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AN AUTECOLOGICAL STUDY OF THE MARINE RED ALGA GIGARTINA STELLATA (STACKHOUSE) BATTERS

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AN AUTECOLOGICAL STUDY OF THE MARINE RED ALGA
GIGARTINA STELLATA (STACKHOUSE) BATTERS

by

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M.S., University of Massachusetts, 1967

A DISSERTATION

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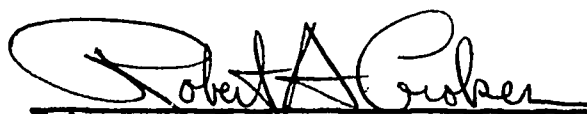
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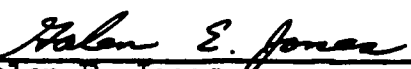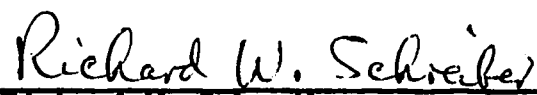
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ABSTRACT

The growth, local distribution and reproductive
periodicity of Gigartina stellata (Stackhouse) Batters are
described relative to a variety of environmental factors.
The effects of harvesting on regrowth and reproduction are
reported. The responses of sporelings in culture, and
manometric investigations of macroscopic plants are related
to the autecology of G. stellata.

Gigartina is a plant of the low littoral zone, exhibits
maximum growth in spring and summer and reproduces by
carpospores from October to March. Annual growth is initi-
ated between February and May depending on the location.
Growth coincides with increasing temperature from February
through July. Populations reach a maximum biomass in
August and September. Salinity is the dominant factor
influencing the distribution of G. stellata. Populations
exhibiting maximum biomass and frond size occur on the open
coast whereas reduced populations of stunted plants are
found in the estuary.

Harvesting in August was least detrimental to the
regrowth of G. stellata provided care was taken not to
damage the holdfasts. August harvesting sacrificed repro-
ductive fronds for the ensuing reproductive season, yet
it was the least detrimental to reproductive potential one
year after harvesting.

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In culture, spores of G. stellata exhibited maximum
germination at 30 °/oo and 11 C. Sporelings exhibited
maximum growth at 19 C and in salinities of 25, 30 and
35 °/oo; above and below these levels growth was substan-
tially reduced.

Light saturation intensity for photosynthesis of
macroscopic plants of G. stellata is higher than that for
many sublittoral plants. Maximum P/R ratios were recorded
at 20 C and at 40 °/oo. Gigartina exhibited a broad toler-
ance to dehydration.

INTRODUCTION

The marine red alga <u>Gigartina</u> <u>stellata</u> (Stackhouse) Batters is a member of the order Gigartinales and family Gigartinaceae. <u>Chondrus</u> <u>crispus</u> Stackhouse and <u>G</u>. <u>stellata</u>, the only members of the family Gigartinaceae occurring on the east coast of North America (Taylor, 1957), are collectively referred to as "carageen" (Marshall, <u>et</u>. <u>al</u>., 1949). They are often harvested in mixed lots as sources of carageenan, a phycocolloid (Mathieson, 1969). Carageenan and other products obtained from <u>G</u>. <u>stellata</u> are widely utilized in the food and pharmaceutical industries. Although <u>G</u>. <u>stellata</u> and related plants form the cornerstone for a multimillion dollar industry, often little is known of their basic biology.

The present paper represents the culmination of a two and one half year study on the autecology of <u>G</u>. <u>stellata</u>. The objectives of this investigation of <u>G</u>. <u>stellata</u> were threefold: 1) to study the <u>in</u> <u>situ</u> seasonal growth and reproduction, 2) to determine the effects of harvesting on growth and reproduction, and 3) to ascertain the major factors influencing growth and local distribution. In order to accomplish these objectives a combination of field and laboratory investigations were employed. The response of <u>G</u>. <u>stellata</u> to variations in light intensity, temperature, salinity and desiccation were tested and correlated with field observations. The combined results of laboratory and

field studies provide a functional understanding of the ecology of G. stellata and contribute to a more effective use and conservation of natural populations of this marine alga.

MATERIALS AND METHODS

Field Studies

Field observations and collections were initiated at three stations (Jaffrey Point, Toll Bridge and Dover Point, New Hampshire) in December 1968 and continued for 13 months (Figure 1). Measurements of surface water salinity, temperature and nutrients (nitrate-nitrogen, nitrite-nitrogen and orthophosphate) were recorded monthly. Salinities were measured with a set of hydrometers and corrected to 15 C. The techniques of Wood et. al. (1967) were used to measure nitrate levels; nitrite concentrations were determined using the method of Bendscheider and Robinson (1952). Orthophosphate levels were determined using the methods of Murphy and Riley (1962).

Growth studies of in situ populations were conducted by removing a 10 X 10 cm sample each month from dense populations of G. stellata occurring on rocks between 0.0 to +1.0m above MLW. The samples were preserved in 4% formalin in seawater and later examined to determine the size of fronds, their weight and the occurrence of reproductive structures. The length of the frond was recorded exclusive of the holdfast. In July 1969, a series of samples was removed from -0.3 to +1.7m above MLW at Jaffrey Point to determine differences in biomass and size of G. stellata relative to elevation.

Between September 1968 and October 1970 a total of 24 dives were conducted along the open coast of New Hampshire and in the Great Bay Estuary (in conjunction with other studies) to determine the sublittoral distribution, if any, of G. stellata.

Harvesting Experiments

Various methods of harvesting were employed at Jaffrey Point by establishing four 30 by 100 cm plots which were treated as follows: (1) unharvested control; (2) careful harvest - only plants longer than 4 cm were removed; (3) moderate harvest - only plants greater than 3 cm were removed; (4) severe harvest - only residual holdfast material was left behind (Figure 2). The plots were established in December 1968 and August 1969. Small (10 x 10cm) samples were removed approximately monthly for one year in order to determine the rate of plant regrowth.

To determine the time required for a totally denuded and sterilized surface to return to control levels, a 30 x 50cm quadrat was established during November 1968 in an algal zone which was primarily composed of G. stellata. All plants were removed. The area was then scoured with a wire brush while applying CLOROX. The treatment was repeated three times. The quadrat was examined periodically for 29 months.

Culture Studies

Cystocarpic fronds of G. stellata were collected at
Jaffrey Point during the fall and winter periods of 1968-
1971. Pieces of fertile plants were washed three times
with a soft brush and then placed in petri dishes with
30 ml of enriched sea water Medium F/2 (Guillard and
Ryther, 1962). The carpospores were usually released with-
in 12 hours. The spores were then pipetted to other petri
dishes and allowed to settle and grow on glass slides.
The response of the germlings to various environmental con-
ditions was determined after one week by measuring the per-
cent germination of the spores and/or the number of cells
per germling. The percent germination was calculated after
examination of 100-300 spores. The average number of cells
per germling was recorded in 30 or more germlings. In
most cases the discoid germlings remained unilayered for
one week facilitating cell counts; after one week they
were usually multilayered and accurate cell counts were
more difficult. Cell counts gave a better index of growth
than diameter measurements because the discoid germlings
remained relatively uniform in size in their early develop-
ment, and the diameter of the older discs seemed to vary
more as a function of spore density than as a function of
the various environmental factors under consideration.

Culture experiments were conducted in Sherer-Gillette
Incubators (Model RI-48-LTP), programmed for a day length
of 12 hours at temperatures of 3, 11, 15 and 19 C. Light

intensities were varied from 130 to 770 foot-candles by
placing the cultures at various distances from a series of
Sylvania Cool White Fluorescent lamps. The relative energy
emissions for various parts of the spectrum, corresponding
to the intensities used in the light experiments are listed
in Table I. It should be noted that the spectral energy
distribution curve for Cool White lamps also has a consid-
erable amount of radiation in the yellow-green portion of
the spectrum (Dunn, et. al. 1968).

In all cases Medium F/2 was used in the culture ex-
periments. The salt concentrations in the salinity experi-
ments were achieved by mixing the standard F/2 stock solu-
tions with three different solutions: 1) concentrated sea
water (by evaporation) with a salinity of 60 °/oo; 2)
normal sea water having a salinity of 30 °/oo; 3) distilled
water, salinity 0 °/oo. Finally, these three enriched
solutions were mixed together in proportions to give Medium
F/2 at any desired salinity between 0 and 60 °/oo.

Photosynthesis and Respiration Studies

Except for minor variations, the manometric tech-
niques employed in the present study are the same as those
of Mathieson (in press). All specimens were collected from
the lower littoral zone at Jaffrey Point. The plants were
transferred immediately (1 hour) to the laboratory where
standard size (6mm) discs were removed with a cork borer
from the thin, flattened portions of the thalli. In most

cases the discs were then immersed in artificial sea water (Chapman, 1962) and stored in the dark at 15 C for 12 to 24 hours prior to use.

The rates of oxygen exchange of the samples were recorded in a Gilsen Differential Respirometer (Model GRP 14) equipped with fourteen 50 watt (Champion) reflector lamps. Photosynthesis experiments were conducted at 2100 foot-candles (unless noted otherwise) and except for the experiments on the effects of temperature the manometric studies were conducted at 15° C. The light intensity was varied with a rheostat. In temperature studies the discs were maintained at each temperature for 12 to 24 hours prior to the measurement of oxygen exchange. In salinity experiments the discs were immersed in the various salinities for four (photosynthesis) or five (respiration) days prior to the initiation of the measurements. The final concentration of carbonate buffers in the artificial sea water was the same in all salinities. During the 4 or 5 day incubation period the discs were maintained under 300 foot-candles and a 12 hour light/dark photoperiod.

Dehydration was accomplished in the desiccation experiments, by allowing the discs to dry at room temperature for various time intervals and by periodically weighing the discs. The percent desiccation represents the percent of the total amount of water the discs would lose at room temperature after 36 hours. The duration of the drying period and the approximate percent desiccation of

discs are given in Table II. In order to start the mano-
metric measurements simultaneously, the discs were set out
at different intervals. In the photosynthesis-dehydration
experiments, the material was dehydrated, placed in a reac-
tion vessel, flooded with 5 ml of artificial sea water, and
within 15 minutes the measurements were initiated. The
respiration-dehydration studies were conducted in two steps
as follows: 1) the discs were dehydrated and oxygen con-
sumption was measured in the dehydrated state (i.e. no
aqueous phase) for one hour; 2) 5 ml of artificial sea
water were then poured into the reaction flask, and the
oxygen consumption was again recorded for one hour.

DESCRIPTION OF STUDY AREAS AND ENVIRONMENTAL FACTORS

Monthly field observations and collections were conducted at Jaffrey Point, Newcastle; the Toll bridge, Portsmouth; and Dover Point, Dover. The stations exhibit a natural gradient from an open coastal location, to an intermediate brackish water location, to an even more brackish estuarine site.

Jaffrey Point is a semiexposed open coastal site with the littoral and sublittoral fringe zones composed of massive rock outcrops. The Toll Bridge is a sheltered location on the Piscataqua River with rock outcrops and a granite wall providing substrate for G. stellata. Dover Point, although the most estuarine of the stations, is described as maintaining a flora similar to that on the open coast (Mathieson et. al in press, b). The stations have been aptly described by several authors (Jaffrey Point: Mathieson et. al. in press a; Toll Bridge: Hehre and Mathieson, 1970; Dover Point: Reynolds, 1971).

The variation of surface water temperatures at the three stations during 1969 is shown in Figure 3. The water temperature at Jaffrey Point ranged from 2 C in January to 15 C in August. The maximum annual variation occurred at Dover Point, ranging from a minimum of -0.5 C in January to a maximum of 19 C in July.

A comparison of the annual variation in surface water salinity is given in Figure 4. Jaffrey Point exhibited

the least fluctuation in salinity. The maximum fluctuation
occurred at Dover Point, while intermediate values were
evident at the Toll Bridge.

The annual variations in inorganic N and P of sur-
face waters at Jaffrey Point, the Toll Bridge and Dover
Point are depicted in Figures 5, 6 and 7. Figure 5 shows
the annual variation in nitrate-nitrogen at each station.
In general, nitrate concentrations were similar at each
station with peak concentrations recorded during the winter
months from December into March, followed by a sharp de-
cline at the end of March into April. Intermediate con-
centrations of nitrate were recorded during the summer
and the levels declined again in August. An increase in
nitrate occurred in November with a maximum being recorded
at Dover Point.

Although considerably more variable, similar fluctua-
tions were recorded for nitrite-nitrogen at each station
(Figure 6). In general the levels were slightly higher
at Dover Point than at the Toll Bridge or Jaffrey Point.
Higher values occurred at each station during the winter,
summer and late fall; lower values were recorded in the
spring and late summer.

Figure 7 illustrates the annual fluctuation of ortho-
phosphate in surface waters at each station. Intermediate
concentrations were registered from December to March. A
noticeable decrease occurred in April resulting in minimum
concentrations in May. A general increase resulted in
maximum levels in early August into September.

GROWTH AND REPRODUCTION IN SITU

Seasonal Growth

When quadrats of G. stellata were examined on an annual basis, both seasonal and spatial differences in populations are evident. Seasonal changes in biomass at the three stations are illustrated in Figure 8. The Toll Bridge maintained an intermediate biomass with higher and lower values recorded at Jaffrey Point and Dover Point, respectively.

Growth was initiated at Jaffrey Point between February and March. Biomass increased from March to the late summer and decreased from October through January. At the Toll Bridge, the initiation of growth occurred somewhat later. Maximal growth took place from May through the summer attaining peak biomass in September; a decrease in biomass was apparent from October until January. Populations of G. stellata exhibited only slight changes in biomass at Dover Point. A meager increase was evident between June and August, followed by a corresponding decrease in biomass from September to December.

The percent frequency of different size classes of fronds at each station is depicted in Figure 9. Gigartina fronds at Jaffrey Point were consistently longer than those at the other two stations. The population at the Toll Bridge was characterized by fronds of intermediate length; the shortest fronds were found in the Dover Point population.

Figure 9 also illustrates the seasonal changes in population structure at each station. The initiation of growth at Jaffrey Point occurred in February and corresponded to an increase in fronds between 0-0.9cm. From February through August a general increase in length occurred. In February the largest fronds were 5-5.9cm but they represented only 2% of the population. By July more than 20%, and by September more than 34% of the fronds were longer than 5.9cm. The maximum frond length attained was 9.9cm. From October through January a decrease in frequency of larger fronds was occurred.

A similar but less striking change in population structure occurred at the Toll Bridge. An increase in fronds of 0-0.9cm size class occurred in February. From March through August the length of fronds increased. In March the largest plants were 4-4.9cm and they comprised 1% of the population. Thereafter, rapid growth followed and by August, 20% of the population was longer than 4.9cm. The maximum frond length attained was 7.9cm. From September through January the percent of longer fronds declined.

The initiation of annual growth at Dover Point was delayed until April. In March, the longest fronds were 3-3.9cm, representing less than 1% of the population. A marked increase in the frequency of small fronds (0-0.9cm) was evident in April. Thereafter, moderate growth continued and by August 30% of the population was longer than 3.9cm. The maximum frond length attained was 6.9cm. A reduction

in the percent of longer plants was initiated in September
and the population remained strikingly stunted through
January 1970.

Vertical Profile of Gigartina stellata at Jaffrey Point

The changes in biomass and size of G. stellata through
its littoral range are shown in Figures 10 and 11 respect-
ively. The maximum biomass of G. stellata was recorded at
+0.45 to +1.0m above MLW. Similarly the largest plants
also occurred within this vertical range (Figure 11), with
the maximum frequency of large plants (25% longer than 5cm)
being found at +0.45m. Conversely, less than 5% of the
population was longer than 5cm above +1.0m, and less than
2% was longer than 5cm below MLW.

Seasonal Periodicity of Reproduction

Reproduction of G. stellata was confined to the fall
and winter, although a few papilla-bearing thalli were found
throughout the year. Cystocarpic papillae developed on
fronds during June and July. Cystocarps matured in August
and carpospores were released from October through March.
The period of maximum spore discharge was from October
through December.

EFFECTS OF HARVESTING ON GROWTH

Harvesting in December

The regrowth of G. stellata at Jaffrey Point following various intensities of harvesting is shown in Figure 12. The control plot exhibited a decrease in biomass between January and February when a minimum biomass was recorded. Thereafter, rapid growth occurred and in August a maximum biomass of $99g/100cm^2$ was attained. A noticeable decrease in biomass was evident after October.

The carefully and moderately harvested plots also decreased in biomass between January and February, but unlike the control plot, the biomass continued to decrease into March. An increase in biomass was evident in the carefully and moderately harvested plots in April, reaching a maximum in September. The maximum biomass attained in the carefully $(61g/100cm^2)$ and moderately harvested $(55g/100cm^2)$ plots was substantially lower than control levels.

Because of the paucity of plant material in the severely harvested plot, samples were not taken until July. An increase in biomass was evident until November when the severely and moderately harvested plots were indistinguishable.

An analysis of the percent occurrence of fronds in each size class is illustrated in Figure 13. Growth was initiated in the control plots in February, and continued through August. The population structure remained relatively stable

from August to October. Thereafter, a reduction of longer fronds occurred.

As described above, the carefully harvested plot exhibited a substantial decrease in biomass from January to March. However, this reduction was not reflected in any important change in population structure (Figure 13). In March the longest plants were 3-3.9cm, and they represented only 2% of the population. From April through August an increase in length occurred, resulting in 19% of the fronds being longer than 3.9cm in August. The maximum frond length attained was 8.9cm. From September through November a gradual reduction in the frequency of larger plants occurred.

