalculated for algae alone, the composition of the drift standing crop and the feeding observations did correlate significantly (p < 0.05). The seagrasses did not appear to be selected or rejected over algae; their high proportion in the drift feeding observations was due to their small average particle size and scattered distribution. The positive correlations between the composition of the available drift material and the utilized drift material suggest that _P. miniata_ did not select or show preference for any particular types of drift plant material.

Pyloric Caecal and Gonadal Indices. - The total fresh body weight (not including the perivisceral fluid) of the individually dissected _P. miniata_ ranged from 15.7 to 124.0 gm. The pyloric caecal index ranged from 3.5 to 12.1,but did not correlate significantly with the total

body weight of the individual batstars. No repeated
cyclical changes or long-term trends were evident in the
seasonal index means which ranged from 6.5 to 8.9 (Figure
23). The temporal changes were not statistically signifi-
cant, with one exception: the mean pyloric caecal index
was significantly higher in Summer, 1974 than in all other
seasons (t-test, $p < 0.05$).

The batstars which were starved or fed fresh or aged
kelp in the laboratory showed no significant changes in
blotted or submerged weight during the 4 month period.
These batstars were generally smaller than those collected
from the field for seasonal index determinations; their
total fresh body weight (not including the perivisceral
fluid) ranged from 2.7 to 26.2 gm. The mean pyloric caecal
indices of these three groups were all significantly
different from each other; the starved group had the
lowest mean index, and the group that was fed aged kelp
had the highest (Figure 23). The mean pyloric caecal
indices of each of these three groups were significantly
lower than all of the seasonal mean indices of the stars
collected from the study area.

Only the four largest of the P. miniata which were
held in the laboratory had measurable gonads, so mean
gonadal indices could not be compared for the three groups.
This was probably due to the small size of the batstars;

Figure 23. Mean pyloric caecal and gonadal indices
(± 1 standard error) of $\underline{P}$. $\underline{miniata}$ fed a) no
drift kelp, b) fresh drift kelp, and c) aged
drift kelp for four months in the laboratory,
and of batstars collected seasonally from the
study area.
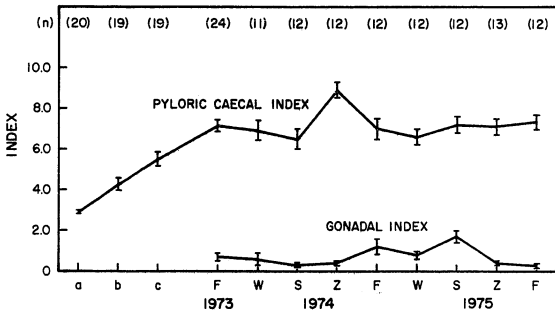
of seven batstars collected from the field population, each with a total body weight less than 30 gm, not one was found to have measurable gonads. The individual P. miniata collected from the field had gonadal indices ranging from 0.0 to 4.8, but showed no correlation between gonadal index and total body weight or pyloric caecal index. Nor did these batstars show a well-synchronized reproductive cycle. The mean gonadal index was uniformly low in all seasons, except in Spring, 1975 when it increased significantly (Figure 23). Typically, each seasonal sample included two or three batstars with relatively high gonadal indices and the remaining stars had poorly developed gonads.

DISCUSSION AND CONCLUSIONS

Patiria miniata maintains a high population density and biomass in the Point Cabrillo kelp forest. The average density determined during this study was 4.1 batstars/m^2. Gerard (1971) found an average live weight of 75 gm/batstar in an adjacent and overlapping study area. Therefore, the batstar population contributes approximately 300 gm/m^2 to the community at Point Cabrillo.

The population of P. *miniata* in the study area seemed stable over time. The density of these asteroids did not change significantly during this 27 month study and, although rates of recruitment and mortality were not determined, both appeared low. Small batstars were not common in the study area, and Gerard (1971) found less than 15% of the population with a live weight of 20 gm or less. This size distribution could have been due to a low rate of recruitment, or to high rates of both recruitment and juvenile mortality. As no measurable growth was found in small batstars which were fed drift kelp for four months in the laboratory, a low rate of growth is predicted for the field population. Araki (1964) noted a lack of predation on P. *miniata*, and no evidence of adult mortality was found during the present study. However, Vandevere (1969) listed batstars among the food items of

the sea otter, _Enhydra lutris_, and batstars were
occasionally found during the present study with one arm
missing, apparently bitten off by a sea otter. The tem-
poral stability of the batstar population suggests
dependence on a constantly available energy source.

