AN ABSTRACT OF THE THESIS OF

Chris Kelvin Kjeldsen for the Doctor of Philosophy in Botany (Phycology)
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Title EFFECTS OF VARIATONS IN SALINITY AND TEMPERATURE ON SOME ESTUARINE MACRO-ALGAE

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(Major professor)

Yaquina Bay, an estuary on the central Oregon Coast was studied to determine the factors limiting the seasonal occurrence and spatial distribution of the macro-algae. The physical and chemical properties of the waters, in Yaquina Bay and estuary, are strongly influenced by the prevailing climatological conditions. Temperature and salinity were studied as ecological parameters in the field and in the laboratory. Field studies involved determination of algal species, their habitats, location within the intertidal zone, spatial distribution, seasonal occurrence, and tolerance to variations in salinity and temperature as determined from the physical-chemical regime of the estuary. The majority of the species had optimum growth in, or were limited to, salinities of 35 to 30‰ and temperatures of 10 to 13 C.

Four zones were defined in the estuary: zone one, extending one and one-half kilometers into the estuary, where the flora consisted primarily of open coast forms; zone two, a transitional area

extending nine kilometers into the estuary occupied by brackish water species and a few of the more tolerant forms also found in zone one; zone three, a brackish water area extending 21 kilometers into the estuary to the town of Toledo with typical brackish water inhabitants; and zone four, above the town of Toledo inhabited by fresh water forms.

Eight species, Ulva expansa, Enteromorpha linza, Laminaria saccharina, Sargassum muticum, Alaria marginata, Odonthalia floccosa, Iridaea splendens and Gigartina californica, were used in laboratory studies to determine the effect of variations in temperature and salinity on rates of respiration and photosynthesis, thus determining the control these ecological factors may exert in nature. Two methods were employed to detect changes in concentration of oxygen in the medium during respiration and photosynthesis. These were manometric methods using a Gilson differential respirometer, and Winkler titration of water samples from a 50-liter photosynthesis-respiration chamber. The experiments determined hourly rates of respiration and photosynthesis in decreased salinities at 10, 15, and 20 C. A series of experiments were also undertaken to determine the the effect of adaptive exposure upon the metabolic rates of macroalgae in media of various salinities.

In laboratory experiments it was found: a) rates of respiration increased with increasing temperatures, however, in experiments in

the Gilson respirometer, using tissues from Laminaria, Sargassum, Odonthalia, and Iridaea, there was an inhibition of respiration at 20 C resulting in rates below those at 15 C; b) rates of respiration increased in reduced salinities down to 11‰; c) rates of photosynthesis were markedly reduced in salinities of less than 11‰; d) in several experiments the rates of photosynthesis were enhanced in salinities of 22‰; e) rates of photosynthesis, with three exceptions, were higher with increasing temperatures; f) photosynthesis was more sensitive to extreme dilutions than respiration, but respiration was more sensitive to temperature changes than photosynthesis, and g) adaptation to salinities above 11‰ does not alter the mode of protoplasmic response to variations of salinity, but does reduce the magnitude of the response.

Ulva expansa, Laminaria saccharina, Sargassum muticum, Alaria marginata, and Gigartina californica showed tolerances to variations in salinity and temperature in laboratory experiments correlating with their distribution in the estuary, and with its physical-chemical regime. In laboratory experiments, Enteromorpha linza, Odonthalia floccosa, and Iridaea splendens showed tolerance to variations of salinity and temperature exceeding the variations they encountered in nature and therefore, their distribution must be limited by some other factors.

EFFECTS OF VARIATIONS IN SALINITY AND TEMPERATURE ON SOME ESTUARINE MACRO-ALGAE

by

CHRIS KELVIN KJELDSEN

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Professor of Botany
In Charge of Major

Redacted for Privacy

Chairman of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

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EFFECTS OF VARIATIONS IN SALINITY AND TEMPERATURE ON SOME ESTUARINE MACRO-ALGAE

INTRODUCTION

Estuaries afford a unique opportunity to study aquatic ecology, because of diverse ecological conditions resulting from the presence of an ecotone between marine and fresh water, which is characterized by gradients of salinity, turbidity, and temperature. The existence of these diverse conditions and the unique biota of estuaries raises questions as to the influence these factors exert on the distribution and periodicity of the biota. The macro-algae growing in this ecotone are continually exposed to relatively drastic changes in ecological conditions, during the tidal cycle and throughout the year, which directly or indirectly influence their distribution, abundance, and physiology. The causal analysis of growth and distribution of benthic macro-algae necessitates a full understanding of the relationship between the metabolism of the organism, particularly the process of photosynthesis since this is the first step in the growth of plants, and the environmental variables. The study of metabolic rates under natural or simulated conditions and of the factors influencing these rates has helped provide a fundamental understanding of the physiological ecology of macro-algae (Feldmann, 1951; Biebl, 1962; Chapman, 1964; and Round, 1965). It has been found by Biebl

(1962) and others that, on the whole, the salinity tolerance of algae parallels the ecological conditions under which they normally grow. Biebl (1962), Montfort (1935), and Ehrke (1929, 1931 as reviewed by Blinks, 1951) have shown that the same is true for temperature tolerance of algae.

A complex relationship exists between the biological effects of temperature and salinity, in that temperature can modify the effects of salinity and enlarge, narrow, or shift the range of salinity tolerance of a species and conversely salinity can modify the effects of temperature. In spite of the important physiological and ecological influences of these factors, there is a conspicuous lack of information concerning their combined effects on macro-algae.

There are two basic approaches to the study of an ecological problem, the use of field methods or the laboratory approach. Possibly for reasons of convenience these approaches usually are undertaken on an exclusive basis. Both of these methods have advantages and limitations, but Yaquina Bay is favorably located and the construction of the Oregon State Marine Science Center at Yaquina Bay made possible the integration of these two approaches. The present study combines these two methods in an investigation of the effects of variations in salinity and temperature on the distribution and seasonal occurrence of the benthic macro-algae in Yaquina Bay, Lincoln County, Oregon. Eight species from the diverse flora in

the bay and estuary were used in detailed laboratory studies to determine the effect of variations in temperature and salinity upon rates of photosynthesis and respiration. In conjunction with the laboratory experiments, field studies were also undertaken to relate seasonal and spatial distribution of the macro-algal inhabitants to variations in temperature and salinity, through physical measurements in the estuary. Previous field investigations on the Pacific Coast have been primarily descriptive of the algae of the open coast (Doty, 1947a, 1947b; Sanborn and Doty, 1944; and numerous papers by Setchell and Gardner). The estuarian macro-algae of the Pacific Coast have been omitted or treated only incidentally in descriptions of the coastal flora.

Description of Survey Area

Yaquina Bay, including the estuary, is located between 44° 34' and 44° 40' north latitude and 123° 51' and 124° 04' west longitude (Figure 1). Yaquina estuary lies west of the Coast Range on the central Oregon Coast. The estuary extends 37 kilometers inland, although the head of fresh water is only 16 kilometers due east of the shoreline in the vicinity of Elk City, where a tidal reversal is observable. The bay and estuary were formed by subsidance and submergence of an ancient river channel. The maximum width of the estuary is near the city of Newport where it broadens to 3.2

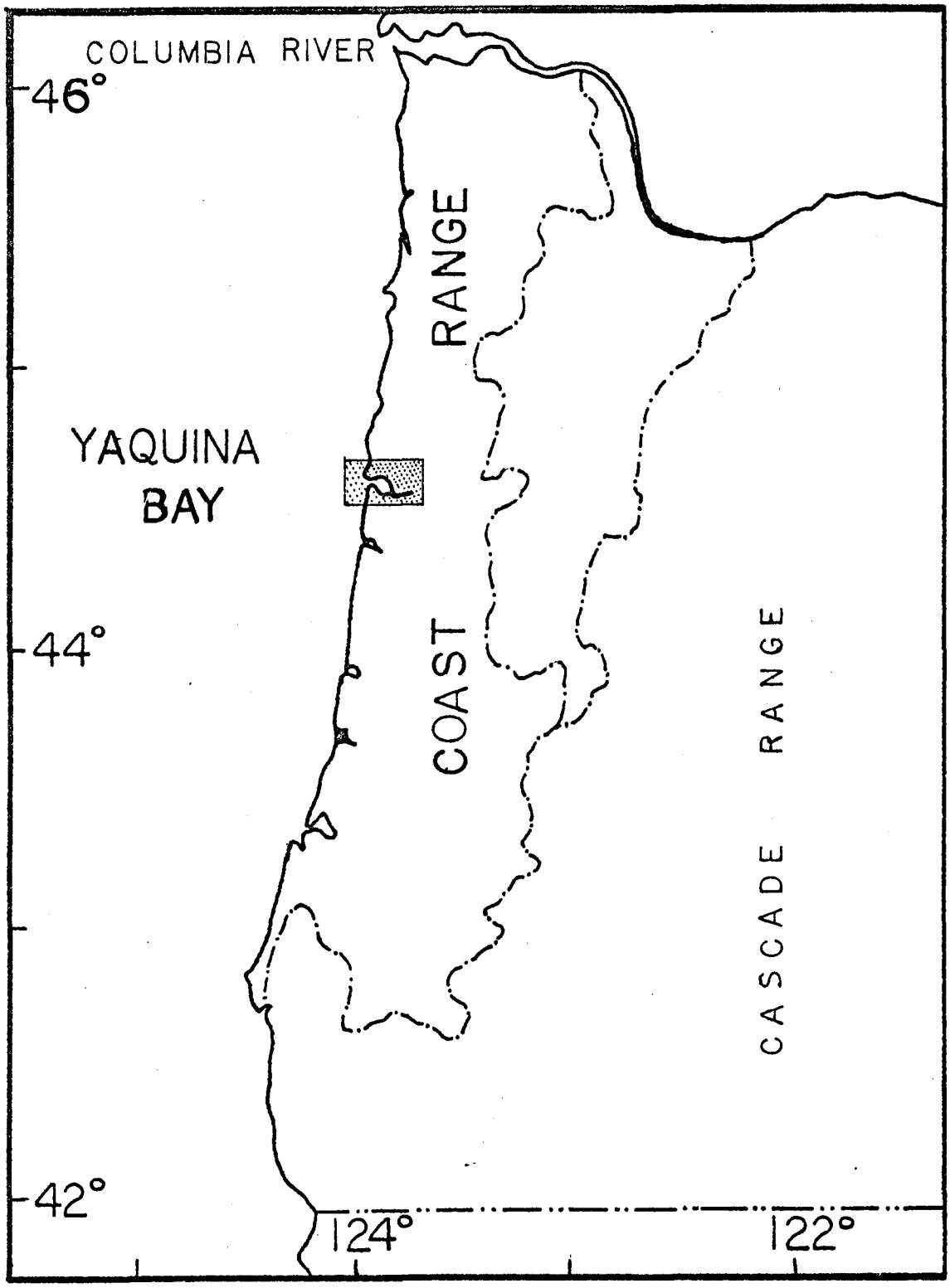


Figure 1. Location map showing Yaquina Bay, Oregon.

kilometers. It then narrows gradually to the head of the estuary near Elk City. The mouth is located between the cities of Newport and South Beach in Lincoln County, Oregon. At the mouth there are twin jetties one kilometer long and approximately 0.2 kilometers apart. The channel between the jetties is maintained at an average depth of seven meters by dredging and by the scouring action of tidal currents whose speed is enhanced by a series of six laterals (spurs) on the south jetty.

The bathymetry of the estuary has been considerably changed due to man's efforts to industrialize the area. Kulm (1965) notes the changes by comparison of the early navigational charts with present conditions. The maintenance of the twin jetties at the mouth and frequent dredging have modified and stabilized the estuary. Presently a channel depth of 3.6 meters is maintained up to Toledo for navigational purposes. There has been considerable filling and draining of some marginal marshlands along the estuary. For a complete description of the geomorphology and sediments of the estuary see Kulm (1965).

Physical Factors Operating in Yaquina Bay

The variations in physical and chemical properties of estuarine waters are much greater than in waters off the open coast or in the open sea because of tidal variations, fresh water runoff, and

meteorological conditions. The climate of the Yaquina Bay area is classified as (Csb) in the Koppen classification of climate (Kulm, 1965) and is typified by extremely dry summers and wet winters.

Precipitation

The mean annual precipitation at Newport, Oregon is 1333 mm, however, deviations of 500 mm are not uncommon. The drainage basin of Yaquina Bay extends from the ocean to the crestline of the central Oregon Coast Range (Figure 2). This system drains approximately 380 square kilometers with the Yaquina River being the main stream. Big Elk Creek is the only other stream of significance.

Seasonal fluctuations in precipitation are closely related to variations in fresh water runoff. Figure 3 shows the average precipitation for the drainage system computed from the average monthly precipitation recorded by the U. S. Weather Bureau at Newport at the mouth of the drainage system and at Summit, located near the crest of the central Oregon Coast Range. Weekly data concerning the runoff into the estuary was obtained from Waldemar Seton of Georgia Pacific Corporation for the four years from 1962 to 1966. These data are expressed as monthly averages in Figure 3. During the summer months the average runoff is approximately 150 cubic feet per second, while during the winter, it is approximately 1000 cfs. Figure 3 shows the close correlation between

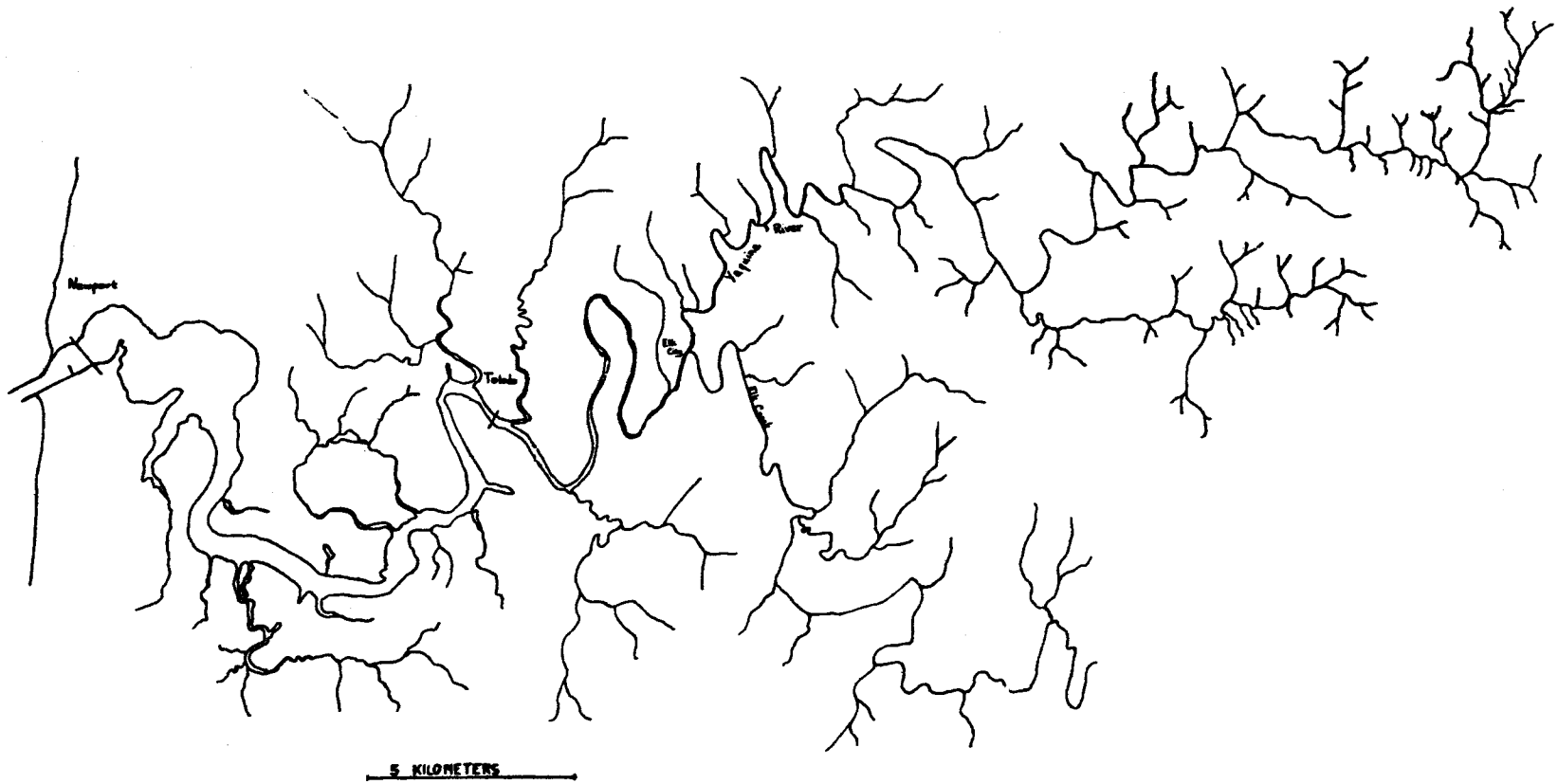


Figure 2. Drainage basin of the Yaquina estuary.

