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

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by

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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 initiated 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 reproductive fronds for the ensuing reproductive season, yet it was the least detrimental to reproductive potential one year after harvesting.

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 substantially 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 tolerance to dehydration.

INTRODUCTION

The marine red alga Gigartina stellata (Stackhouse) Batters is a member of the order Gigartinales and family Gigartinaceae. Chondrus crispus Stackhouse and G. stellata, the only members of the family Gigartinaceae occurring on the east coast of North America (Taylor, 1957), are collectively referred to as "carageen" (Marshall, et. al., 1949). They are often harvested in mixed lots as sources of carageenan, a phycocolloid (Mathieson, 1969). Carageenan and other products obtained from G. stellata are widely utilized in the food and pharmaceutical industries. Although G. stellata 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 G. stellata. The objectives of this investigation of G. stellata were threefold: 1) to study the in situ 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 G. stellata 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 within 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 conditions was determined after one week by measuring the percent 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 development, 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 considerable 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 experiments. The salt concentrations in the salinity experiments were achieved by mixing the standard F/2 stock solutions 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 techniques 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 manometric measurements simultaneously, the discs were set out at different intervals. In the photosynthesis-dehydration experiments, the material was dehydrated, placed in a reaction 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 consumption 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 surface 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 decline at the end of March into April. Intermediate concentrations 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 fluctuations 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 orthophosphate 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 respectively. 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; nevertheless, 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 samples 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 initiation 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 biomass 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 °/oo at 11 C, 20-50 °/oo at 19 C and 25-40 °/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 °/oo and 11 C. At 3 and 19 C, the optimum germination occurred at 35 °/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 °/oo; growth was greatly reduced at salinities of 20 and 40 °/oo. At 11 C the optimal growth occurred in 30 and 35 °/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 °/oo; above 40 °/oo and below 16 °/oo there was a

significant reduction. Maximum photosynthesis was recorded at 40 °/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 °/oo), whereas respiration was relatively constant over a broad range of higher salinities (32 to 60 °/oo). Five days immersion in 0 °/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 residual 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 following fall. However, moderate harvesting drastically reduced the reproductive potential the following season; severe harvesting completely eliminated carposporic plants the following 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 harvested plots approached control levels of reproductive potential 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 sublittoral alga Chondrus crispus using older upright thalli (Ring, 1970).

Gigartina 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.

Gigartina exhibited a restricted tolerance to reduced salinities at 19 C. Spores did not germinate at 15 °/oo and they exhibited a low percent germination at 20 °/oo. Such responses are reflected in the local distribution of this species. Gigartina thrives on the open coast and it exhibits a restricted estuarine distribution. Indeed, G. stellata 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 G. stellata (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). Results 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 intensity 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 sublittoral forms. Summer temperatures, 15-20 C, offer maximum potential for growth. The combined results of culture and photosynthesis-respiration experiments indicate a relatively narrow tolerance to salinity fluctuations sheding light on its restricted estuarine distribution and infrequent occurrence in tide pools. Gigartina's ability to recover from desiccation permits it to succeed on vertical rock faces in the littoral zone. Field studies indicate that August harvesting of G. stellata allows maximum regrowth if care is taken to not damage the holdfast. Harvesting 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 Gigartina stellata.

Intensity (ft-c)	W/cm^2 Red	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 Gigartina stellata 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.

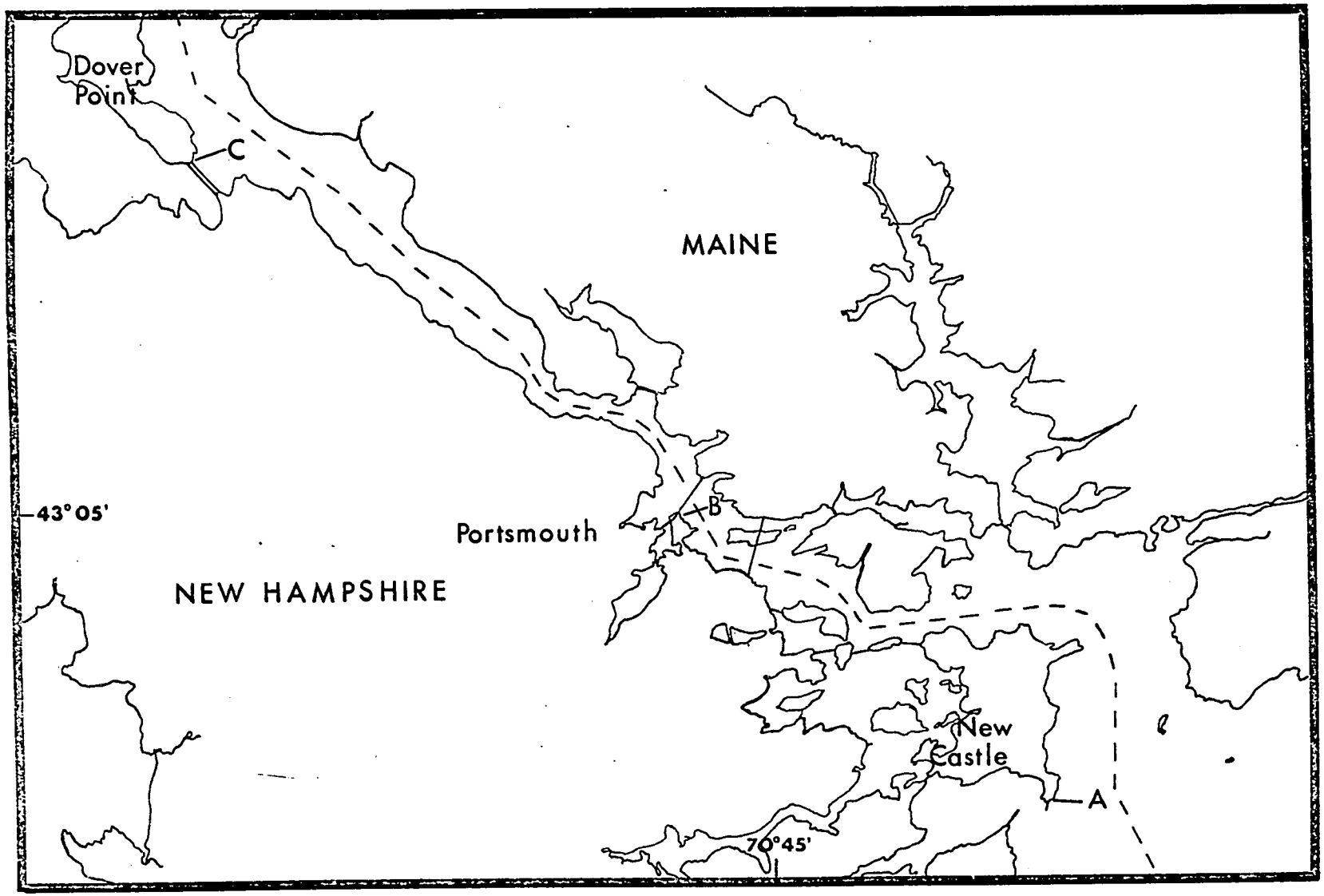

Dover
Point
C
MAINE
43°05'
Portsmouth
B
NEW HAMPSHIRE
New
Castle
A
70°45'

Figure 2. Harvesting plots of Gigartina stellata, August, 1969. (A=Control; B=Careful Harvest; C=Moderate Harvest; D=Severe Harvest).

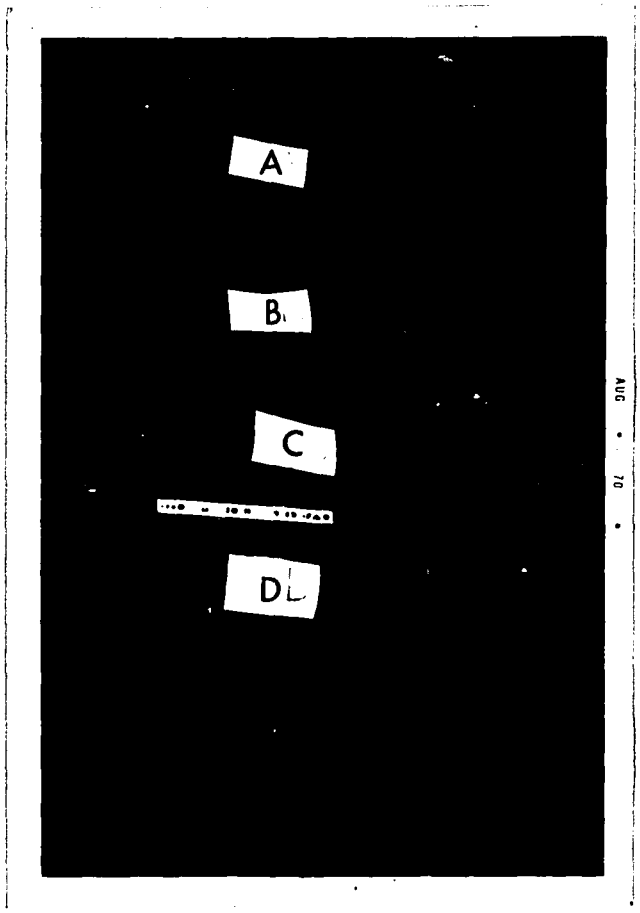

A
B
C
D
AUG • 70 •

Figure 3. Variation in surface water temperature between January 1969 and January 1970 at Jaffrey Point, Toll Bridge and Dover Point.

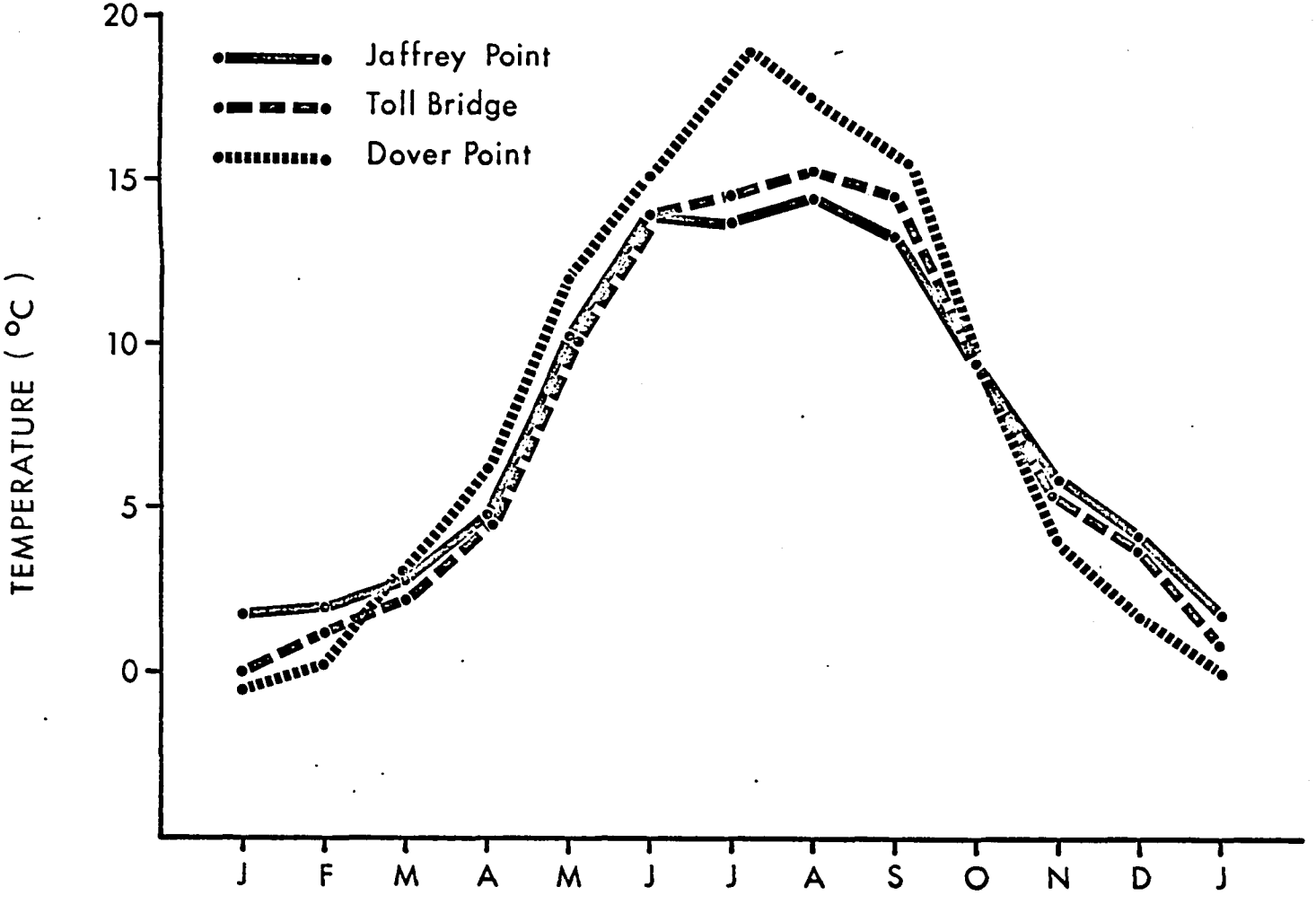

20
15
10
5
0
TEMPERATURE (°C)
Jaffrey Point
Toll Bridge
Dover Point
J
F
M
A
M
J
J
A
S
O
N
D
J

Figure 4. Variation in surface water salinity between January 1969 and January 1970 at Jaffrey Point, Toll Bridge and Dover Point.