Moderate harvesting produced more immediate and severe effects than careful harvesting. A reduction in the frequency of fronds longer than 1.9cm was observed between January and March (corresponding to the loss of biomass observed in Figure 12). A gradual increase in length occurred from March through July. Nevertheless, only 2% of the fronds were longer than 3.9cm in July, and the maximum length attained in the moderately harvested plot was only 6.9cm.

Severe harvesting produced a significant reduction in biomass (Figure 12) and distinctive changes in population structure (Figure 13). From January until June all of the fronds were less than 2cm in length, and the scantiness of material discouraged extensive sampling. In July, 14% of

the population was longer than 2cm, and unlike the control
and other harvested plots, growth continued through November.
The maximum length (7.9cm) exceeded that of the moderately
harvested plants. In November over 17% of the fronds in
the severely harvested plot were longer than 3.9cm; never-
theless, the overall biomass of the plot was exceedingly
low (Figure 12).

The distribution of biomass among various size classes
is depicted in Figure 14. During January and February the
major portion of the biomass (54-61%) in the control sam-
ples was provided by fronds of 3-4.9cm. Rapid growth was
initiated in March, and it continued for the next 5 months.
Thus in August and September over 75% of the biomass was
provided by plants longer than 7cm. From October through
November a gradual reduction of biomass supplied by larger
fronds occurred.

In February and March, the carefully harvested plot
had 60% of its biomass provided by plants 1-2.9cm long. In
August, after spring and summer growth, more than 95% of
the biomass was furnished by plants longer than 3cm. Even
so, the biomass was spread relatively evenly among plants
from 3-8.9cm.

In January the major portion of the biomass (45%) in
the moderately harvested plot was contributed by fronds
1-1.9cm long. Samples taken in April and May exhibited a
relatively uniform distribution of biomass among fronds
2-3.9cm in length. Following the spring and summer growth

period, the major portion of the biomass (74%) was furnished
by the 3-5.9cm class.

In July the biomass in the severely harvested plot was
relatively evenly distributed among fronds 1-3.9cm. The
biomass was relatively balanced among fronds between 2-7.9cm
long in November.

Harvesting in August

The rate of regrowth of G. stellata following various
degrees of harvesting in August 1969 at Jaffrey Point is
shown in Figure 15. The control plot exhibited a decrease
in biomass from October to March 1970. Following the initia-
tion of annual growth in late March, the biomass increased
until a maximum of $93g/100cm^2$ was recorded in August.

The carefully harvested plot exhibited only a slight
decrease in biomass from October through February. Rapid
growth between March and August resulted in a maximum bio-
mass of $90g/100cm^2$ in August - one year after harvesting.

The moderately harvested plot remained relatively
stable from September to January and exhibited only a slight
decline in biomass between January and February. Spring and
summer growth resulted in a maximum of $83g/100cm^2$ in August.

Severe harvesting produced a drastic and long-term
reduction in biomass. The maximum biomass attained 12
months after harvesting was $29g/100cm^2$ or 30% of the control
level.

An analysis of the percent frequency of different size

fronds following various degrees of harvesting in August is illustrated in Figure 16. In the control quadrat a reduction in larger fronds occurred from October through March. Thus, 43% of the fronds were longer than 4.9cm in October, whereas less than 1% were that large in March. From March through August a general increase in length occurred, resulting in a population having 39% of its fronds longer than 4.9cm in September.

Both the carefully and moderately harvested plots remained relatively stable until March. Rapid growth beginning in March produced populations similar to control levels in biomass and population structure (compare Figure 15 and 16). In September, the control, carefully harvested and moderately harvested plots had 39%, 42% and 36% of their fronds longer than 4cm respectively. The maximum length attained in each of these plots was 9-9.9cm.

Severe harvesting resulted in fronds with a maximum length of only 6.9cm. Indeed, thirteen months after harvesting only 6% of the fronds were longer than 4.9cm.

The percent of the total biomass provided by each size class following harvesting is shown in Figure 17. In September over 75% of the biomass in the control sample was provided by plants longer than 7cm. From October to March, a gradual reduction in biomass contributed by the longer fronds occurred. Growth in the spring and summer once again resulted in over 75% of the biomass being supplied by plants 7-9.9cm in August and September.

Carefully and moderately harvested plots underwent no size-class changes until March. Ensuing growth in spring and summer resulted in September populations which had over 75% of their biomass provided by plants longer than 7cm. However, severe harvesting resulted in a stunted population. Indeed 70% of the biomass was furnished by fronds between 4-5.9cm long thirteen months after harvesting.

EFFECT OF HARVESTING ON REPRODUCTION

Harvesting in December

In order to determine the effects of harvesting on reproduction, the number of carposporic papillae per plant was counted in all samples taken from control and experimentally harvested plots. The absolute number of papillae per plant varied from 0-1200. However the numbers of papillae presented in Figures 18 and 19 are average values for all fronds in the 100cm^2 samples and therefore they are substantially lower than one would find on a single reproductive frond.

Figure 18 depicts the number of carposporic papillae per plant for control and harvested samples during one year of regrowth. In control samples, the number of carposporic papillae decreased steadily from January through May. During the period of most active growth the fronds were relatively devoid of papillae. Thereafter, the number of papillae increased reaching a maximum in August. From September to January the number of papillae gradually decreased during the period of active spore release. Viable spores for culture experiments could only be obtained between November and January.

Fronds from the carefully harvested plot lacked papillae through July. The number of papillae reached control levels in August and September, and then declined steadily through the following January.

Moderate harvesting reduced the reproductive potential of fronds for one year. Thus, fronds lacked papillae until August and only a scant number were observed from August to January. No carposporic papillae were observed on any fronds in the severely harvested plot after one year's regrowth.

Harvesting in August

The effects of an August harvest on reproduction are shown in Figure 19. In control samples, the maximum numbers of papillae were recorded from September through December, with decreasing numbers from January through June. From April through July the plants virtually lacked papillae. A rapid increase in production of papillae occurred after July with maximum levels being recorded from August through October. Viable spores could only be obtained from late September through February.

Harvesting in August 1969 deprived all plots of any reproductive potential for eleven months - until the following reproductive season. By August 1970, both the carefully and moderately harvested plots were at control levels. However, after one year no reproductive fronds were found on the severely harvested plots.

RECOLONIZATION AFTER STERILIZATION

Studies of the denuded and sterilized quadrat indicated that at least 3 years were required before control conditions would be reached. Periodic observations indicated that the primary algal colonizers were diatoms followed by spring and summer annual green algae. Approximately one year after sterilization a few small plantlets of G. stellata were observed in the crevices (Figure 20, 21). The plants were 9 to 12 months old and they had a maximum length of 3cm. Ten fronds of Fucus vesiculosus and several fronds of Porphyra umbilicalis were also observed in the quadrat at this time. Figure 22, taken 29 months after sterilization, shows that the denuded and sterilized quadrat could still be distinguished from the surrounding unharvested community.

CULTURE STUDIES

The responses of spores and sporelings of G. stellata to a variety of environmental factors are illustrated in Figures 23 through 26. When cultured under various light intensities, G. stellata showed a gradual increase in growth from 130 to 770 foot-candles (Fig. 23). Similarly, sporelings exhibited an increase in growth correlated with an increase in temperature from 3 to 19 C (Fig. 24). The rate of increase in growth was greater between 3 and 11 C than between 11 and 19 C.

The interacting effects of temperature and salinity on germination of spores are shown in Figure 25. Spore germination occurred in salinities of 15-50 ^{o}/oo at 11 C, 20-50 ^{o}/oo at 19 C and 25-40 ^{o}/oo at 3 C. Thus the lowest temperature was the most restrictive, while the intermediate temperature was the least restrictive. Optimum germination occurred at 30 ^{o}/oo and 11 C. At 3 and 19 C, the optimum germination occurred at 35 ^{o}/oo.

The growth of sporelings at various temperatures and salinities is illustrated in Figure 26. The maximum growth occurred at 19 C in salinities of 25, 30 and 35 ^{o}/oo; growth was greatly reduced at salinities of 20 and 40 ^{o}/oo. At 11 C the optimal growth occurred in 30 and 35 ^{o}/oo; above and below these salinities growth was substantially reduced. Only minimum growth occurred at 3 C.

PHOTOSYNTHESIS AND RESPIRATION OF MACROSCOPIC PLANTS

The rate of apparent photosynthesis of G. stellata at 5 and 15 C and under a variety of different light intensities is shown in Figure 27. The apparent photosynthesis increased with an increase in light intensity up to approximately 2100 foot candles, and there was a slight increase in apparent photosynthesis between 2100 and 5000 foot-candles. Thus light intensities of less than 2100 foot-candles were probably suboptimal (particularly at 15 C), whereas light intensities of 5000 foot-candles were not inhibitory - although they may be saturating.

Figure 28 illustrates the rate of apparent photosynthesis at various temperatures and 2100 foot-candles. Apparent photosynthesis increased with an increase in temperature up to 20 C, thereafter it decreased. Figure 29 indicates that the respiration of G. stellata was relatively uniform over a broad range of temperatures (i.e. 8-20 C). From 26 to 32 C there was a substantial increase in respiration. A comparison of Figures 28 and 29 indicates that the maximum ratio of photosynthesis to respiration occurred at 20 C whereas the minimum photosynthesis/respiration ratio was at 32 C.

The rate of apparent photosynthesis at 2100 foot-candles in various salinities is shown in Figure 30. Apparent photosynthesis of G. stellata was relatively uniform between 16 to 40 $^{o}/oo$; above 40 $^{o}/oo$ and below 16 $^{o}/oo$ there was a

significant reduction. Maximum photosynthesis was recorded at 40 ^{o}/oo.

Figure 31 illustrates the rate of respiration of G. stellata after 5 days immersion in various salinities. Maximum respiration occurred at the lower salinities (i.e. 8 and 16 ^{o}/oo), whereas respiration was relatively constant over a broad range of higher salinities (32 to 60 ^{o}/oo). Five days immersion in 0 ^{o}/oo was apparently lethal.

The effects of various degrees of desiccation on the apparent photosynthesis is shown in Figure 32. A slight decrease in oxygen evolution occurred after a 65% water loss; increased desiccation caused a corresponding decrease in apparent photosynthesis.

Figure 33 illustrates the respiration of G. stellata at various degrees of dehydration and its recovery after rehydration. A slight dehydration (30%) brought about an increase in respiration. Further desiccation produced a decrease in respiration. Gigartina was able to recover from 88% dehydration.

DISCUSSION AND CONCLUSIONS

Growth of Gigartina stellata in situ

Annual growth of G. stellata was initiated between February and May, depending upon the location. Growth continued through the summer, with populations reaching maximum biomass and size in August and September. A general decrease in biomass and length occurred during the reproductive period (October to February), presumably because rough seas fragmented the heavier, reproductive thalli.

In addition to seasonal fluctuations, differences in growth and standing crop were evident at different sites. The occurrence of large plants and maximum biomass at Jaffrey Point suggests that G. stellata thrives on semi-exposed coastal locations. Intermediate and minimal sized populations at the Toll Bridge and Dover Point indicate that its growth and distribution into the estuary is restricted.

The period of maximum growth coincided with the increasing temperatures from February through July. A comparison of the nutrient data indicated that although a pronounced seasonal fluctuation existed, the monthly nutrient levels were similar at the three stations. The sharp decline in nutrient levels observed during April coincided with the rapid spring growth of G. stellata as well as with a bloom of spring-summer annuals observed by Mathieson et. al. (in press, a,b).

A salinity gradient exists between the three stations, and Dover Point consistently exhibits the lowest salinities. Not only did the depressed biomass of G. stellata correspond to the lower salinities at Dover Point, but an apparent lag in growth was evident during spring run-off. Rosenvinge (1931) has described limited growth of G. stellata in areas of low salinity in Denmark, and similar distributional patterns along salinity gradients have been recorded on the coast of Ireland (Anon. 1939). Marshall et. al. (1949) conducted extensive surveys of G. stellata in Great Britain and noted stunted populations in areas of low salinity. Thus, salinity is a dominant factor influencing the local distribution and growth of G. stellata.

Vertical Distribution

The vertical profile studies conducted at Jaffrey Point indicated that maximum length and biomass of G. stellata occurred from +0.45m to +1.0m above MLW. Gigartina extended to -1.0m but rarely to -2.0m. Thus it is predominantly a plant of the littoral zone with some extension into the sublittoral zone.

Effects of Harvesting

The results of the December harvesting experiments indicated that winter harvesting was detrimental to G. stellata. Both the carefully and moderately harvested plots decreased in biomass through March; in contrast, the control plot increased in biomass during March. The thinning out

process resulting from harvesting apparently weakened resi-
dual fronds, making them more vulnerable to rough seas.
Severe harvesting was the most detrimental to G. stellata.
None of the December plots reached control levels within
one year of harvesting.

The degree of harvesting was reflected in differential
reproduction. Careful harvesting had little or no effect
on the number of carposporic papillae produced the follow-
ing fall. However, moderate harvesting drastically reduced
the reproductive potential the following season; severe
harvesting completely eliminated carposporic plants the fol-
lowing reproductive season. Thus, winter harvesting of
G. stellata should be discouraged, because of detrimental
effects on biomass and reproduction.

Harvesting G. stellata in August provided the maximum
biomass. It also appeared to be the least detrimental to
regrowth and future yields. Both carefully and moderately
harvested plots approached control levels of biomass the
following August. Severe harvesting once again produced
extremely harmful effects on future regrowth.

As expected, harvesting in August deprived the plots
of any reproductive plants for the immediate reproductive
season. Nevertheless, both carefully and moderately har-
vested plots approached control levels of reproductive po-
tential the following season. Severe harvesting in August
1969 prevented the appearance of carposporic thalli in

August 1970; therefore, severe harvesting in August sacrificed at least two seasons of reproductivity.

In August, in the most dense populations of G. stellata, greater than 75% of the biomass was composed of fronds longer than 7cm (See Fig. 16). Careful and moderate harvesting in this situation allowed regrowth to control levels of biomass, population structure and reproduction in one year. However, the reproductive potential of these plants was sacrificed for the immediate season. Therefore it is advisable always to leave some zones of reproductive plants unharvested. The fact that denuded and sterilized quadrats of G. stellata required longer than three years to re-establish themselves underscores the need for caution in harvesting.

Culture Studies

Previous studies have indicated that littoral algae have higher light requirements than sublittoral plants (Boney and Corner, 1962,1963). Although light intensities of less than 800 foot candles were employed in the culture experiments, G. stellata responded well in this narrow light regime (See Figure 23). The gradual yet consistent increase in growth exhibited by G. stellata from 130 to 770 foot candles may be attributed to a high light requirement for G. stellata. It is unfortunate that higher light intensities could not be provided in these experiments. In contrast, much lower saturation values (approximately 130 foot

candles) have been established for the growth of the sub-littoral alga <u>Chondrus</u> <u>crispus</u> using older upright thalli (Ring, 1970).

<u>Gigartina</u> exhibited an increase in growth with an increase in temperature up to 19 C. Field observations show a good correlation between maximum population growth during the summer months and optimum temperatures.

<u>Gigartina</u> exhibited a restricted tolerance to reduced salinities at 19 C. Spores did not germinate at 15 ^{o}/oo and they exhibited a low percent germination at 20 ^{o}/oo. Such responses are reflected in the local distribution of this species. <u>Gigartina</u> thrives on the open coast and it exhibits a restricted estuarine distribution. Indeed, <u>G</u>. <u>stellata</u> is represented by poorly developed communities of smaller plants in estuarine locations (see Figure 8&9). Among others, Druehl (1967), Norton and South (1969) and Sundene (1962) have demonstrated similar results when comparing the growth in culture of laminarian algae relative to their distribution.

Photosynthesis and Respiration Studies

According to Stocker and Holdeheide (1938) the saturation light intensity for littoral algae is usually greater than that for sublittoral algae. Accordingly it is not surprising that the optimum light intensity for <u>G</u>. <u>stellata</u> (approximately 2100 foot candles) was higher than that (approximately 1000 foot candles) reported for sublittoral

plants such as Egregia laevigata (Chapman, 1962) and
Macrocystis pyrifera (Clendenning and Sargent, 1957). Re-
sults similar to those reported here were obtained using a
Gigartina species from the West Coast of North America
(Emerson and Green, 1939), and the European littoral brown
alga Fucus serratus (Rabinowitch, 1956). Saito (1956) has
recorded an increase in optimal light intensity for Undaria
pinnatifida at higher temperatures. The optimal light in-
tensity for G. stellata also seems to be correlated with
water temperature for there was a trend towards reduced
light saturation at 5 C as compared to 15 C.

The optimum temperature for apparent photosynthesis of
G. stellata was approximately 20 C. A good correlation
exists between optimum temperature requirements for maximum
rates of apparent photosynthesis and peak population growth.
The lower photosynthetic rates of G. stellata in this series
of experiments was primarily due to the thickened thalli
(August) used in these experiments. During the early part
of the summer the photosynthetic rate per unit weight of
the blades was greater.

The respiration rate of G. stellata was relatively
stable over a broad range of temperatures (i.e. 8 to 26 C).
Respiration was depressed below 8 C but increased sharply
above 26 C at which point the plants may have been damaged.
Newell and Pye (1968) have recorded similar findings with
C. crispus except that they did not record a sharp rise in

respiration above 26 C. The maximum photosynthesis/respiration ratios (approximately 7/1) were recorded at 20 C. Comparable P/R ratios have been reported for Egregia planifolia (Chapman, 1962) and the older blades of Macrocystis pyrifera (Clendenning and Sargent, 1957), but they are much less than the values recorded for Phaeostrophion irregulare (Mathieson, in press).