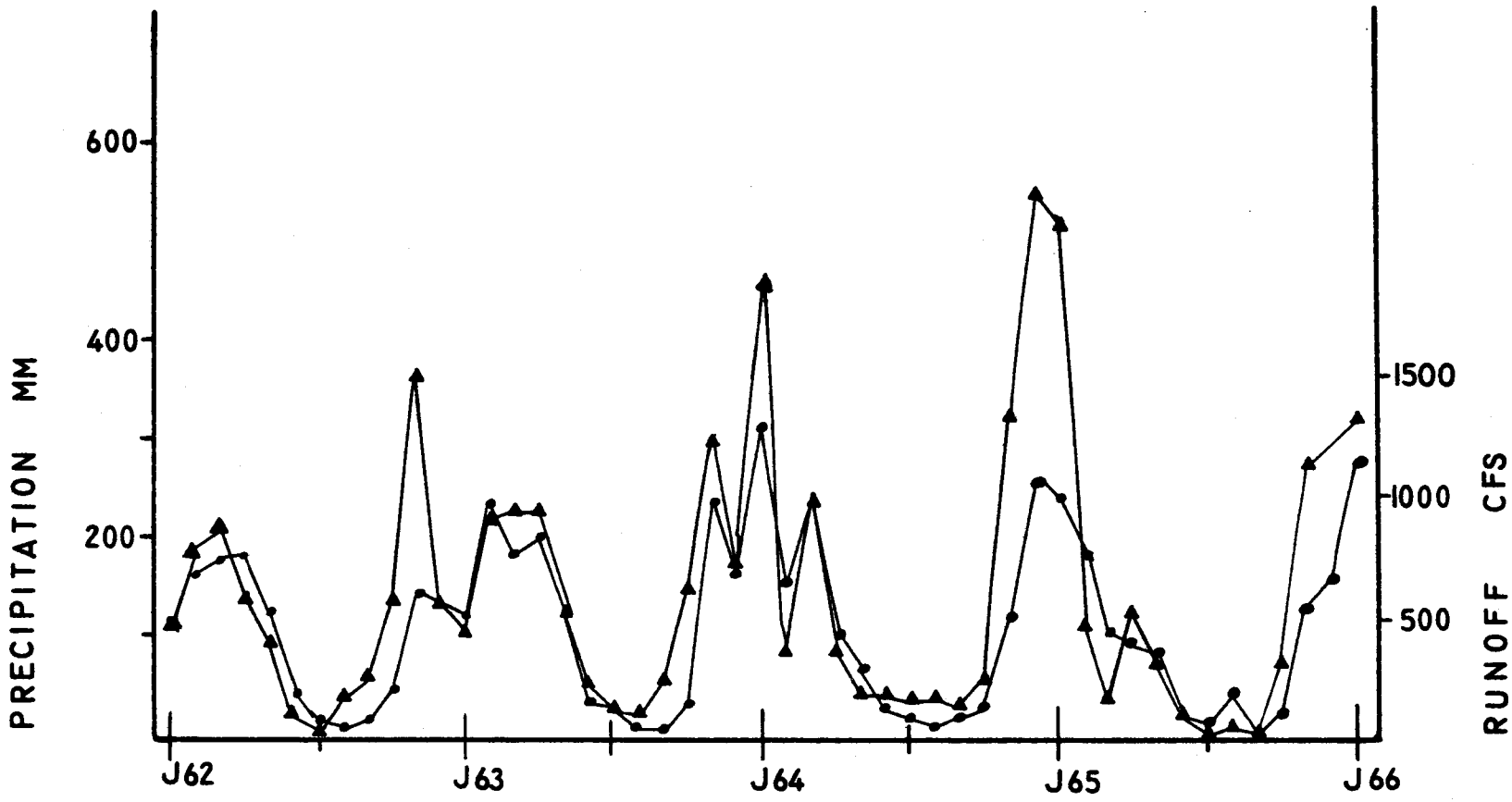


Figure 3. Correlation between precipitation and runoff. The average monthly precipitation for Newport and Summit. The monthly average calculated from data of weekly runoff in cfs. ▲ Precipitation ⁎ Runoff

runoff and precipitation. This will be discussed further as it relates to the salinity regime of the estuary.

Temperature

The mild temperatures in the area result from the oceanic influence. The area characteristically has warm summers and mild winters with an annual mean air temperature of 11 C.

The temperature of the water of an estuary is a function of the temperature of entering streams and of the entering tidal sea water, both of which are modified by effects of solar radiation. Because Yaquina estuary is a shallow flowing system there is little heat storage from one season to the next. A decrease in temperature of surface water begins in November and low temperatures continue through March. The lowest temperatures in the estuary occur during January and February. In winter the low temperatures of the surface water are correlated with low temperatures in the drainage basin and are derived from the cold streams of the inner Coast Range. The bottom waters in winter are generally warmer but appear to have little effect on the temperature at the surface, in fact, they in turn are little altered and are generally slightly colder than offshore waters (Kulm, 1965). The lowest temperatures of the bottom water occur in summer during offshore upwelling that is carried several kilometers into the estuary by tidal currents.

Generally, the temperatures at the bottom and surface are highest in the spring and late fall, but the highest surface water temperatures, according to Kulm, occur in the summer and early fall. Kulm (1965) notes two temperature inversions between the surface and bottom water, one in October and November and the other occurring between March and April.

Weekly records of the temperature of the water at the surface at five stations in the estuary and one station off the north jetty were provided by Waldemar Seton of Georgia Pacific Corporation. In Figure 4 these data are plotted as average monthly values. Dr. Kenneth Chew provided daily maximum and minimum temperature readings at Marker 26, which is off the Oregon Oyster Company. Daily maximum and minimum temperatures at this point have been converted to average monthly maximum and minimum temperatures to illustrate the variation possible at a given station. Variations at Marker 26 show an average difference between maximum and minimum readings of 6 to 8 C in the summer and 2 to 4 C in the winter. The average annual variation in temperatures in winter and summer determined from the four years data was: 5.6 C off the north jetty; 8 C at Marker 15; 11 C at Markers 25 and 26; 13 C at Marker 47; and 14 C at the Toledo bridge. Frolander (1964) noted the following temperature variations during a tidal cycle late in the summer; 4 C at the Newport bridge; 7 C at Marker 15; 10 C at Marker 21; 5 C at Marker 29; 3 C

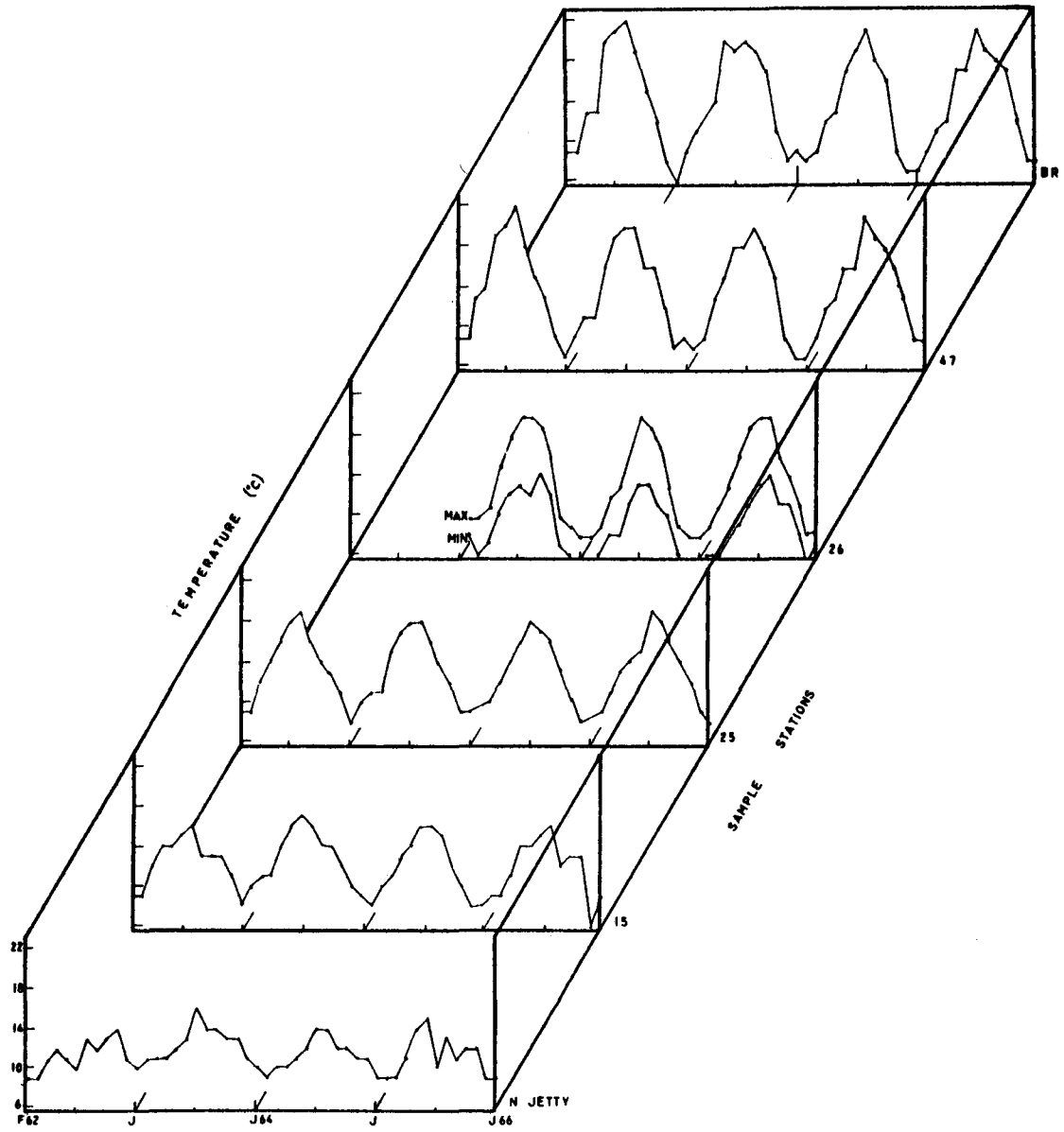


Figure 4. Temperature regime at six stations in Yaquina Bay. Average monthly values in degrees Centigrade calculated from weekly readings. At Marker 26 the average monthly maximum and minimum temperatures calculated from daily readings are plotted.

at Marker 39; and 2 C at Marker 45. Seasonal variation increases as one proceeds into the estuary, but the greatest tidal variation in temperature is found 8.5 kilometers from the mouth.

Wind

Wind is one of the prominent features of the Oregon coastal climate. As noted by Cooper (1958) at Newport, the summer winds with a velocity of 4 m.p.h. and more are north or northwest onshore winds. Of these, the north winds seem to predominate. The occurrence of winds of more than 16 m.p.h. although their frequency is less, follows the same trend. Cooper found that during the winter there is a marked difference in the wind patterns. Offshore winds of more than 4 m.p.h. but less than 16 m.p.h. are the most frequent winter winds. The frequency of high velocity winds in winter is less than the frequency of high velocity winds in summer. The strong, but relatively infrequent, onshore winter winds are from the south to southwest and strike the coast at an acute angle or run parallel to the coast. The spring and fall are characterized as transitional periods in-so-far as the wind regime is concerned.

Turbidity

Turbidity data (Figure 5) concerning four years of weekly samples at six stations were obtained from Georgia Pacific Corporation.

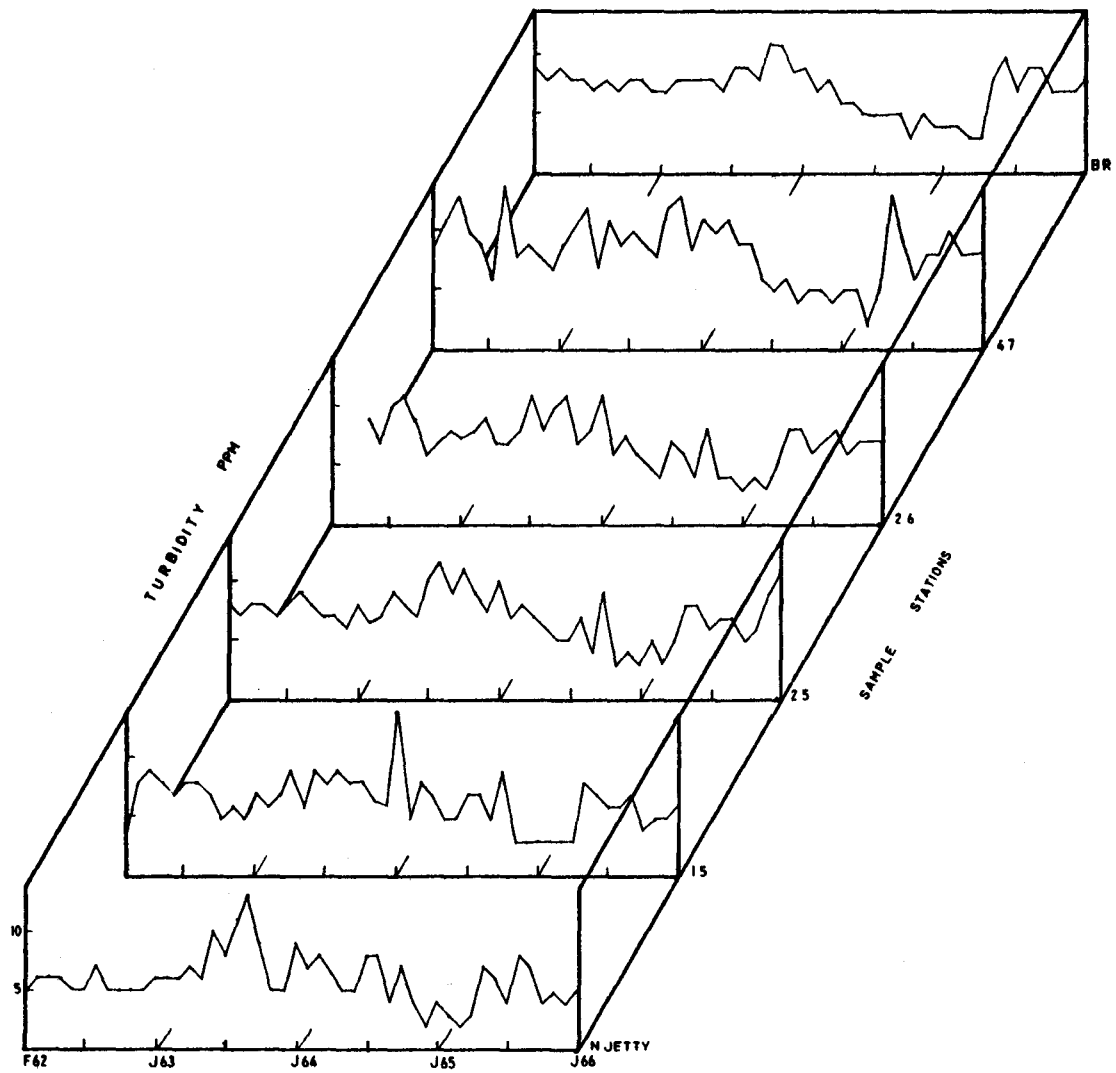


Figure 5. Turbidity regime at six stations in Yaquina Bay. Average monthly values in parts per million SiO_2 calculated from weekly readings.

The values, expressed as ppm SiO_2, are irregular but some trends can be observed. The monthly average of weekly turbidity readings was lowest near the mouth of the estuary and highest between Markers 26 and 47. When expressed as monthly averages, there is no consistent correlation between precipitation and turbidity data, runoff and turbidity, or salinity and turbidity such as has been noted in other estuaries. If any trend is shown in these data it is an inverse relationship, i. e. some of the least turbid conditions occur during months of high precipitation, high runoff and low salinity. It is my contention that the irregular occurrence of turbid conditions and their unusual distribution within the bay is directly related to the occurrence of onshore winds. This was also noted by Conover (1964) in estuaries in Texas. Certainly some of the turbid conditions in the estuary are due to the silt load carried in by runoff during winter storms, when the estuary will be turbid throughout, but a rapid setling of the suspended matter has been observed and solids will not remain in suspension unless the water is in motion. Diurnal variations in turbidity are created by tidal movement, but rapid settling of suspended particles is noticeable during the slack of high and low tides. The wind regime of the area contributes to water movement and the wave action thus created resuspends settled particles. In winter the winds are of higher velocity, but infrequent. In the summer the winds are not of exceptionally high velocity, but they are constant and contribute to the high turbidity. In the summer, turbidity has a diurnal fluctuation also created by the typical wind pattern. In the late spring and summer the winds are light in

the mornings, but as the land mass is warmed by radiation a thermal wind develops by noon, and during the afternoons onshore winds are quite strong. Plankton blooms may also contribute to the turbid conditions encountered in the summer.

Salinity

Two types of estuaries have been recognized on the basis of tides, runoff, and the resulting salinity: a) the normal, or positive type, in which there is a reduction in salinity due to fresh water inflow; and b) the hypersaline, or negative type, in which higher than oceanic salinities exist due to evaporation. Yaquina Bay is generally the positive type, and only during a few weeks in the summer do parts of it approach the negative type.

Yaquina Bay and estuary have been classified on the basis of patterns of circulation and distribution of salinity by Burt and McAlister (1959). Although the data upon which this was based are incomplete, they suggest that the Yaquina estuary is partly-mixed in the winter and spring, showing a salinity difference of 4 to 19‰ between top and bottom waters, and completely mixed in the summer and fall with a salinity difference of less than 3‰ between top and bottom waters.

The mixing of fresh and saline waters in an estuary is a function of tidal energy runoff and wind. The tides in Yaquina Bay are

semidiurnal tides characteristic of the North Pacific, with two high and low tides of unequal amplitude in a 24.8-hour period. Tidal access between the jetties at the mouth of the estuary is free throughout the year. The tidal amplitude is also a significant factor in mixing, and in Yaquina Bay the average tidal height of 1.6 meters is conducive to mixing, especially during periods of low flow.

The first systematic recordings of salinity in Yaquina Bay were made by Professor R. E. Dimick in conjunction with studies of the native oyster. Subsequent to these studies there have been several studies of the salinities in the bay. A very informative study was made by Frolander (1964) of variations in salinity during the complete tidal cycle on 9 and 10 August 1963 at each of six stations along a transect extending nine nautical miles in the estuary. This study showed that during the late summer, when the estuary is well mixed, there is very little variation in salinity near the mouth of the estuary, but at Marker 21 there was a difference of 6‰ between high and low tide. At Marker 39 he found differences of 10‰ and at Marker 45 differences of 6‰ during the tidal cycle.