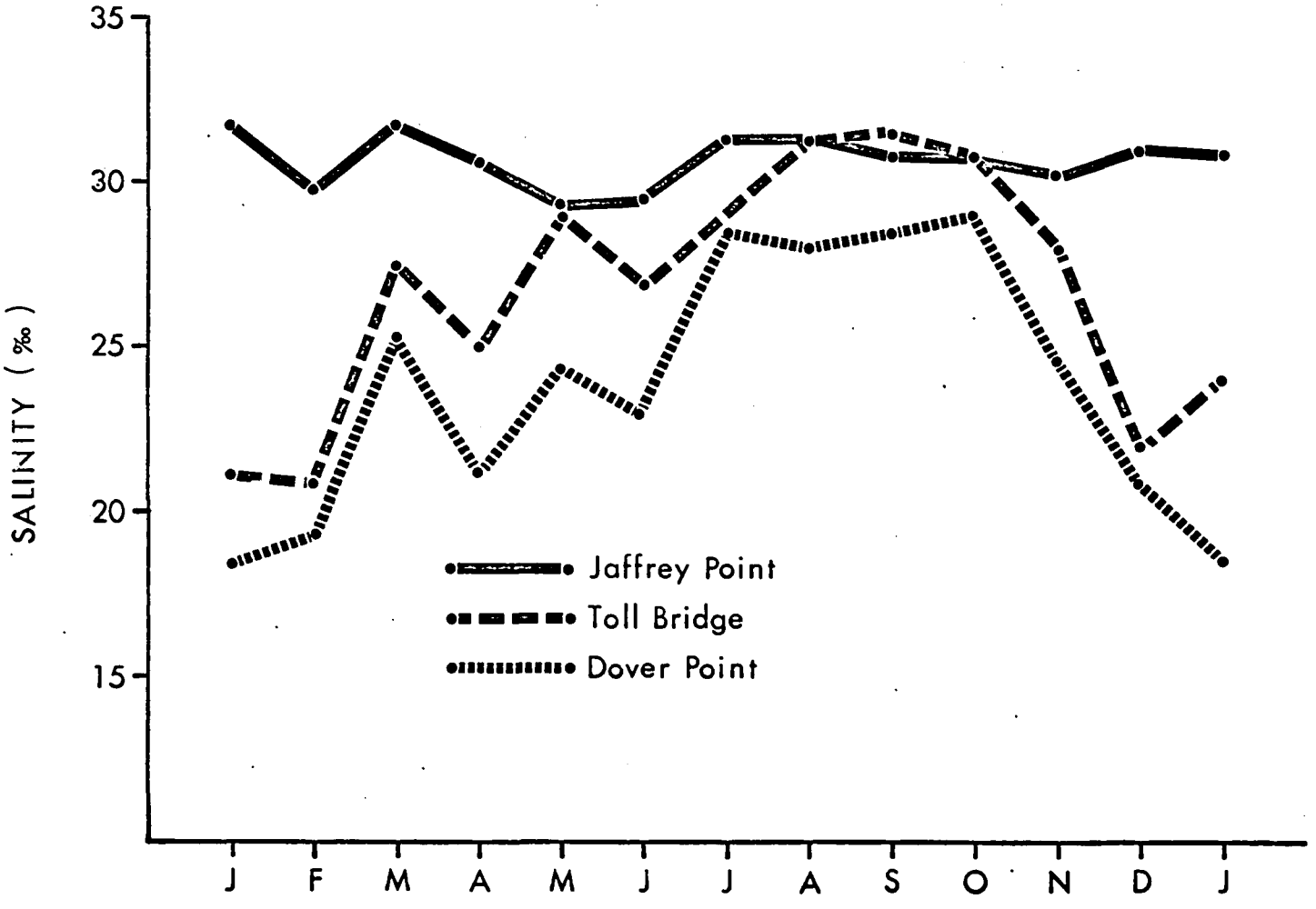

35
30
25
20
15
SALINITY (‰)
Jaffrey Point
Toll Bridge
Dover Point
J
F
M
A
M
J
J
A
S
O
N
D
J

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

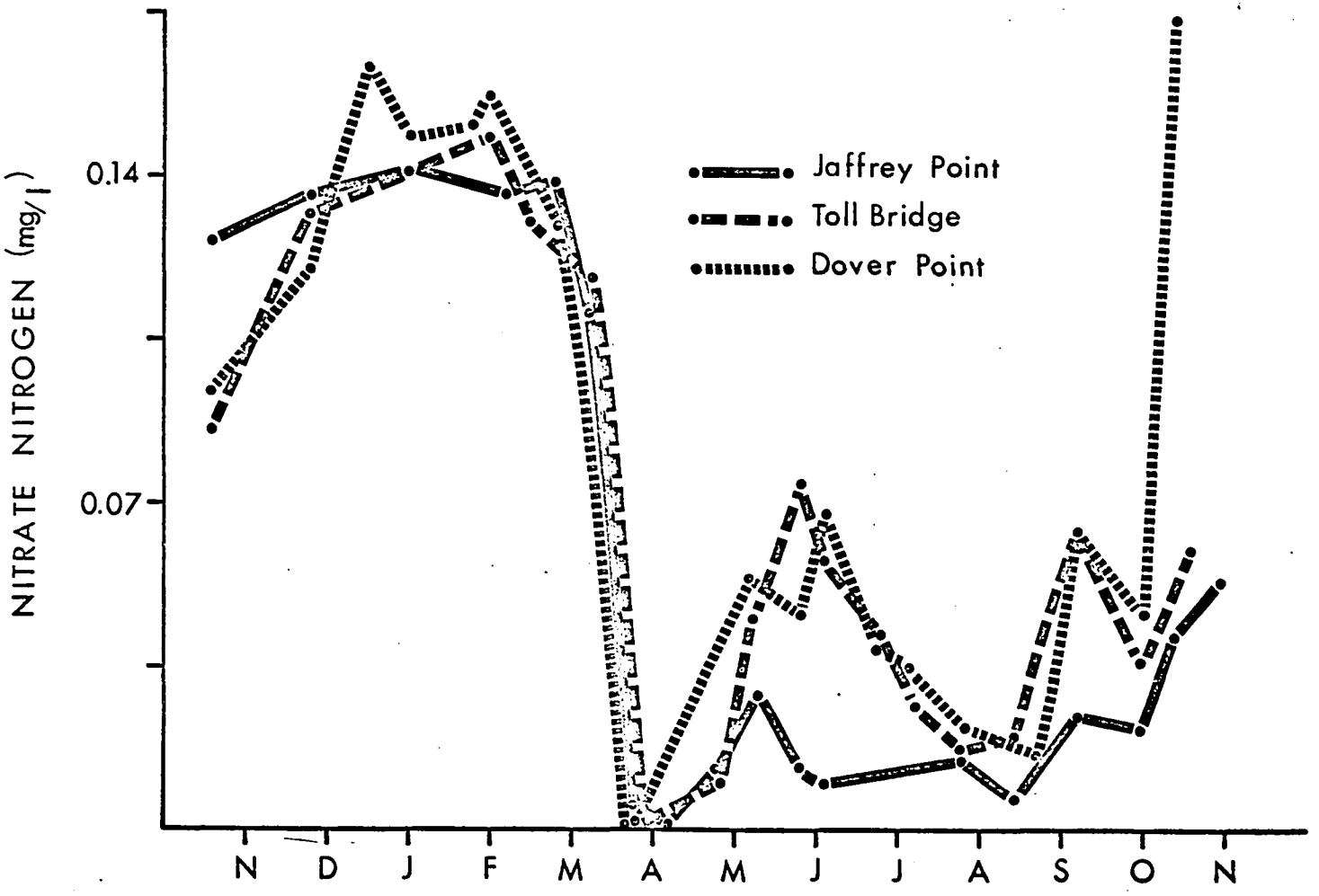

NITRATE NITROGEN (mg/l)
0.14
0.07
Jaffrey Point
Toll Bridge
Dover Point
N
D
J
F
M
A
M
J
J
A
S
O
N

Figure 6. Variation in Nitrite-Nitrogen between November 1969 and November 1970 at Jaffrey Point, Toll Bridge and Dover Point.

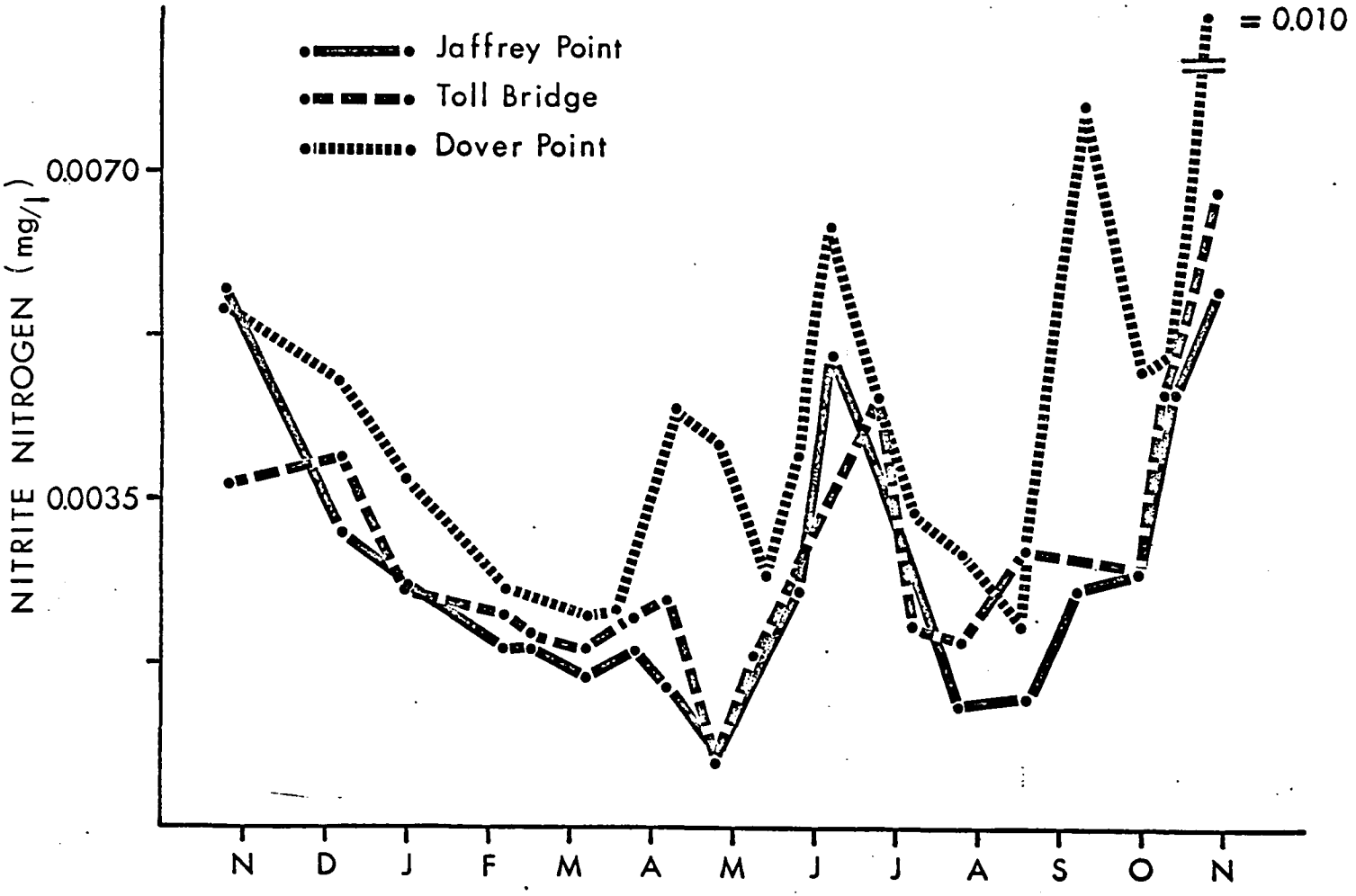

Jaffrey Point
Toll Bridge
Dover Point
= 0.010
NITRITE NITROGEN (mg/l)
0.0070
0.0035
N
D
J
F
M
A
M
J
J
A
S
O
N

Figure 7. Variation in orthophosphate between November 1969 and November 1970 at Jaffrey Point, Toll Bridge and Dover Point.

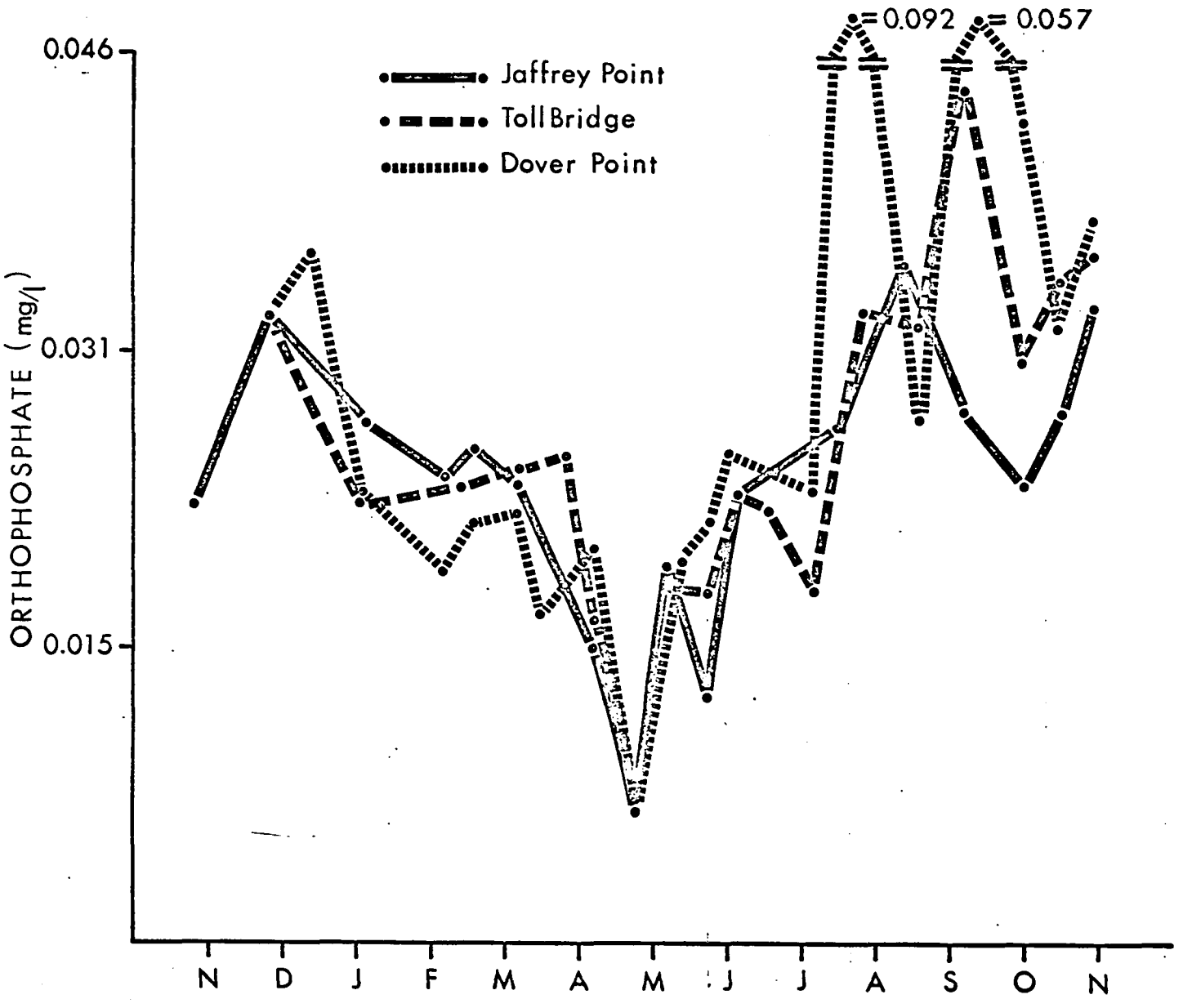

0.046
0.031
0.015
ORTHOPHOSPHATE (mg/l)
Jaffrey Point
Toll Bridge
Dover Point
= 0.092
= 0.057
N
D
J
F
M
A
M
J
J
A
S
O
N

Figure 8. Variations in biomass of Gigartina stellata between January 1969 and January 1970 at Jaffrey Point, Toll Bridge and Dover Point.