The salinity experiments indicated that G. stellata showed its maximum photosynthesis and minimum respiration at 40 °/oo. High P/R ratios in elevated salinities would favor growth in open coastal waters as opposed to estuarine salinities. Ogata and Takada (1968) have postulated that hypertonicity suppresses the respiration of marine plants. Both Hammer (1968) and Ogata and Matsui (1965) have emphasized that salinity may indirectly affect photosynthesis due to differences in carbon dioxide supply. All the salinities in this study were provided with the same concentration of carbon dioxide, and the plants were incubated for four days prior to the measurement of photosynthesis. Thus it appears that maximum photosynthesis in G. stellata occurs in salinities where there is a minimum of osmotic stress.

Ogata (1968) and Ogata and Matsui (1965) conducted extensive manometric investigations of intertidal plants after dehydration; they also related their experiments to specific growth habitats of the algae. Ogata (1968) suggested that a good indication of the tolerance of a plant to dehydration was its ability to recover metabolically

(relative to control levels) after reimmersion. Gigartina's
photosynthetic and respiratory responses indicate a broad
tolerance to desiccation, which is reflected in its local
abundance on vertical rock faces, that rapidly drain during
emersion.

General Conclusions

On the basis of field and laboratory investigations
several general conclusions may be made concerning the
autecology of G. stellata. Gigartina is a perennial plant
of the low littoral zone, exhibiting maximum growth in
spring and summer, and reproducing via carpospores from
October to March. Responses in culture and photosynthetic
experiments indicate a higher light requirement than sub-
littoral forms. Summer temperatures, 15-20 C, offer maxi-
mum potential for growth. The combined results of culture
and photosynthesis-respiration experiments indicate a
relatively narrow tolerance to salinity fluctuations shed-
ing light on its restricted estuarine distribution and
infrequent occurrence in tide pools. Gigartina's ability
to recover from desiccation permits it to succeed on verti-
cal rock faces in the littoral zone. Field studies indicate
that August harvesting of G. stellata allows maximum re-
growth if care is taken to not damage the holdfast. Har-
vesting at other times of the year may severely impede
reproduction, alter population structure and retard future
growth of G. stellata.

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Table I. *Light conditions for the growth of
sporelings of <u>Gigartina</u> <u>stellata</u>.

Intensity (ft-c)	Red	W/cm^2 Far-Red	Blue	Total
770	2.70	1.6	3.6	17.3
440	1.65	0.8	1.6	6.5
250	0.80	0.2	1.0	3.4
130	0.41	0.0	0.7	1.9

Table II. Experimental conditions for the
dehydration of discs of <u>Gigartina</u>
<u>stellata</u> prior to photosynthesis-
respiration experiments.

drying time (min)	0	15	30	60	90
% dehydration	0	30	66	83	91

*Light measurements were made with a "Plant
Growth Photometer" Model IL 150, provided
by International Light, Inc., Newburyport,
Massachusetts.

Figure 1.   Map indicating the location of A,
            Jaffrey Point; B, Toll Bridge; C,
            Dover Point.

Dover
Point

C

MAINE

43°05'

Portsmouth
B

NEW HAMPSHIRE

New
Castle

A

70°45'
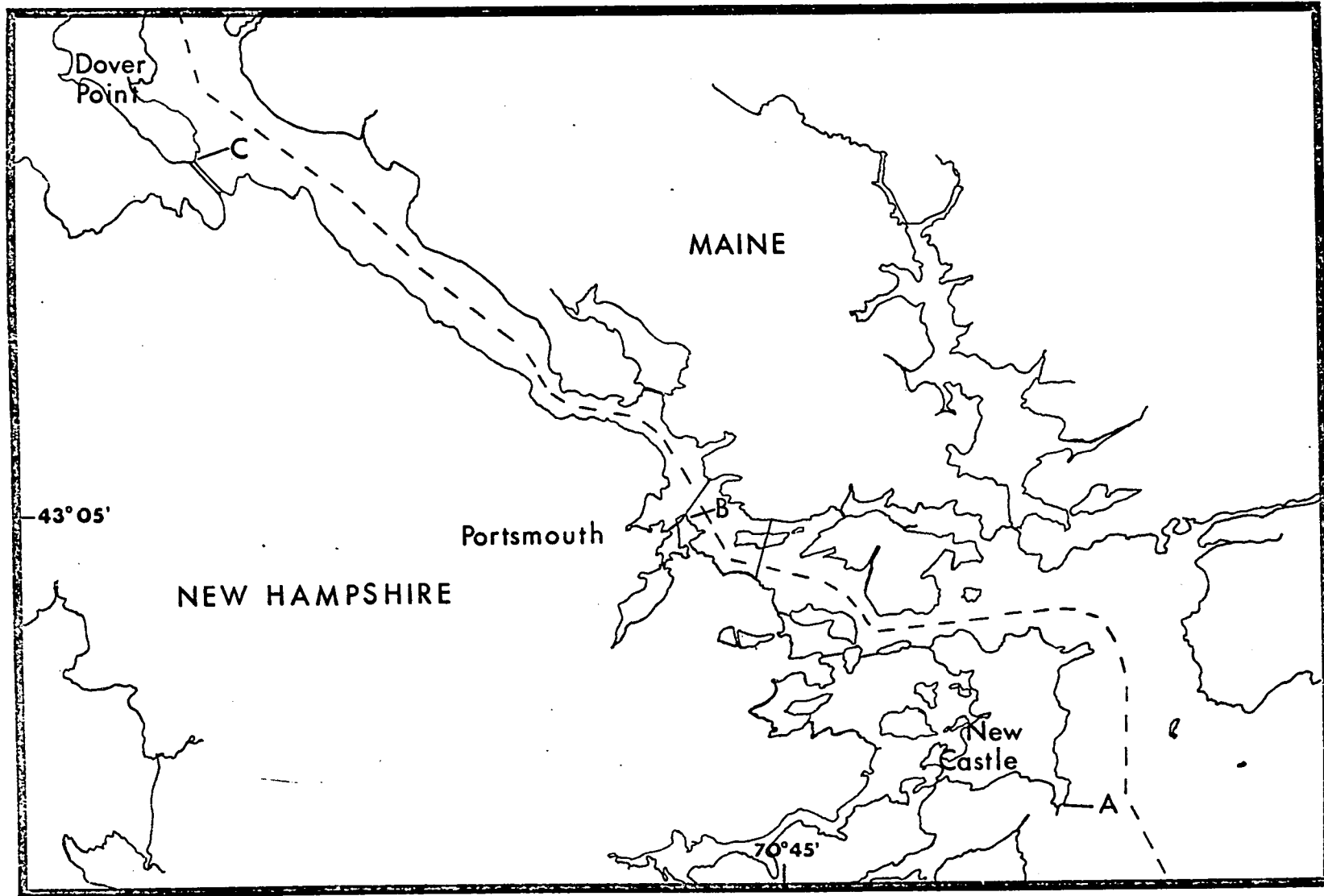
Figure 2.   harvesting plots of <u>Gigartina stellata</u>,
             August, 1969. (A=Control; B=Careful
             Harvest; C=Moderate Harvest; D=Severe
             Harvest).
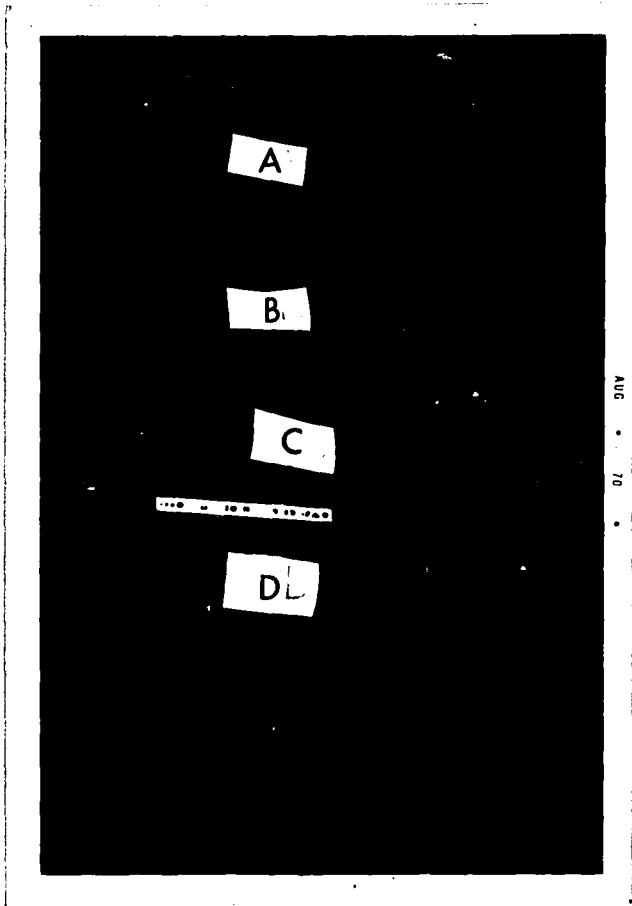
Figure 3.   Variation in surface water temperature
            between January 1969 and January 1970
            at Jaffrey Point, Toll Bridge and Dover
            Point.

44
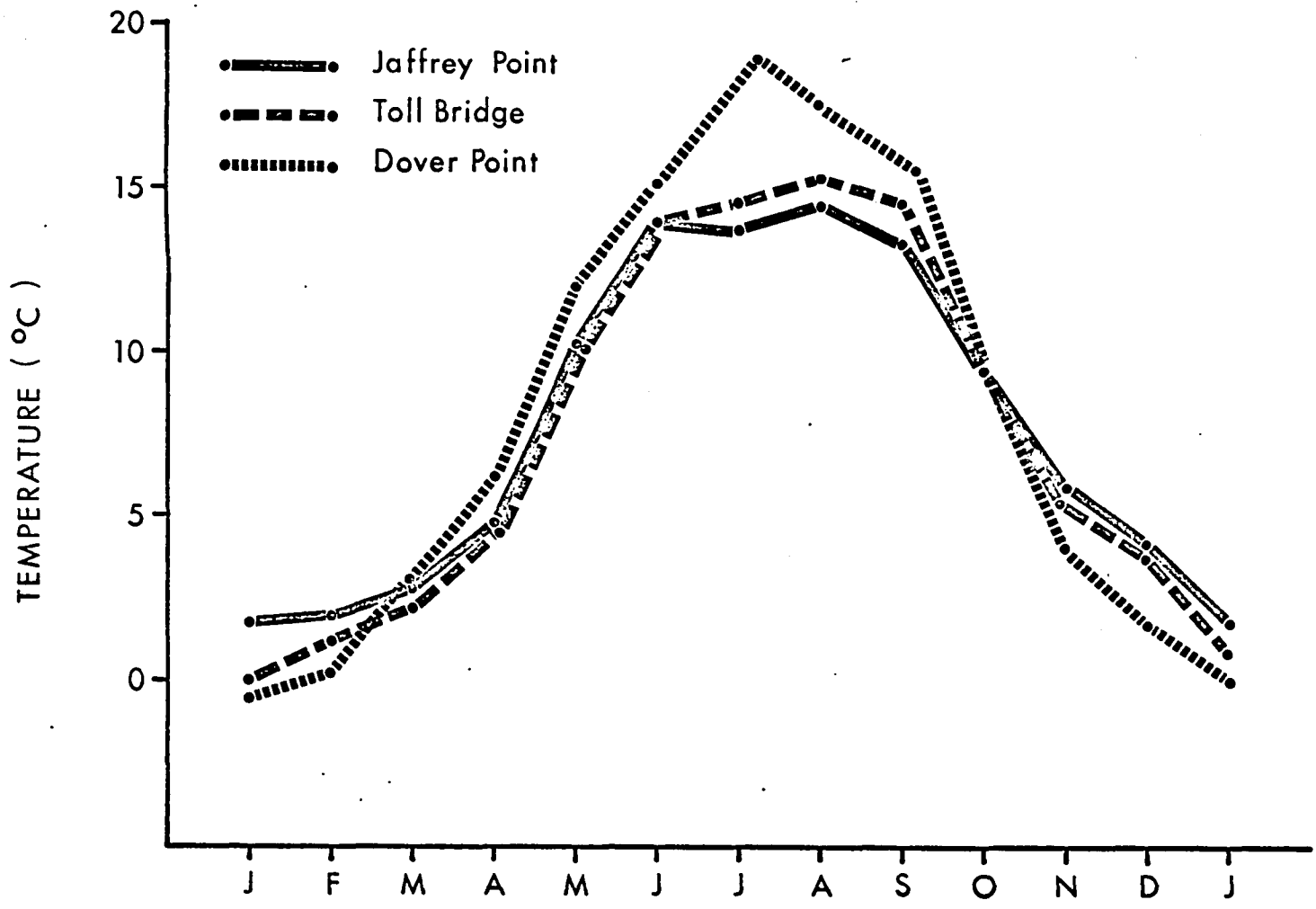
Figure 4.   Variation in surface water salinity be-
             tween January 1969 and January 1970 at
             Jaffrey Point, Toll Bridge and Dover
             Point.

46
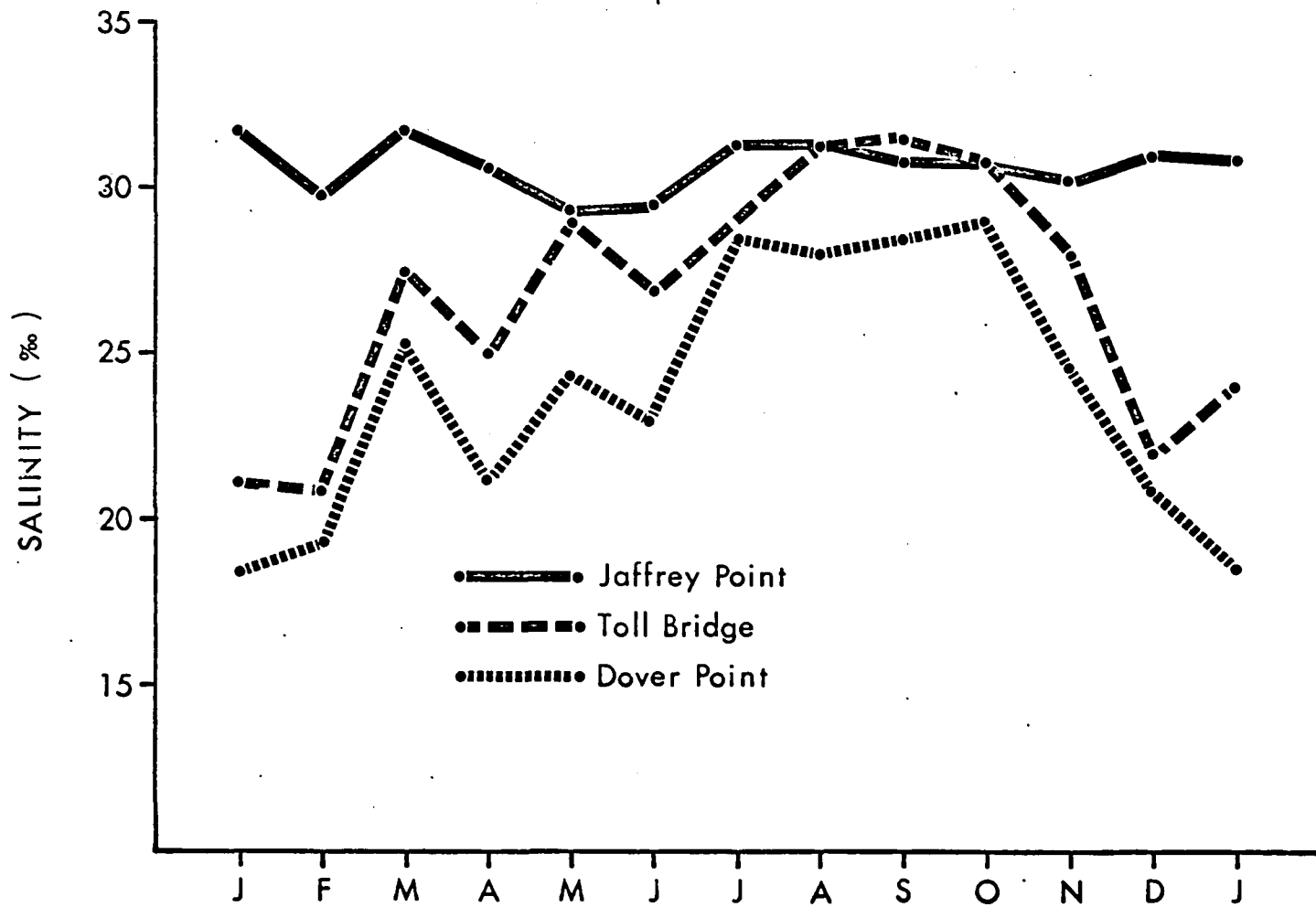
Figure 5.   Variation in Nitrate-Nitrogen between
             November 1969 and November 1970 at
             Jaffrey Point, Toll Bridge and Dover
             Point.