At present Raymond Jones of Georgia Pacific Corporation is conducting a survey of physical and chemical characteristics of surface waters in Yaquina Bay. Salinity data from weekly samples taken at six different stations in the estuary at various times during the tidal cycle for the period February 1962 to January 1966 have

been made available by Waldemar Seton of Georgia Pacific. The salinities of the weekly samples were converted to monthly averages (Figure 6). It is realistic to consider surface water as it influences the benthic algae since turbidity limits the depth of their growth in the estuary. While Frolander's work shows there is variation during the tidal cycle, I feel that monthly averages of weekly samples, which for practical purposes can be considered as being taken at random, present a generalized picture of the salinity regime at various points in the estuary.

The mean salinities determined from weekly samples were 33‰at the jetties with a mean variation of 5‰ between winter and summer. At Marker 25 the mean was 28‰ with an average variation between winter and summer of 26‰, and variations during a tidal cycle in the late summer of approximately 5‰. At Marker 47 the mean salinity was 11‰ and the average variation between summer and winter 16‰, with variations during a tidal cycle of 6‰ in late summer.

Seasonal fluctuations in precipitation determine variations in the amount of runoff and correlate directly with changes in salinity in the estuary. The relationship between variations in salinity and the amount of rainfall is evident when comparing Figures 3 and 5. This correlation was noted by Kulm (1965) when he compared precipitation and the average monthly difference in salinity of water

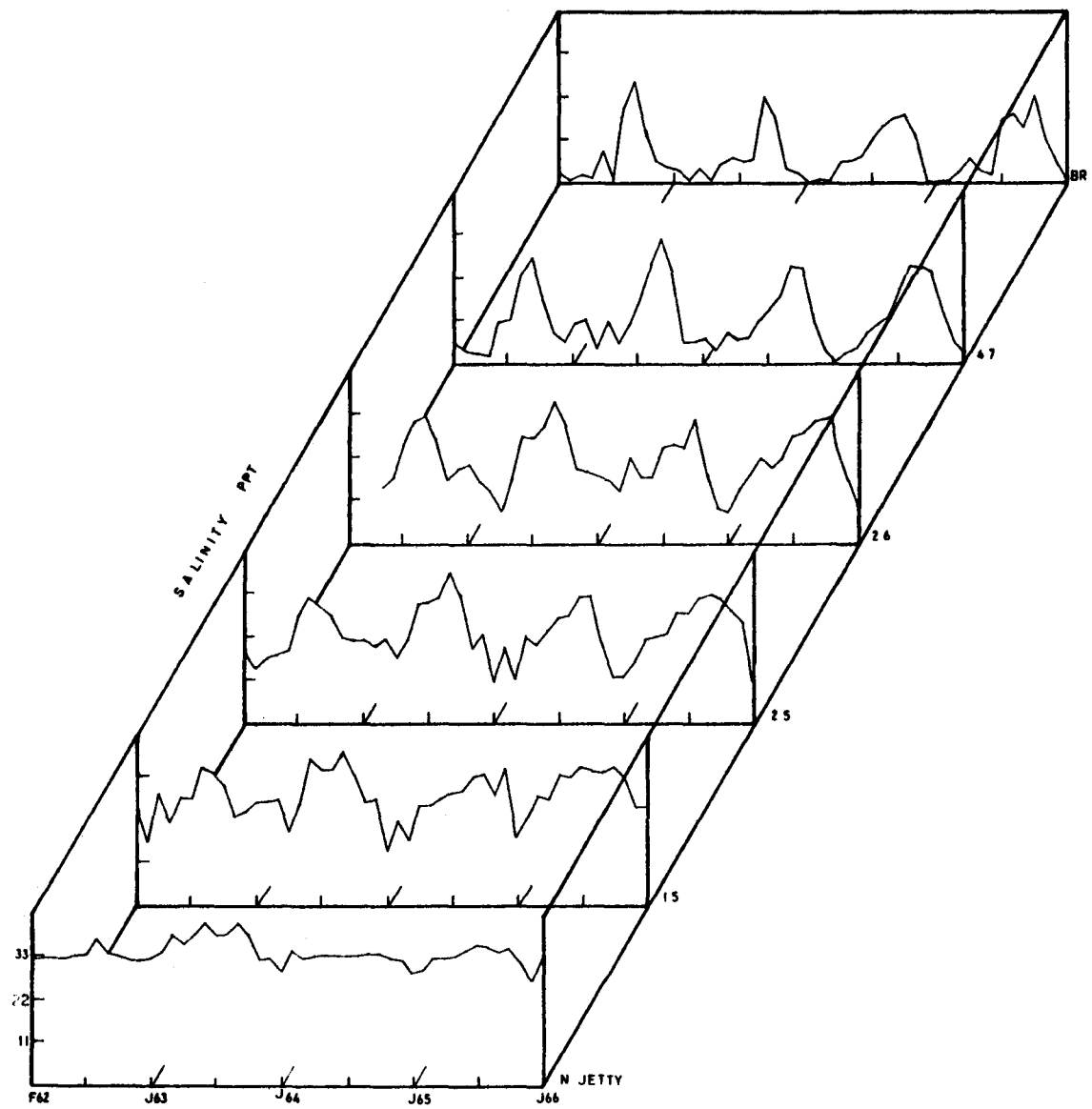


Figure 6. Salinity regime at six stations in Yaquina Bay. Average monthly values in ‰ salinity, calculated from weekly readings.

at the surface and bottom. However this relationship is demonstrated, it gives evidence of the strong local climatic control of the estuarine system. There is a time lag during the fall when the first precipitation occurs after the summer drouth. The marked increase in precipitation in October is not reflected by variations in salinity until some time later, presumably due to the time required to saturate the soil of the watershed. After saturation the influence of precipitation upon variation in salinity can generally be detected in approximately 24 hours.

Coastal upwelling of cold, mineral rich water from the offshore bottom as well as precipitation and runoff contribute to the physical-chemical characteristics of the estuary. Coastal upwelling occurs during the summer, as a result of the onshore winds, and exerts its influence near the mouth of the estuary. The upwelling bottom waters have salinities ranging between 33 and 34‰ and temperatures near 10 C. The influence of this water diminishes rapidly with distance inland from the mouth of the estuary.

Currents

In an estuary two opposing current systems meet, the unidirectional currents of the stream and the fluctuating tidal currents. The meeting of these currents strongly influences sedimentation and mixing of the waters in the estuary.

Seasonal patterns of currents in Yaquina Bay are not clearly delimited. Some general patterns can be deduced from the patterns of mixing in the estuary. Mixing and current patterns appear to be seasonal and influenced by climatic conditions.

From the tidal prism and the cross-sectional area at the entrance of Yaquina Bay, Kulm (1965) calculated the velocity of the tidal current to average 77 cm/sec with a maximum of 109 cm/sec. Burt (as noted in Kulm, 1965) measured current velocities at various locations in the bay by means of current drags and, as expected, the velocities decrease rapidly with increasing distance from the mouth.

MATERIALS AND METHODS

Laboratory Studies

Nine species of macro-algae were selected for laboratory study from the diverse flora occurring in Yaquina Bay. The selection of these species was determined by: 1) a desire to have representatives from each of the three Divisions; 2) their size and ease in handling; 3) abundance; and 4) their distribution in relation to the tidal zones. The species used for experiments in the Gilson differential respirometer and photosynthesis-respirometer chamber were: a) two species of green-algae (Chlorophyta), Ulva expansa Setchell and Gardner, from the first spur and Marker 21 and Enteromorpha linza (L) J. Agardh, from the sand flats west of the Oregon State Marine Science Center; b) three species of brown-algae (Phaeophyta), Laminaria saccharina Lamouroux, from the Coast Guard dock, Sargassum muticum (Yendo) Fensholt, from the first spur, and Alaria marginata Postels and Ruprecht, from the third spur; and c) four species of red-algae (Rhodophyta), Odonthalia floccosa (Esper) Falkenberg, Iridaea splendens (Setchell and Gardner) Papenfuss, Gigartina californica J. G. Agardh, and Polyneura latissima (Harvey) Kylin, all four of which were collected from the first spur of the south jetty. Specimens obtained from the Coast Guard dock were taken off

the log floats. Specimens from the south jetty were collected from the subtidal zone by SCUBA diving or as low as possible in the intertidal during low tides. Thus, all of these algae can be considered as normal inhabitants of the subtidal zone with the exception of Enteromorpha linza which was collected from shells in the intertidal zone.

The specimens collected for these studies were all mature, healthy plants. The condition of the plants collected for laboratory experiments was of vital importance and this condition proved rather difficult to maintain, particularly for those used in the manometric experiments in the Gilson differential respirometer which was located in Corvallis. The photosynthesis-respirometer chamber experiments, which will be described later avoided this problem as experimental material could be collected and placed immediately in the chamber or maintained for the interim in flowing sea water.

Studies Using the Gilson Differential Respirometer

Experimental materials for use in the manometric experiments were found to be best preserved if they were wrapped separately in moist newspaper, placed in plastic bags, and transported to Corvallis at low temperature and used the afternoon or evening of the same day that they were collected. Storage for periods longer than 24 hours damaged the plants to such an extent that erratic and unreliable data resulted. Once the procedure for collecting and handling

the material was established, reproducible data were obtained.

Warburg-type of manometric measurements were recorded using the "one vessel" method involving only oxygen exchange between the gas and liquid phase. Mixture number nine of a carbonate-bicarbonate, carbon dioxide-buffer solution, as given by Umbreit, et al. (1964), was employed. Two methods of using the buffer were tried, first, as an additive to the sea water, and, second, placed in the center well with a filter paper wick. The first procedure proved undesirable as it was an added dilutent in the sea water. The latter procedure was employed throughout the manometric experiments. Shaking was maintained at a rate of 120 oscillations per minute during all manometric experiments.

The algal tissue used in the manometric experiments was washed in sea water and a number seven cork borer used to cut disks approximately 11 mm in diameter from the thallus of the blade-like forms. The branching forms, such as Odonthalia and Sargassum, did not lend themselves to this technique and consequently small portions of branches were cut off and placed in the reaction vessels. Six disks, or a small branch estimated to weigh approximately 50 milligrams when dry, were placed in each 15-ml reaction vessel containing 3 ml of a particular salinity concentration, together with 0.2 ml of the buffer in the center well with a filter paper wick. It was difficult to control exactly the amount of tissue placed in each

reaction vessel and the dry weights express this variability. It was proven that in extreme cases, this variance would influence the results even when they were expressed as microliters of oxygen per milligram of dry weight. In the small volume of sea water contained in the reaction vessel different amounts of tissue were exposed to different rates of diffusion and light penetration.

The sea water used in the manometric experiments was collected 50 kilometers off the Oregon Coast and had a salinity of 33.2‰. The water was aged for three months and then micropore filtered before use in the experiments. The control was the filtered sea water of 32.2‰ salinity and dilutions of 22.0‰ (2/3 sea water), 11.6‰ (1/3 sea water) and 0.0‰ (fresh water) were obtained by using distilled water.

Initially, the manometric experiments were performed in a Bancroft-Warburg apparatus. These experiments were subject to temperatures above ambient room temperature and were maintained at 26 C. Since this temperature was abnormally high compared to natural environmental conditions, a refrigeration unit was adapted to the apparatus so that a temperature approximating nature (15 C) could be employed. Measurements of respiration were taken in a dark room for a very dim light was found to affect the results. Fluorescent light of approximately 300 foot candles intensity was used in measurements of rates of photosynthesis in the

Bancroft-Warburg apparatus.

To obtain more precise control over temperature and a better source of light, a series of experiments were performed in a Gilson differential respirometer (Gilson, 1963) when it became available. This apparatus had distinct advantages over the previous instrument, principally precison of control and ease of operation.

When the Gilson differential respirometer was used, measurements of changes in gas volume as a result of photosynthesis and respiration were taken every 30 minutes for a period of two hours following equilibration of the reaction vessels. Rates of photosynthesis were determined in incandescent light of 1100 foot candles intensity as measured by a Weston Model 756 Sunlight Illumination Meter. The temperatures employed were 20, 15, and 10 C. In studies of Laminaria saccharina the experiments were extended to include 25 and 5 C. Upon conclusion of an experiment the plant tissue was removed from the reaction flask and placed on weighed filter paper and dried for 24 hours in an oven of 90 C. The dry weight obtained and the gas exchange measured were expressed as microliters of oxygen change per hour per milligram dry weight of tissue. In all manometric experiments each salinity was represented in triplicate.

The measured net rate of photosynthesis was converted to an estimate of gross photosynthesis by adding to the oxygen evolved

during the period of illumination the amount of oxygen consumed during an equivalent period of darkness.

Studies Using the Photosynthesis-Respiration Chamber

The advantages of using manometric methods are the ease with which experiments can be duplicated, the accuracy with which experimental conditions can be maintained, and the precise measurements of changes in oxygen volume. However, there are certain limitations inherent in the use of the manometric respirometer. The method involved the use of small pieces of deliberately damaged tissue taken from only a part of a plant that had been transported to Corvallis under abnormal conditions of light and temperature. With this in mind, further experiments were designed to use whole plants in a photosynthesis-respiration chamber described by McIntire, et al. (1964) with modifications and changes in technique. The chamber, a rectangular enameled steel tank, 60 cm long by 50 cm wide and 17 cm deep, was coated with a nontoxic, water-proof enamel. A 75 liter head jar for fresh water, a 150 liter tank for settling suspended matter in the sea water, and a 75 liter head jar for sea water were assembled with the chamber in the Oregon State Marine Science Center at Yaquina Bay.

The sea water used in the respirometer chamber experiments was taken from the laboratory supply. This water was pumped from

a depth of two meters below the surface at the Oregon State University Marine Science Center dock, through a glass pipe into a large reservoir supplying the laboratory system. The sea water in this laboratory system at all times flows through polyvinyl-chloride plumbing.

In view of the volume of water required, it was not practical to use distilled water for dilution in these experiments, consequently the fresh water supply of the laboratory was used. This fresh water came from the South Beach water supply system and was transported through "Transite" pipe into the laboratory where it passed through 20 feet of galvanized pipe and then by black, polyethylene plastic pipe to the fresh water head jar. The fresh water had several undesirable biological characteristics, a pH of 8-10, turbidity for the water was not absolutely clear, and possible presence of toxic metal ions following passage through the galvanized pipe.

From the two head jars the water passed through two flowmeters, with which the salinity was regulated, and then into a 40 liter mixing and temperature control jar. Temperature control was accomplished by either cooling or heating the water depending upon the temperature required. A two-ton York compressor was used to cool a 300 liter bath of diethylene glycol containing coils of one-half inch, thin walled, stainless steel pipe carrying fresh water and sea water. The cooling unit reduced the temperature of the

incoming water approximately 5 C. In order to obtain more precise control and higher temperatures when needed, a stainless steel immersion heater, controlled by a National Appliance Company series 1000 safety thermostat, was placed in the head jar in which fresh and sea water were mixed. Water from the temperature control and salinity mixing head jar passed either to the chamber or circulated through the water bath surrounding the chamber. Thus, both the salinity and temperature were controlled in this apparatus.

Photosynthesis and respiration of the experimental plants could be measured in the respirometer chamber, under varying conditions of salinity and temperature by noting the changes in concentration of dissolved oxygen i. e. the amounts of oxygen evolved during photosynthesis and oxygen consumed during respiration. The concentration of dissolved oxygen was measured by the unmodified Winkler method (American Public Health Association, 1955).

The experimental plants were cleaned of all visible epiphytes, washed in sea water, and secured in the chamber with stainless steel clamps. The effluent lines were closed and the chamber filled with water and sealed by clamping the plexiglass cover in place, excluding all contact with the atmosphere and eliminating the problem of change in gas concentration by diffusion between the water and the atmosphere. The inflow lines were clamped off and the water in the chamber mixed by circulation provided by two centrifugal pumps.

It was assumed that the concentration of gas in the water leaving the chamber would be the same as that of the water in the chamber.

Once the plexiglass cover was secured, the chamber was covered with sheets of black polyethylene and allowed to come to equilibrium. After a period of equilibration, a sample of water was withdrawn and the dissolved oxygen determined by the Winkler method. One hour later a second water sample was taken and the difference in the concentration of dissolved oxygen between the two samples used as an index of the rate of respiration.

It was realized that errors may result from the respiration of microorganisms contained in the water supplied to the chamber. Attempts were made to sterilize the water supply by passing it through ultraviolet light, but subsequent blank runs showed this to have insignificant effect. A filtration system was discussed but the expense would have been exorbitant. It was thought that a correction factor could be obtained by determining oxygen consumption during operation of the chamber in the absence of experimental plants. After five blank runs, the change in dissolved oxygen was found to be so small as to be insignificant compared to the changes obtained in the presence of experimental plants.

After determining the rate of oxygen consumption by respiration during one hour the polyethylene sheets were removed and the lights switched on. A measurement was then obtained of the change

in the concentration of dissolved oxygen caused by the oxygen evolved by photosynthesis during an equivalent period of time. The light used for photosynthesis was supplied by a bank of six, four foot fluorescent tubes (G. E. Power Groove Deluxe Cool White) producing 800 foot candles illumination intensity at the center of the chamber with the plexiglass cover in place. The net rate of oxygen change for photosynthesis and respiration was computed according to the following expression:

$$\text{Net oxygen change per hour} = \frac{V}{t}(D_1 - D_o)$$

where

V = volume of water in the chamber

t = time in hours

D_o = dissolved oxygen concentration in milligrams/liter of the effluent water at the beginning of the time interval.