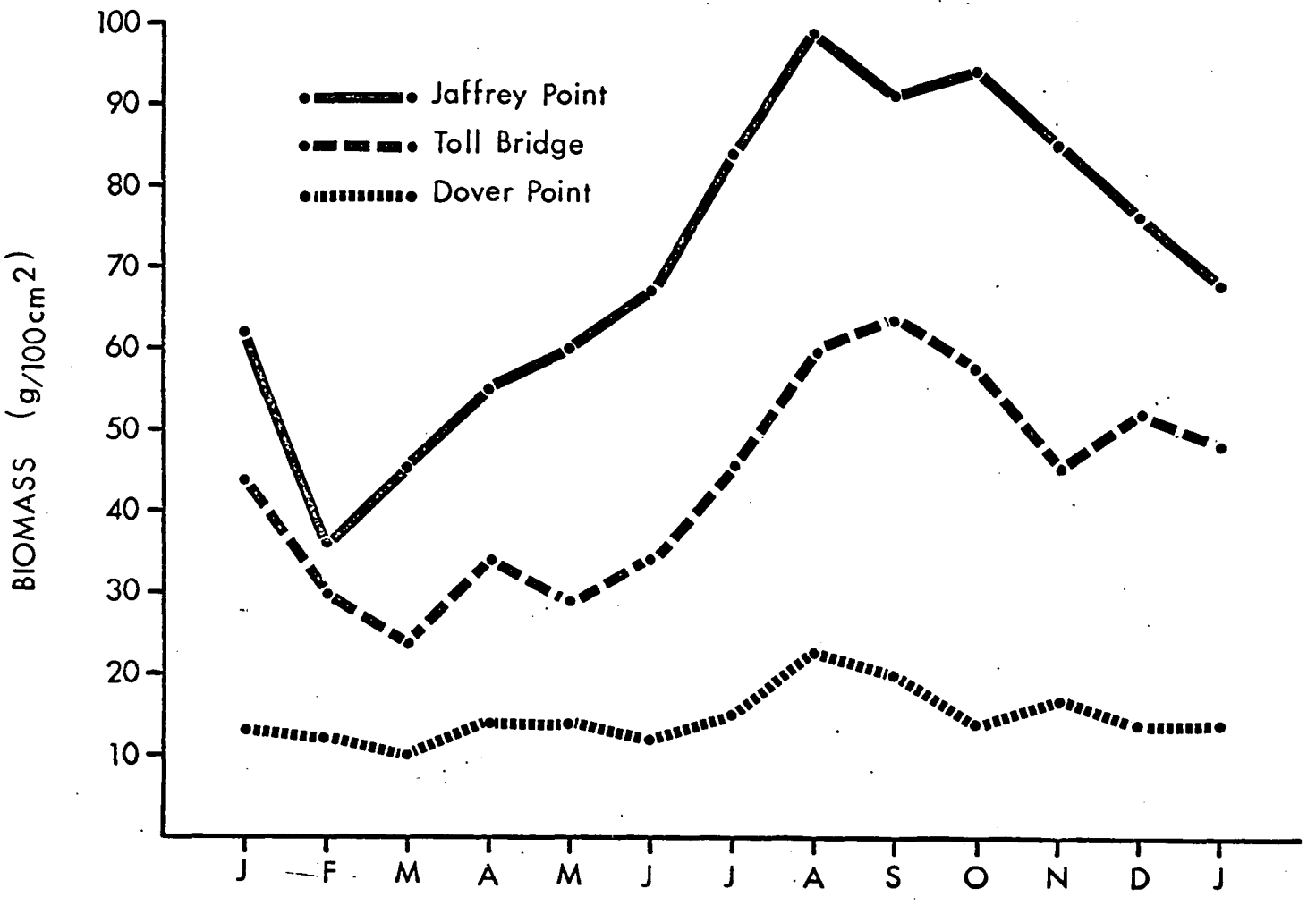

BIOMASS (g/100cm2)
100
90
80
70
60
50
40
30
20
10
Jaffrey Point
Toll Bridge
Dover Point
J
F
M
A
M
J
J
A
S
O
N
D
J

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.

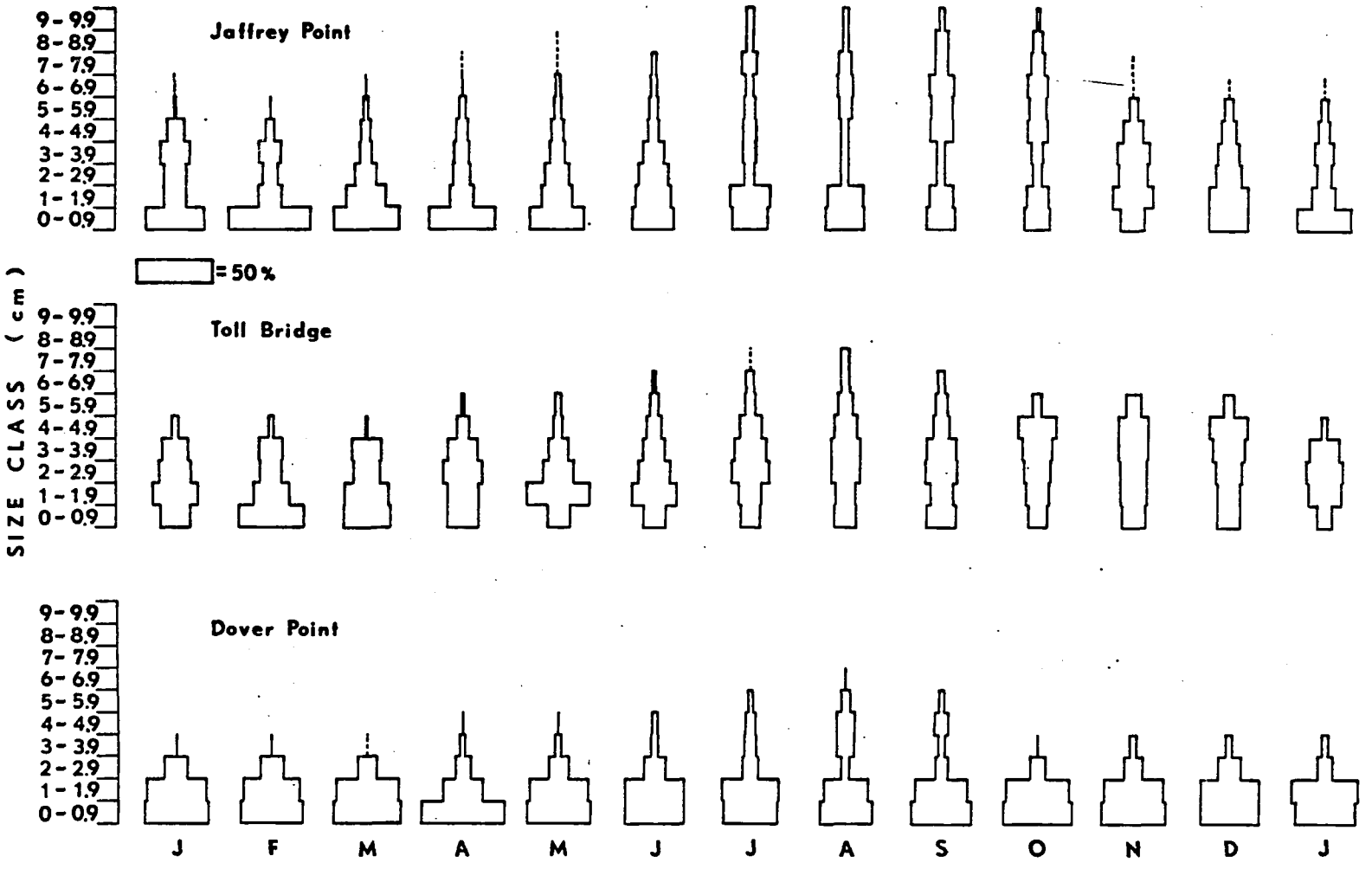

Jaffrey Point
Toll Bridge
Dover Point
SIZE CLASS (cm)
9-9.9
8-8.9
7-7.9
6-6.9
5-5.9
4-4.9
3-3.9
2-2.9
1-1.9
0-0.9
=50%
J
F
M
A
M
J
J
A
S
O
N
D
J

Figure 10. Variation in biomass of *Gigartina stellata* relative to elevation.

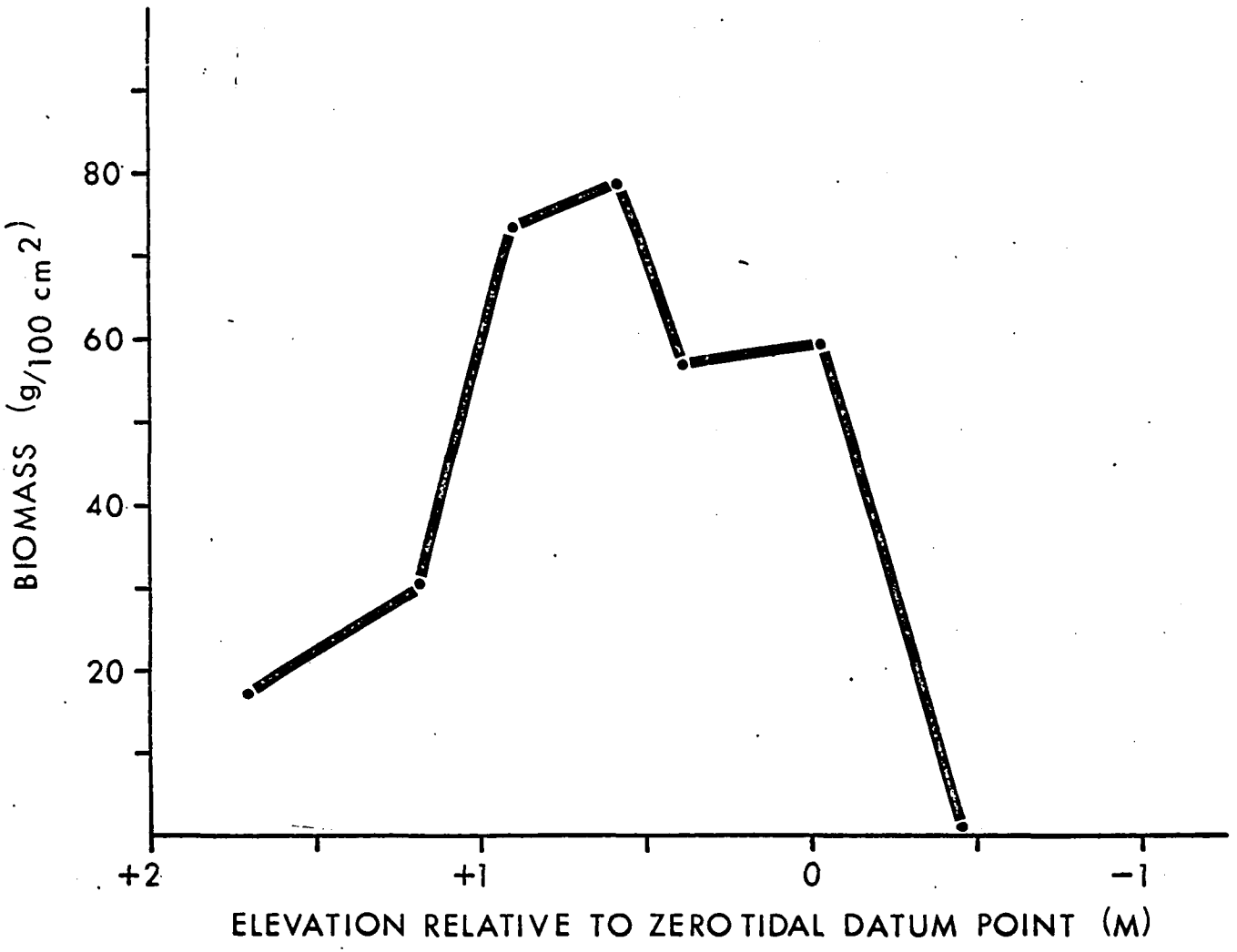

BIOMASS (g/100 cm2)
80
60
40
20
+2
+1
0
−1
ELEVATION RELATIVE TO ZERO TIDAL DATUM POINT (M)

Figure 11. Percent frequency of different size classes of Gigartina stellata relative to elevation.