NITRATE NITROGEN (mg/l)

0.14

0.07

Jaffrey Point
Toll Bridge
Dover Point

N D J F M A M J J A S O N
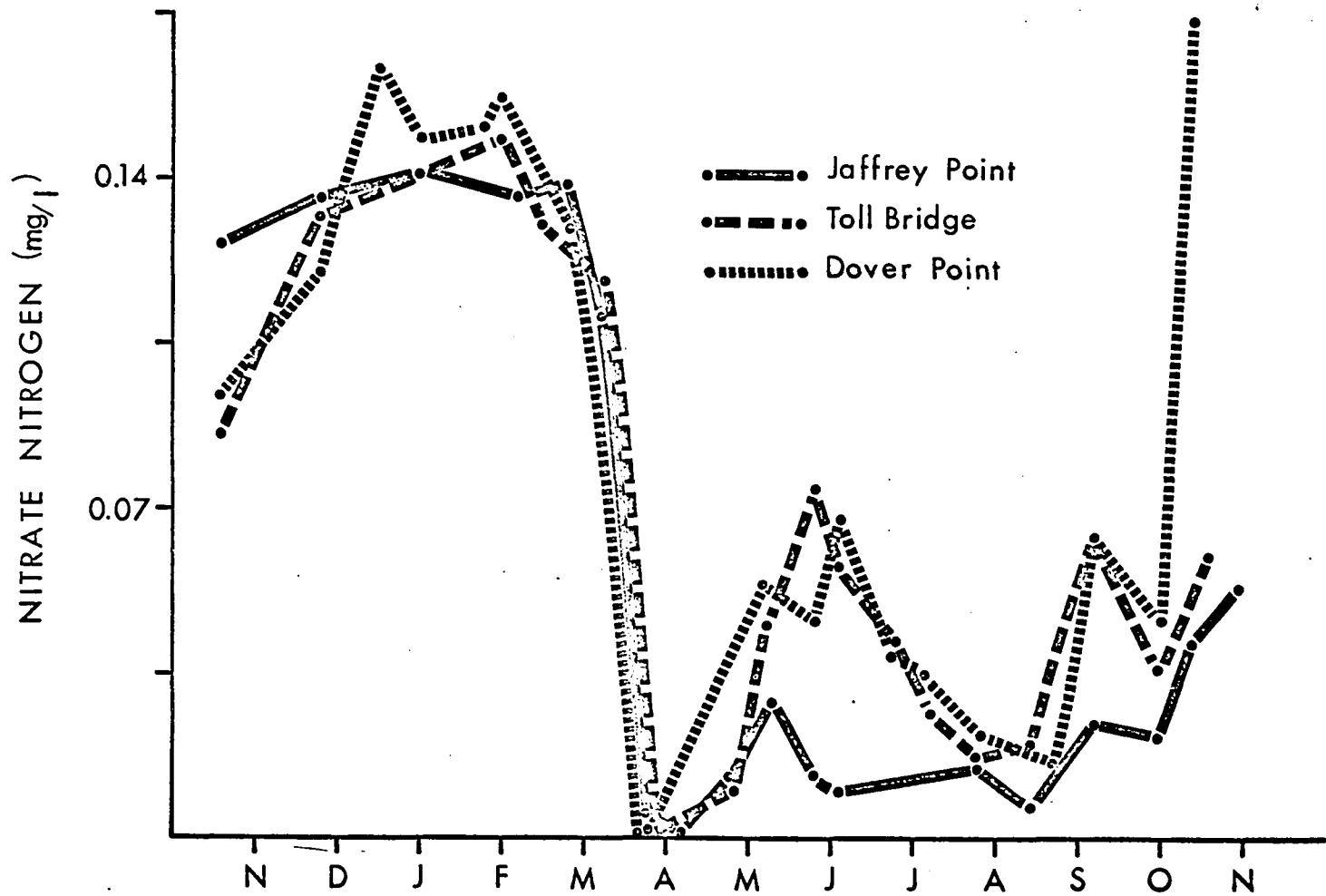
Figure 6.   Variation in Nitrite-Nitrogen between
            November 1969 and November 1970 at
            Jaffrey Point, Toll Bridge and Dover
            Point.

Figure showing Nitrite Nitrogen (mg/l) versus month (N D J F M A M J J A S O N) for Jaffrey Point, Toll Bridge, and Dover Point. Y-axis marks at 0.0035 and 0.0070, with scale marker = 0.010.
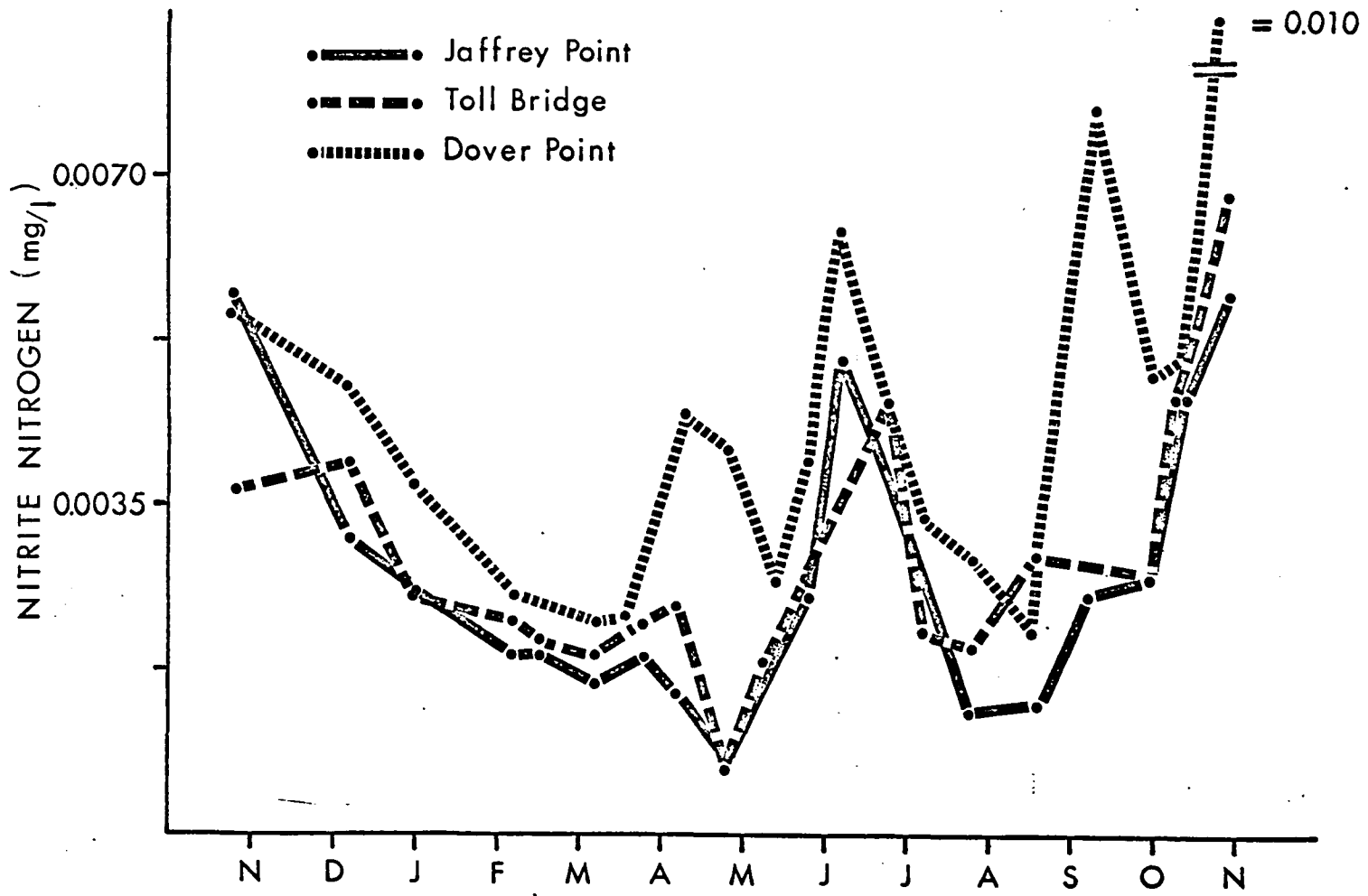
Figure 7.   Variation in orthophosphate between
             November 1969 and November 1970 at
             Jaffrey Point, Toll Bridge and Dover
             Point.
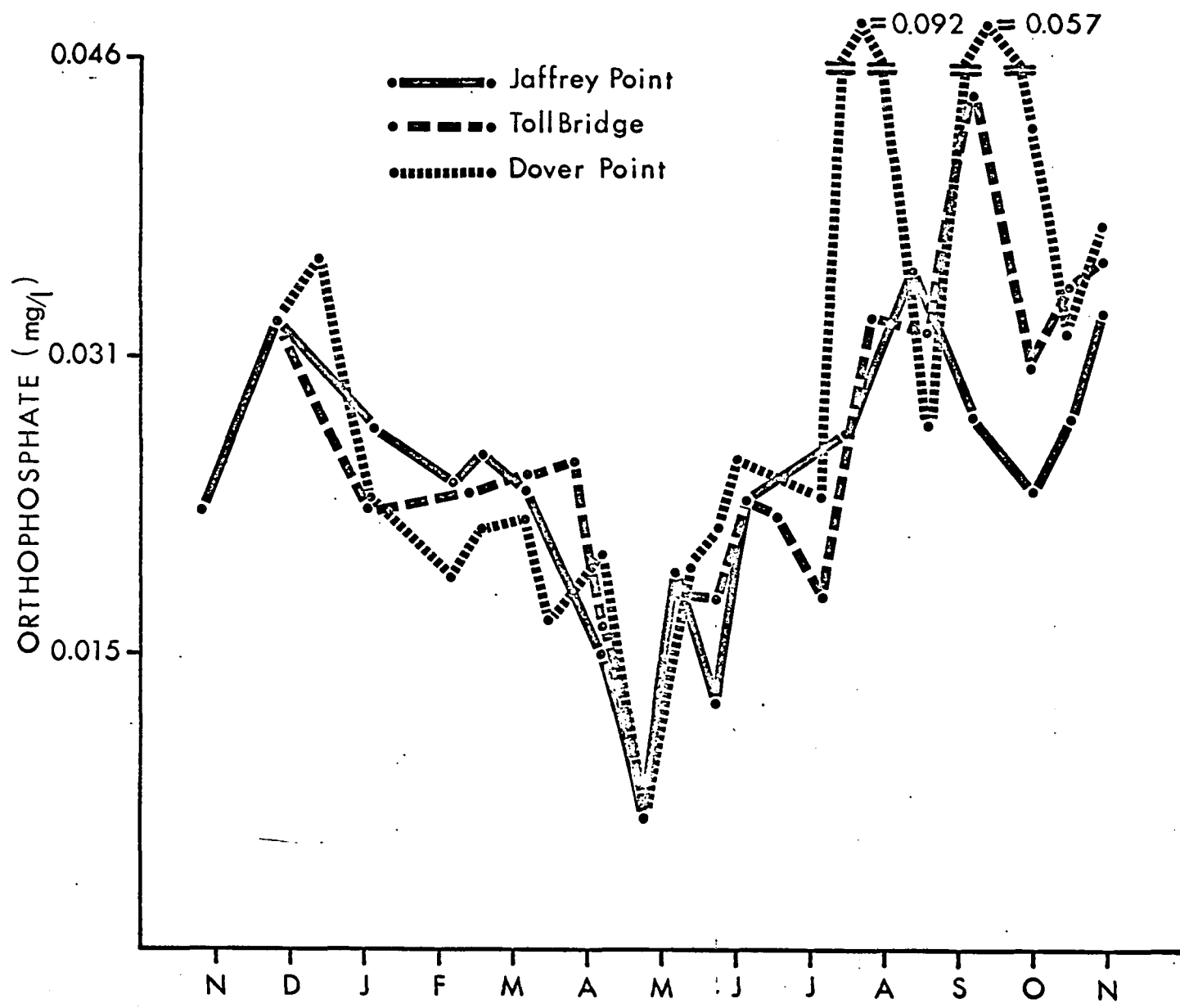
Figure 8. Variations in biomass of Gigartina
           stellata between January 1969 and
           January 1970 at Jaffrey Point, Toll
           Bridge and Dover Point.

54
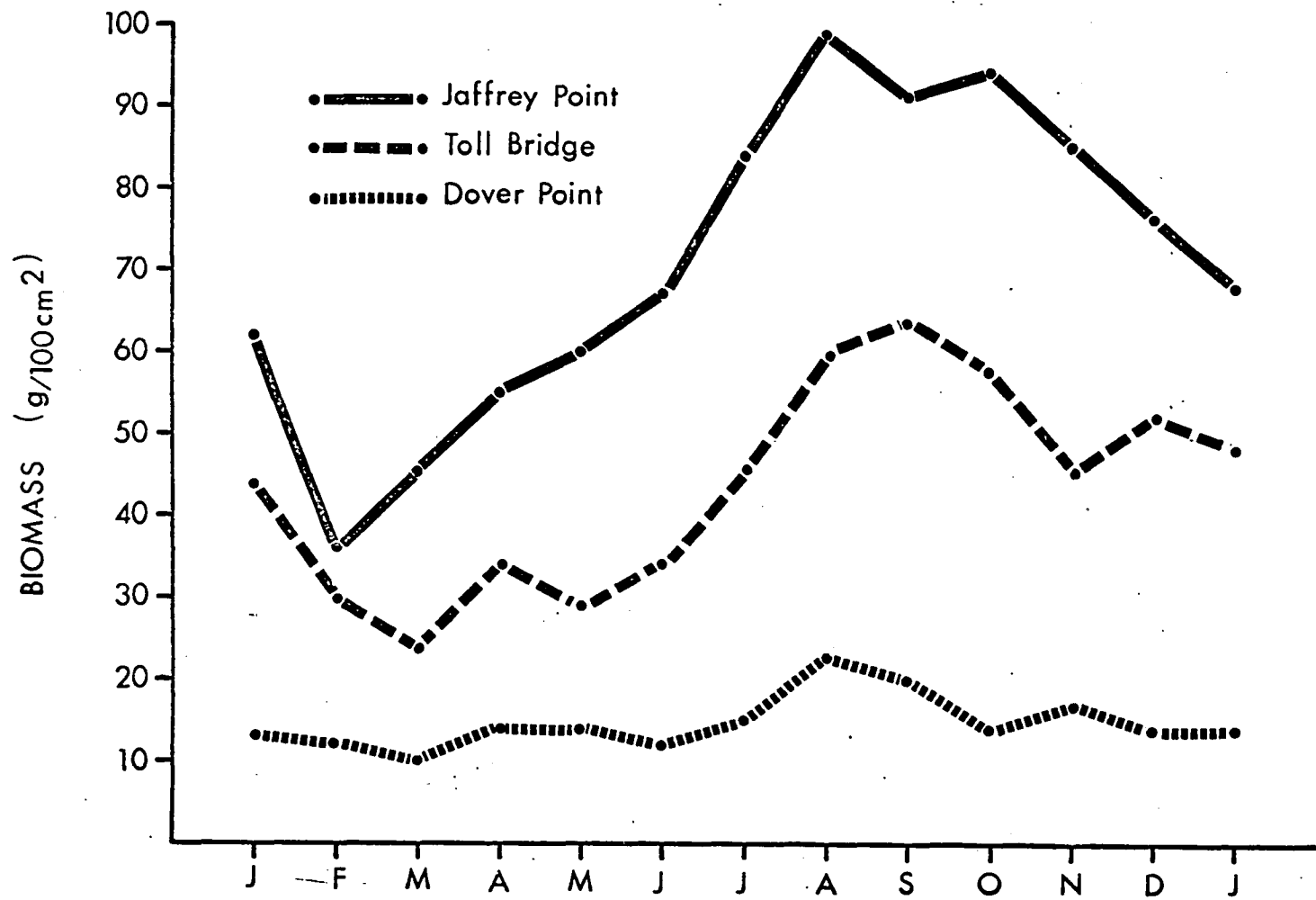
Figure 9.   Percent frequency of different size
             classes of _Gigartina_ _stellata_ between
             January 1969 and January 1970 at
             Jaffrey Point, Toll Bridge and Dover
             Point.