D_1 = dissolved oxygen concentration in milligrams/liter of the effluent water at the end of the time interval.

The net rate of photosynthesis was converted to an estimation of gross photosynthesis by adding the net oxygen evolved during the period of illumination to the amount of oxygen consumed during an equivalent period of darkness.

Following the initial measurements of respiration and photosynthesis in sea water, the first dilution of salinity was initiated by flushing the chamber with fresh water. When the desired salinity of 22.0‰ had been obtained, as indicated by the specific gravity of the effluent water, the system was closed, equilibrated, and measurements of rates of respiration and photosynthesis at that salinity were taken. This process was repeated at a dilution of approximately 11‰, and finally at a dilution of less than 5‰ salinity, the equivalent of fresh water. Therefore, in order to obtain the experimental treatments at each temperature, it required four, two hour runs with the additional time required to exchange the water to obtain the next salinity desired and for equilibration before each treatment. A total of 12 hours was required for each experiment and 28 experiments were conducted.

Upon conclusion of an experiment the plants were removed from the chamber, allowed to drip dry, and then placed on a weighed sheet of aluminum foil. The tissue was dried at 90 C in an oven for 24 hours or longer, and then weighed. The results were expressed as milligrams of oxygen change per hour per gram dry weight of tissue.

Studies of the Effects of Adaptation

The studies of salinity and temperature tolerance in the P-R

chamber were supplemented by a series of experiments concerning long term adaptation of five species to decreased salinities.

The apparatus consisted of two 25-liter head jars, one for fresh water and the other for sea water. Suitable plumbing was installed to distribute water from the head jars to regulate the salinity in each of 12 large mouth carboys. Mixing was accomplished by an aerator in each carboy. It was considered desirable to control temperature by a continuous flow of water into each of the jars, however, silt suspended in the sea water supply for the laboratory made this impossible. The sea water lines became filled with silt and the desired salinity could not be maintained. The jars also became loaded with silt, and algae and mud near the bottom became anaerobic resulting in destruction of the experimental plants. Consequently, this method was abandoned and the plants were adapted by placing them in the P-R chamber at a selected salinity controlled by flow meters. This arrangement was not as desirable as the previous one because it occupied the P-R chamber for long periods and fewer experiments could be performed. In one respect it was advantageous in that temperature could be controlled during the time of adaptation.

The experimental plants were secured in the P-R chamber and provided with an ample flow of water of the desired salinity and temperature. The lights regulated by a timer gave a photoperiod

approximating the daylength at the time of the experiment. After a period of adaptation, which varied from two to four days, the influent and effluent lines were pinched off and determination made of the rates of respiration and photosynthesis under the conditions of adaptation. Sea water was then flushed in and similar readings taken. Determinations were made also at dilutions of 22, 11, and less than 5‰ salinity. These data were expressed in the same manner as in the previous experiments.

Field Studies

Collecting was begun in the spring of 1963 for the purpose of determining the species present and their distribution in the estuary. The reference navigational markers locating regularly sampled areas are presented in Figure 26. Other collecting stations in the estuary are listed in Appendix D. Most specimens collected from the south jetty were obtained by SCUBA diving, others were collected on low tides. The only other location in the bay sampled by SCUBA diving was the Coast Guard dock. The remaining locations in the estuary were sampled at low tides except for the dock floats which could be sampled at any time. An attempt was made to sample these areas at least once a month from the spring of 1964 to the spring of 1966. Specimens were identified and mounted as a permanent record. Duplicates of the specimens have been deposited in the hebarium

of the Oregon State Marine Science Center and in the collection of Dr. Harry K. Phinney.

Successional studies of denuded natural areas were attempted. Some information was obtained but it was difficult to return to the denuded area for observations and impossible to make this study at different locations in the estuary because of the lack of suitable substrates. Studies of the colonization of artificial substrates were attempted using cement blocks placed in triplicate at five locations in the bay. The 2 x 8 x 16 inch blocks were washed in dilute hydrochloric acid to remove some of the lime from the surface and placed in the bay by diving. The blocks were secured in place by a one meter length of 1/4 inch reinforcing steel inserted through a hole drilled in the block and driven into the substrate. It was intended that these blocks be studied for stages in colonization and succession of algae. They were also to be placed in the P-R chamber at different stages of their development to determine the salinity tolerance of the community. These studies failed to materialize because of the rapid silting over of the blocks. At one location on the east side of the first spur they were covered by two meters of sand.

RESULTS

The results of laboratory and field work on the tolerance of algae toward variations in salinity and temperature are presented under two headings: 1) the tolerance of selected species to variations of salinity and temperature as revealed through Gilson respirometer and P-R chamber studies, and 2) field studies on the algal species present, their habitat, distribution, seasonal occurrence, and tolerance to variations in salinity and temperature.

Tolerance of Selected Species to Variations of Salinity and Temperature as Revealed Through Gilson Respirometer and P-R Chamber Studies of Their Rates of Photosynthesis and Respiration

Results of Gilson Differential Respirometer Studies

During the spring and summer of 1964 a series of experiments on salinity tolerance of several marine algae from Yaquina Bay were started using a Bancroft-Warburg apparatus. The species used were Ulva expansa Setchell and Gardner, Laminaria saccharina Lamouroux, Iridaea splendens (Setch. and Gard.) Papenfuss, and Polyneura latissmia (Harv.) Kylin. The latter was abundant at that time but was not available in any quantity the following year. The results of these experiments demonstrated that variations in salinity had noticeable effects on respiration and photosynthesis, and that

through further experiments an understanding of salinity tolerance might possibly be gained. It also became apparent that temperature was closely associated and integrated with the tolerance to variations in salinity. To measure temperature and salinity tolerance with greater accuracy the experiments were repeated and expanded using the Gilson differential respirometer when this instrument became available. The results are presented for each species summarizing the rates in sea water and the response at each temperature to variations in salinity.

Ulva expansa (Figure 7). In water of 33‰ salinity, the rates of respiration varied from 0.61 µl/hr/mg at 20 C to 0.33 µl/hr/mg at 10 C. The rate of respiration at 20 C in decreased salinities was enhanced markedly at 22‰ salinity but with further dilution the rate was unchanged from the rate at 22‰ salinity. At 15 and 10 C, decreased salinities essentially did not alter the rates of respiration.

In water of 33‰ salinity, the rates of photosynthesis varied from 6.25 µl/hr/mg at 20 C to 3.55 µl/hr/mg at 10 C. The rate of photosynthesis at 20 C attained a maximum at 22‰ salinity, and then decreased in lower salinities to a minimum in fresh water. At 10 C, the rate was unchanged in dilutions of 22‰ salinity, but in salinities of less than 22‰ the rate was markedly depressed.

Laminaria saccharina (Figure 8). Measurements of respiration were taken at temperatures of 5, 10, 15, 20, and 25 C. In water

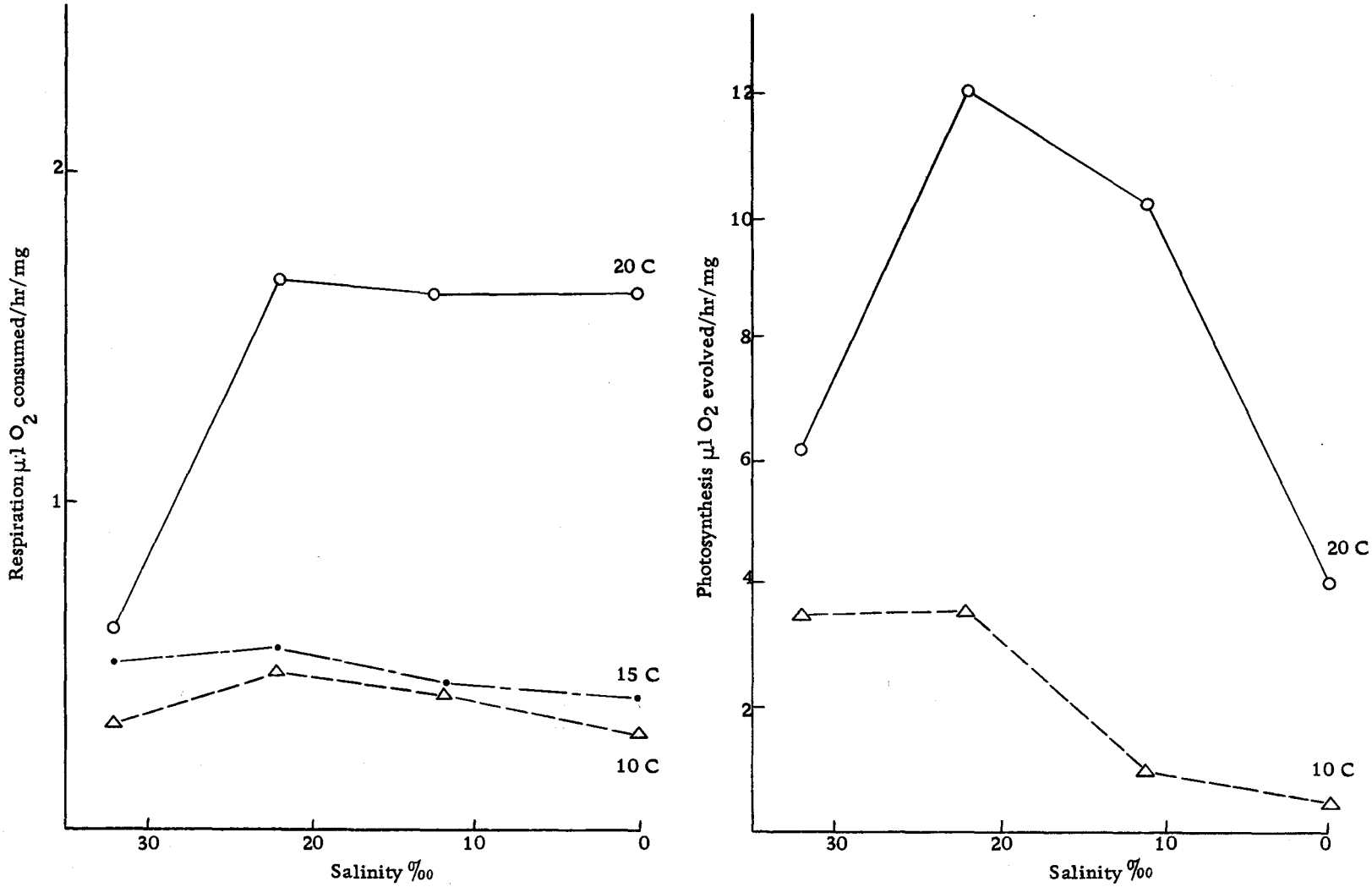


Figure 7. Rates of respiration and photosynthesis in Ulva expansa at various temperatures and salinities as measured in the Gilson differential respirometer.

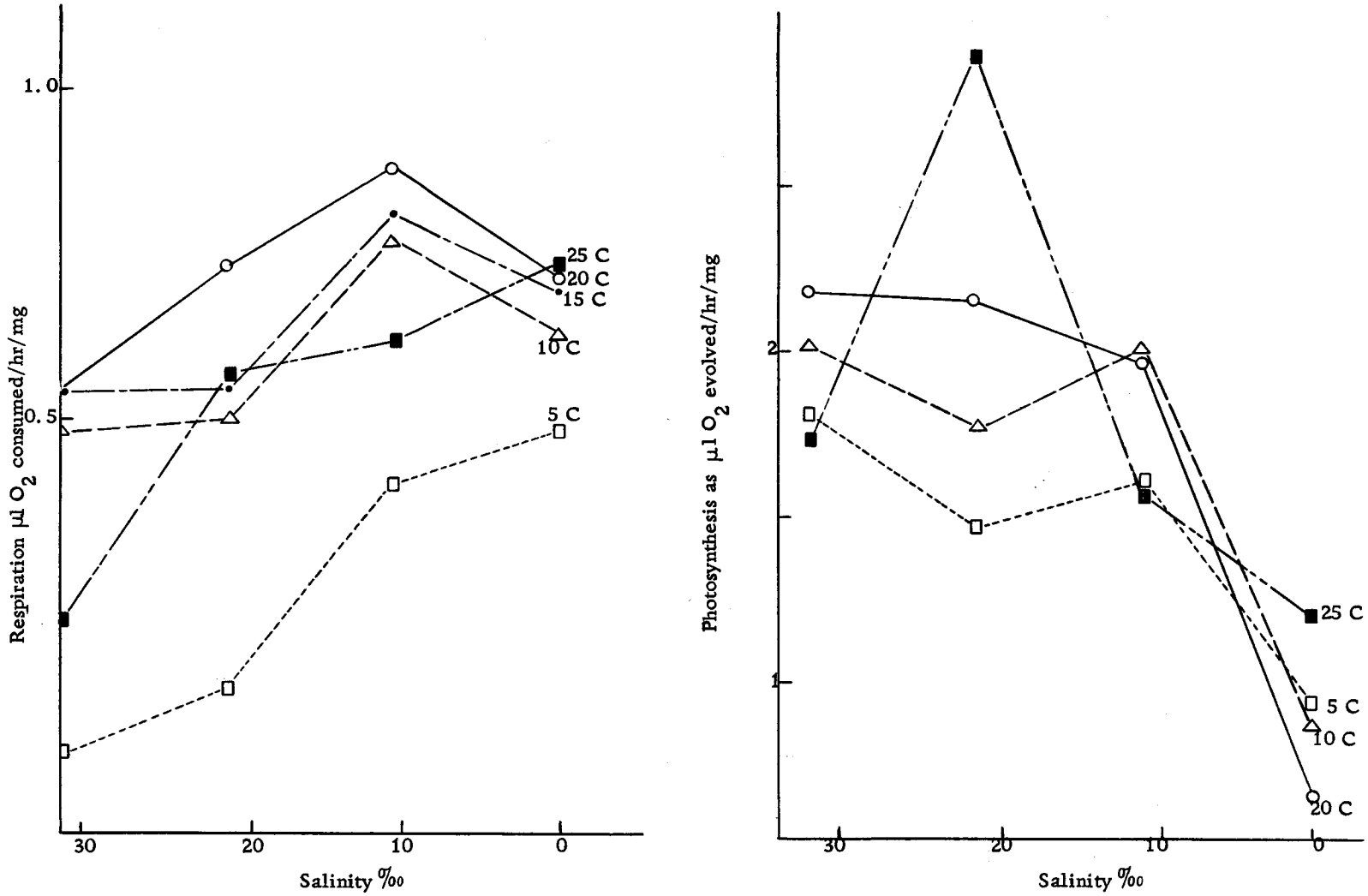


Figure 8. Rates of respiration and photosynthesis in Laminaria saccharina at various temperatures and salinities as measured in the Gilson differential respirometer.

at 33‰ salinity, the rates of respiration varied from 0.55 µl/hr/mg at 15 C to 0.10 µl/hr/mg at 5 C. At all temperatures there was an increase in the rate of respiration with each dilution to 11‰ salinity. The rates of 5 and 25 C, in decreased salinities showed the greatest change from the rates in sea water. It was also significant that the rates of respiration at 25 and 20 C in sea water were less than the rate at 15 C.

In water of 33‰ salinity, the rates of photosynthesis varied from 2.19 µl/hr/mg at 20 C to 1.81 µl/hr/mg at 5 C. At all temperatures, in salinities of less than 11‰, the rates of photosynthesis were depressed. In sea water, the rates of photosynthesis at 20 and 25 C were below the rates of 5 and 10 C.

Sargassum muticum. (Figure 9). In water of 33‰ salinity, the rates of respiration varied from 0.71 µl/hr/mg at 10 C to 0.53 µl/hr/mg at 20 C. At all temperatures, the rates of respiration with decreasing salinity were higher than the rates in sea water.

In water of 33‰ salinity, the rates of photosynthesis varied from 4.01 µl/hr/mg at 20 C to 1.71 µl/hr/mg at 10 C. At all salinities, the rates of photosynthesis were higher with increasing temperature. At all temperatures, the rates of photosynthesis in 22‰ salinity were higher than the rates in sea water, but in salinities of less than 22‰, the rates were lower.