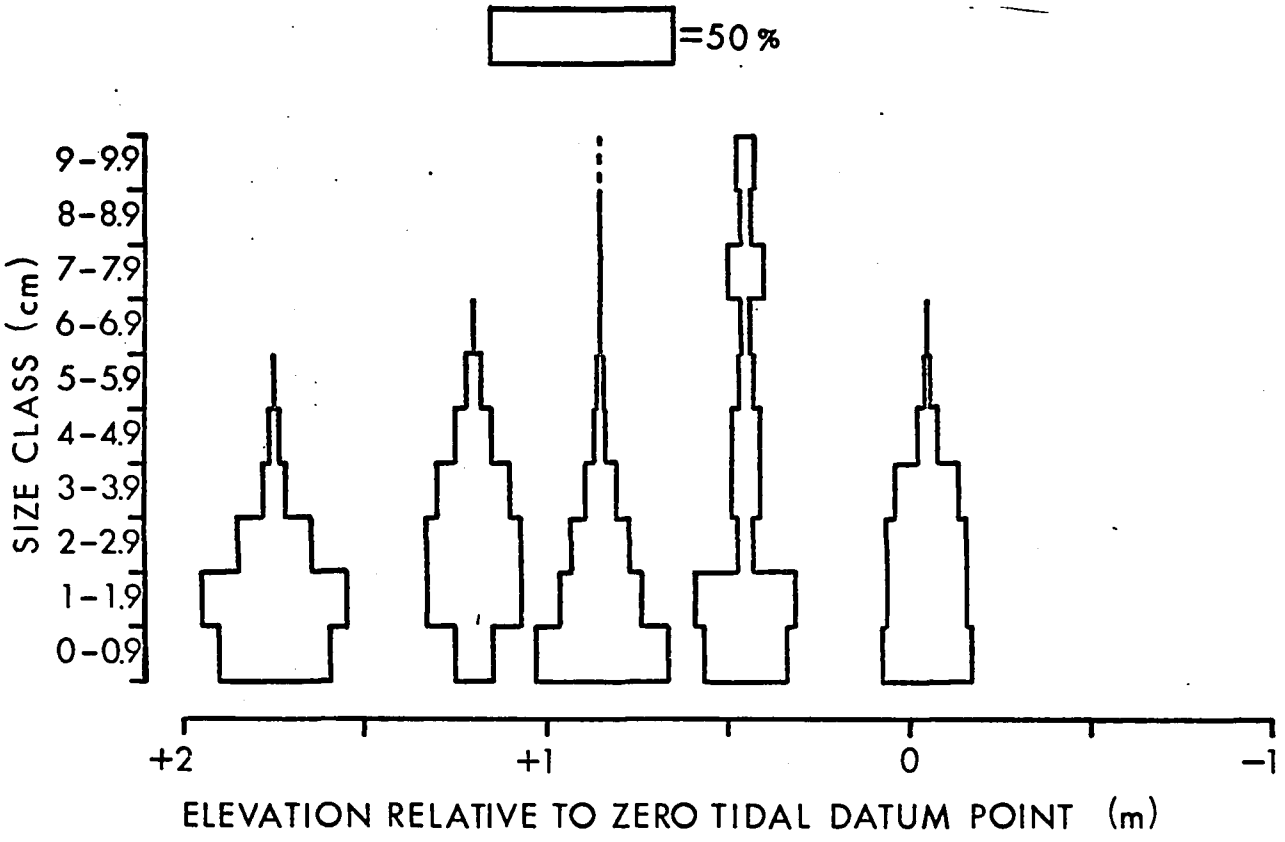

=50 %
SIZE CLASS (cm)
9-9.9
8-8.9
7-7.9
6-6.9
5-5.9
4-4.9
3-3.9
2-2.9
1-1.9
0-0.9
+2
+1
0
−1
ELEVATION RELATIVE TO ZERO TIDAL DATUM POINT (m)

Figure 12. Changes in biomass of Gigartina stellata following various degrees of harvesting in December 1968.

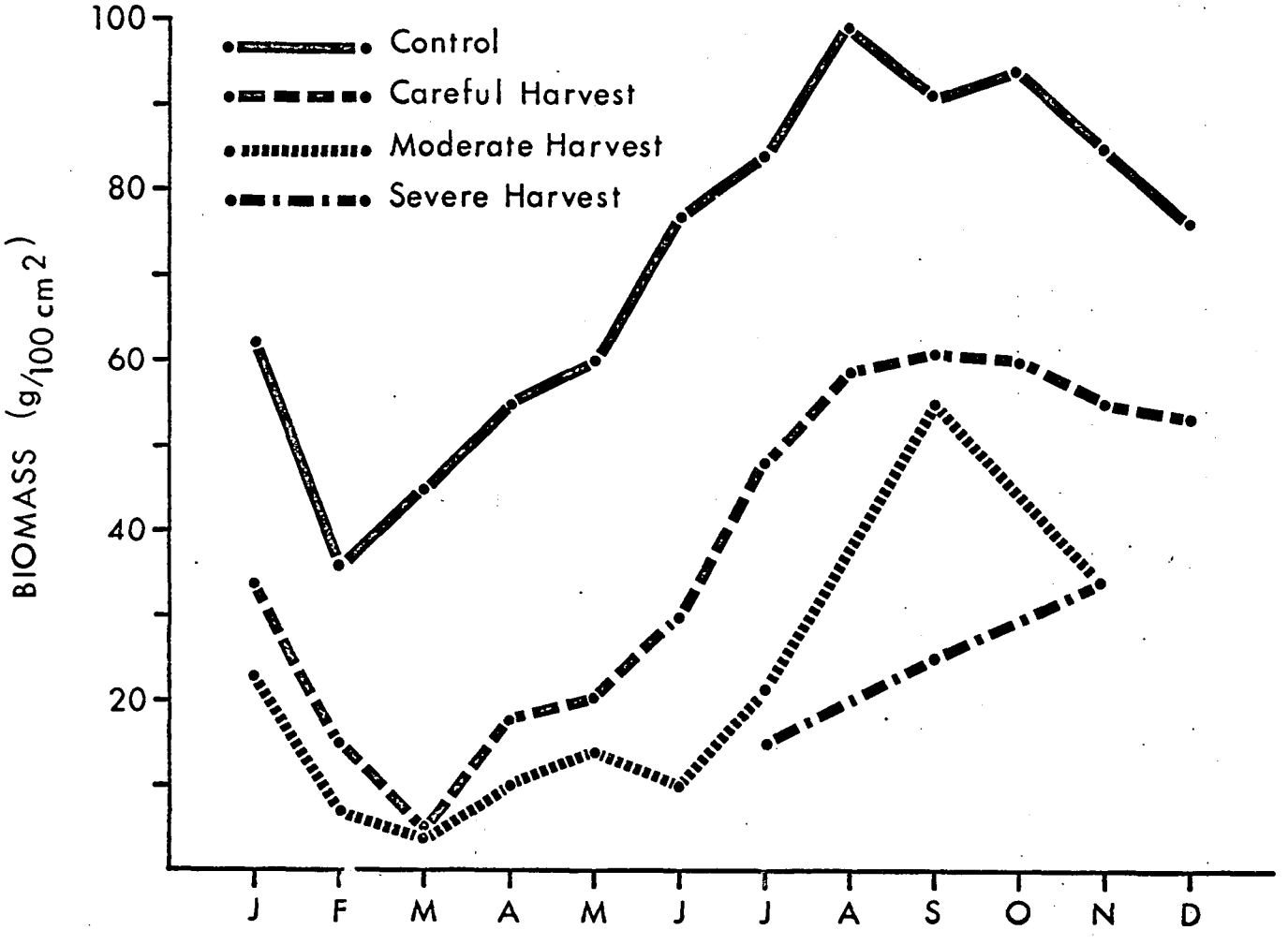

Control
Careful Harvest
Moderate Harvest
Severe Harvest
BIOMASS (g/100 cm 2)
100
80
60
40
20
J
F
M
A
M
J
J
A
S
O
N
D

Figure 13. Percent occurrence of different size fronds following various degrees of harvesting in December, 1968.

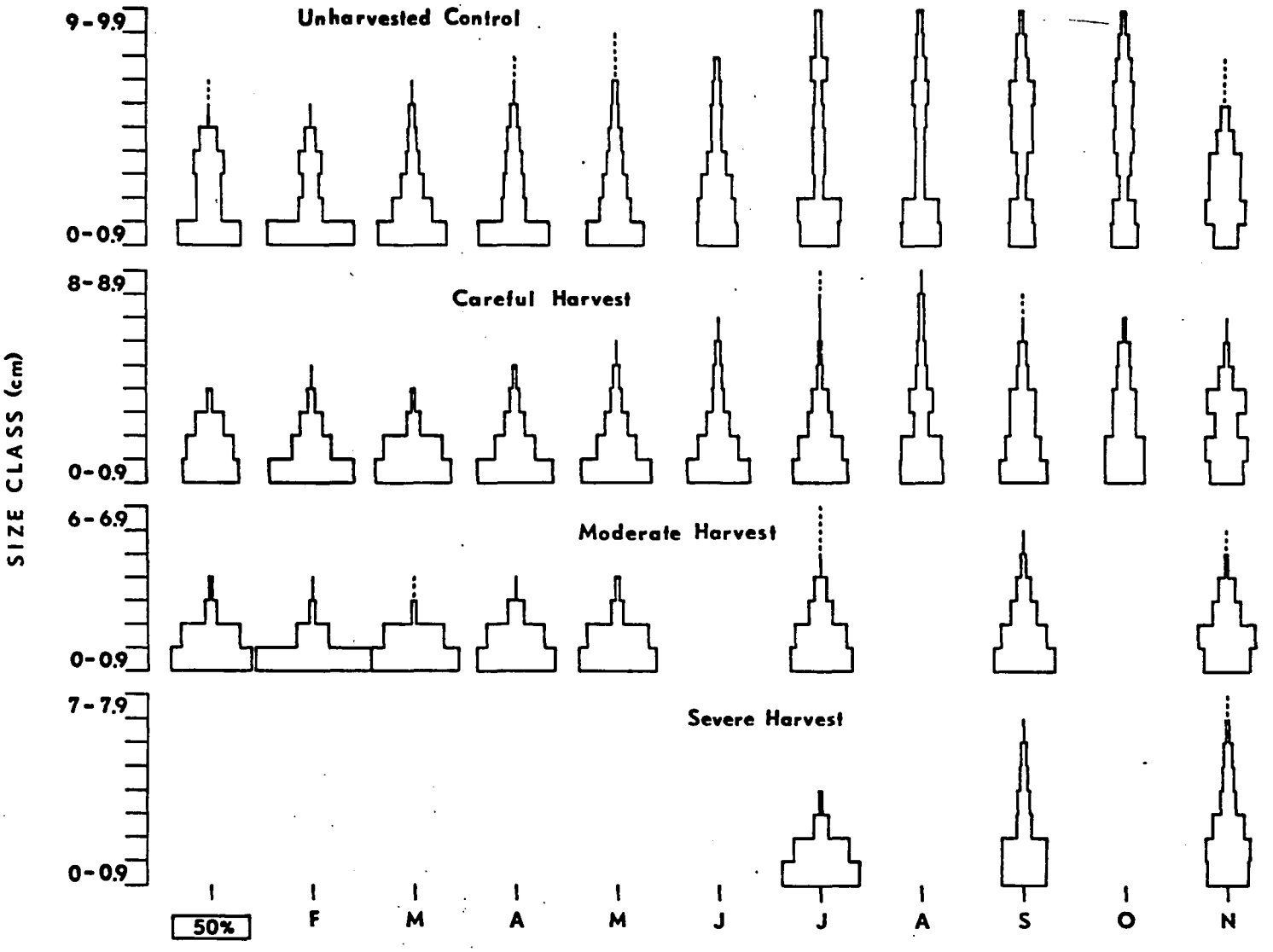

Unharvested Control
Careful Harvest
Moderate Harvest
Severe Harvest
SIZE CLASS (cm)
9-9.9
0-0.9
8-8.9
0-0.9
6-6.9
0-0.9
7-7.9
0-0.9
50%
F
M
A
M
J
J
A
S
O
N

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

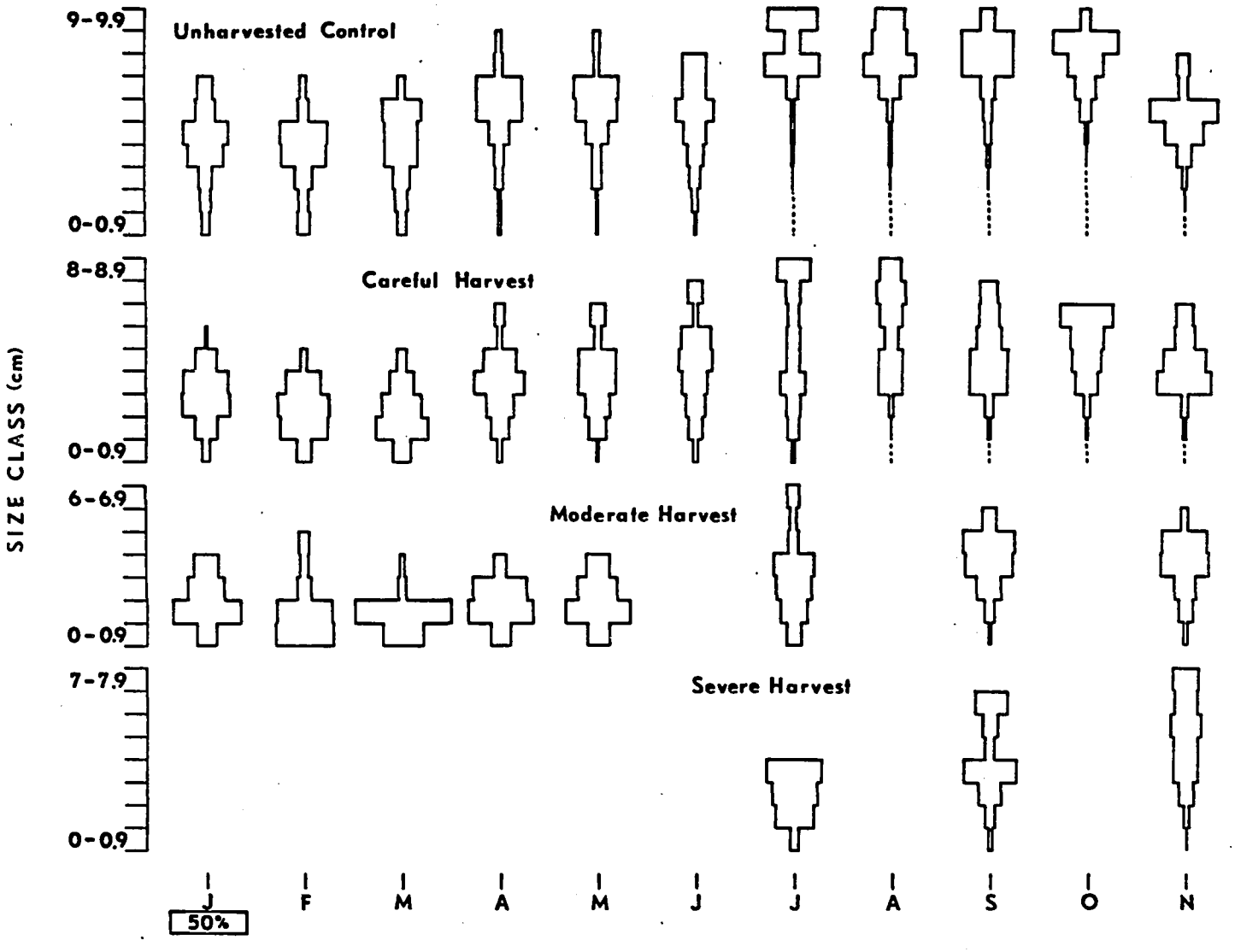

SIZE CLASS (cm)
9-9.9
0-0.9
Unharvested Control
8-8.9
0-0.9
Careful Harvest
6-6.9
0-0.9
Moderate Harvest
7-7.9
0-0.9
Severe Harvest
J
F
M
A
M
J
J
A
S
O
N
50%

Figure 15. Changes in biomass of Gigartina stellata following various degrees of harvesting in August, 1969.