At least 50% of the batstar population was found to be
feeding at any time during the present study. However, the
factors that influence feeding frequency were not success-
fully determined. The percent feeding varied between
semiseasonal samples, but no temporal patterns or effects
of physical factors, such as water movement intensity and
temperature, were evident. It is possible that the varia-
tion in the feeding frequency was related to changes in
the frequency of intraspecific and/or interspecific inter-
actions, such as those described by Wobber (1975) who
found 20-25% of the batstars at the Monterey breakwater
engaged in agonistic behavior at any time. However, Wobber
also found that the batstars were able to feed during the
majority of those interactions, and that asteroid density
had a significant influence on the frequency of this
behavior. At Point Cabrillo, density was not found to
affect feeding frequency.

The abundance of benthic drift algae and seagrasses
did not appear to limit the total feeding frequency of the
P. miniata population. Temporal changes in the feeding

frequency did not correspond to changes in the standing crop of drift material; when the standing crop was low, a higher proportion of the feeding observations consisted of non-drift food sources. Similarly, both Poore (1972) and Shepherd (1973) found that abalones grazed more frequently on attached algae when and where drift material was scarce. Overall, 68% of the observed batstars were found to be feeding. This high proportion suggests that little time is spent searching for and capturing food items.

As Shepherd (1973) concluded, drift algae and seagrasses provide a convenient food source, because they require little effort in search and capture. Moving water transported drift material to the batstars whose spatial distribution was similar to that of their drift food: both had highest densities in areas with rock crevices and sand patches, and lowest densities on extensive sand plains and rock surfaces with dense algal cover. Water movement intensity determined the rate of drift turnover (see Chapter II) and, thus, the rate of supply of drift material to the batstars. However, the abundance of this food source was also influenced by water movement intensity, but in an inverse manner (see Chapter II), so the rate of supply was highest when the amount supplied was lowest. Therefore, although the proportion of drift feeding observations and the mean amount of drift material held

by feeding batstars showed a positive correlation with the drift standing crop, drift algae and seagrasses made up a large percentage of their food items even during the time of lowest drift standing crop (Figure 22).

Patiria miniata showed no preference for specific types of benthic drift algae or seagrasses; all drift material was utilized according to its relative abundance. Because the composition of the drift standing crop varied little over time (see Chapter II), the composition of the batstars' drift algal diet also showed little temporal variation (Table 6). This lack of selectivity is consistent with the batstars' opportunistic feeding habits, and consistent with Poore's (1972) conclusion that the abalones most dependent on drift material as a food source showed the least selectivity in their diets.

The fragmented and decomposed state of most drift algae and seagrasses is an important factor in determining their value as food items. Patiria miniata is unable to digest the external layers of intact algae, and needs broken edges with internal portions exposed (Araki, 1964). Thus, intact attached algae are not a suitable food source, although invertebrate epiphytes may be utilized. Decomposition of the drift kelp enhanced its nutritive value, at least for the laboratory batstars. This may have been due to increased proportions of protein or

nutrients, as have been found in other decomposing plant material (Teal, 1962; Gosz, Likens,and Bormann, 1973; Schultz and Quinn, 1973; De la Cruz, 1975; Harrison and Mann, 1975). Other studies have illustrated the importance of the microbial component of detritus to consumers (Newell, 1965; Fenchel, 1970; Cummins et al., 1973), so increasing colonization by bacteria and/or fungi may be important to drift consumers. Patiria miniata may also absorb dissolved organic material (DOM) leached from the decomposing drift material.

Batstars were found to utilize a variety of non-drift food sources. Living, motile animals can usually escape the batstars (Araki, 1964) and so were not often eaten, but sessile invertebrates, such as sponges, bryozoans, and ascidians, that are abundant on the rocky floor of the kelp forest were observed relatively often as food items. Foster (1975) showed that this predation could influence the benthic community by reducing space competition between the sessile invertebrates and attached algae. Patiria miniata that were found with their stomachs extruded over visibly barren rock and sand may have been absorbing DOM, and were probably ingesting small detritus particles by flagellary mucoid feeding (Araki, 1964).

Preference for non-drift food sources was not quantitatively determined by this study; however,

preference for animal macrodetritus was obvious from
qualitative observations. Feeding batstars were found to
congregate in large piles on top of dead fish, scyphozoans,
and other carcasses. Wobber (1975) demonstrated this
convergent feeding behavior using dead squid as bait.
Araki (1964) found that proteins and soluble protein deriva-
tives (such as those released by decomposing animal
material) elicited a strong feeding response in the labora-
tory. It is possible that P. miniata depends on this
infrequent and unpredictable food source for the nutrition
it requires to grow, build up pyloric caecal reserves, and
produce gametes. When animal macrodetritus is not avail-
able, the batstars maintain themselves on other food sources
that are available: drift algae and seagrasses, sessile
invertebrates, detritus, and DOM. This hypothesis could
explain the observed difference between the pyloric caecal
indices of the laboratory stars and the field population;
the stars held in the laboratory had no access to animal
macrodetritus. However, this difference in pyloric caecal
indices does not provide conclusive evidence for the
hypothesis, because the stars were subject to other
environmental differences between the field and laboratory,
and differed in size, as well. Gonor (1972) cautions
against comparing indices in animals of different sizes.