Odonthalia floccosa (Figure 10). In water of 33.2‰ salinity, rates of respiration varied from 0.67 µl/hr/mg at 15 C to 0.32

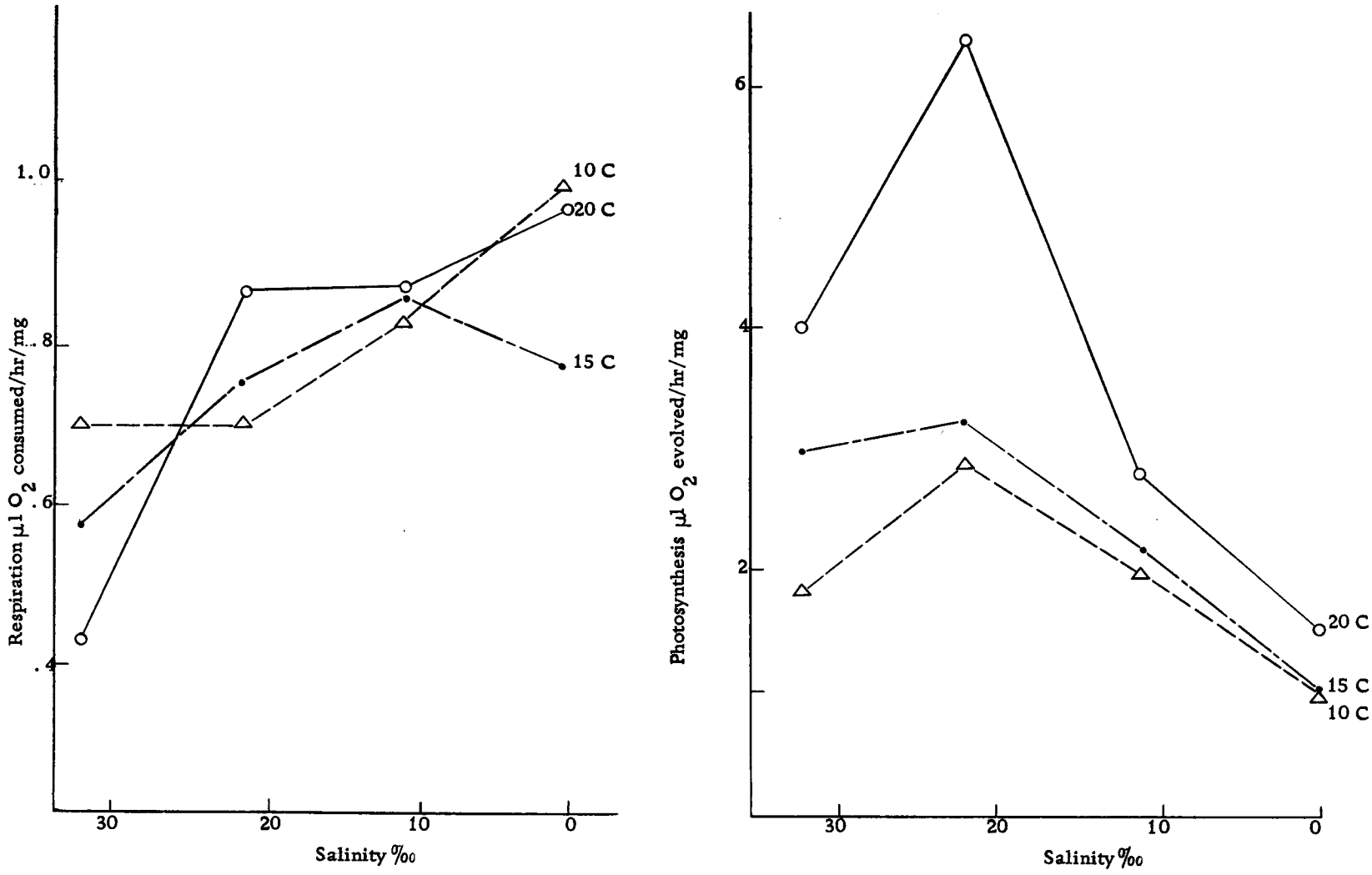


Figure 9. Rates of respiration and photosynthesis in Sargassum muticum at various temperatures and salinities as measured in the Gilson differential respirometer.

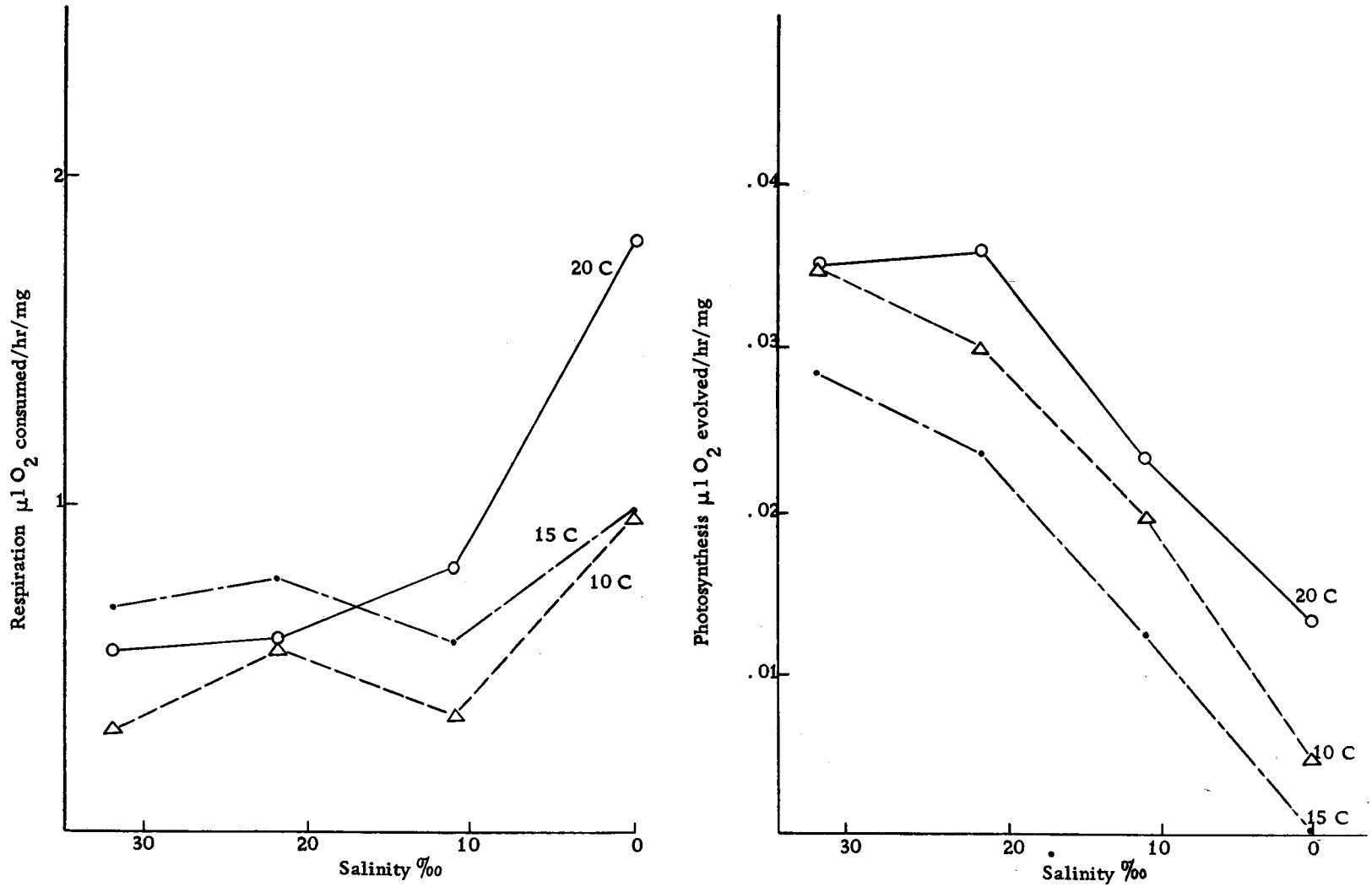


Figure 10. Rates of respiration and photosynthesis in Odonthalia floccosa at various temperatures and salinities as measured in the Gilson differential respirometer.

µl/hr/mg at 10 C. The rates of respiration were not markedly altered from those in sea water at salinities above 11‰, but in dilutions of less than 11‰ the rates were decidedly higher.

In water of 33‰ salinity, the rate of photosynthesis varied from 3.75 µl/hr/mg at 10 C to 2.71 µl/hr/mg at 15 C. At 20 C, the rate of photosynthesis in 22‰ salinity was higher than the rate in sea water, but in dilutions of less than 22‰ it was markedly depressed. At 15 and 10 C, the rates of photosynthesis decreased with decreasing salinities.

Iridaea splendens (Figure 11). In water of 33‰ salinity, rates of respiration varied from 0.15 µl/hr/mg at 15 and 20 C to 0.11 µl/hr/mg at 10 C. At 20 C, the rate was not altered in 22‰ salinity but with further dilution the rate was markedly enhanced. At 15 C, the rate of respiration was slightly enhanced at each dilution above the rate in sea water. At 10 C, the rate of respiration attained a maximum at 22‰, and with further dilution the rate decreased.

In water of 33‰ salinity, the rate of photosynthesis at 10 C was 1.05 µl/hr/mg which was almost double the rate at 20 C (0.65 µl/hr/mg). At 20 C, the rate of photosynthesis was not significantly altered by decreasing salinity, but at 10 C the rate was depressed.

Gigartina californica (Figure 12). In water of 33‰ salinity, the rates of respiration varied from 0.36 µl/hr/mg at 20 C to 0.31 µl/hr/mg at 10 C. The rates of respiration increased above those

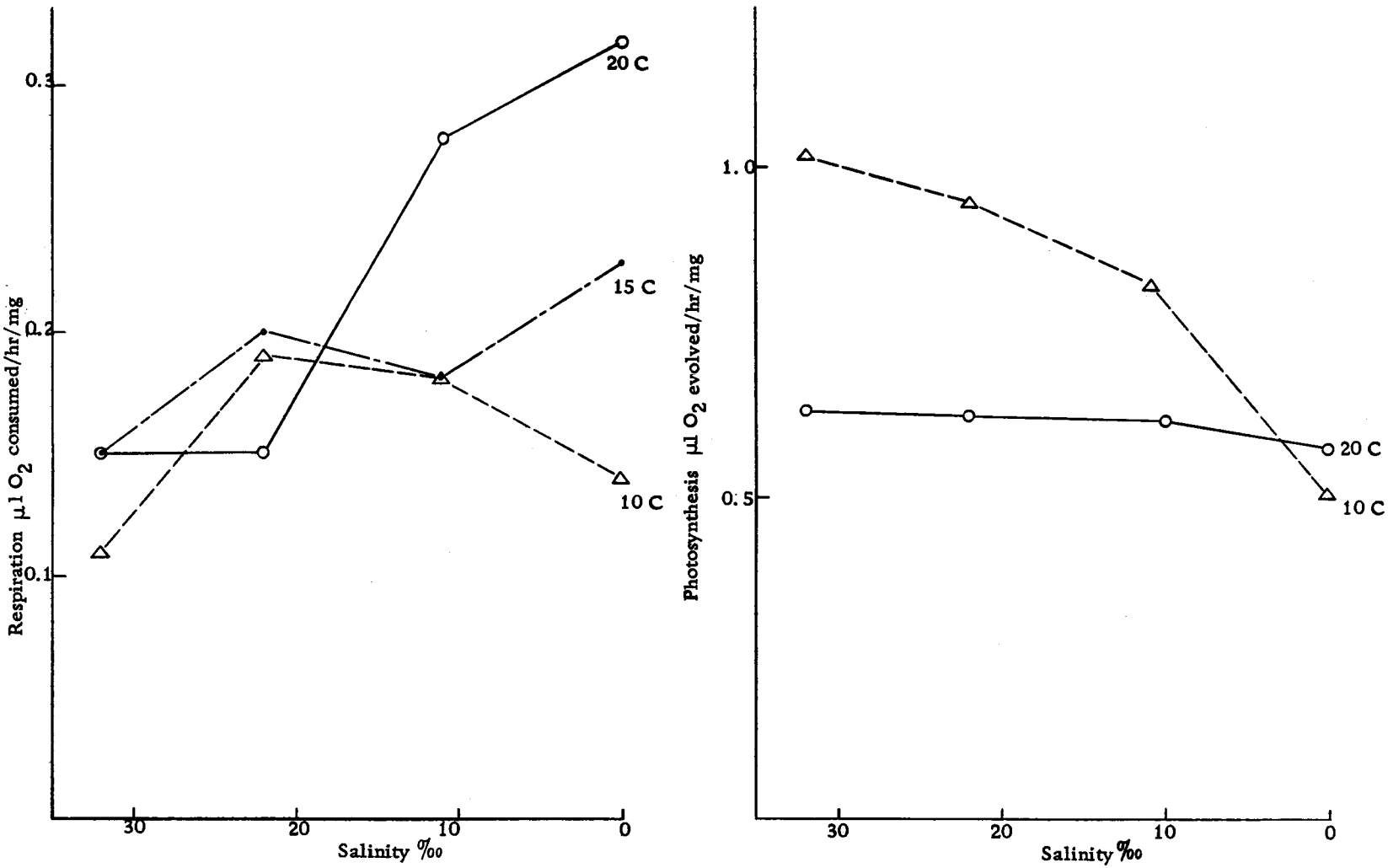


Figure 11. Rates of respiration and photosynthesis in Iridaea splendens at various salinities and temperatures as measured in the Gilson differential respirometer.

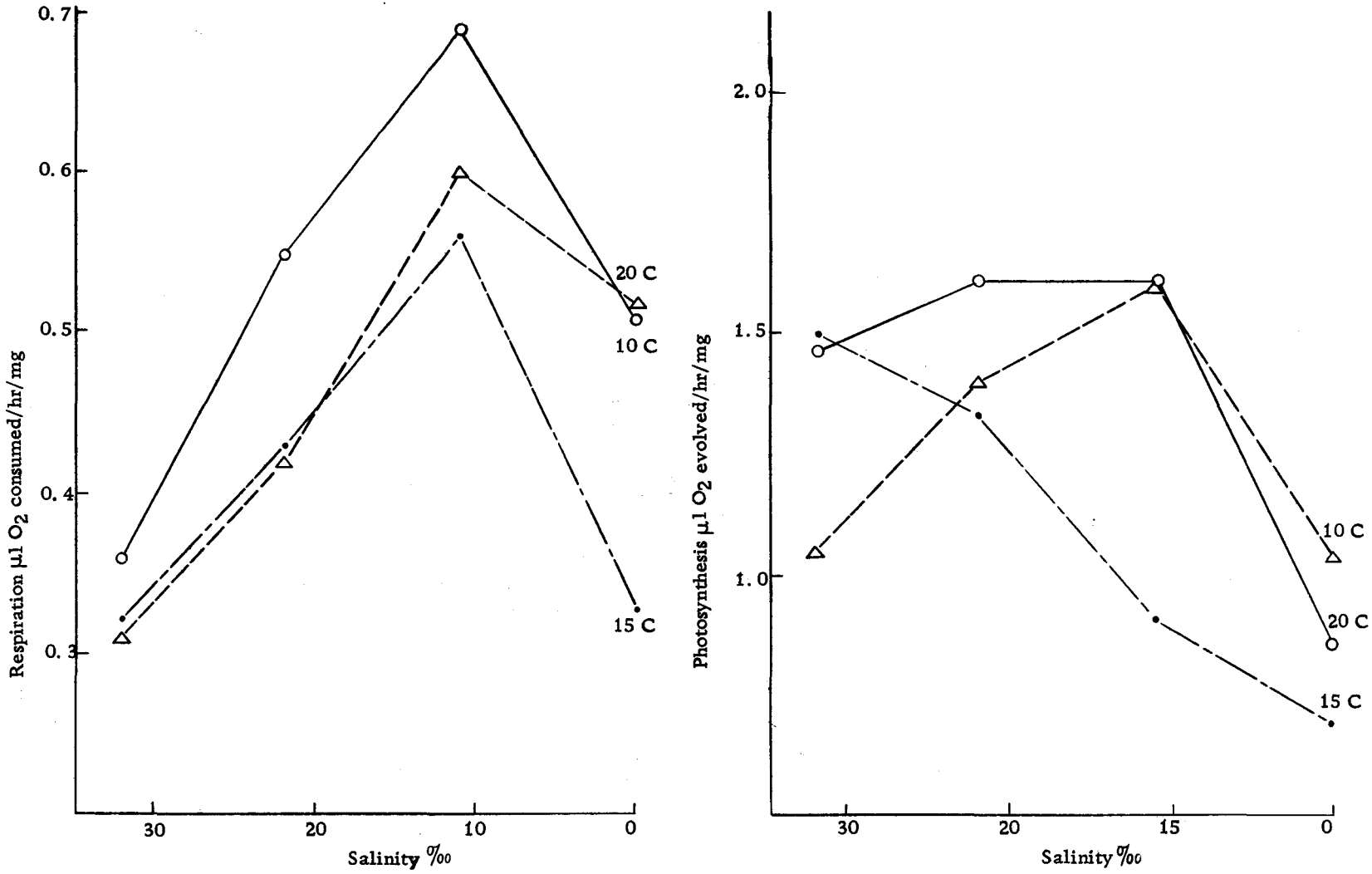


Figure 12. Rates of respiration and photosynthesis in Gigartina californica at various salinities and temperatures as measured in the Gilson differential respirometer.

in sea water with dilution to 11‰ salinity, but with further dilution the rates were depressed.

In 33‰ salinity, the rates of photosynthesis varied from 1.50 µl/hr/mg at 15 C to 1.06 µl/hr/mg at 10 C. At 10 and 20 C, the rates of photosynthesis increased above those in sea water with decreasing salinity to 11‰, but with further dilution the rates were below the rates obtained in sea water. At 15 C, photosynthesis decreased with decreasing salinity.

Results of P-R Chamber Studies

Construction of the P-R chamber and necessary supporting apparatus was completed August 10, 1965. Preliminary experiments were immediately initiated and followed by the studies that are to be presented. Rates of photosynthesis and respiration were determined at hourly intervals at salinities above 30‰, or sea water, and in dilutions of approximately 22‰, 11‰, and in less than 5‰, at temperatures of 10, 15, and 20 C. Data obtained at 10 C are lacking in three of the eight species studied because of malfunction of the cooling system. It was difficult to control precisely the temperature over the duration of the experiment, consequently for each experiment the temperature range and mean temperature are given in Table 1, but in the text the three temperatures will be referred to as 20, 15, and 10 C.

Table 1. Temperature ranges for P-R chamber experiments and mean temperature.