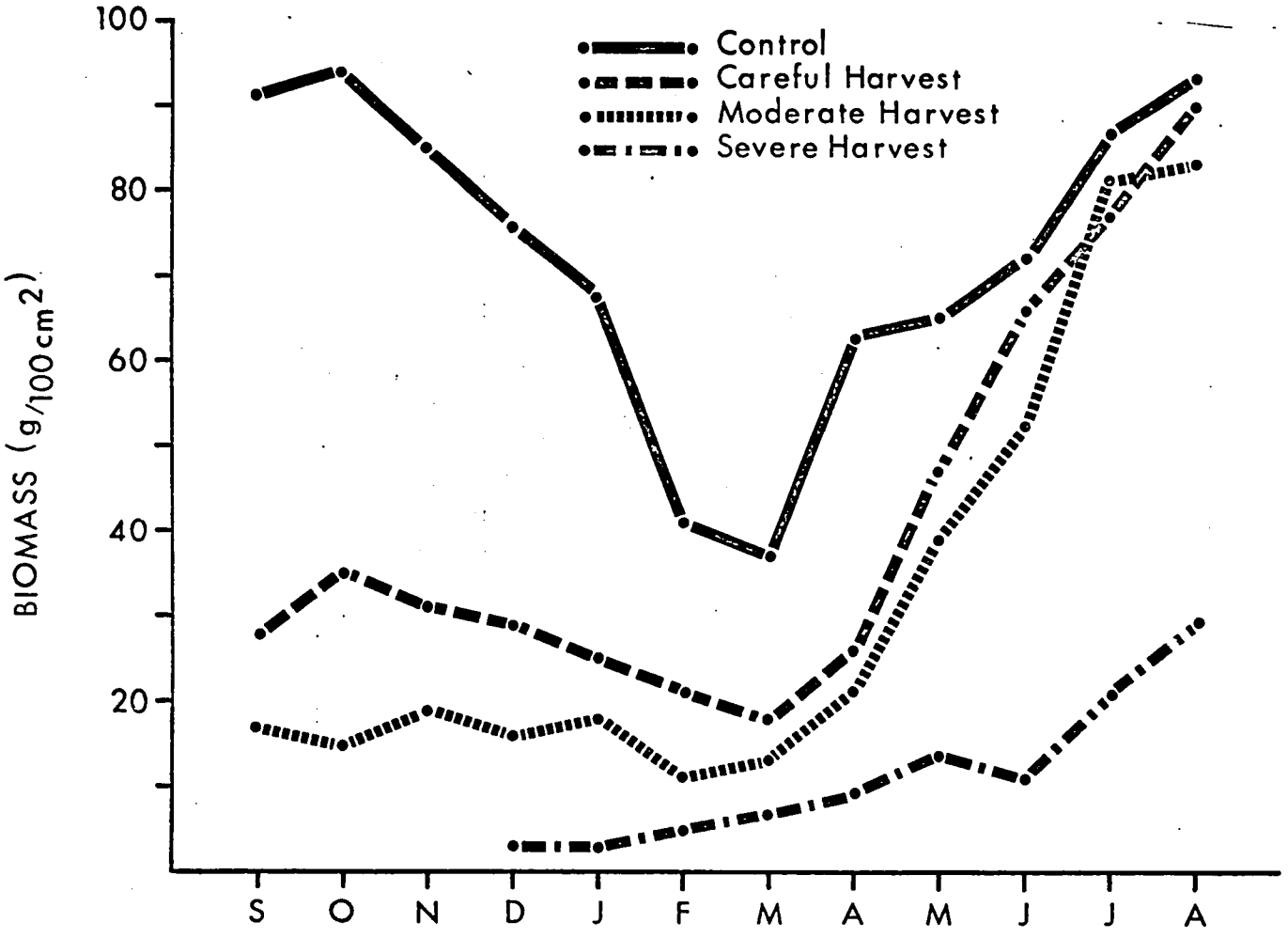

Control
Careful Harvest
Moderate Harvest
Severe Harvest
BIOMASS (g/100cm²)
100
80
60
40
20
S
O
N
D
J
F
M
A
M
J
J
A

Figure 16. Percent occurrence of different size fronds following various degrees of harvesting in August, 1969.

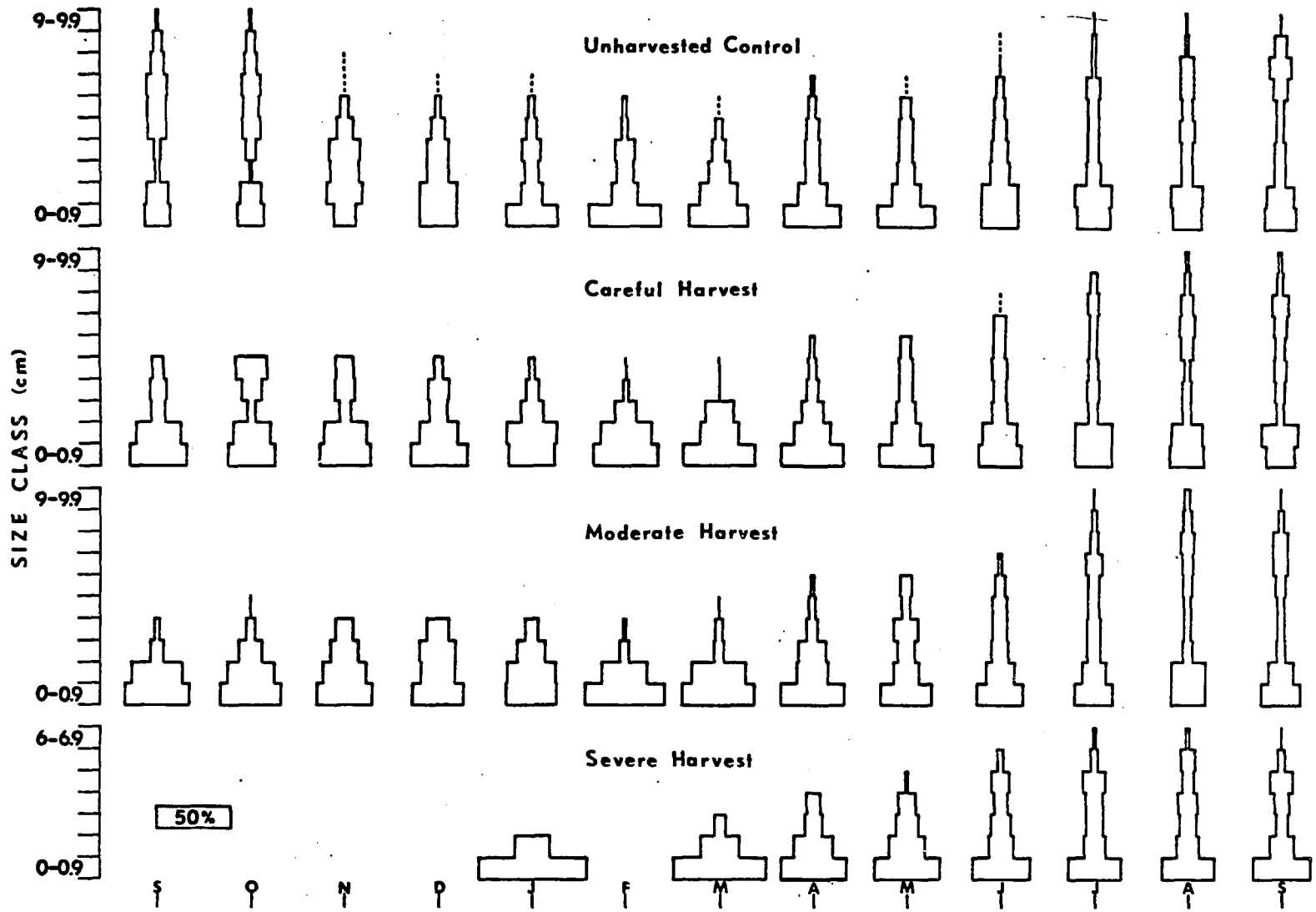

Unharvested Control
Careful Harvest
Moderate Harvest
Severe Harvest
SIZE CLASS (cm)
9-9.9
0-0.9
6-6.9
50%
S
O
N
D
J
F
M
A
M
J
J
A
S

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

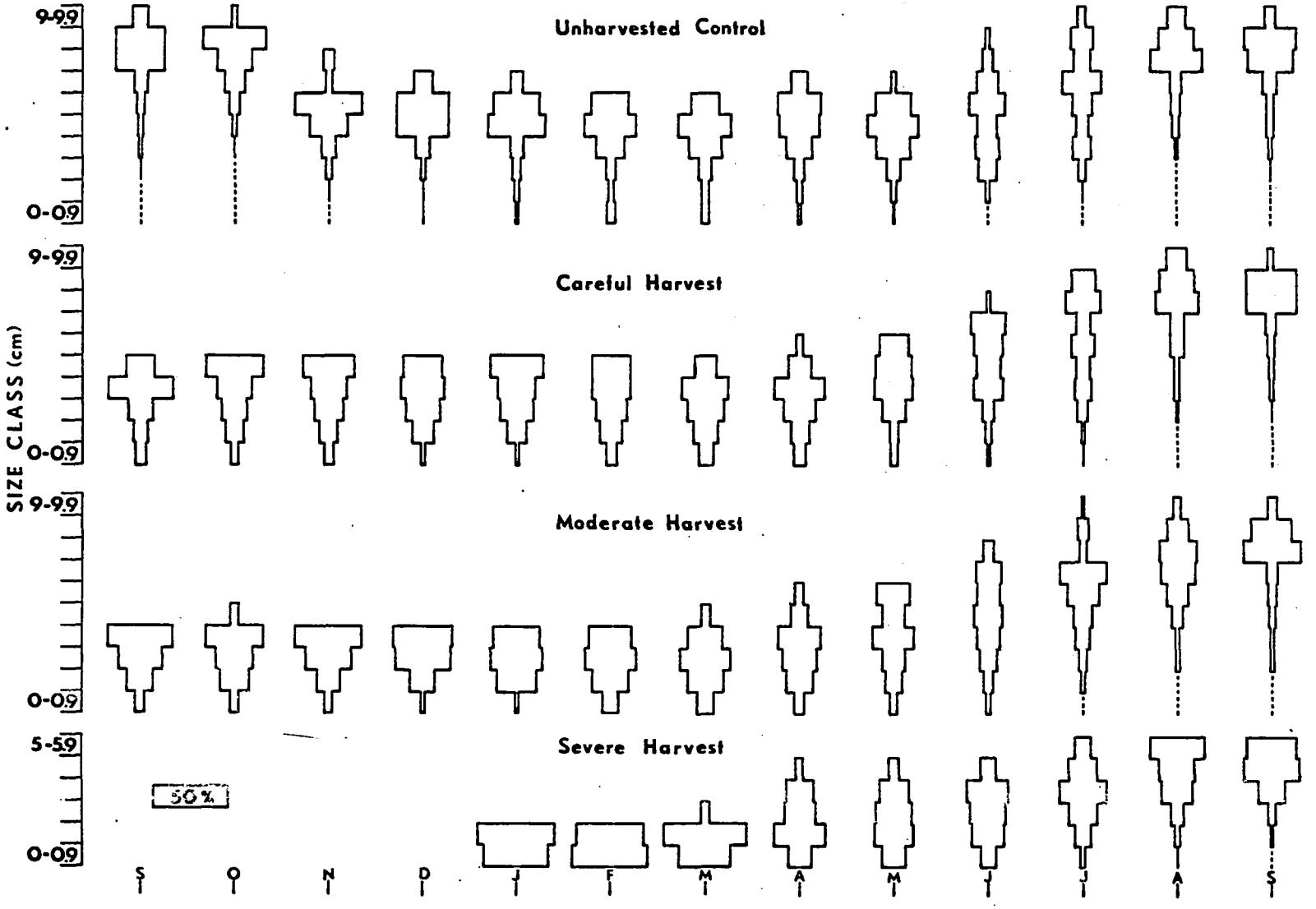

Unharvested Control
Careful Harvest
Moderate Harvest
Severe Harvest
SIZE CLASS (cm)
9-9.9
0-0.9
5-5.9
50%
S
O
N
D
J
F
M
A
M
J
J
A
S

Figure 18. The number of carposporic papillae on Gigartina stellata following various degrees of harvesting in December 1968.