SIZE CLASS (cm)

Jaffrey Point

= 50%

Toll Bridge

Dover Point

J F M A M J J A S O N D J
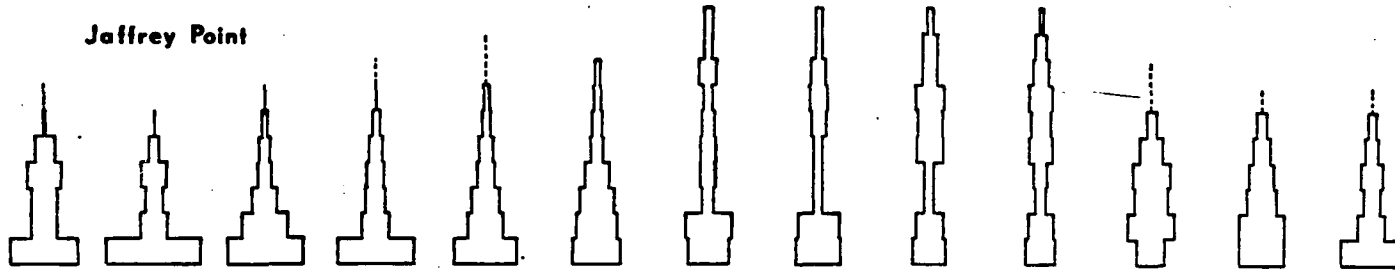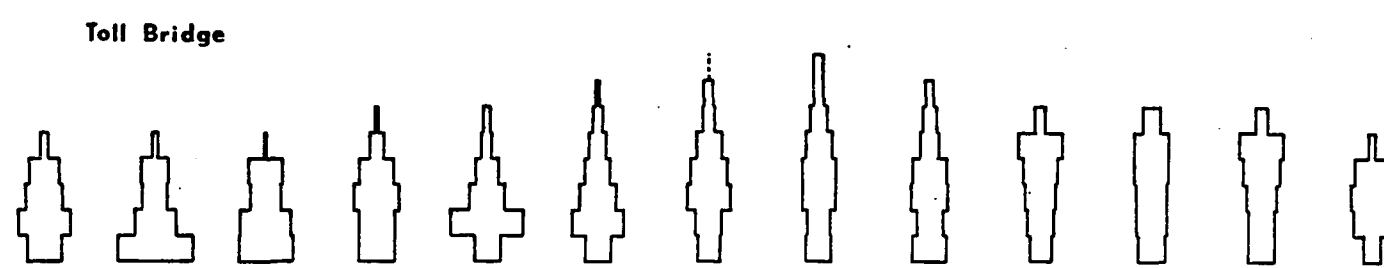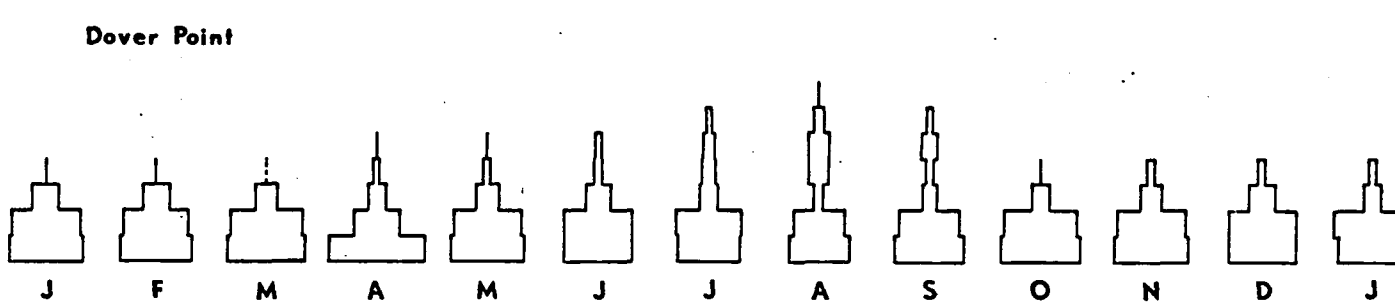
Figure 10. Variation in biomass of _Gigartina stellata_ relative to elevation.

58
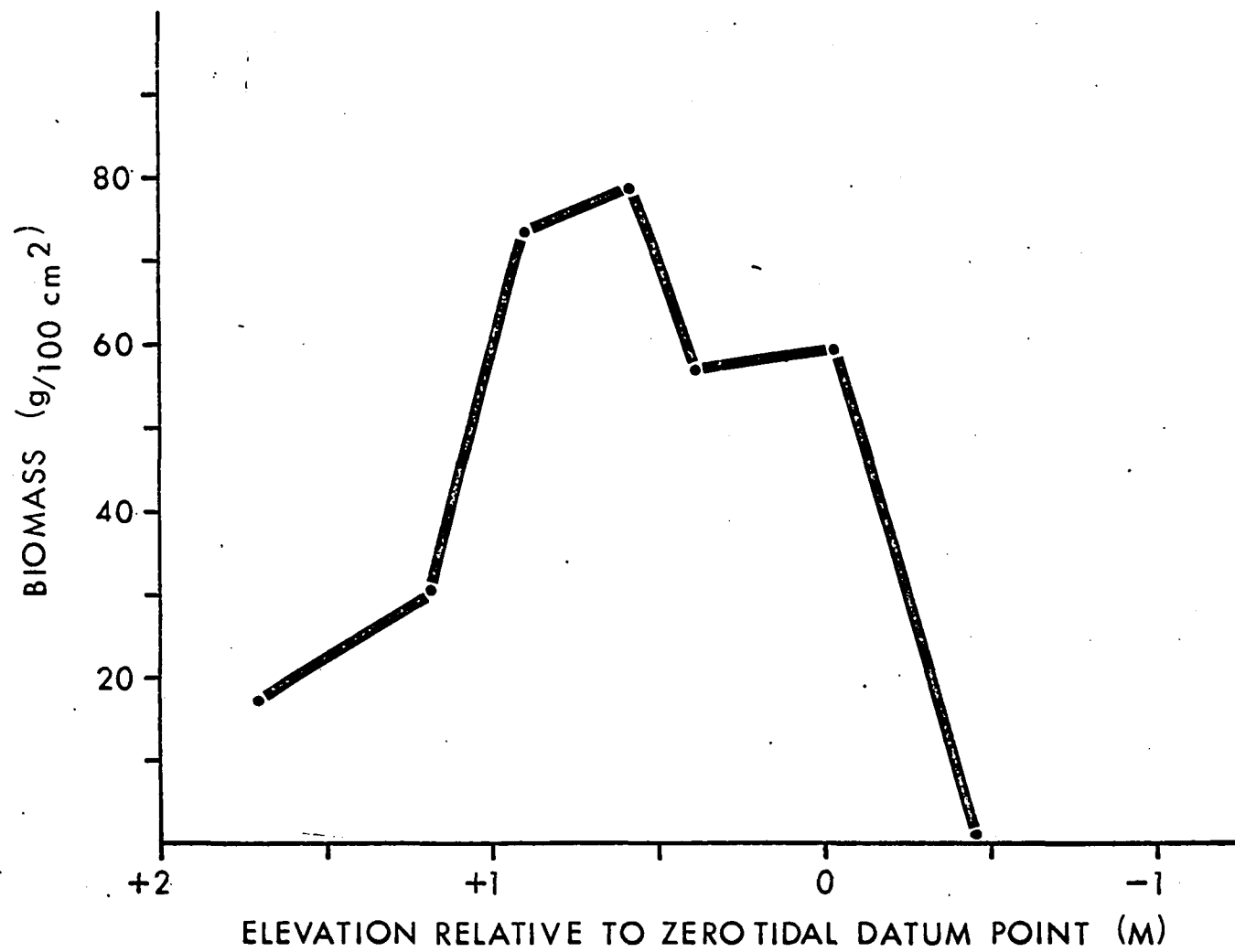
Figure 11.   Percent frequency of different size classes
             of <u>Gigartina</u> <u>stellata</u> relative to elevation.
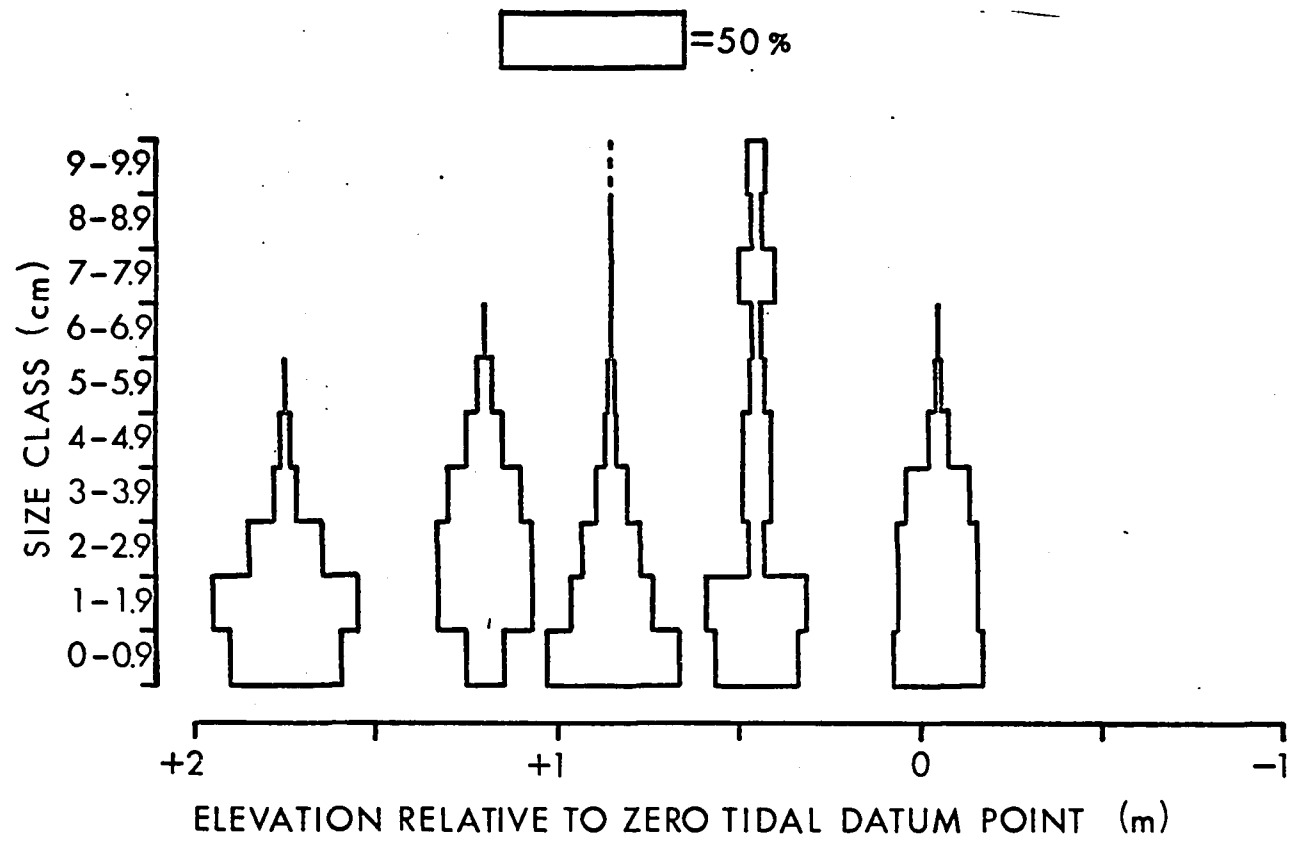
Figure 12. Changes in biomass of <u>Gigartina</u> <u>stellata</u>
            following various degrees of harvesting
            in December 1968.
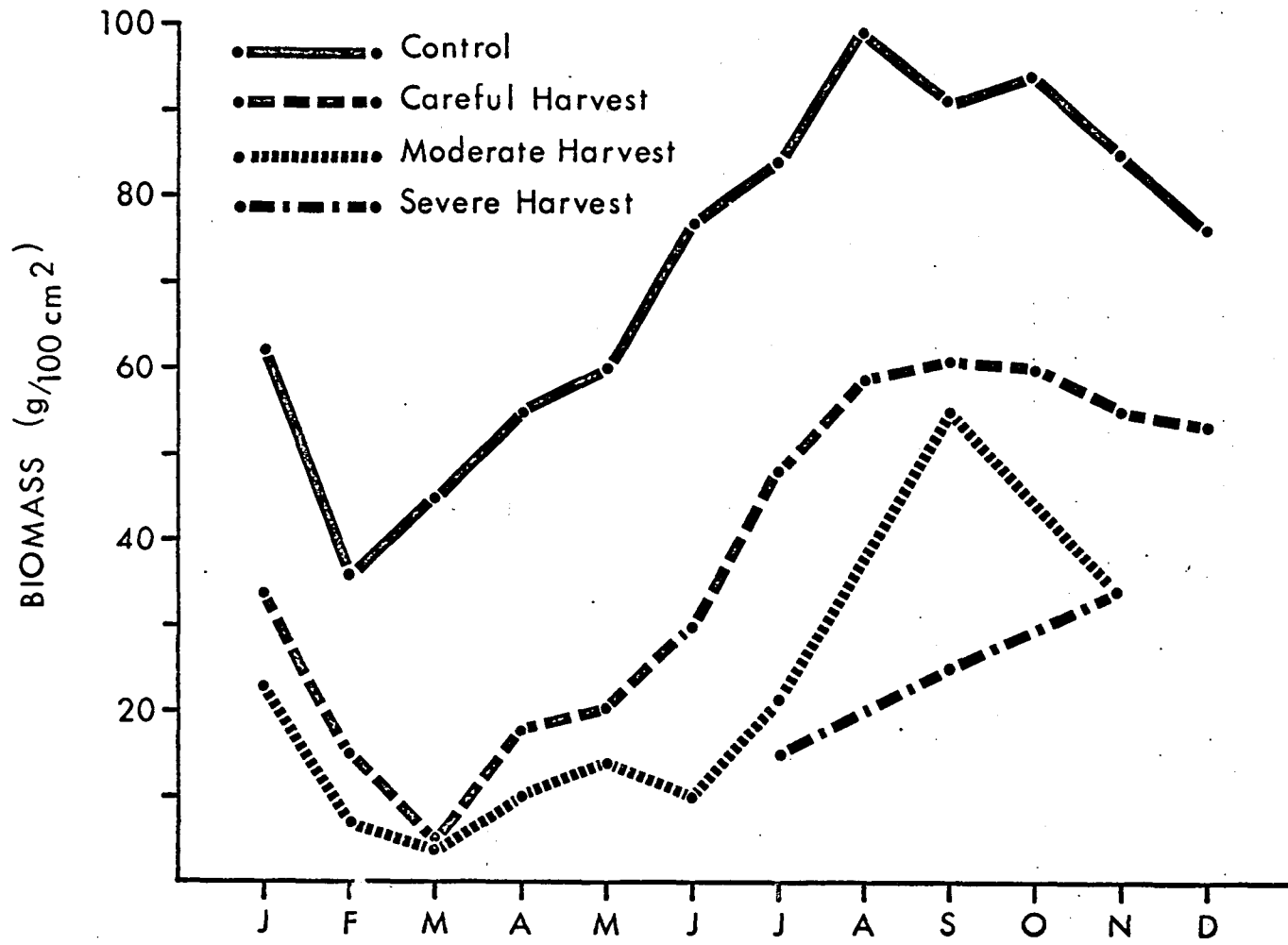
Figure 13. Percent occurrence of different size fronds
following various degrees of harvesting in
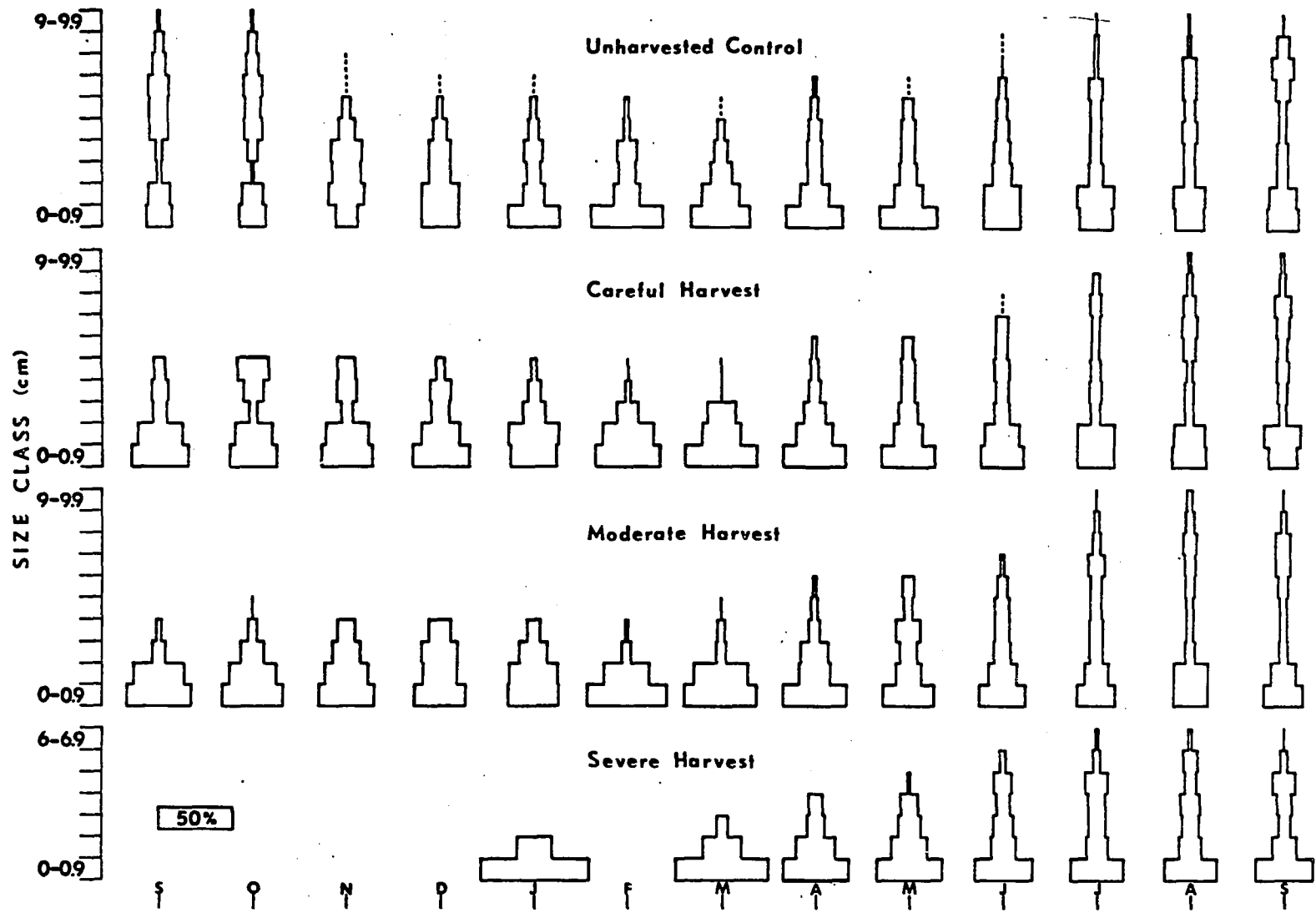December, 1968.