Species	Temperature range over the duration of the experiment	Mean Temperature (°C)
E. linza	20.3 - 19.5	19.9
	15.5 - 14.9	15.3
U. expansa	20.8 - 19.9	20.4
	20.6 - 20.3	20.4
	15.4 - 15.0	15.2
	10.5 - 9.9	10.1
	15.6 - 15.5 adapted	15.6
A. marginata	20.2 - 19.5	19.8
	17.5 - 17.2	17.4
	14.8 - 14.4	14.6
	10.2 - 9.0	9.5
	15.8 -15.5 adapted	15.7
L. saccharina	21.0 - 20.8	20.9
	16.7 - 15.5 average of 2 runs	15.8
	11.0 - 10.0	10.2
	16.5 - 16.0 adapted	16.2
S. muticum	21.0 - 20.6	20.9
	15.3 - 14.9	15.1
	10.5 - 9.5	9.8
	16.0 - 15.0 adapted	15.5
G. californica	20.0 - 19.5	19.8
	17.9 - 16.9	17.4
I. splendens	21.1 - 20.1	20.7
	16.3 - 15.1	15.9
	15.7 - 15.4 adapted	15.5
O. floccosa	20.8 - 20.2	20.5
	16.0 - 15.1	
	15.5 - 15.2	15.5

Ulva expansa (Figure 13). In sea water, the rates of respiration varied from 5.46 mg/hr/g at 20 C to 2.61 mg/hr/g at 10 C. The rates of respiration, at 10 and 15 C, were higher in dilutions of 22 and 11‰ salinity while in salinities below 11‰, respiration was depressed at 15 C, but continued to increase at 10 C. At 20 C, the rate was reduced with decreasing salinities.

In sea water, the rates of photosynthesis varied from 14.6 mg/hr/g at 20 C to 7.1 mg/hr/g at 10 C. At 20 C, the rate of photosynthesis decreased with each salinity dilution. At 15 C, the rate was higher with dilution to 11‰ salinity, but was depressed with further dilution. At 10 C, the rate was higher with dilution to 25‰ salinity and subsequently depressed with further dilution.

Enteromorpha linza (Figure 14). In sea water, the rates of respiration varied from 7.04 mg/hr/g at 20 C to 1.49 mg/hr/g at 15 C. At 15 and 20 C, the rates of respiration were enhanced with dilution to 11‰ salinity, but were depressed with further dilution.

In sea water, the rates of photosynthesis varied from 10.95 mg/hr/g at 20 C to 10.95 mg/hr/g at 15 C. At both temperatures, the rates were only slightly altered with dilution to 11‰ salinity, but further dilutions markedly reduced the rates.

Laminaria saccharina (Figure 15). In sea water, the rates of respiration varied from 1.80 mg/hr/g at 20 C to 0.51 mg/hr/g at 10 C. At 15 and 20 C, the rates of respiration were increased

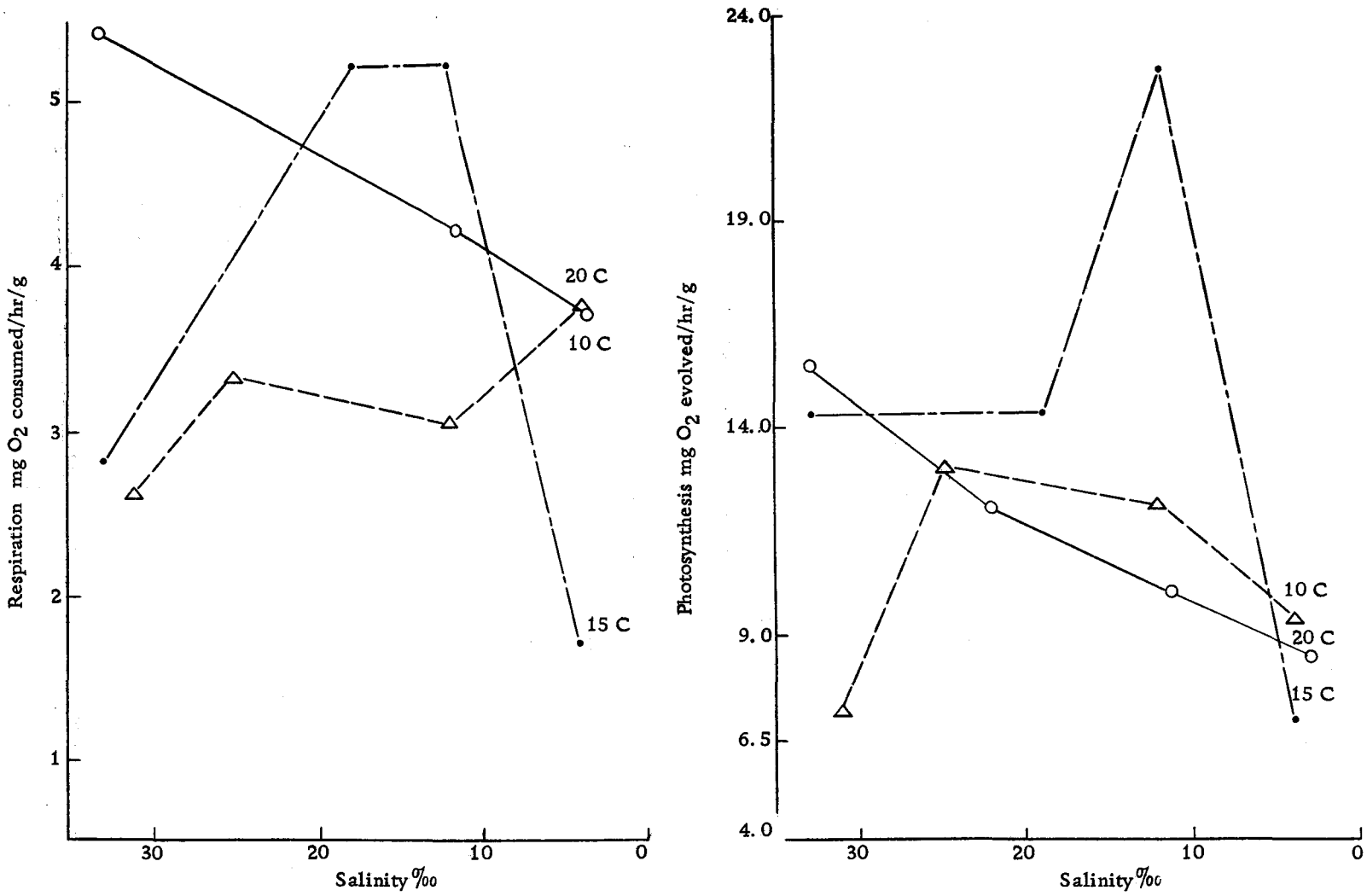


Figure 13. Rates of respiration and photosynthesis in Ulva expansa at various salinities and temperatures as measured in the P-R chamber.

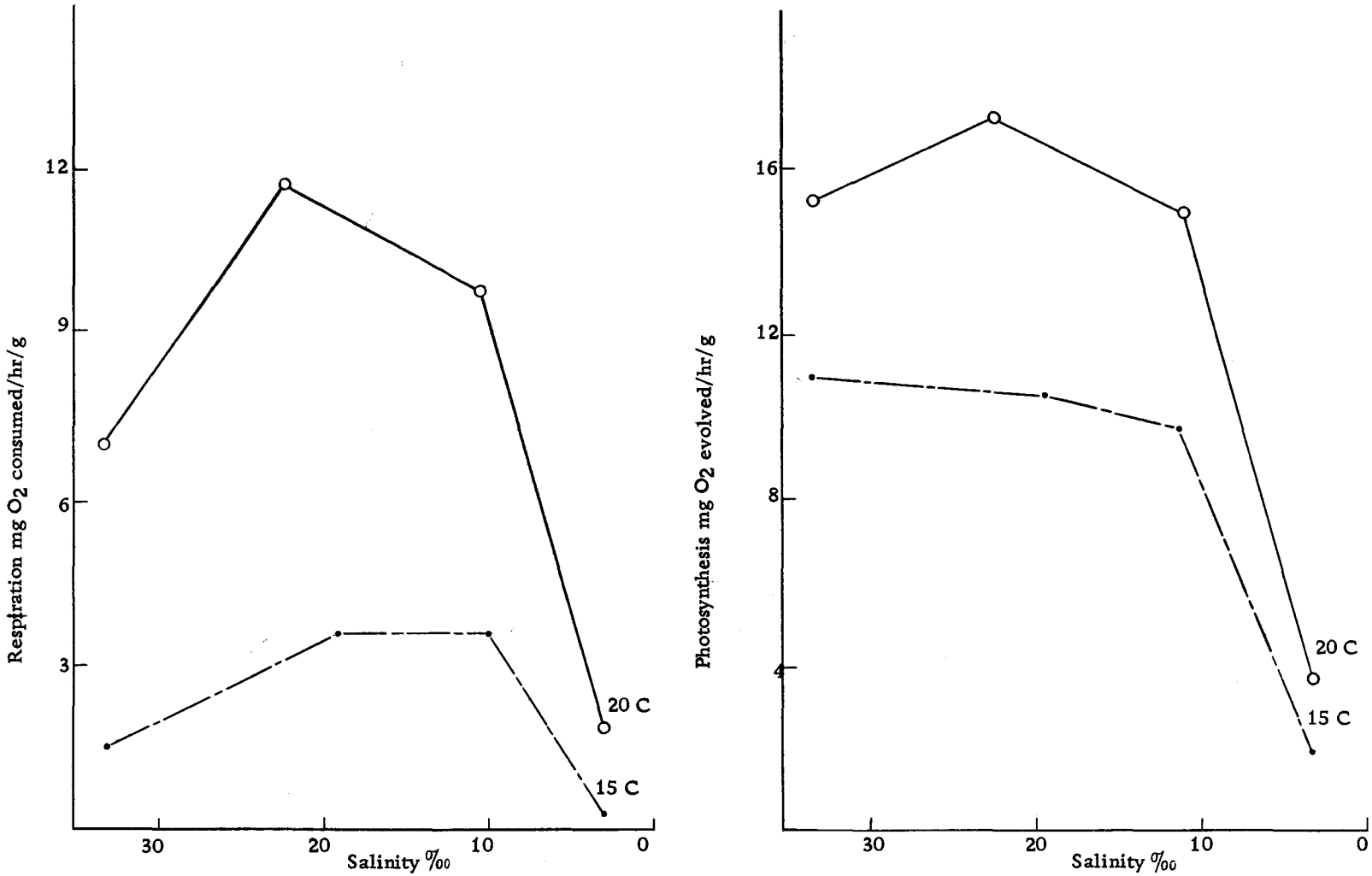


Figure 14. Rates of respiration and photosynthesis in Entermorpha linza at various salinities and temperatures as measured in the P-R chamber.

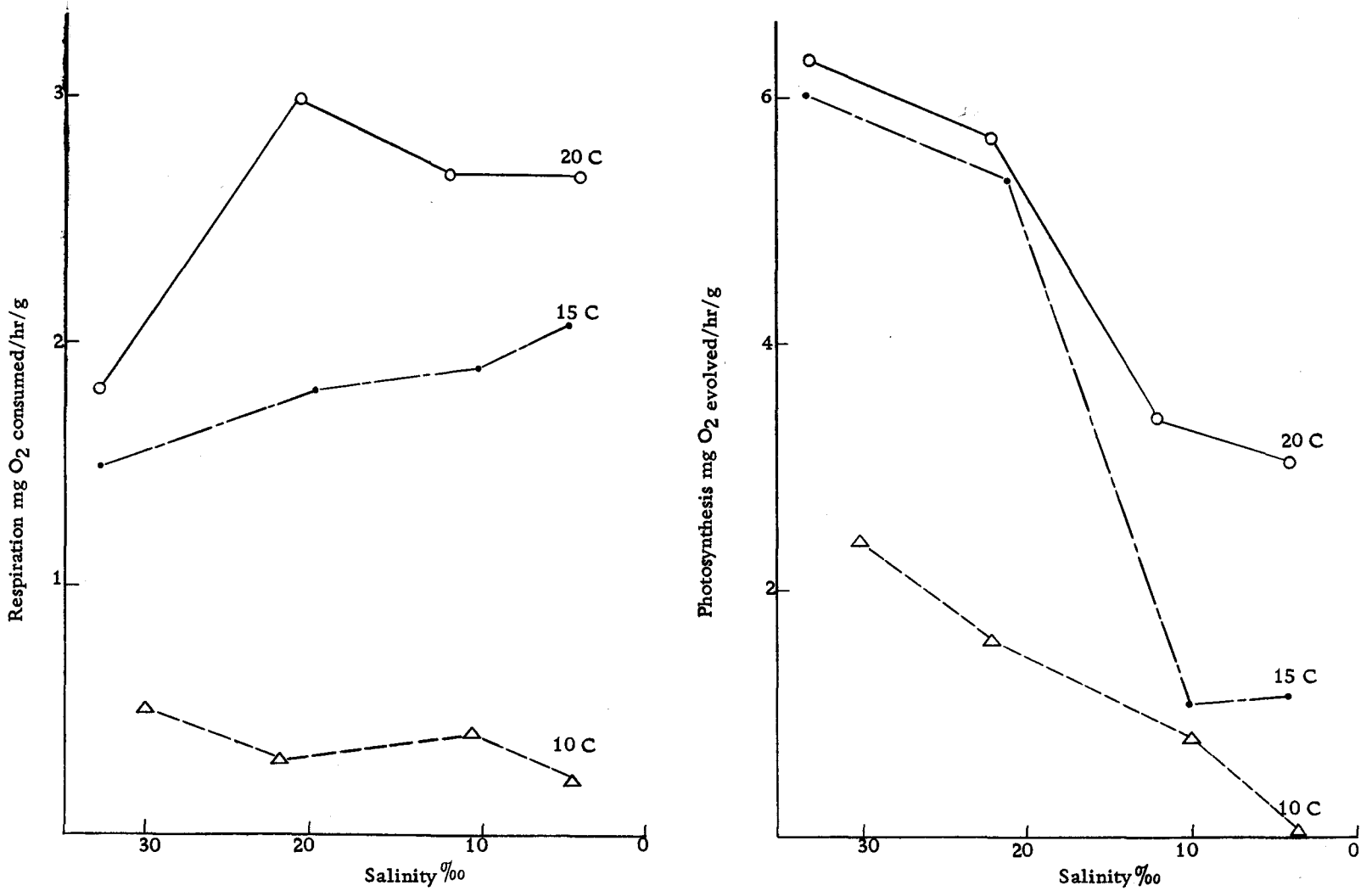


Figure 15. Rates of respiration and photosynthesis in Laminaria saccharina at various salinities and temperatures in the P-H chamber.

with salinity dilution, but at 10 C they were depressed.

In sea water, the rates of photosynthesis varied from 6.31 mg/hr/g at 20 C to 2.32 mg/hr/g at 10 C. At all temperatures, the rates of photosynthesis decreased at lower salinities.

Sargassum muticum (Figure 16). In sea water, the rates of respiration varied from 1.84 mg/hr/g at 20 C to 0.49 mg/hr/g at 15 C. At all temperatures, the rates of respiration increased with decreasing salinities, but the response was greater at 15 C than at 10 and 20 C.

In sea water, the rates of photosynthesis varied from 5.59 mg/hr/g at 15 C to 2.10 mg/hr/g at 10 C. Photosynthesis was not markedly altered with dilution to 22‰ salinity, in fact the rates at 10 and 20 C were slightly higher, but with further dilution, the rates at all temperatures were markedly depressed. At 20 C the rate at each dilution was intermediate between 10 and 15 C.

Alaria marginata (Figure 17). In sea water, the rates of respiration varied from 2.86 mg/hr/g at 20 C to 0.26 mg/hr/g at 10 C. At 20 C, the rate of respiration was increased with salinity dilution to 10‰ and depressed with further dilution. At 15 C, the rate was not significantly altered by dilutions of salinity. At 10 C, the rate was slightly higher at dilutions of less than 5‰ salinity.

In sea water, the rates of photosynthesis varied from 8.69 mg/hr/g at 20 C to 1.28 mg/hr/g at 10 C. Photosynthesis at 15 and

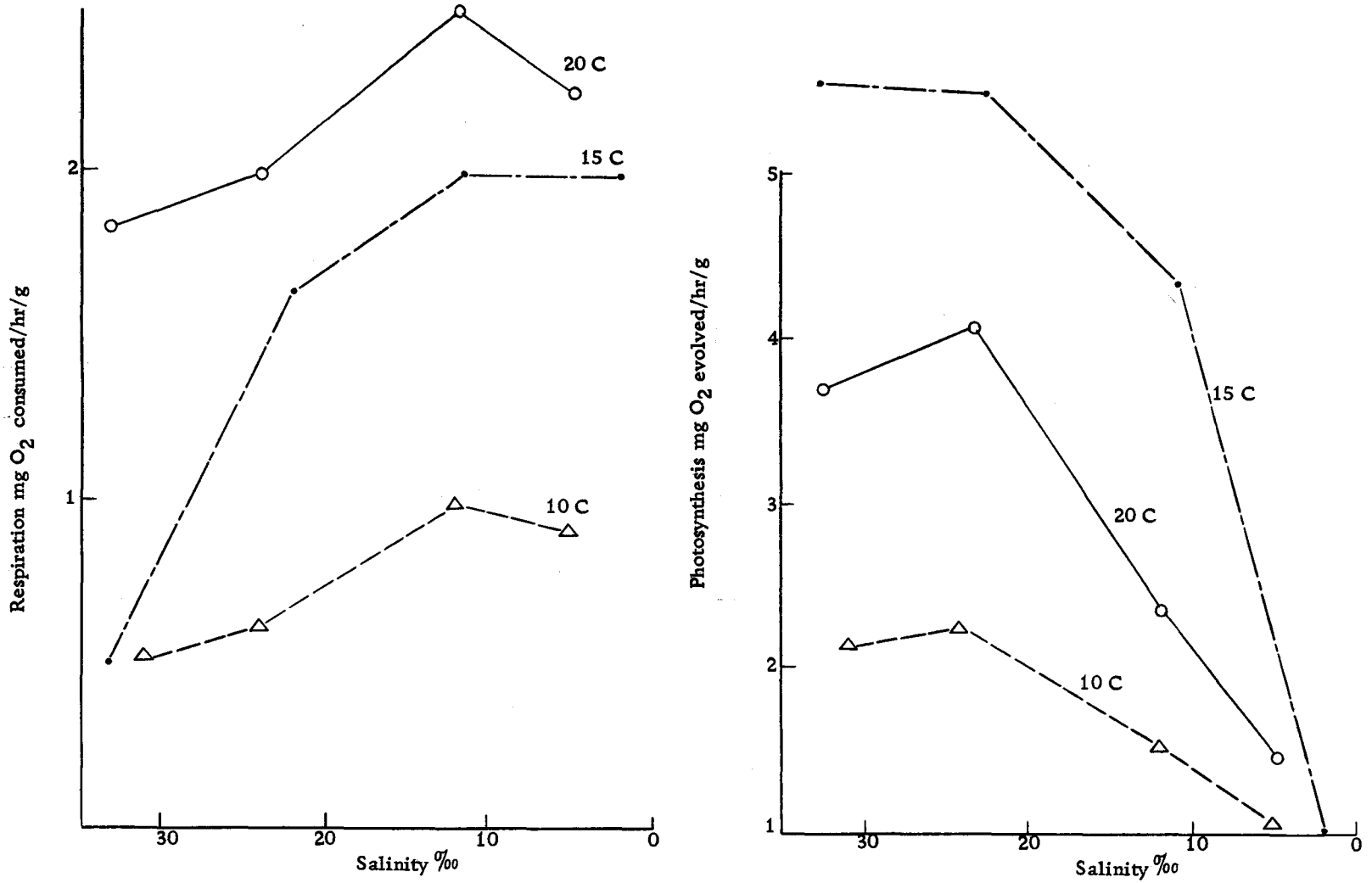


Figure 16. Rates of respiration and photosynthesis in Sargassum muticum at various salinities and temperatures as measured in the P-H chamber.