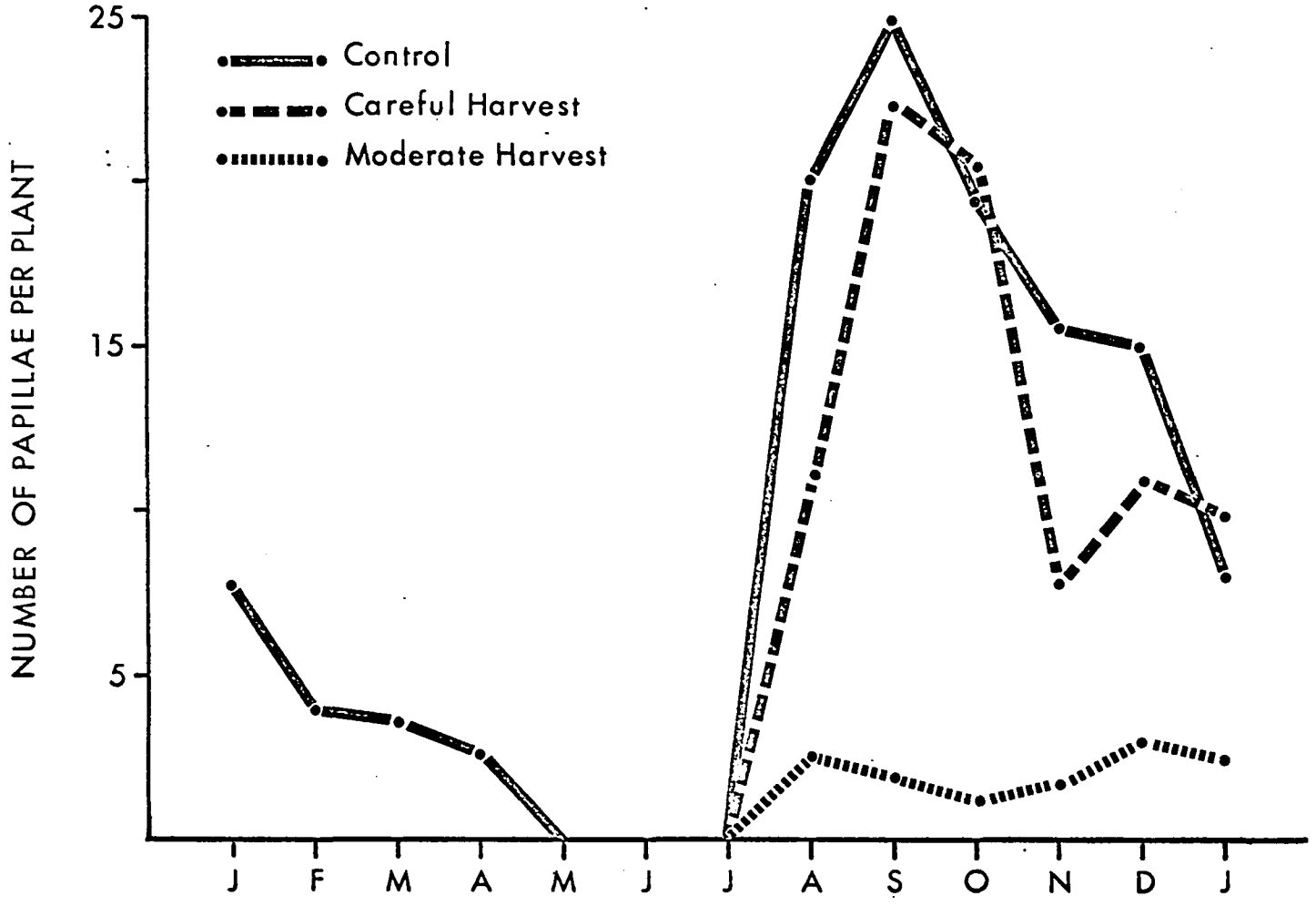

NUMBER OF PAPILLAE PER PLANT
25
15
5
Control
Careful Harvest
Moderate Harvest
J
F
M
A
M
J
J
A
S
O
N
D
J

Figure 19. The number of carposporic papillae on Gigartina stellata following various degrees of harvesting in August, 1969.

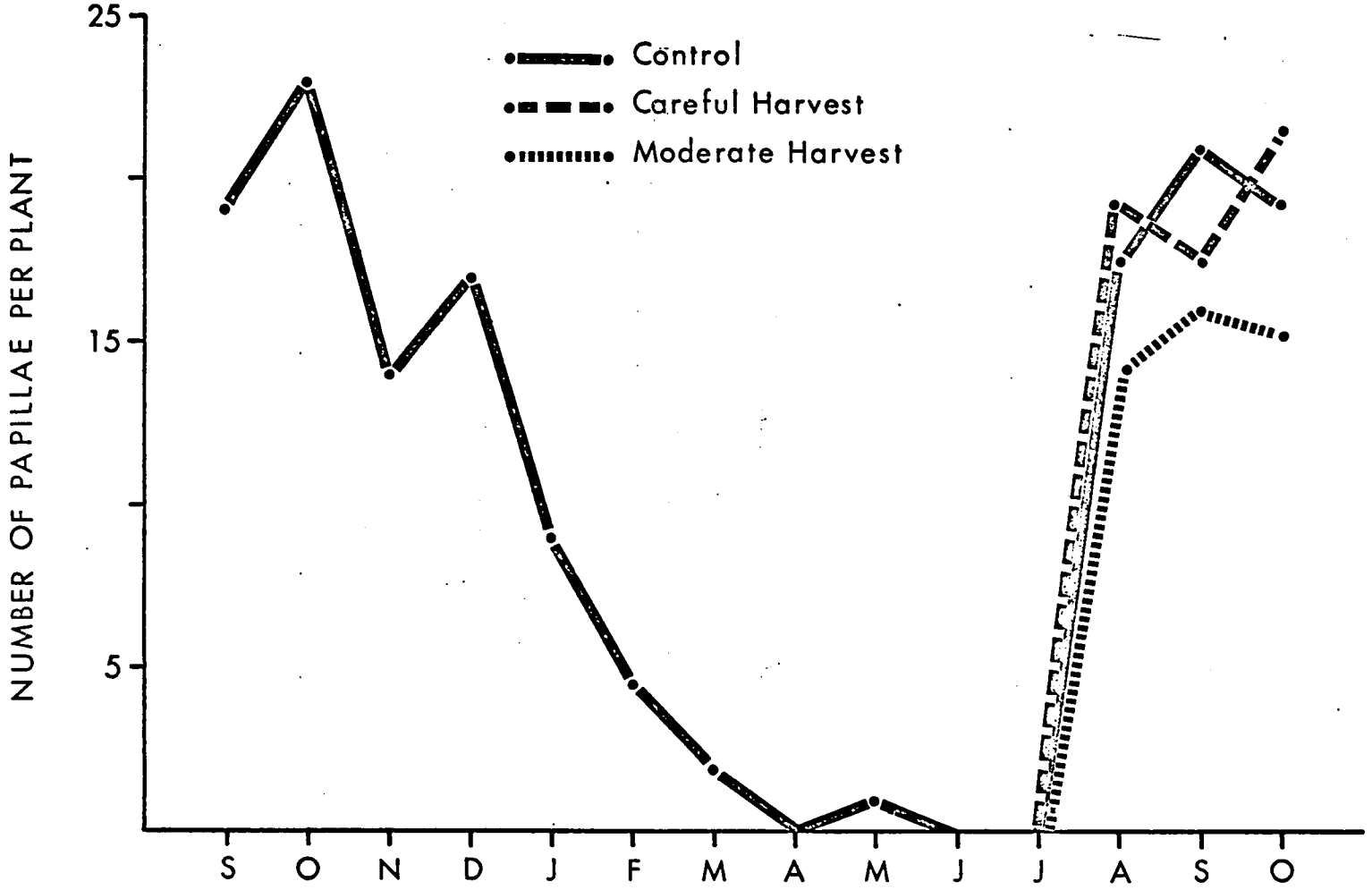
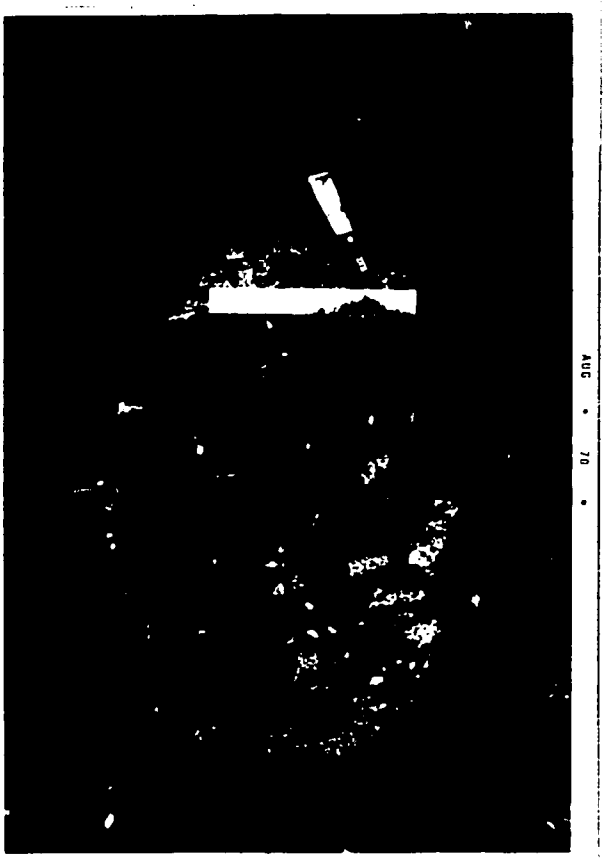

NUMBER OF PAPILLAE PER PLANT
25
15
5
Control
Careful Harvest
Moderate Harvest
S
O
N
D
J
F
M
A
M
J
J
A
S
O

Figure 20. Denuded quadrat, 21 months after sterilization. (August, 1970).

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


AUG • 70 •

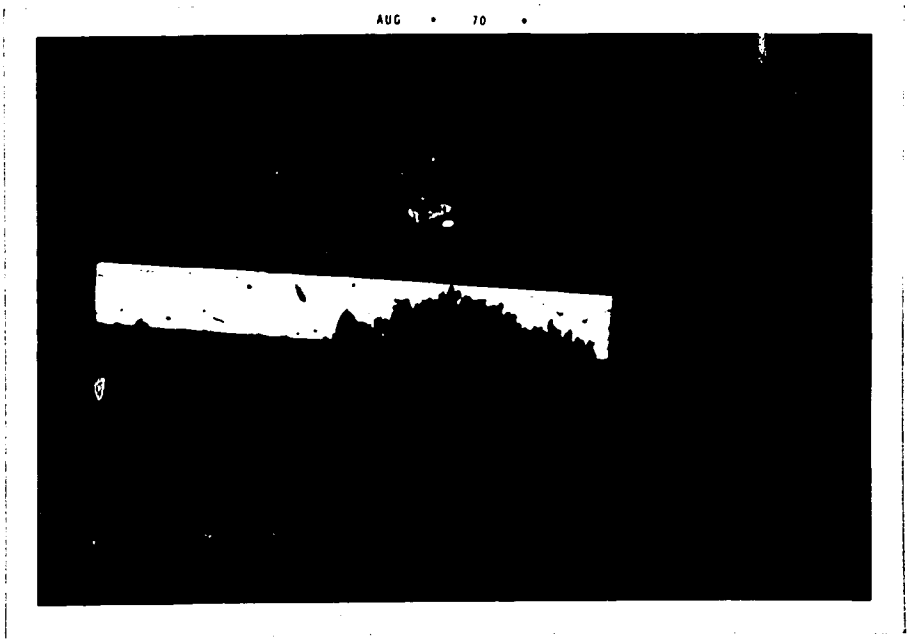

AUG • 70 •

Figure 22. Denuded quadrat, 29 months after sterilization (April, 1971).

Figure 23. The growth of Gigartina stellata at various light intensities at 15 C and a salinity of 30 °/oo.

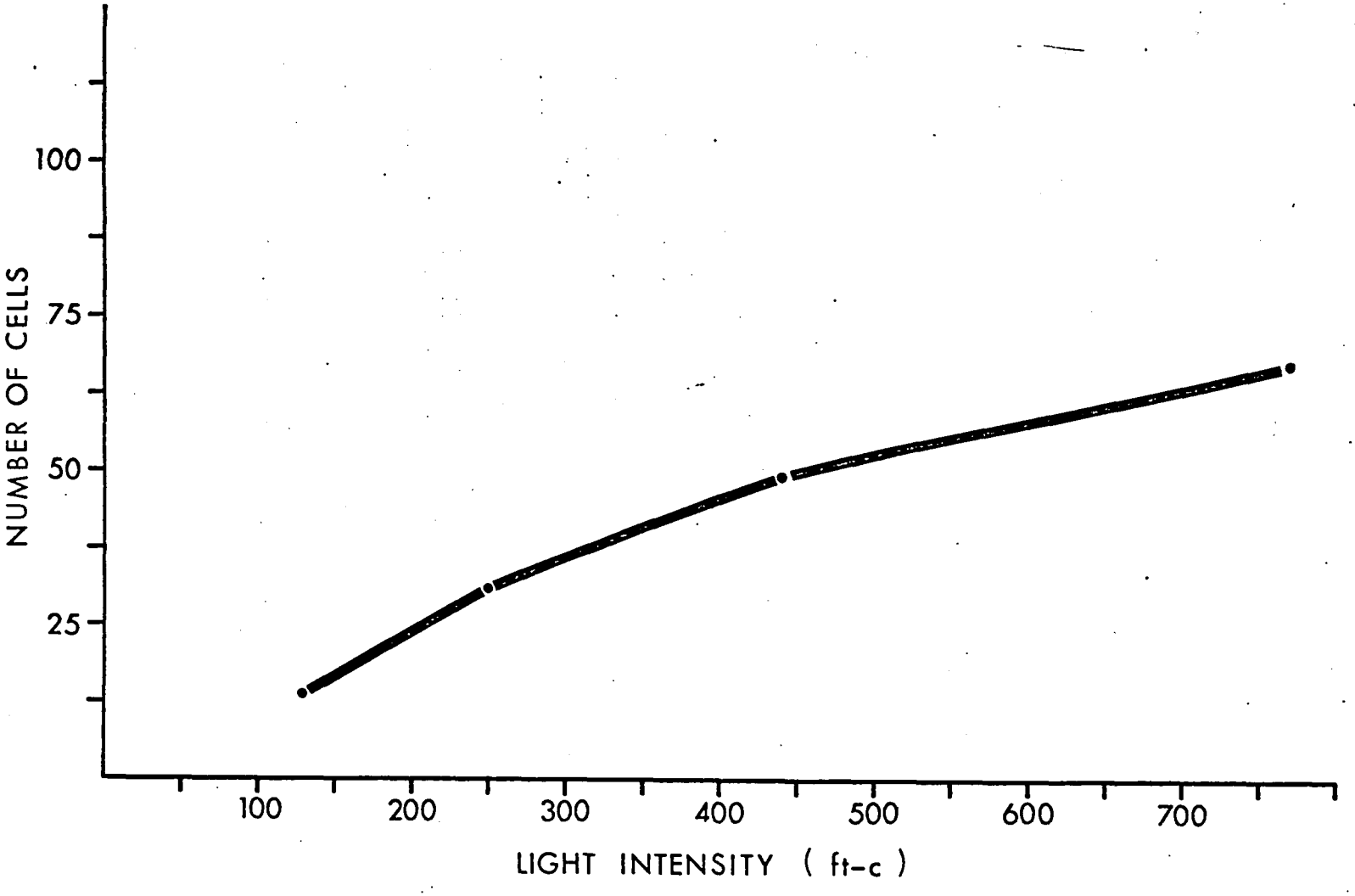

NUMBER OF CELLS
100
75
50
25
100
200
300
400
500
600
700
LIGHT INTENSITY (ft-c)

Figure 24. The growth of Gigartina stellata at various temperatures and at 400 to 440 foot-candles and 30 o/oo salinity.