The mean pyloric caecal index of the batstar population at Point Cabrillo was found to be relatively constant over time. This is not an unexpected result, considering the constant availability of their major food source, drift plant material. Similarly, Farmanfarmaian et al. (1958) found no significant changes in the mean pyloric caecal index of intertidal batstars at Point Cabrillo during a 10 month study. The cause or causes of the significant pyloric caecal index increase in Summer, 1974 are not clear. The increased abundance of drift material during the calm summer weather (see Chapter II) may have been influential, and animal macrodetritus may show a similar summer accumulation due to reduced rates of export from the kelp forest. Crump (1971) found that the abundance of macroscopic food affected the pyloric caecal and gonadal indices of Patiriella regularis which is a New Zealand asteroid with omnivorous feeding habits similar to those of Patiria miniata. However, no other seasonal changes in the mean pyloric caecal index of the batstars were found at Point Cabrillo, although the drift standing crop fluctuated during the entire study (Figure 22d). If drift abundance was the primary influencing factor in Summer, 1974, it must be explained as a threshold effect. Perhaps an increased state of decomposition of the drift material during its long summer residence in the forest

had an additional influence on the nutritional state of the batstars.

All of the seasonal samples included a low percentage of batstars with high gonadal indices. However, the significant increase in the mean gonadal index of the Point Cabrillo batstars in Spring, 1975 reconfirmed the conclusion of Farmanfarmaian et al. (1958) that P. miniata are more reproductively active in late spring and early summer. The lack of a corresponding increase in Spring, 1974 cannot be explained by the information available in this study.

Benthic drift algae and seagrasses provide a major food source for P. miniata in the Point Cabrillo kelp forest. Drift plant material comprised over 60% of the batstars' food items observed during this study. From the point of view of the drift material, the batstars do not appear to have much, if any, effect on its standing crop, composition, or turnover rate. Occasionally, a discoloration was noted in a section of drift material that had been held by a feeding batstar, and this was also observed by Araki (1964). It is possible that the decomposition rate of the discolored fragment was increased due to the actions of the asteroid. However, unlike sea urchins and abalones (see Chapter II), P. miniata actually ingest very little drift material, only the most

decomposed fragments.

Patiria miniata are not limited to a kelp forest
environment; they are common in intertidal communities
and in subtidal areas where no attached kelp occurs. Their
successful existence in a wide variety of habitats must be
at least partially due to their opportunistic feeding
habits. When and where animal macrodetritus is abundant,
P. miniata may not utilize plant foods at all. Even in
the Point Cabrillo kelp forest where animal macrodetritus
was infrequently available, batstars showed preferential
and convergent feeding behavior for this food source.
However, drift algae and seagrasses comprised a much
greater proportion of their food items in the kelp forest
at Point Cabrillo. The importance of drift plant material
to this batstar population was a function of several
characteristics of the resource. First, the fragmented
and decomposing state of the drift plant material made it
a suitable food source, in contrast to intact attached
algae. Second, drift material showed a similar spatial
distribution to the batstars and was transported to them
by water movement. Therefore, it was spatially within
reach and required little effort in search and capture.
Finally, the inverse relationship of the drift standing
crop and turnover rate insured a temporally constant
supply of drift material. The continual availability of

this major food source must at least partially account for the lack of distinct reproductive and nutritional cycles in the batstar population. Thus, _Patiria miniata_ was able to maintain a high and stable population density and biomass in the Point Cabrillo kelp forest by opportunistically utilizing a not highly preferred, but suitable and available resource, benthic drift algae and seagrasses.

CONCLUSIONS

The kelp forest at Point Cabrillo is an extremely productive system characterized by a high standing crop and rapid turnover of _Macrocystis pyrifera_. Standing crop, production, and loss of kelp are interdependent and are greatly influenced by the intensity of water movement, resulting in predictable fluctuations in certain parameters of the kelp population, such as plant density, plant size, and frond size.

Mean plant density (number of plants) and plant size (number of fronds) show a characteristic pattern of change through a long-term cycle of plant loss and recruitment. Recruitment of juvenile kelp plants is typically low in a dense kelp forest, because shading by the canopy prevents their growth. Periodically, high plant losses, due to storms, reduce plant density to an extremely low level and allow sufficient light to reach the forest floor for the growth of juvenile sporophytes. This large recruitment results in a kelp population characterized by a high density of small plants. If no extremely stormy years occur, the mean density will decrease and the mean size will increase, as individual plants or small patches of plants are lost and the remaining plants grow larger. Eventually, equilibrium density and size distributions are

reached, and these may be maintained until a period of intense storms initiates a new cycle.