SIZE CLASS (cm)

Unharvested Control

Careful Harvest

Moderate Harvest

Severe Harvest

9-9.9 ... 0-0.9

8-8.9 ... 0-0.9

6-6.9 ... 0-0.9

7-7.9 ... 0-0.9

50% F M A M J J A S O N

63

64
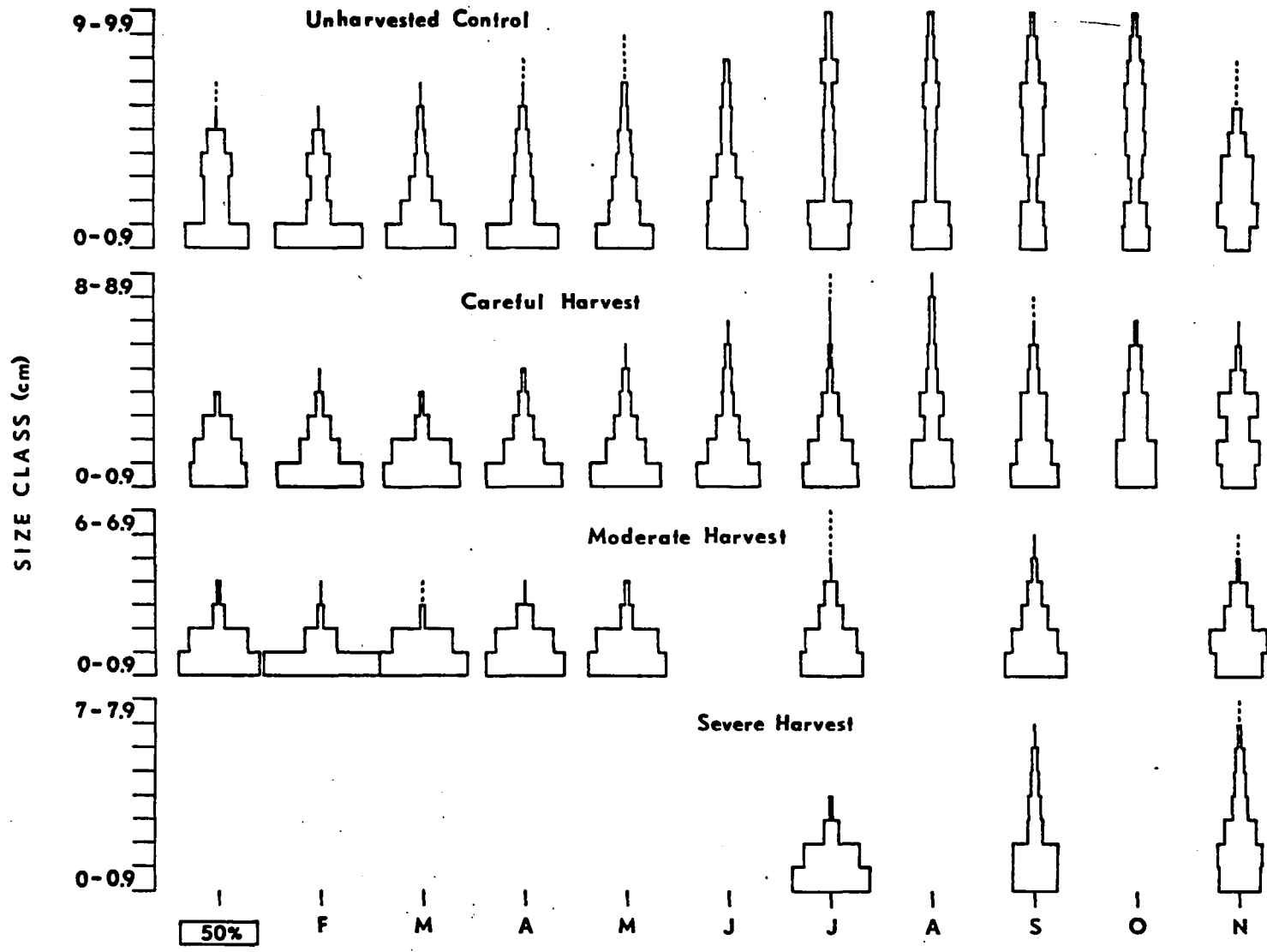
Figure 14. Distribution of biomass among various
size classes following different degrees
of harvesting in December, 1968.

SIZE CLASS (cm)

Unharvested Control

Careful Harvest

Moderate Harvest

Severe Harvest

9-9.9
0-0.9

8-8.9
0-0.9

6-6.9
0-0.9

7-7.9
0-0.9

50%

J F M A M J J A S O N

66
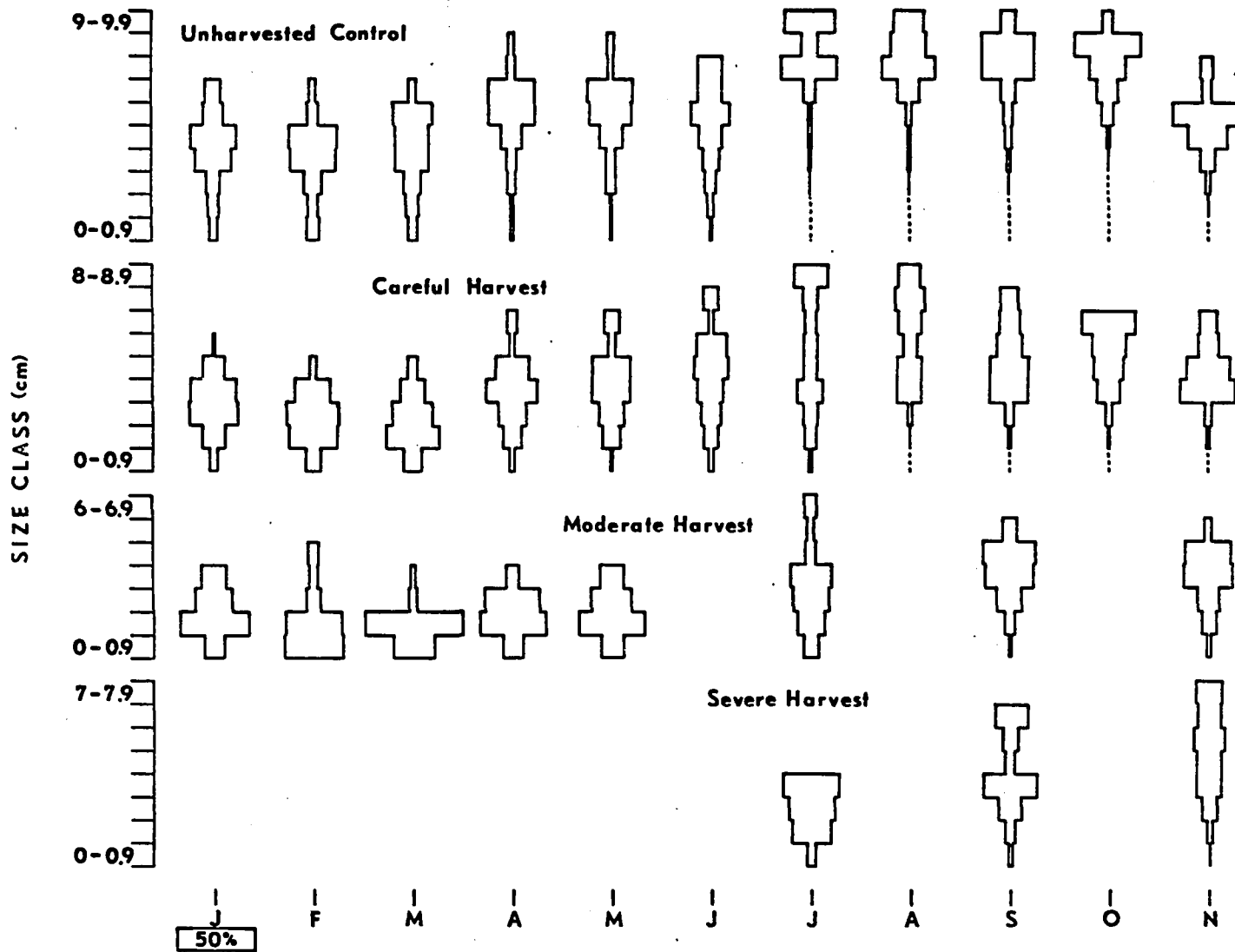
Figure 15. Changes in biomass of <u>Gigartina</u> <u>stellata</u>
following various degrees of harvesting
in August, 1969.
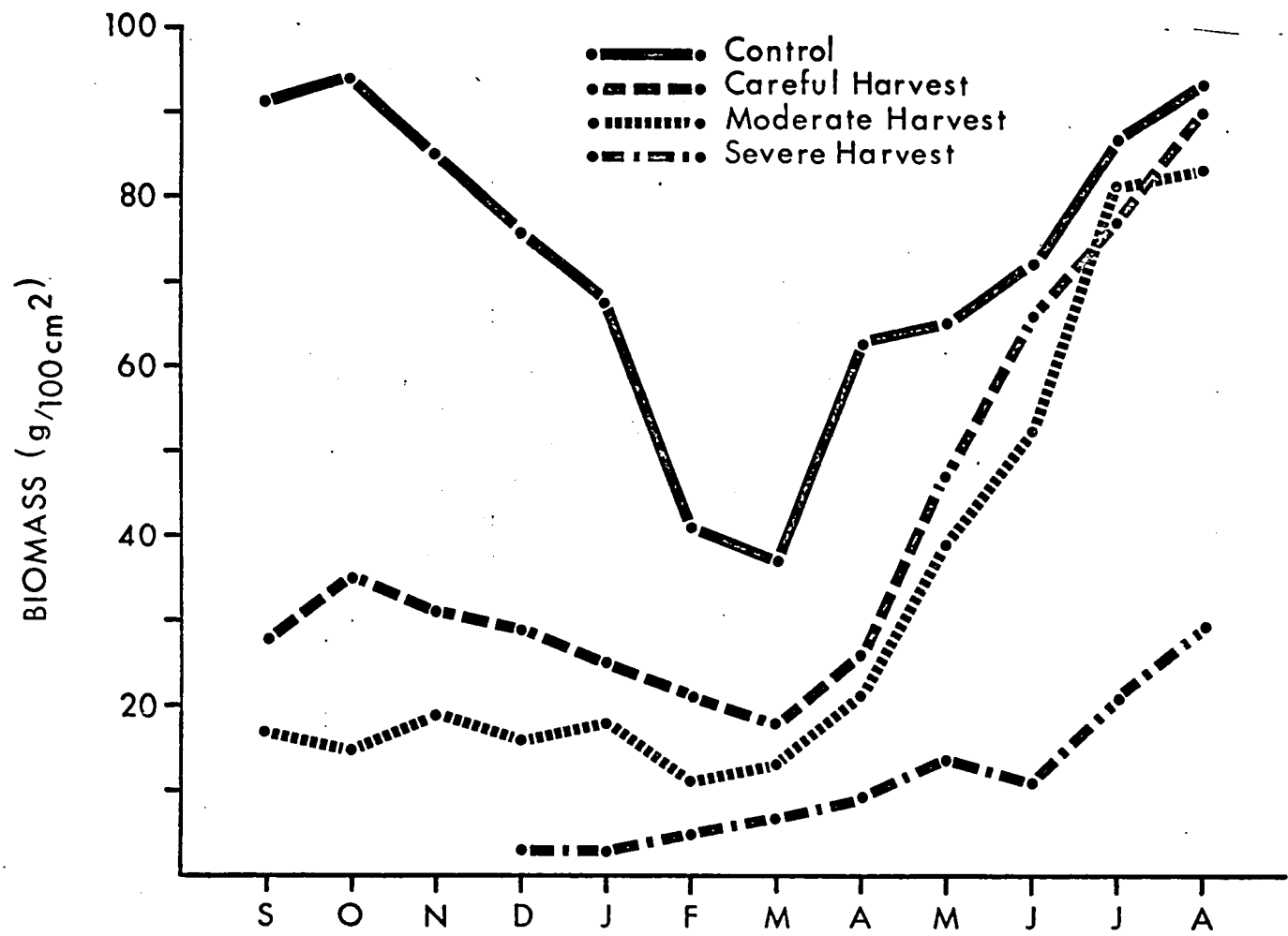
Figure 16. Percent occurrence of different size
fronds following various degrees of
harvesting in August, 1969.

SIZE CLASS (cm)

Unharvested Control

Careful Harvest

Moderate Harvest

Severe Harvest

50%

S O N D J F M A M J J A S

69

Figure 17.   Distribution of biomass among various
             size classes following different degrees
             of harvesting in August, 1969.

SIZE CLASS (cm)