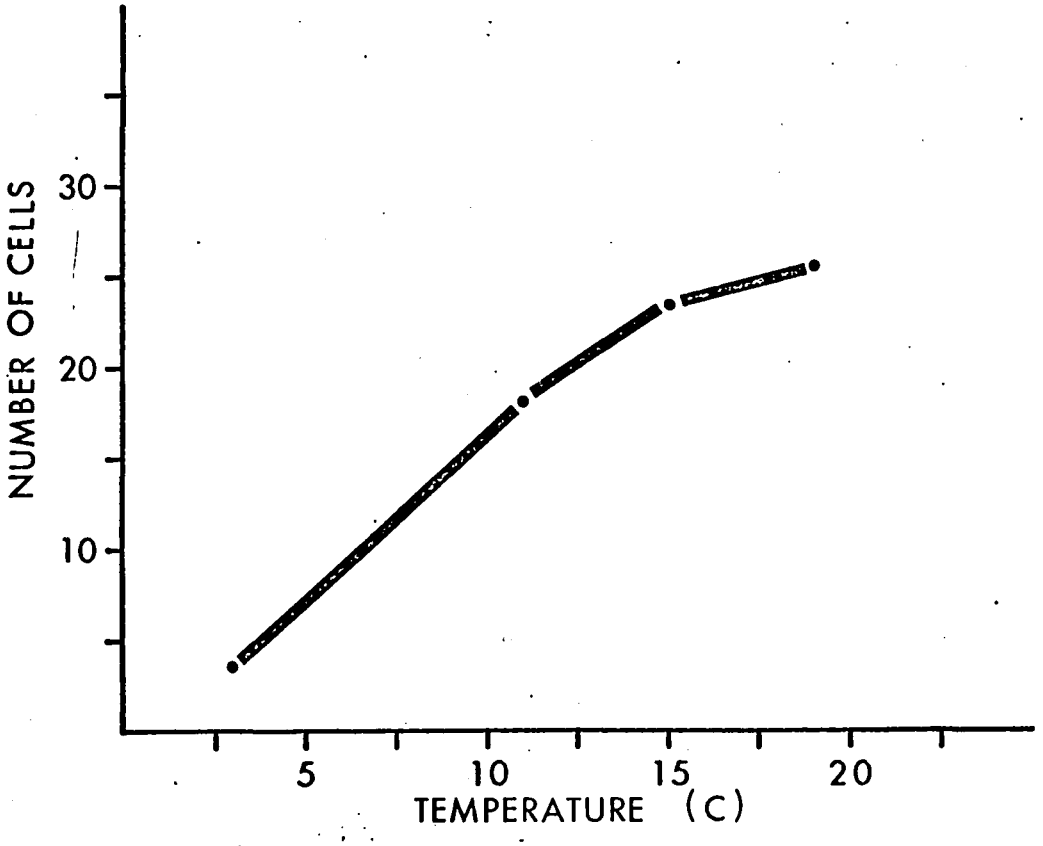

NUMBER OF CELLS
30
20
10
5
10
15
20
TEMPERATURE (C)

Figure 25. The germination of spores of Gigartina stellata at various salinities and temperatures.

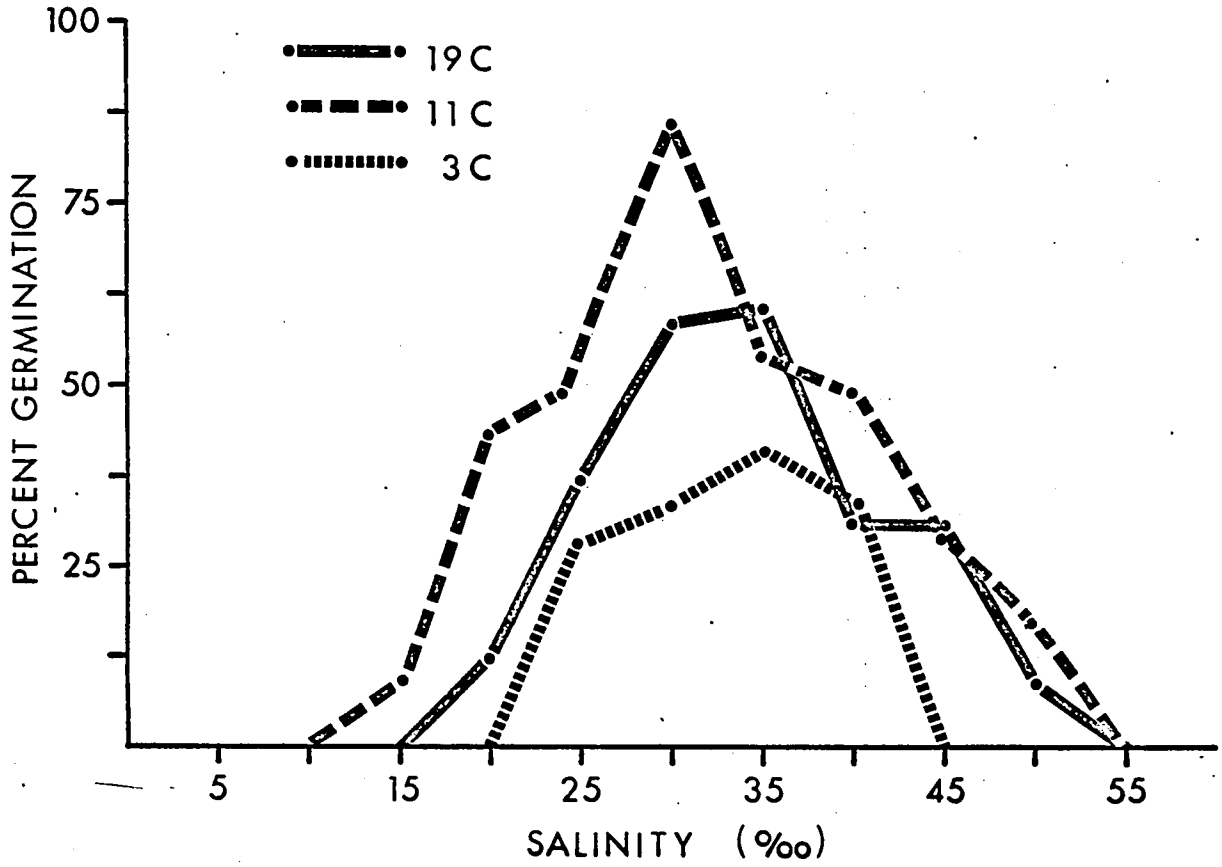

100
75
50
25
PERCENT GERMINATION
19 C
11 C
3 C
5
15
25
35
45
55
SALINITY (‰)

Figure 26. The growth of Gigartina stellata at various temperatures and salinities (after 7 days in culture at 400 to 440 ft-c).

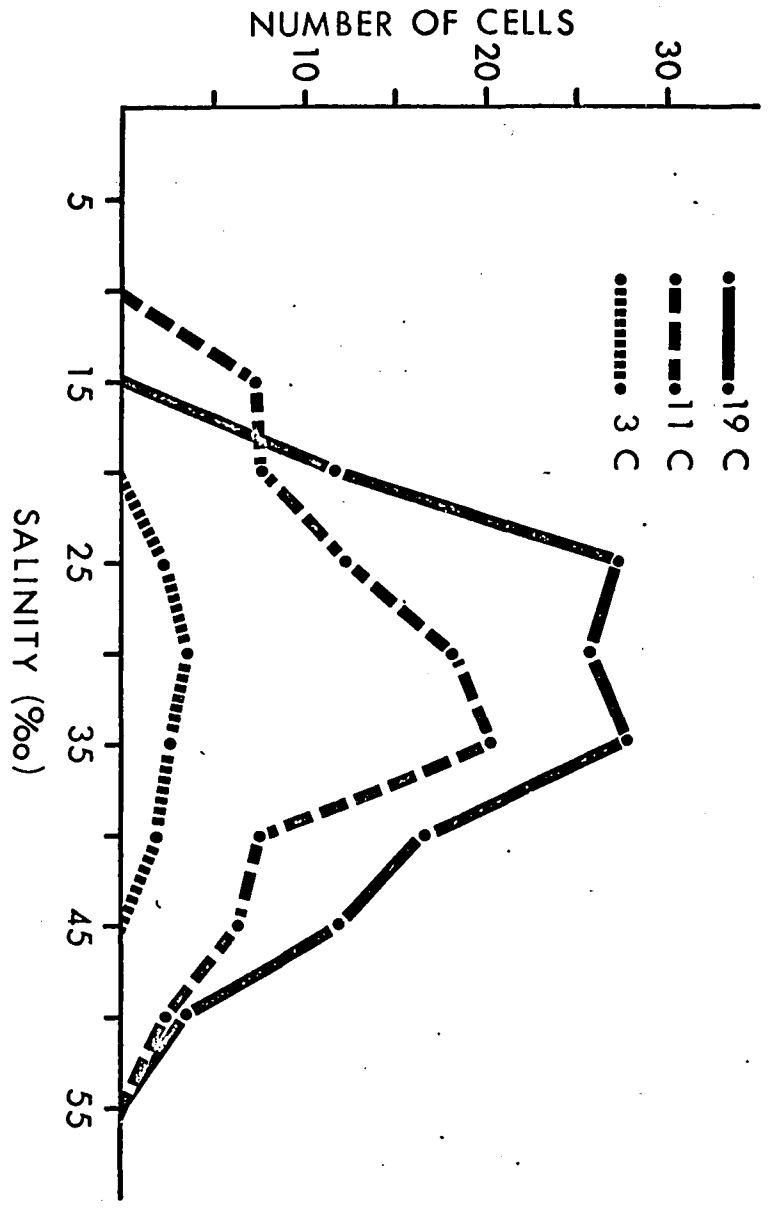

NUMBER OF CELLS
10
20
30
SALINITY (‰)
5
15
25
35
45
55
19 C
11 C
3 C

Figure 27. Apparent photosynthesis of Gigartina stellata at various light intensities.

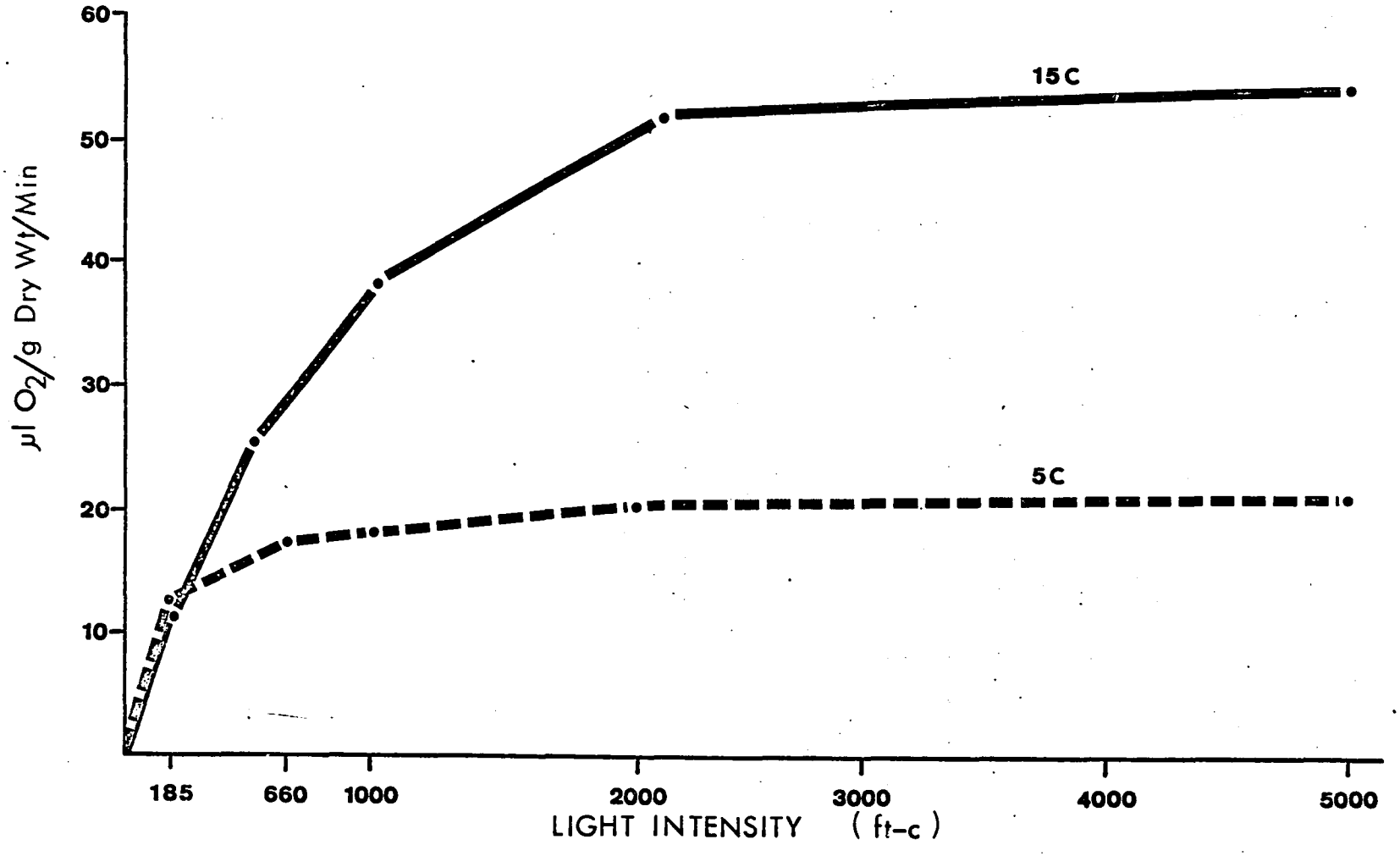

60
50
40
30
20
10
μl O2/g Dry Wt/Min
15C
5C
185
660
1000
2000
3000
4000
5000
LIGHT INTENSITY (ft-c)

Figure 28. Apparent photosynthesis of Gigartina stellata at various temperatures.