Superimposed on this long-term pattern of change is an annual cycle of fluctuation in the frond size distribution. Calm weather in summer allows the persistence of very large, old fronds which are often in poor physical condition. These fronds are selectively removed by the first fall storms, causing a decrease in the maximum and mean frond sizes. Sustained high water movement intensity through the winter maintains the low maximum frond size, but the calmer spring weather again allows an increase, and the cycle is repeated.

The growth rate of individual kelp fronds also follow a predictable pattern of change dependent on frond size. The growth rate (measured as an increase in blade number, length, or weight) increases as the frond becomes larger and then reaches a maximum which is sustained for a month or so prior to terminal blade formation. The maximum frond growth rate did not show any repeated temporal fluctuations during this study at Point Cabrillo. The influences of changing physical conditions on the rate of growth may be too complex or short-term to be determined by monthly measurements in a field population. Similarly, the rate of new frond addition did not fluctuate in a regular manner over time. The frond addition rate is

determined primarily by plant size; and, because both the gross addition and gross loss rates increase with increasing plant size, the net frond addition rate is relatively constant throughout the size range.

Kelp productivity is dependent on the growth rate and standing crop. Because the growth rate is relatively constant, temporal changes in production are mainly due to fluctuations in the standing crop which, in turn, are determined by the relationship of kelp production and loss. Because high water movement intensity causes high losses of kelp and a reduction in standing crop, and because the rate of production is strongly influenced by the standing crop, high water movement intensity can limit the productivity of the kelp forest.

The annual net production of a forest of $\underline{M}$. $\underline{pyrifera}$ is comparable to that of stands of other kelps and of terrestrial forests. In all of these communities, only a small proportion (probably less than 10%) of the net primary production is directly consumed by grazers. In the giant kelp forest, part of the production is lost as detritus and dissolved organic material, but most becomes drift kelp.

The formation of drift kelp depends to some extent on the size and condition of the kelp plants and fronds, but is primarily influenced by water movement intensity.

Tangling with previously detached plants is sometimes an important factor, causing plant loss in conjunction with water movement. Much of the drift kelp that is produced by losses from the attached kelp standing crop is exported from the forest and may provide an important source of allocthonous energy to other marine communities. The influence of temporal fluctuations in attached and drift kelp production on these communities is not known.

Drift kelp that sinks to the forest floor, along with other species of benthic drift algae and seagrasses, forms a resource which is utilized by many inhabitants of the kelp forest. The species composition of this drift plant material is primarily determined by the composition of the local attached flora, although differential rates of export, decomposition, and consumption may also be influential. The species composition is relatively stable over time, with $\underline{M}$. $\underline{pyrifera}$ as the largest single-species component. The benthic drift standing crop, however, fluctuates greatly and follows a predictable annual cycle. The drift standing crop is highest in summer, despite a low rate of drift production, because low water movement intensity allows the accumulation of drift material. High water movement intensity in winter causes a high drift export rate and results in a low drift standing crop, although winter rates of drift production are relatively

high. The rapid rate of export, in conjunction with
relatively high rates of decomposition and consumption
of drift material, cause the drift standing crop to have
a very high rate of turnover. Unlike the litter in
terrestrial forests which decomposes slowly and accumulates
a large standing crop on the forest floor, benthic drift
algae and seagrasses form no large, slowly decomposing
reservoir within the kelp forest. The rapid turnover of
benthic drift material, its spatial availability, and the
inverse relationship of drift standing crop and transport
rate make this resource important to benthic consumers
within the kelp forest, such as sea urchins, abalones,
and batstars.

The condition of the drift material may affect its
suitability as a food source. For example, the batstars
(Patiria miniata) are not able to digest the external
layers of intact algae, but need the broken edges charac-
teristic of algal fragments in the drift material.
Furthermore, changes that occur in the chemical composition
and associated microflora of drift material during
decomposition seem to increase its nutritive value for
P. miniata. Batstars maintain a high and stable popula-
tion density within the forest by utilizing benthic drift
algae and seagrasses, as well as a variety of other food
sources. Although they seem to preferentially feed on

animal macrodetritus when it is available, drift plant material comprises the major part of their diet. Batstars, as opportunists, show no preference for specific types of drift material, but utilize it as it is transported to them by water movement.

Although benthic drift material comprises only a small proportion of the total macrophyte biomass within the kelp forest community, its rapid turnover and spatial and temporal availability to benthic consumers make it an important pathway and a means of retaining energy and materials within the community. The drift pathway may add stability to the community structure, because drift consumers utilize material which has already been lost from the producer biomass, and do not directly affect or limit the primary productivity.

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