Unharvested Control

Careful Harvest

Moderate Harvest

Severe Harvest

50%

9-9.9
0-0.9

S O N D J F M A M J J A S
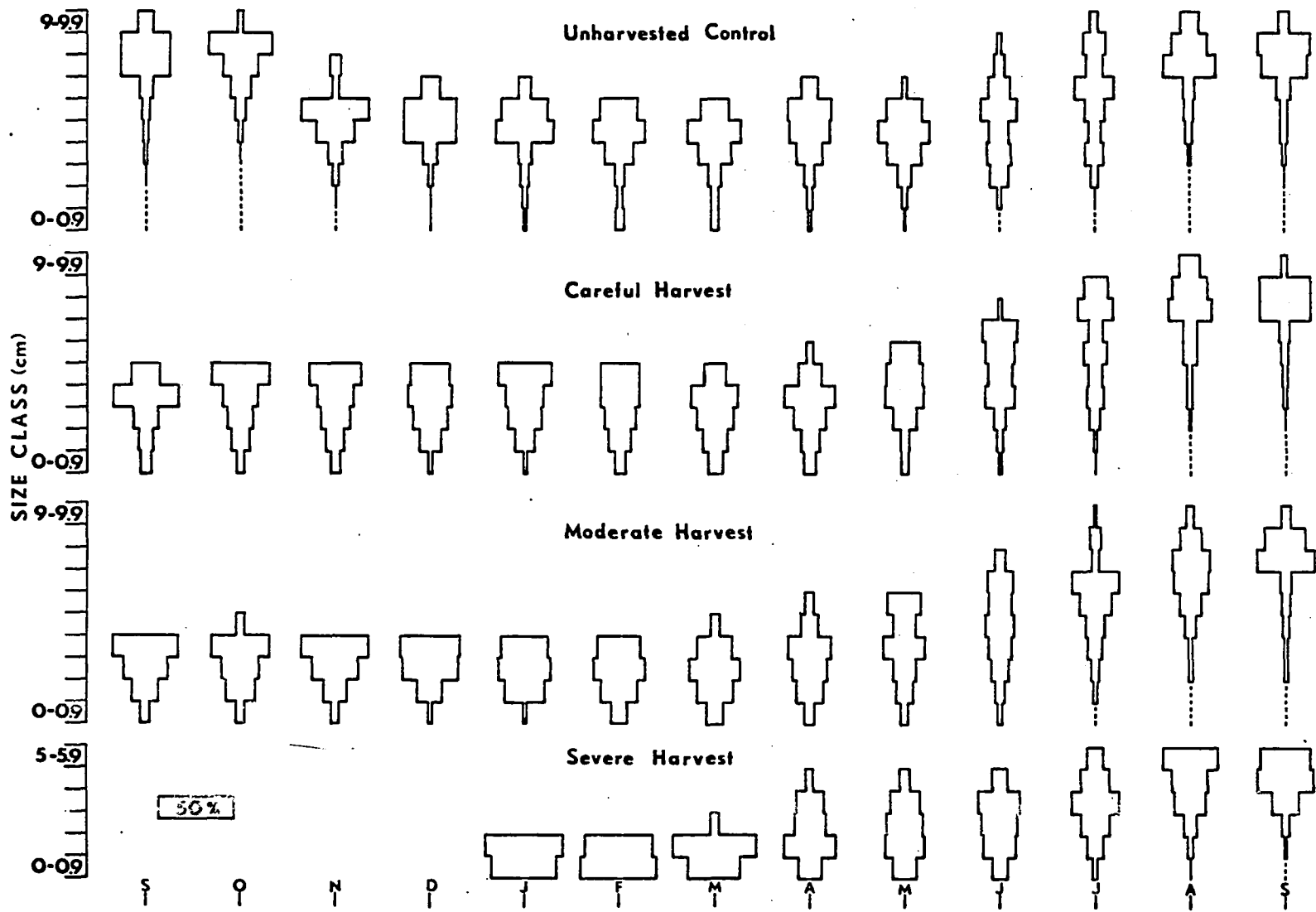
Figure 18. The number of carposporic papillae on
            Gigartina stellata following various
            degrees of harvesting in December 1968.
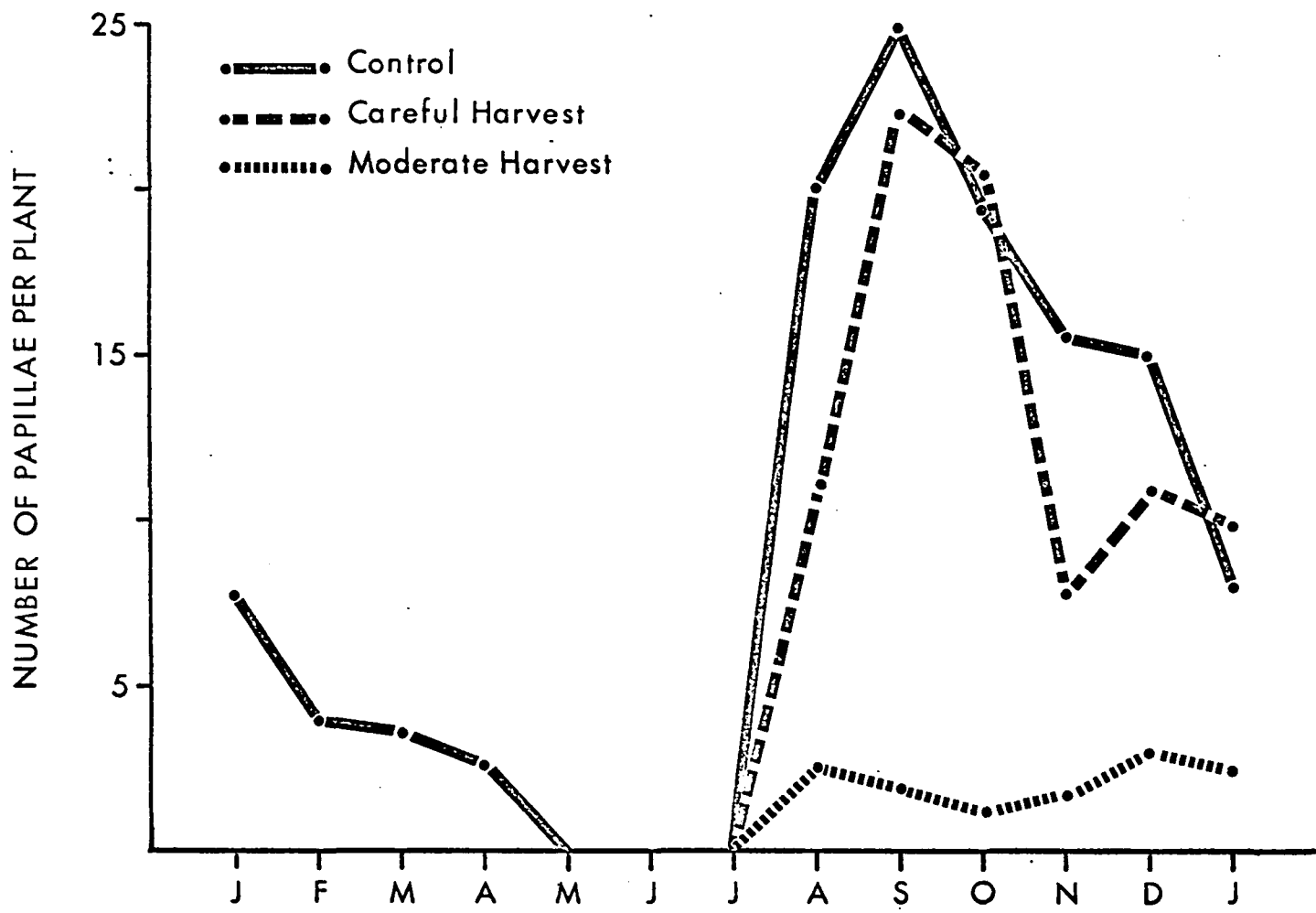
Figure 19. The number of carposporic papillae on
            Gigartina stellata following various
            degrees of harvesting in August, 1969.
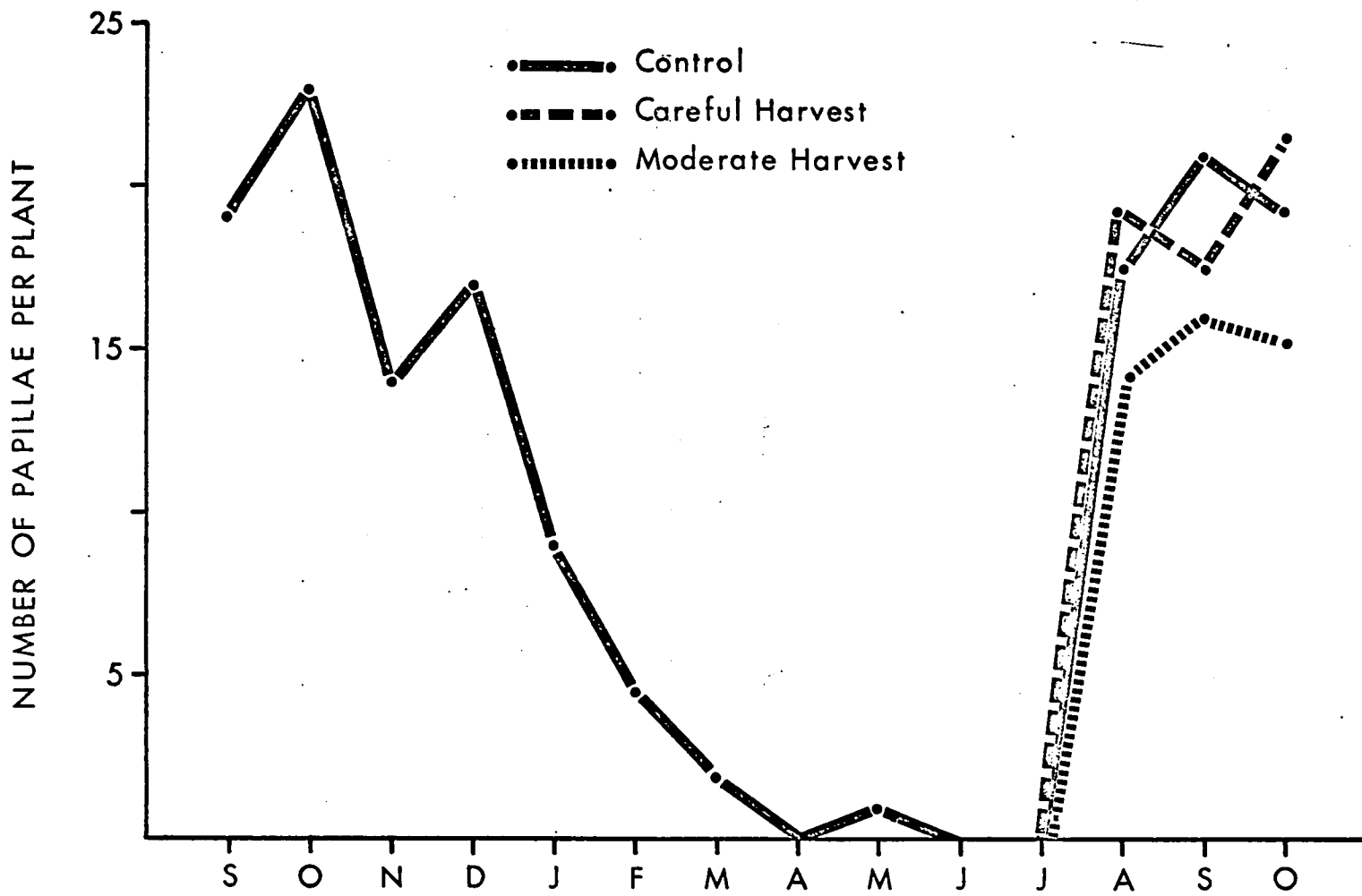
Figure 20. Denuded quadrat, 21 months after steri-
lization. (August, 1970).

Figure 21. Close-up of denuded quadrat taken 21
months after sterilization. (August,
1970).

AUG • 70 •

AUG • 70 •

Figure 22. Denuded quadrat, 29 months after sterili-
zation (April, 1971).

Figure 23.   The growth of <u>Gigartina stellata</u> at
           various light intensities at 15 C
           and a salinity of 30 o/oo.
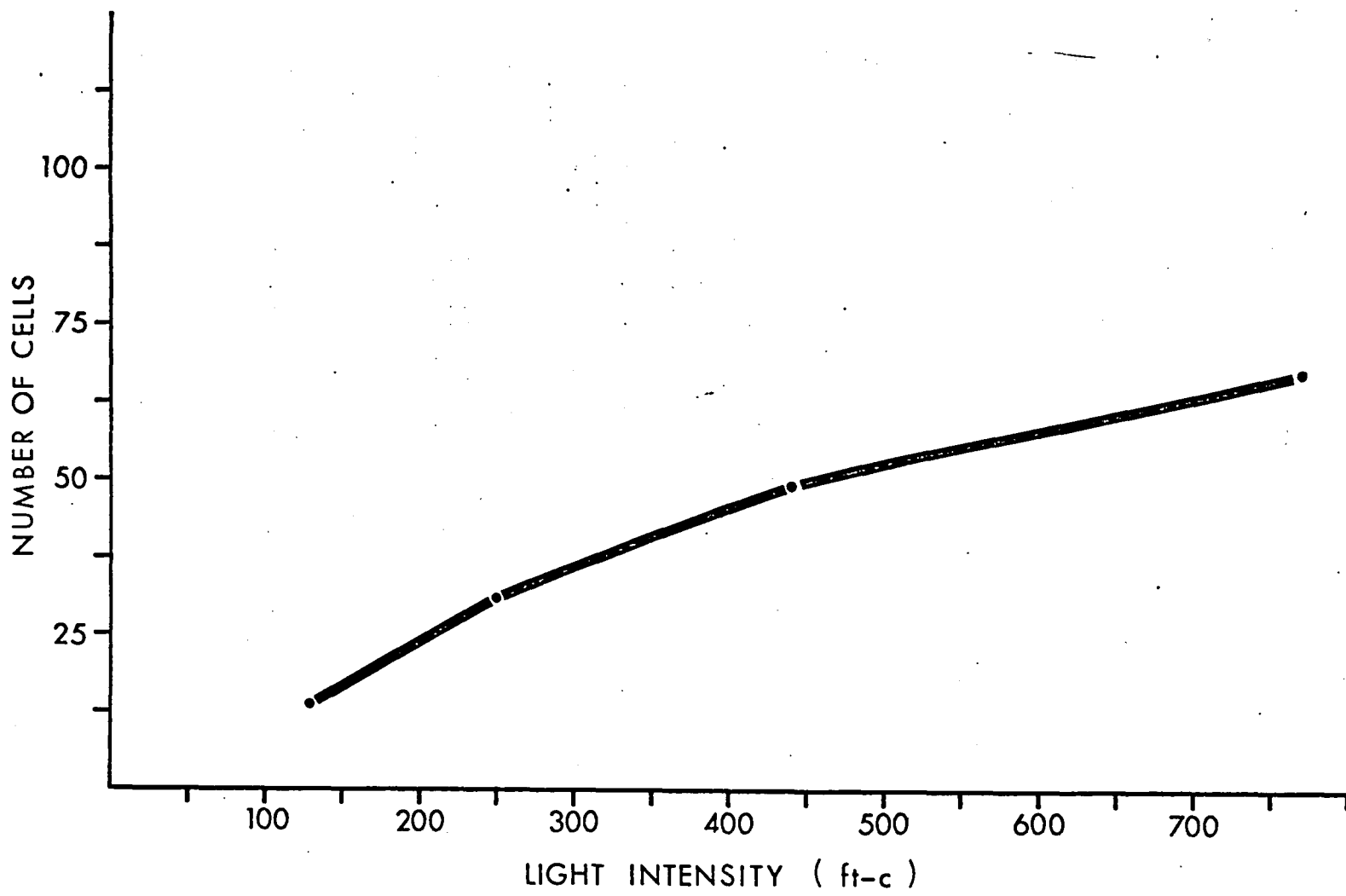
Figure 24.   The growth of <u>Gigartina stellata</u> at
             various temperatures and at 400 to
             440 foot-candles and 30 o/oo salinity.

84
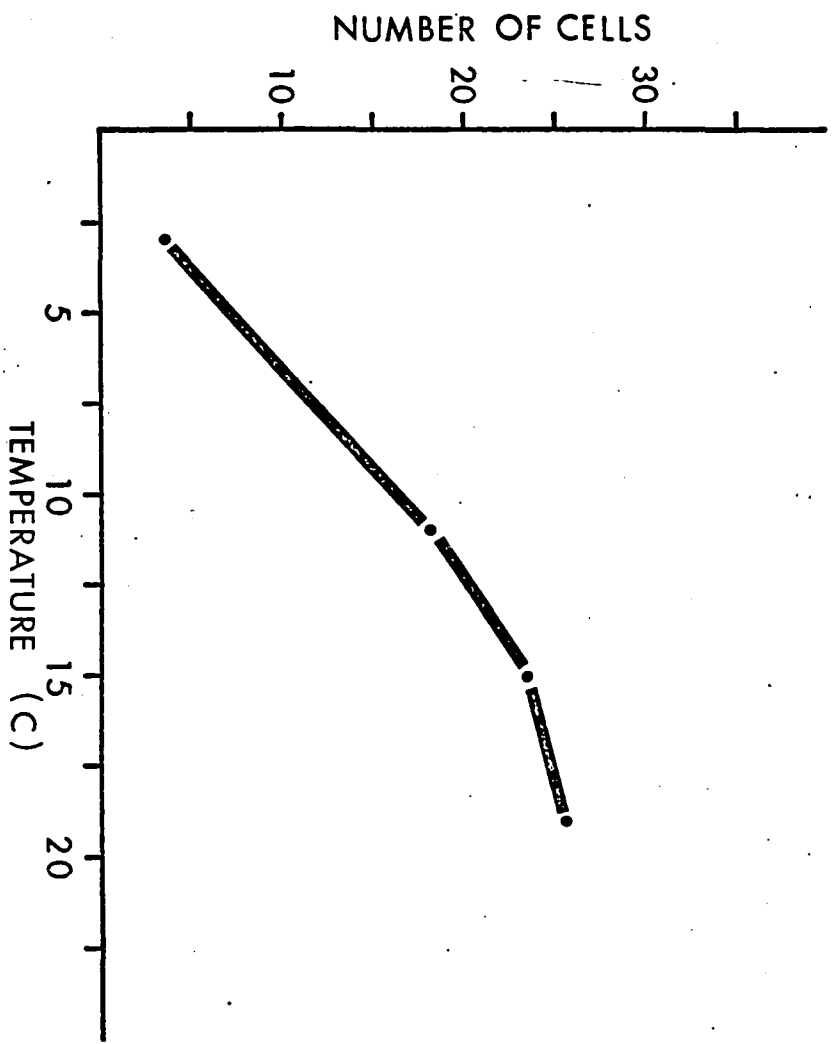
Figure 25. The germination of spores of _Gigartina
stellata_ at various salinities and
temperatures.
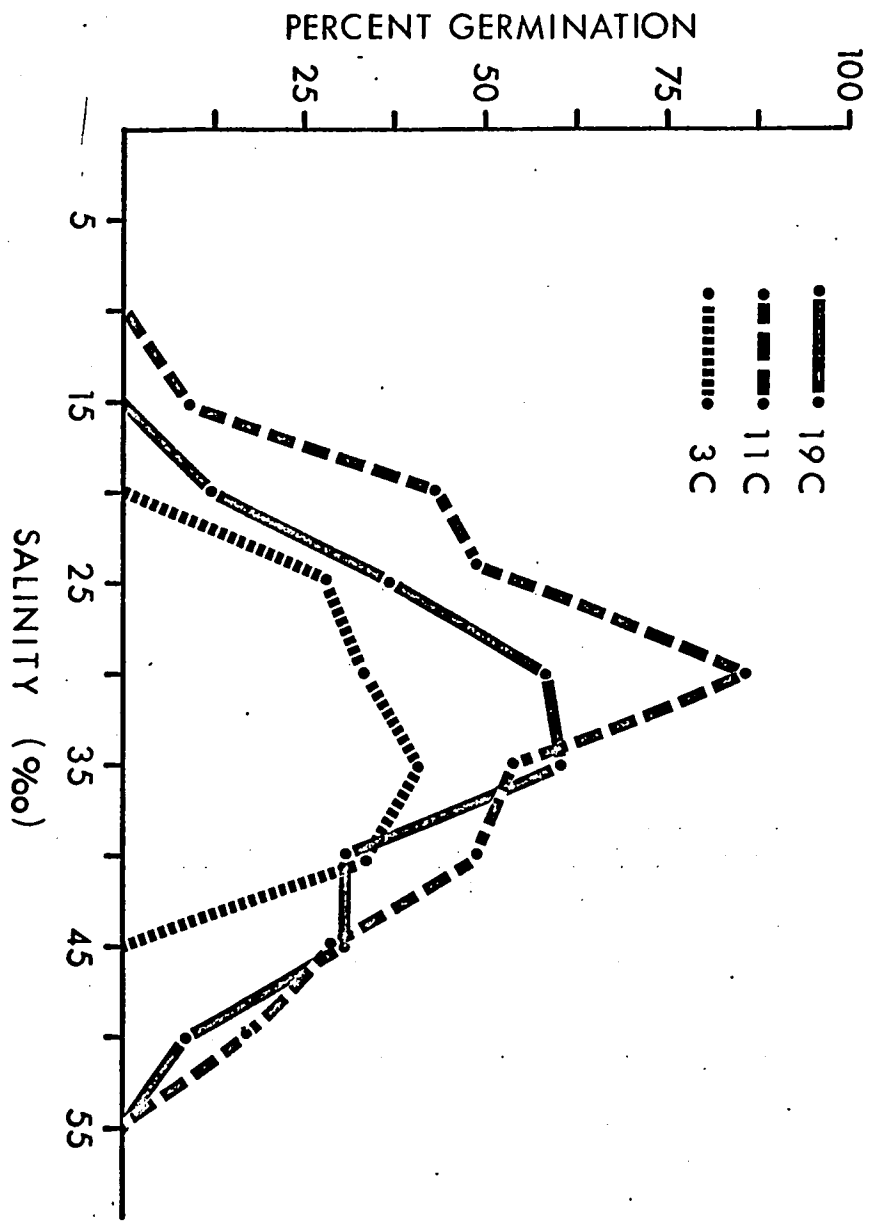
Figure 26. The growth of <u>Gigartina stellata</u> at
various temperatures and salinities
(after 7 days in culture at 400 to
440 ft-c).