Figure 29. Respiration of Gigartina stellata at various temperatures.

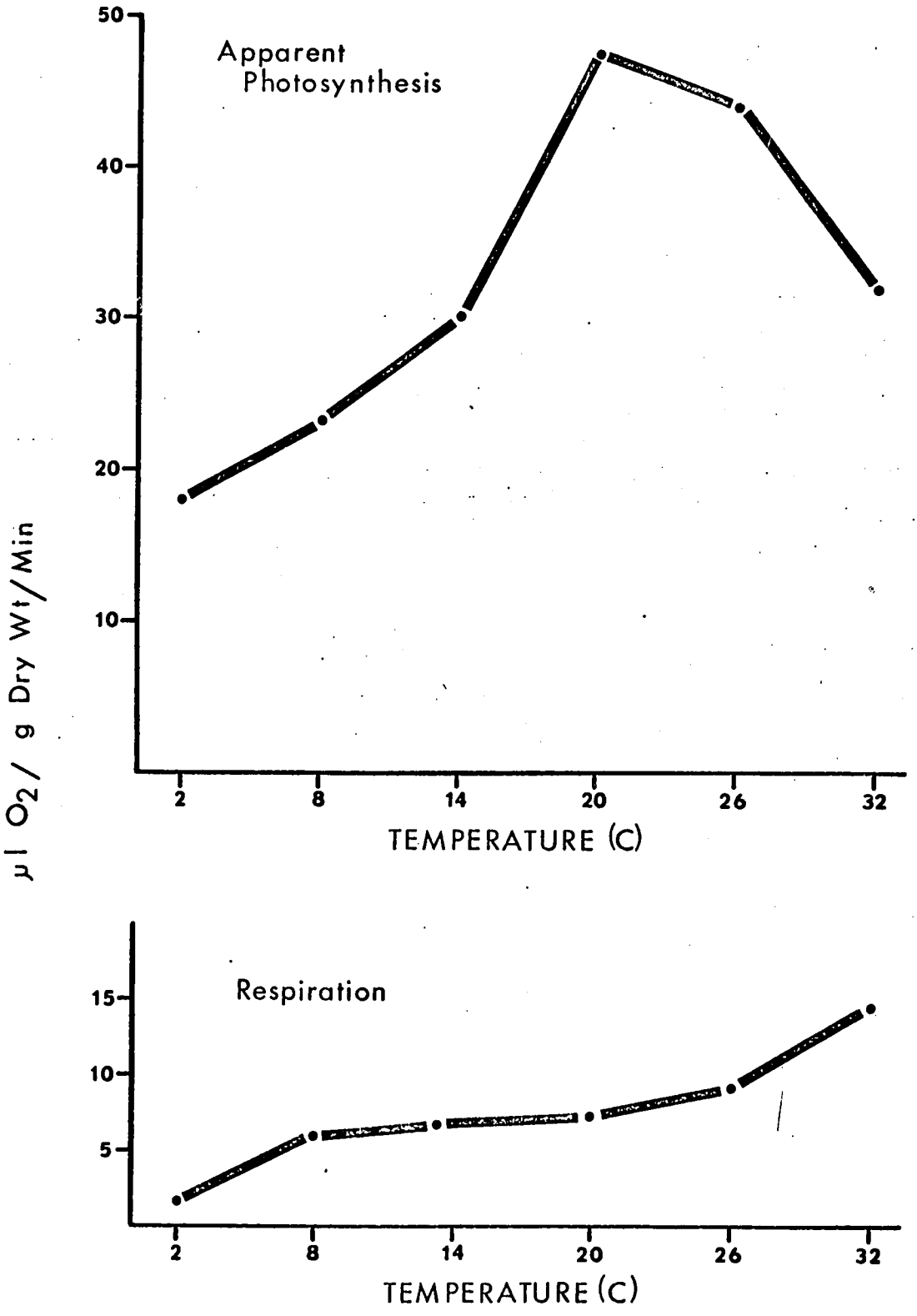

Apparent
Photosynthesis
50
40
30
20
10
2
8
14
20
26
32
TEMPERATURE (C)
µl O2/ g Dry Wt/Min
Respiration
15
10
5
2
8
14
20
26
32
TEMPERATURE (C)

Figure 30. Apparent photosynthesis of Gigartina stellata in various salinities.

Figure 31. Respiration of Gigartina stellata in various salinities.

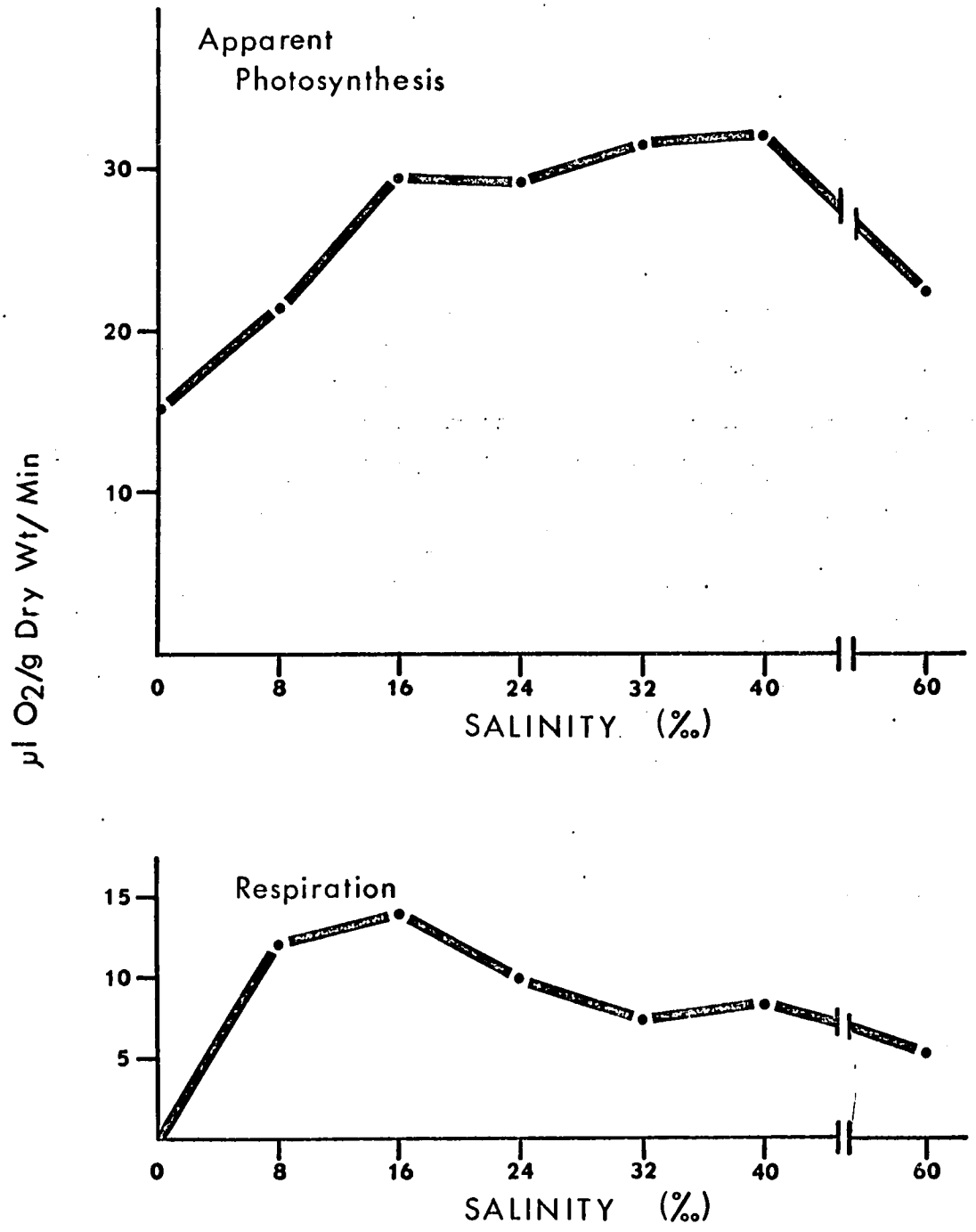
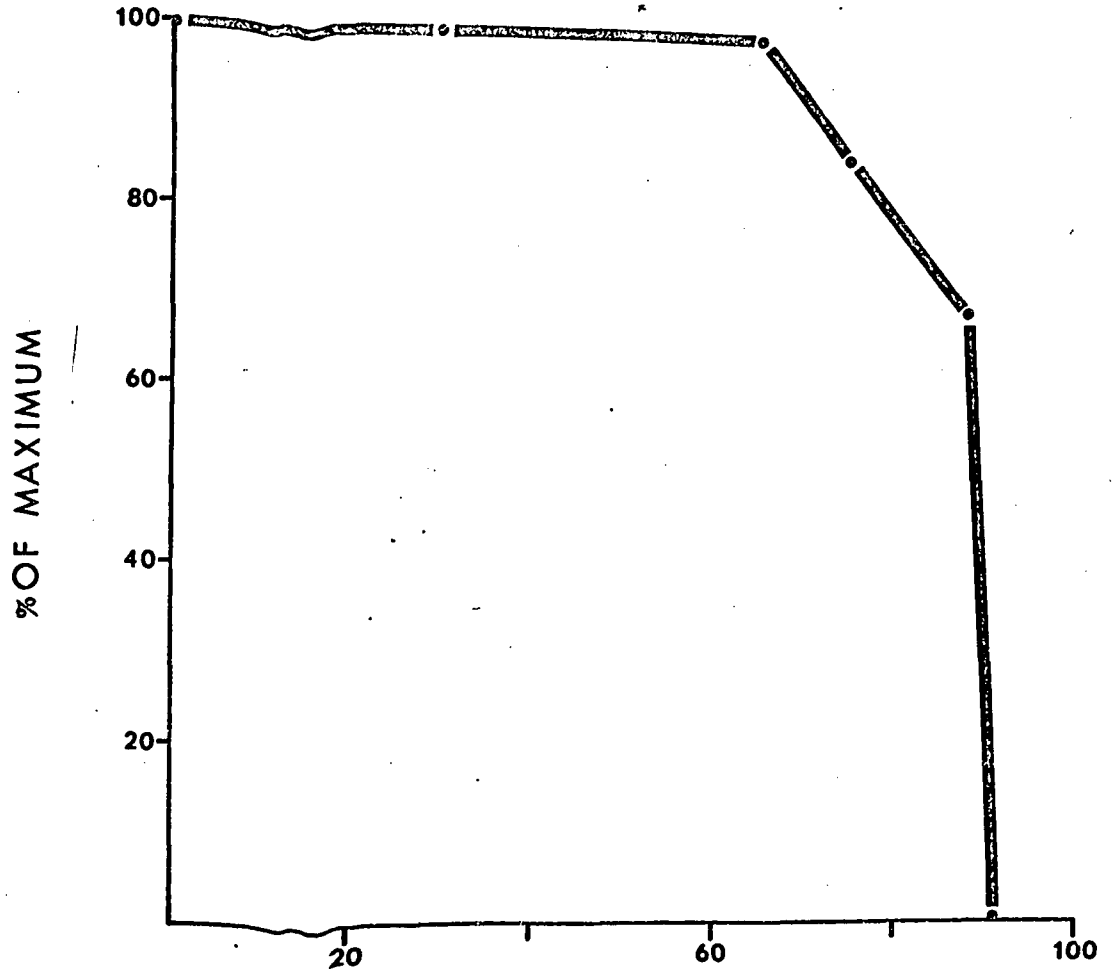
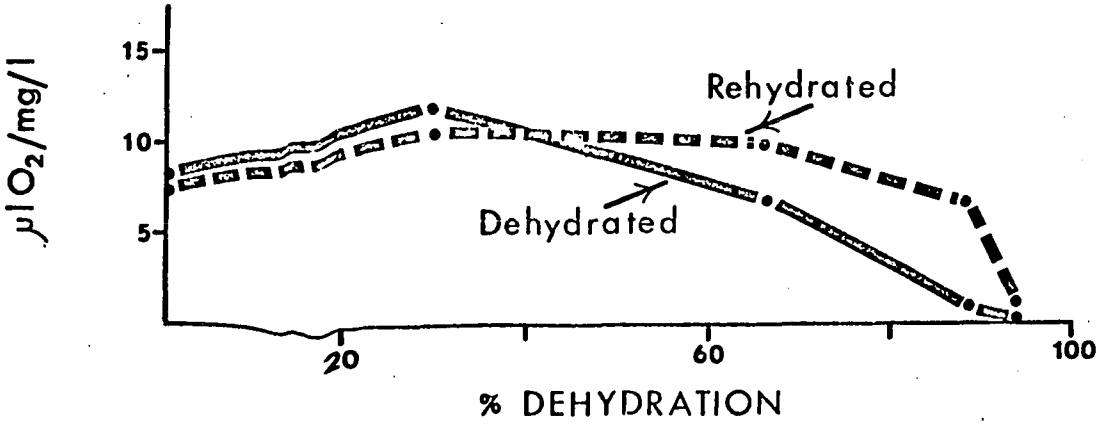

Apparent
Photosynthesis
30
20
10
µl O2/g Dry Wt/ Min
0
8
16
24
32
40
60
SALINITY (‰)
Respiration
15
10
5
0
8
16
24
32
40
60
SALINITY (‰)

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.


100
80
60
40
20
% OF MAXIMUM
20
60
100
% DEHYDRATION


15
10
5
µlO2/mg/l
Rehydrated
Dehydrated
20
60
100
% DEHYDRATION