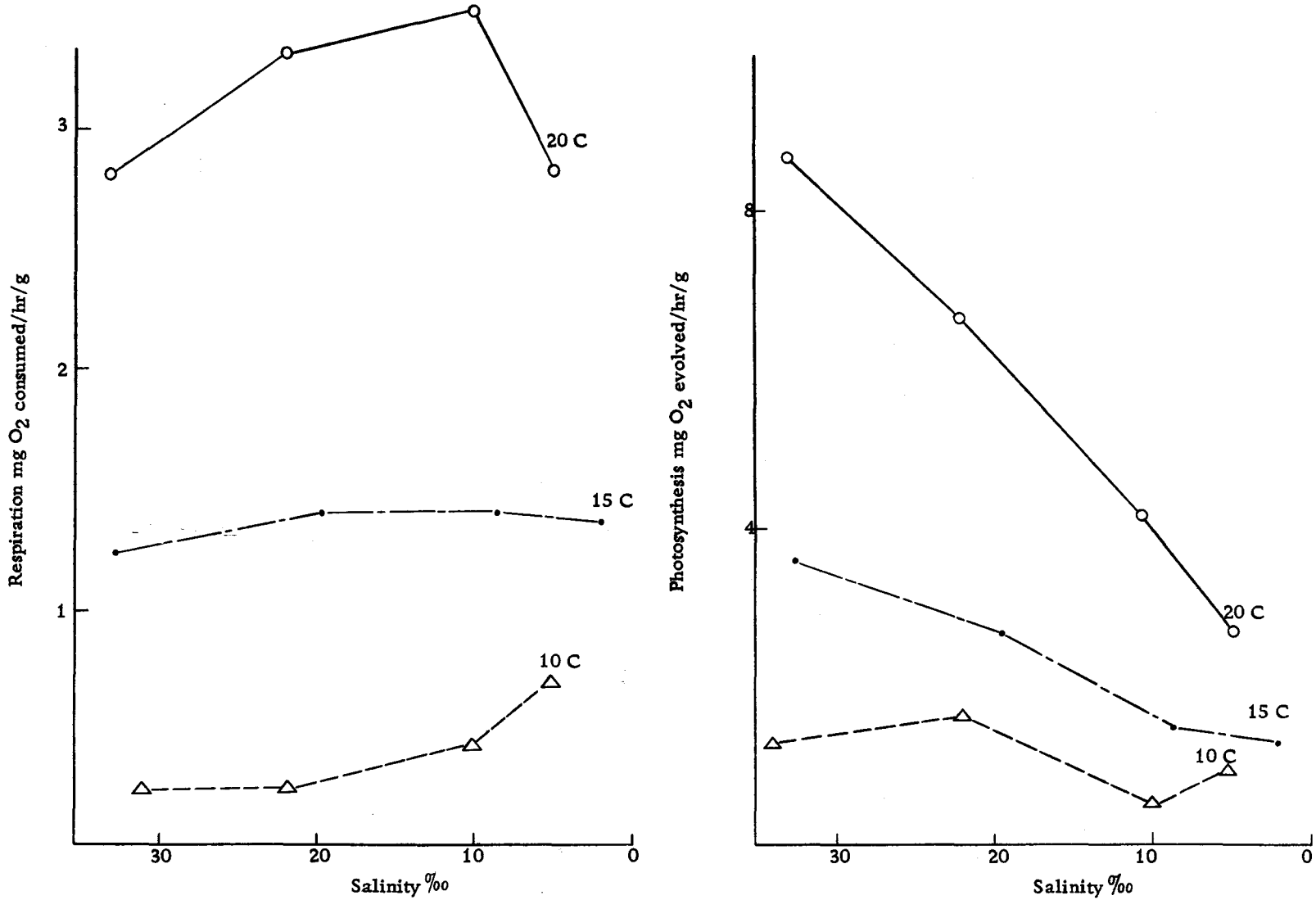


Figure 17. Rates of respiration and photosynthesis in Alaria marginata at various salinities and temperatures as measured in the P-R chamber.

and 20 C was depressed in a linear fashion by decreasing salinities, but at 10 C, the rate was not significantly altered.

Odonthalia floccosa (Figure 18). In sea water, the rates of respiration varied from 7.44 mg/hr/g at 20 C to 3.92 mg/hr/g at 15 C. At 20 C, the rate was not markedly altered with dilutions in salinity to less than 5‰, but at 15 C, the rate increased with salinity dilutions of less than 5‰.

In sea water, the rates of photosynthesis varied from 13.59 mg/hr/g at 20 C to 8.17 mg/hr/g at 15 C. At both temperatures the rates of photosynthesis increased with dilutions to 22‰ salinity, but with further dilution the photosynthetic activity decreased.

Iridaea splendens (Figure 19). In sea water, the rates of respiration varied from 2.04 mg/hr/g at 20C to 0.30 mg/hr/g at 15 C. At 20 C, the rate of respiration decreased in dilutions of 23‰ salinity and with further dilution the rate increased again to a value slightly less than that obtained in sea water. At 15 C, the rate increased with dilutions to less than 5‰ salinity.

In sea water, the rates varied from 6.27 mg/hr/g at 20 C to 2.81 mg/hr/g at 15 C. At both temperatures, the rates of photosynthesis were depressed with decreasing salinities.

Gigartina californica (Figure 20). In sea water, the rates of respiration varied from 2.65 mg/hr/g at 20 C to 1.01 mg/hr/g at 17 C. At 20 C, the rate of respiration increased with decreasing

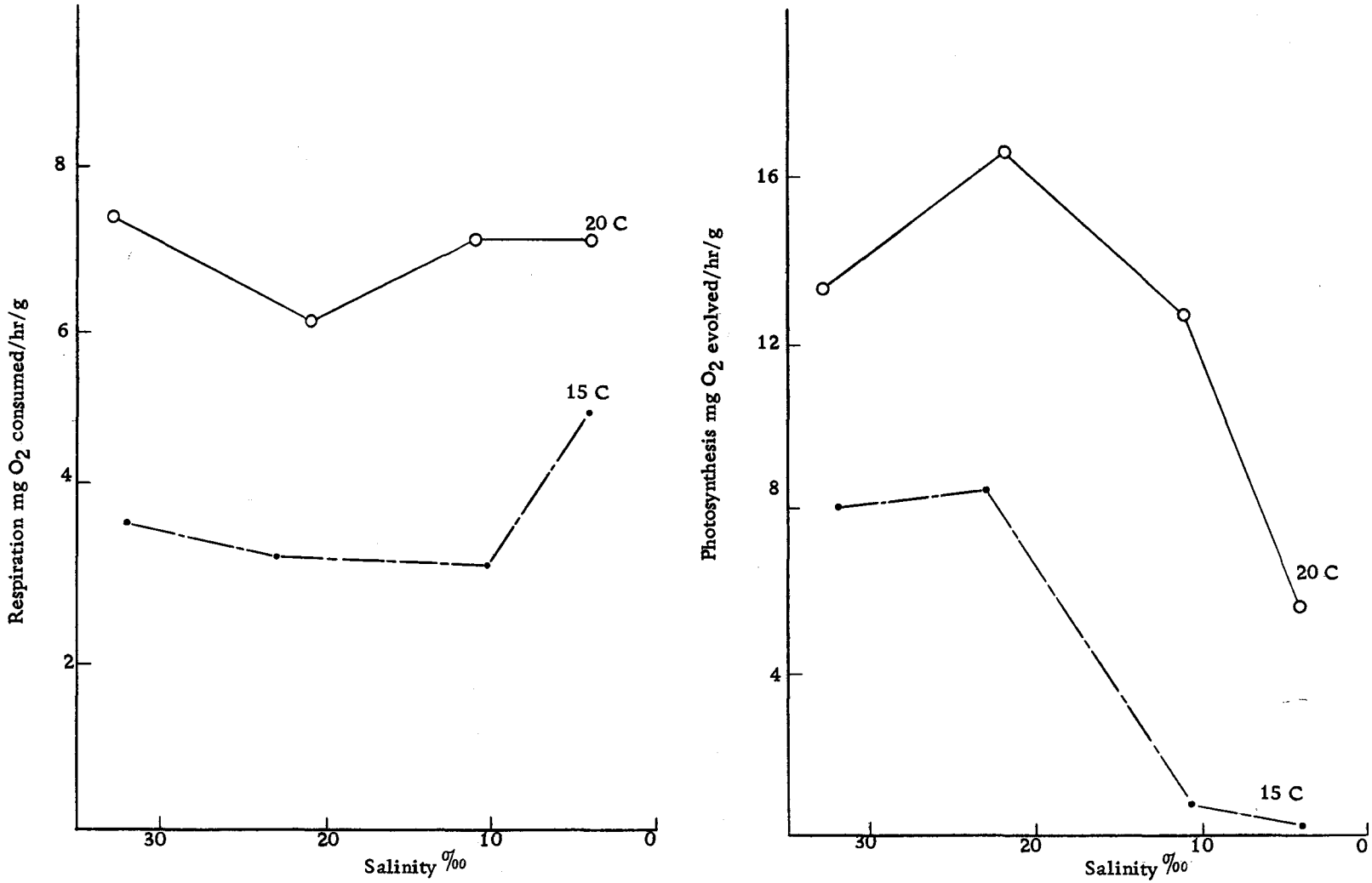


Figure 18. Rates of respiration and photosynthesis in Odonthalia floccosa at various salinities and temperatures as measured in the P-R chamber.

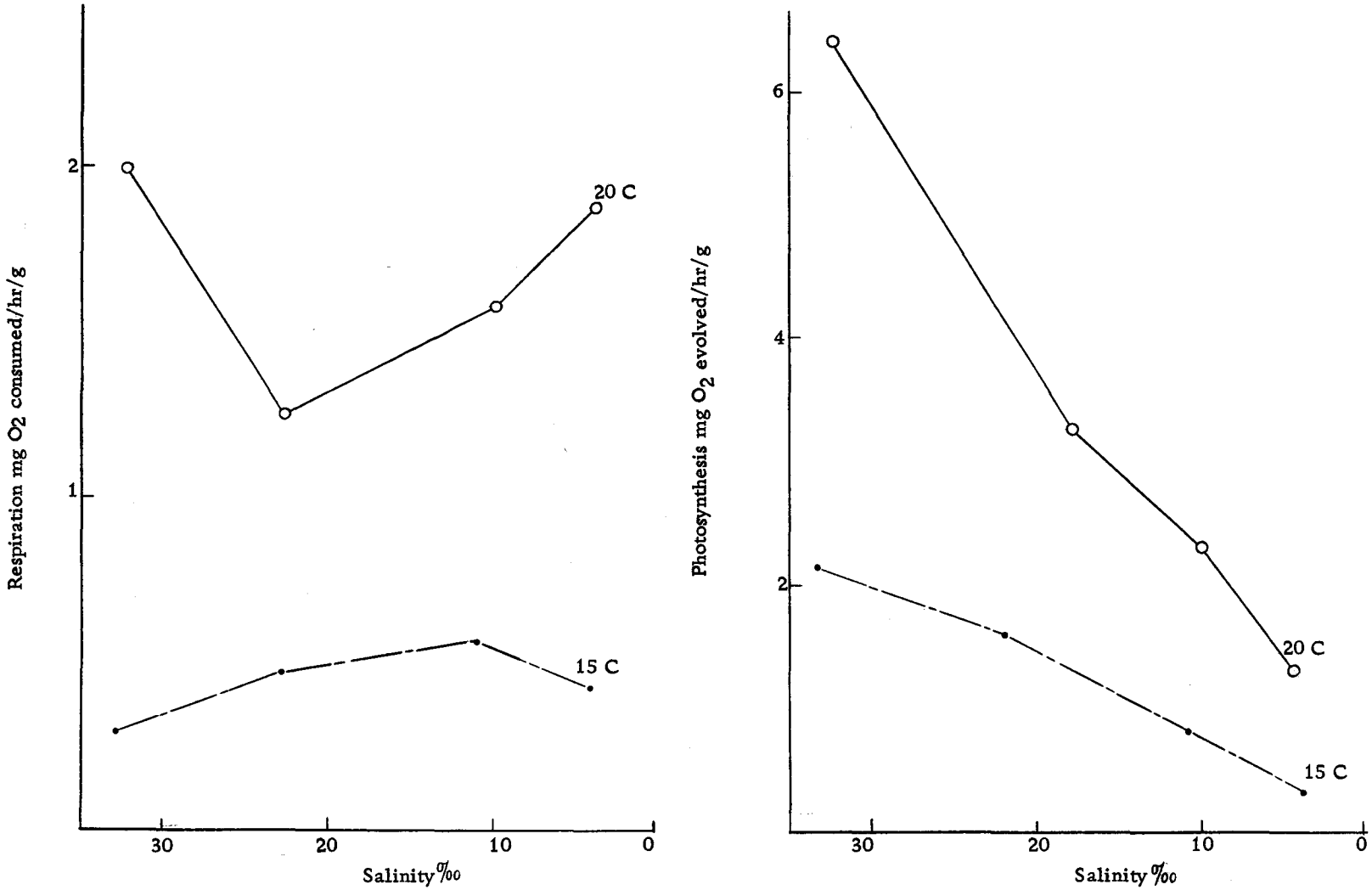


Figure 19. Rates of respiration and photosynthesis in Iridaea splendens at various salinities and temperatures as measured in the P-R chamber.

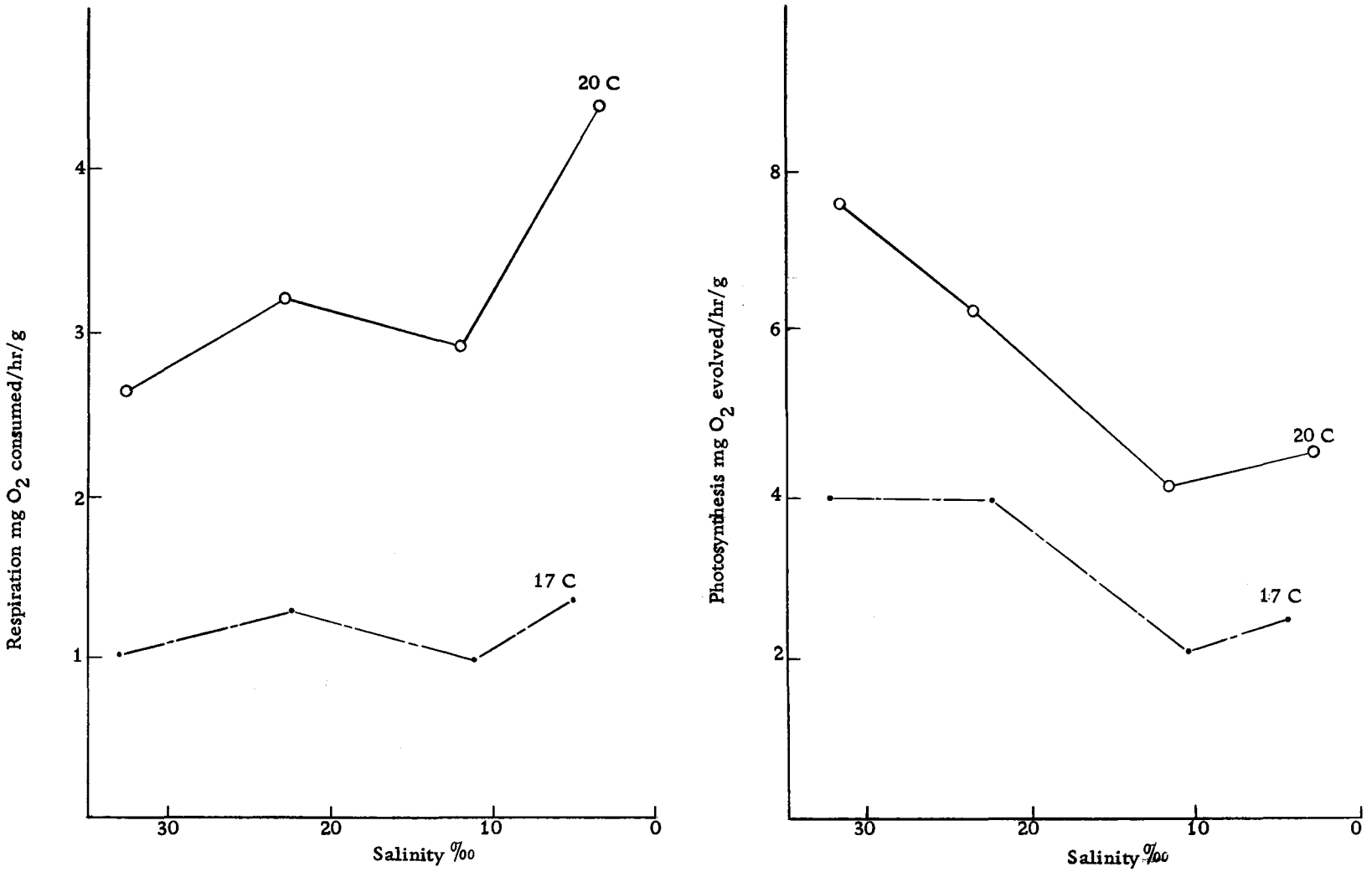


Figure 20. Rates of respiration and photosynthesis in Gigartina californica at various salinities and temperatures as measured in the P-R chamber.

salinities, but at 17 C, the rate was not significantly altered.