88
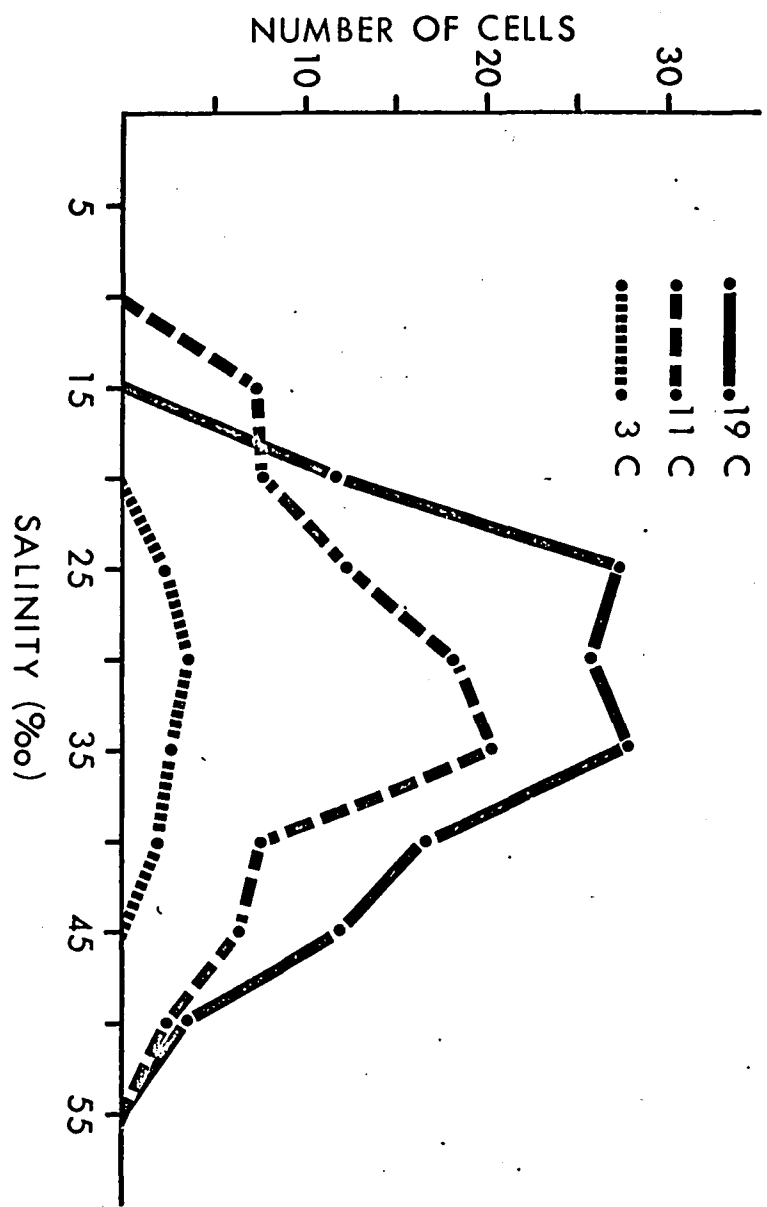
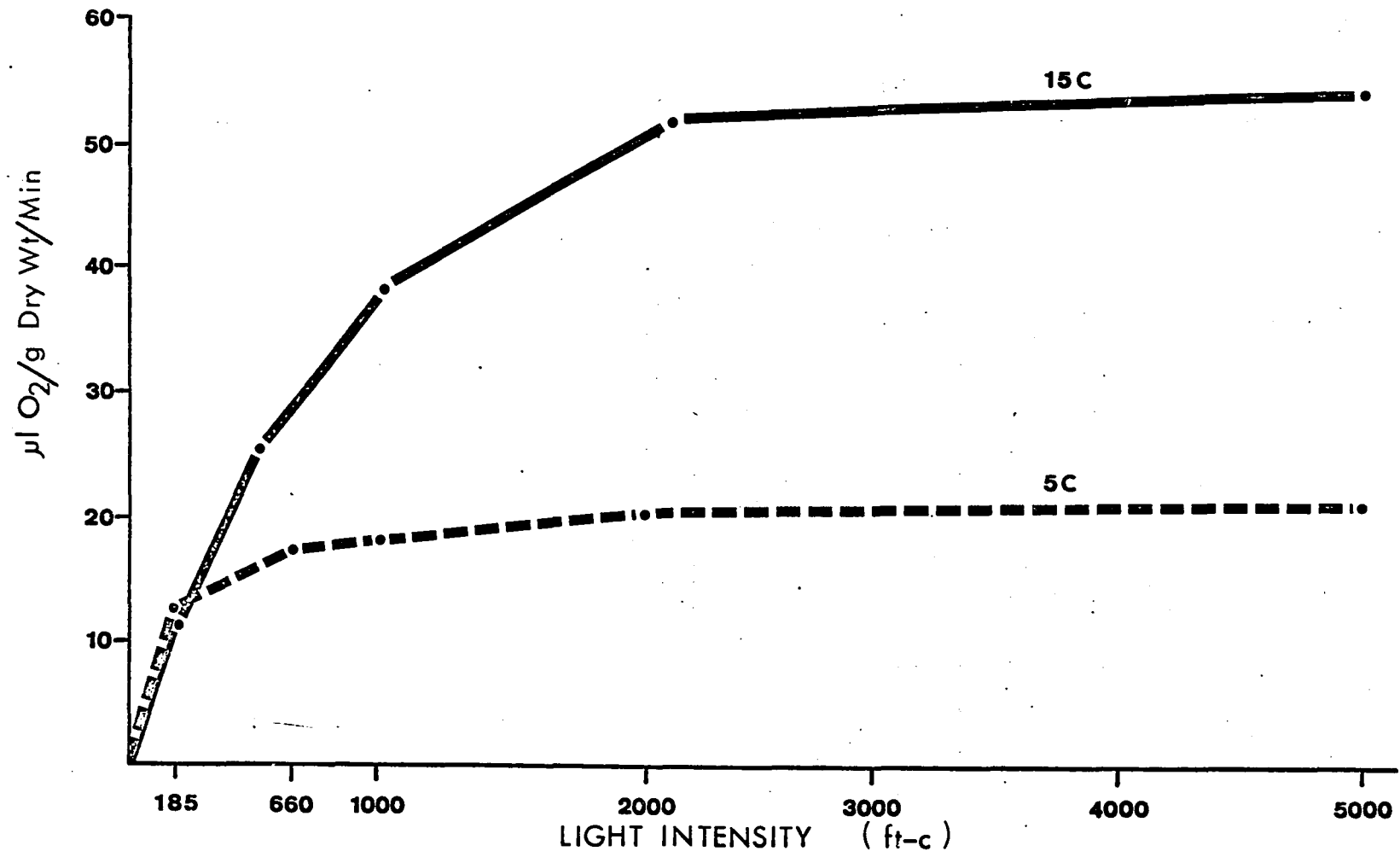Figure 27. Apparent photosynthesis of <u>Gigartina</u>
<u>stellata</u> at various light intensities.

Figure 28. Apparent photosynthesis of <u>Gigartina</u> <u>stellata</u> at various temperatures.

Figure 29. Respiration of <u>Gigartina</u> <u>stellata</u> at various temperatures.
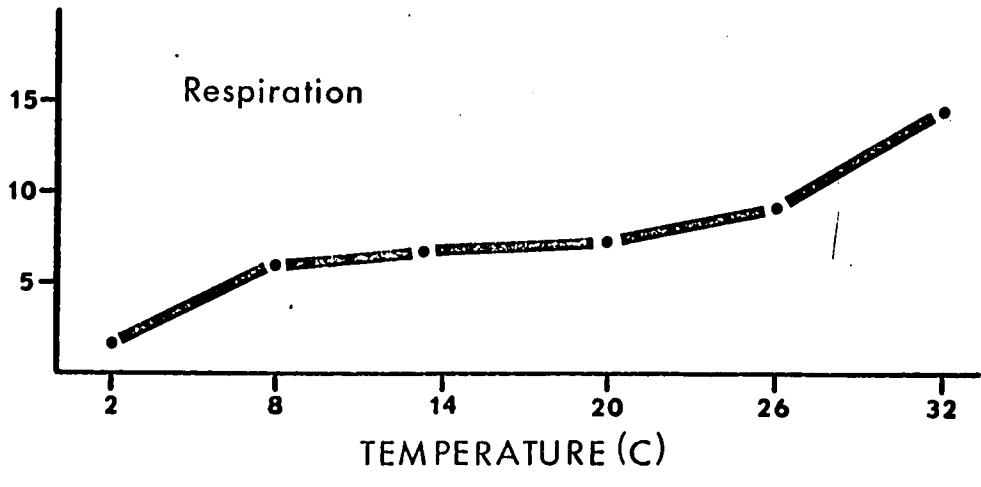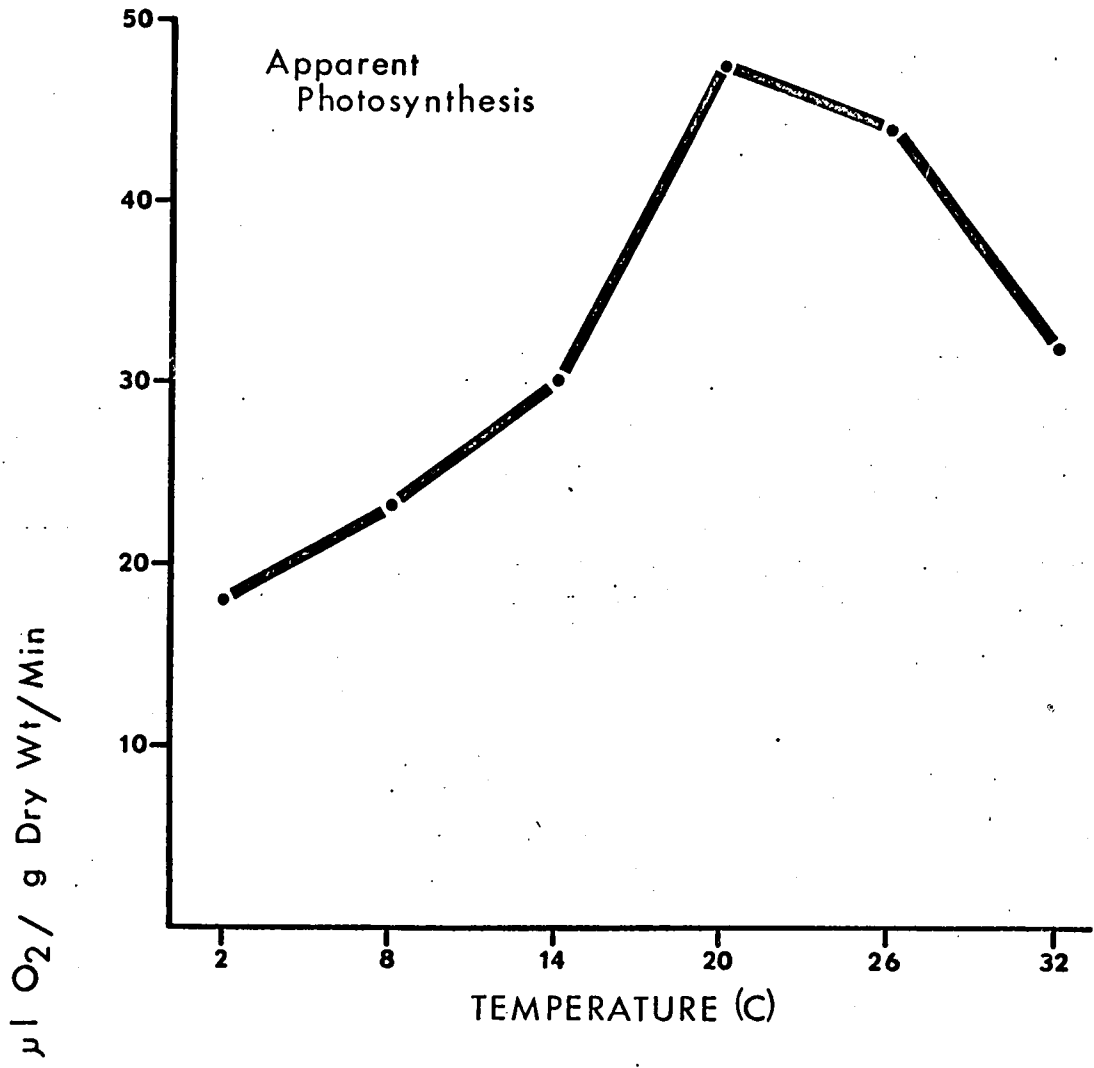
Figure 30. Apparent photosynthesis of Gigartina
            stellata in various salinities.

Figure 31. Respiration of Gigartina stellata in
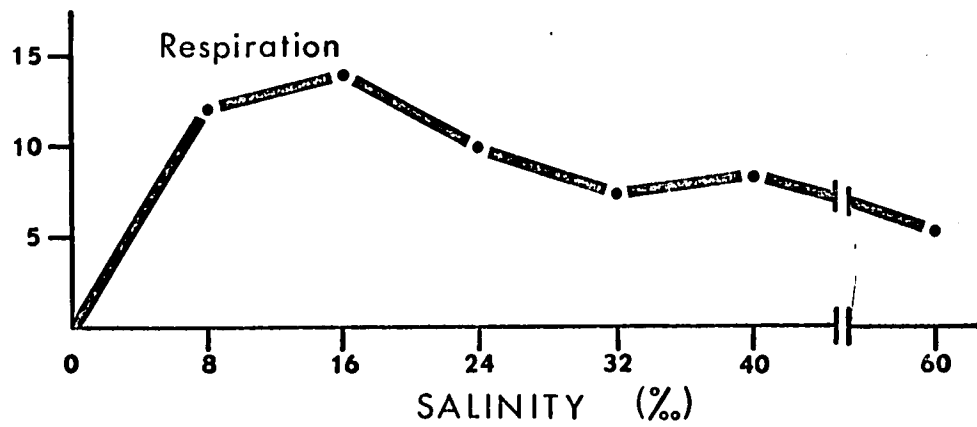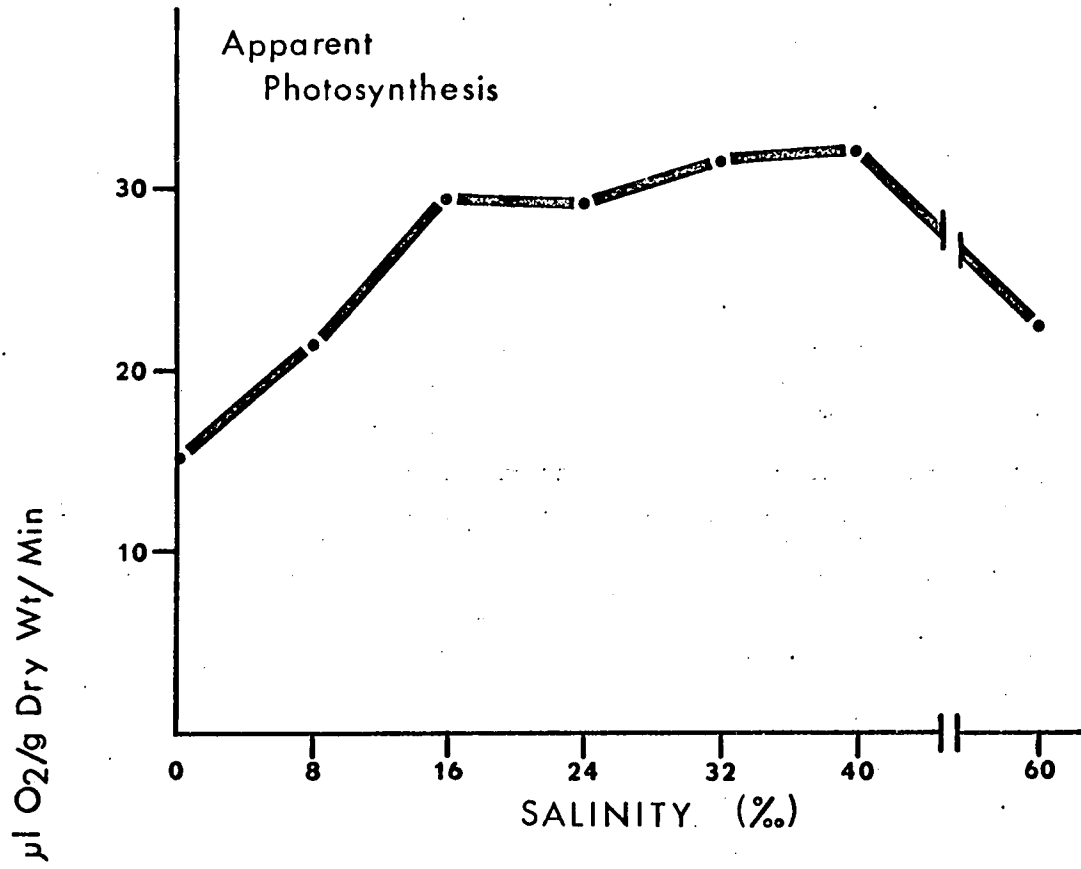   various salinities.

Figure 32. The effect of dehydration on the
apparent photosynthesis of _Gigartina_
stellata expressed as the percent
of maximum photosynthesis.

Figure 33. Respiration of _Gigartina stellata_
at various degrees of dehydration
and after rehydration.