In sea water, the rates of photosynthesis varied from 7.65 mg/hr/g at 20 C to 4.04 mg/hr/g at 17 C. At both temperatures the rates of photosynthesis decreased with decreasing salinities.

Results of Adaptation Studies

Since the previous experiments were all short term and could have been measuring an osmotic shock reaction, a series of experiments on adaptation to reduced salinities were conducted with Ulva expansa, Laminaria saccharina, Sargassum muticum, Alaria marginata, and Iridaea splendens. The experiments were designed to determine whether the species under study were able to adapt and survive at a given salinity over a period of time. The plants were adapted in salinities of less than 30‰ for times varying from two to four days and oxygen consumption and evolution were measured under these conditions. In order to check the effects of adaptation, measurements of respiration and photosynthesis were taken in sea water, dilutions of approximately 22 and 11‰, and in fresh water. The results as they relate of non-adapted plants at the same temperature are shown in Figures 21 to 25 and in Appendix A.

Ulva expansa (Figure 21). This species was adapted in water of 8.9‰ salinity at 15.5 C for a period of two days and the rate of respiration under these conditions was 2.81 mg/hr/g. The rate of

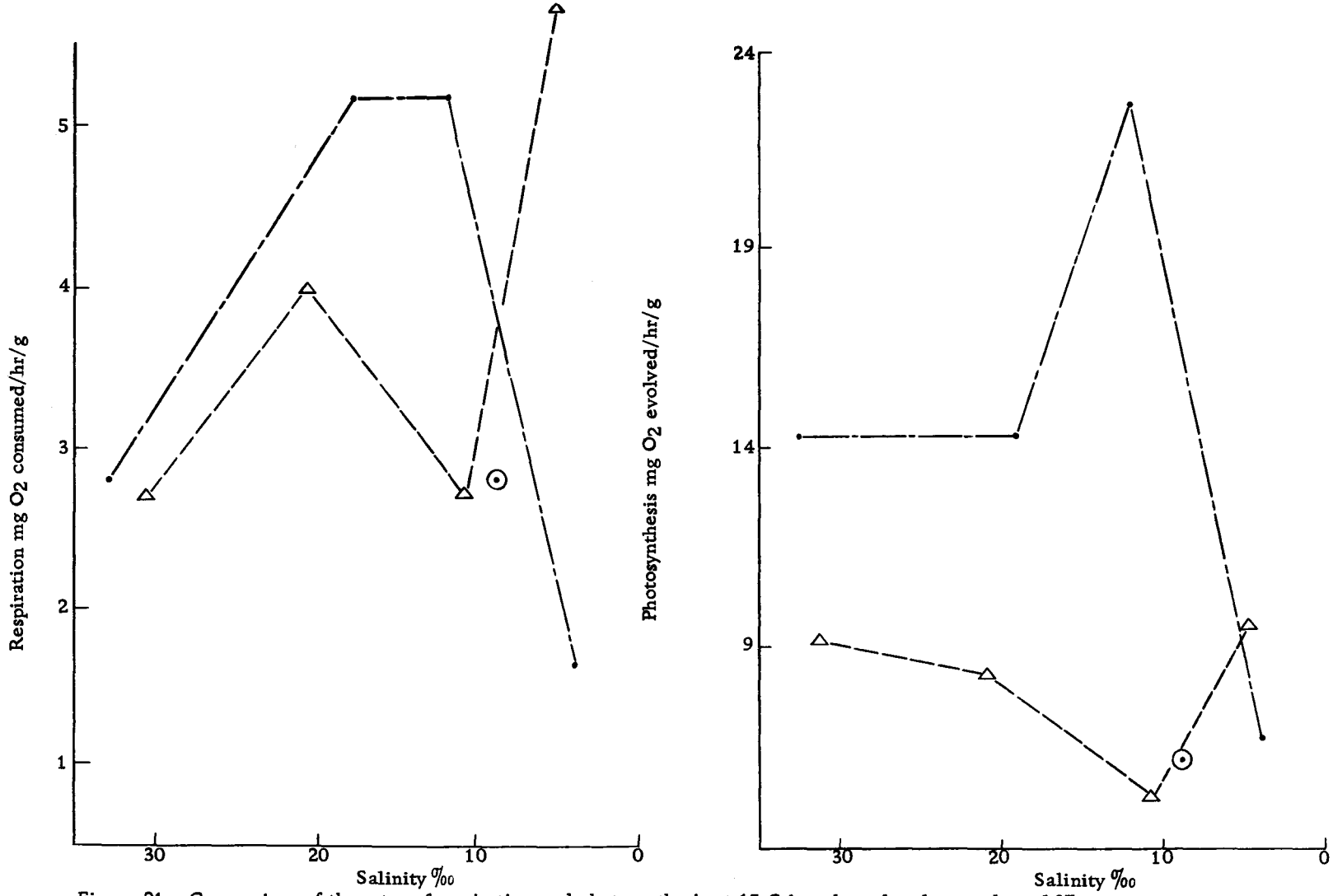


Figure 21. Comparison of the rates of respiration and photosynthesis at 15 C by adapted and non-adapted Ulva expansa.

△ Adapted rate • non-adapted rate ⊙ Rate and conditions of adaptation

respiration of the adapted plants in salinities ranging from sea water to fresh water, varied from 2.72 mg/hr/g in sea water to 14.4 mg/hr/g in fresh water, whereas the rate for non-adapted plants varied from 5.22 mg/hr/g at 12‰ to 1.70 mg/hr/g in fresh water.

The rate of photosynthesis under the conditions of adaptation was 6.04 mg/hr/g. The rate of photosynthesis of the adapted plants, in salinities ranging from sea water to fresh water, varied from 9.52 in sea water to 4.66 mg/hr/g in fresh water. Rates for non-adapted plants varied from 22.61 at 12‰ salinity to 6.96 mg/hr/g in fresh water.

Laminaria saccharina (Figure 22) This species was adapted in water of 27.8‰ salinity for two days at 16 C, and the rate of respiration under these conditions was 0.36 mg/hr/g. The rate of respiration of adapted plants in salinities ranging from sea water to fresh water, varied from 0.33 mg/hr/g in sea water to 1.49 mg/hr/g in fresh water, while that of non-adapted plants varied from 1.50 in sea water to 2.09 mg/hr/g in fresh water.

The rate of photosynthesis under the conditions of adaptation was 2.75 mg/hr/g. Rates of photosynthesis, in salinities ranging from sea water to fresh water, varied from 2.79 mg/hr/g in sea water to 1.08 mg/hr/g in fresh water for adapted plants and from 6.05 in sea water to 1.15 mg/hr/g in fresh water for non-adapted plants.

Sargassum muticum (Figure 23). This species was adapted

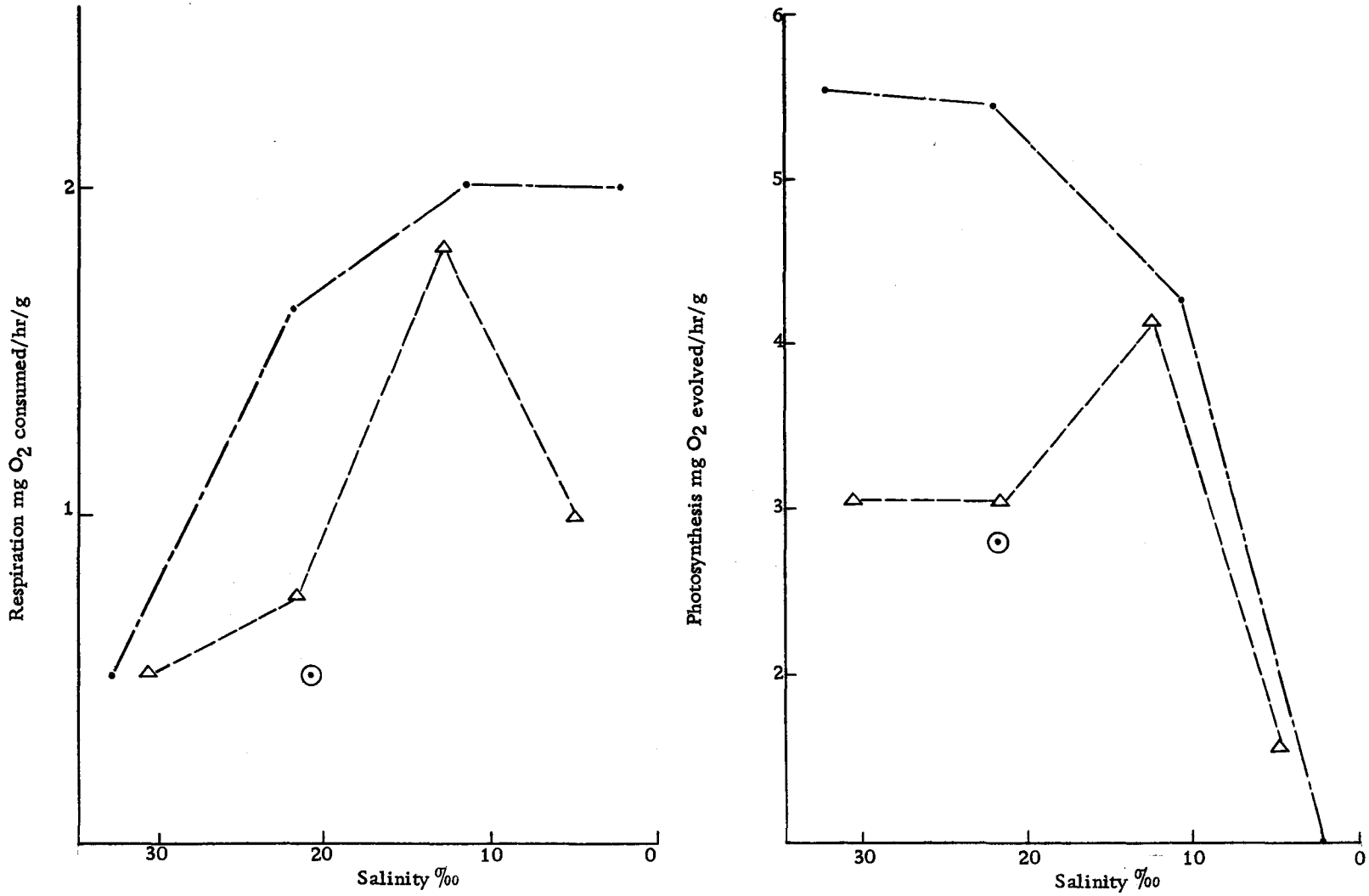


Figure 22. Comparison of the rates of respiration and photosynthesis at 15 C by adapted and non-adapted Sargassum muticum.
△ Adapted rate • non-adapted rate ⊙ Rate and conditions of adaptation

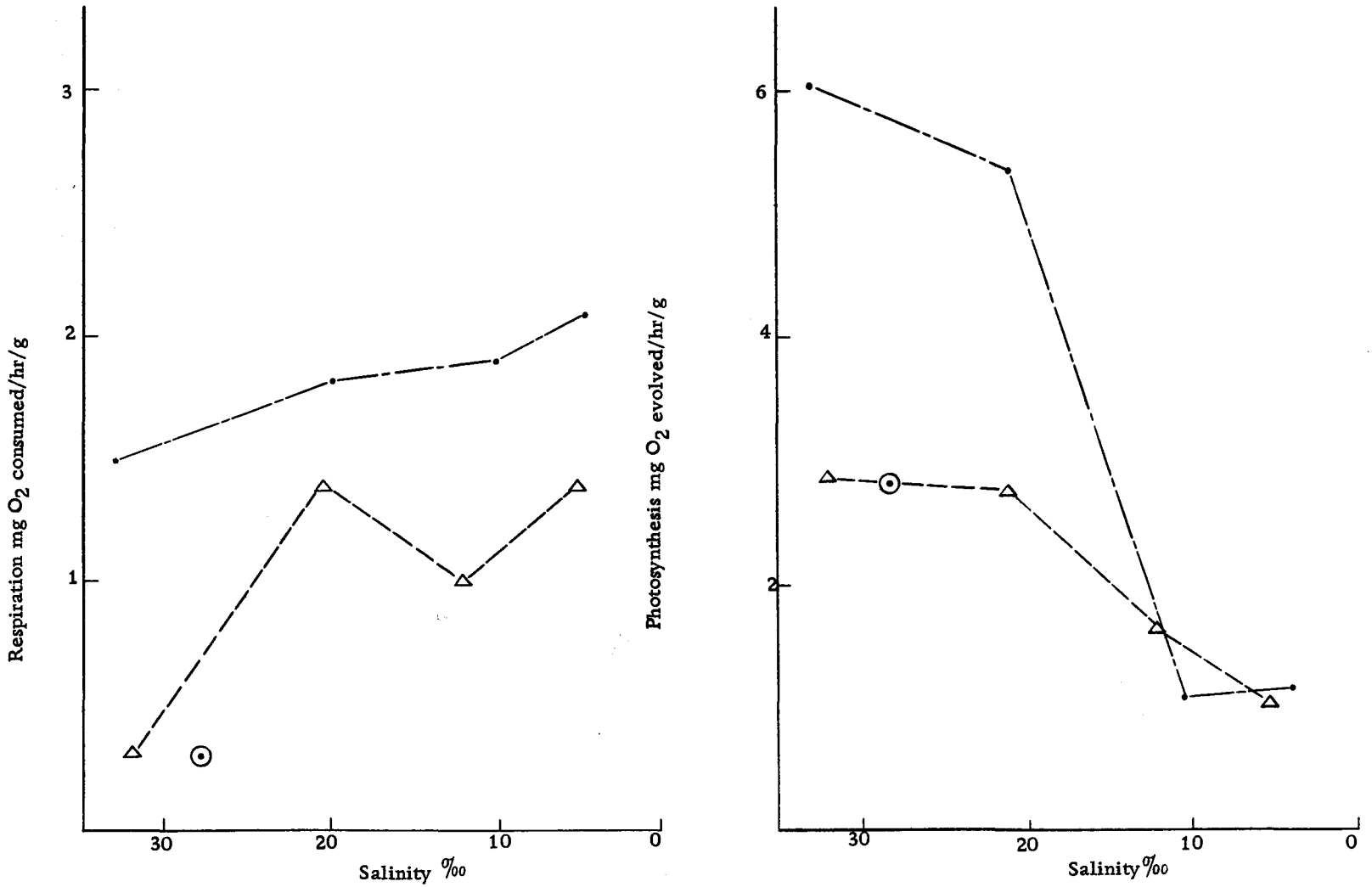


Figure 23. Comparison of the rates of respiration and photosynthesis at 15 C by adapted and non-adapted Laminaria saccharina.
△ Adapted rate • non-adapted rate ⊙ Rate and conditions of adaptation

in water of 21.6‰ salinity for four days at 15.5 C, and the rate of respiration under these conditions was 0.59 mg/hr/g. Rates of respiration of the adapted plants in salinities ranging from sea water to fresh water varied from 0.50 mg/hr/g in sea water to 1.82 mg/hr/g at 10‰ salinity, whereas rates for non-adapted plants varied from 0.49 mg/hr/g in sea water to 2.06 mg/hr/g in 12‰ salinity.

The rate of photosynthesis under the conditions of adaptation was 2.86 mg/hr/g. The rate of photosynthesis of the adapted plants in salinities ranging from sea water to fresh water, varied from 4.22 mg/hr/g in 10‰ salinity to 1.63 mg/hr/g in fresh water, whereas the rates for non-adapted plants varied from 5.59 mg/hr/g in sea water to 0.90 mg/hr/g in fresh water.

Alaria marginata (Figure 24). This species was adapted in water of 19‰ salinity at 15.5 C for a period of 30 hours, and the rate of respiration under these conditions was 0.45 mg/hr/g. The rate of respiration for adapted plants, in salinities ranging from sea water to fresh water, varied from 0.52 mg/hr/g in 21‰ salinity to 1.16 mg/hr/g in fresh water and for non-adapted plants between 1.26 mg/hr/g in sea water and 1.41 mg/hr/g in 9‰ salinity.

The rate of photosynthesis under the conditions of adaptation was 1.79 mg/hr/g. The rate of photosynthesis for the adapted plants, in salinities ranging from sea water to fresh water, varied from 1.29 mg/hr/g in sea water to 2.81 mg/hr/g in fresh water, whereas the

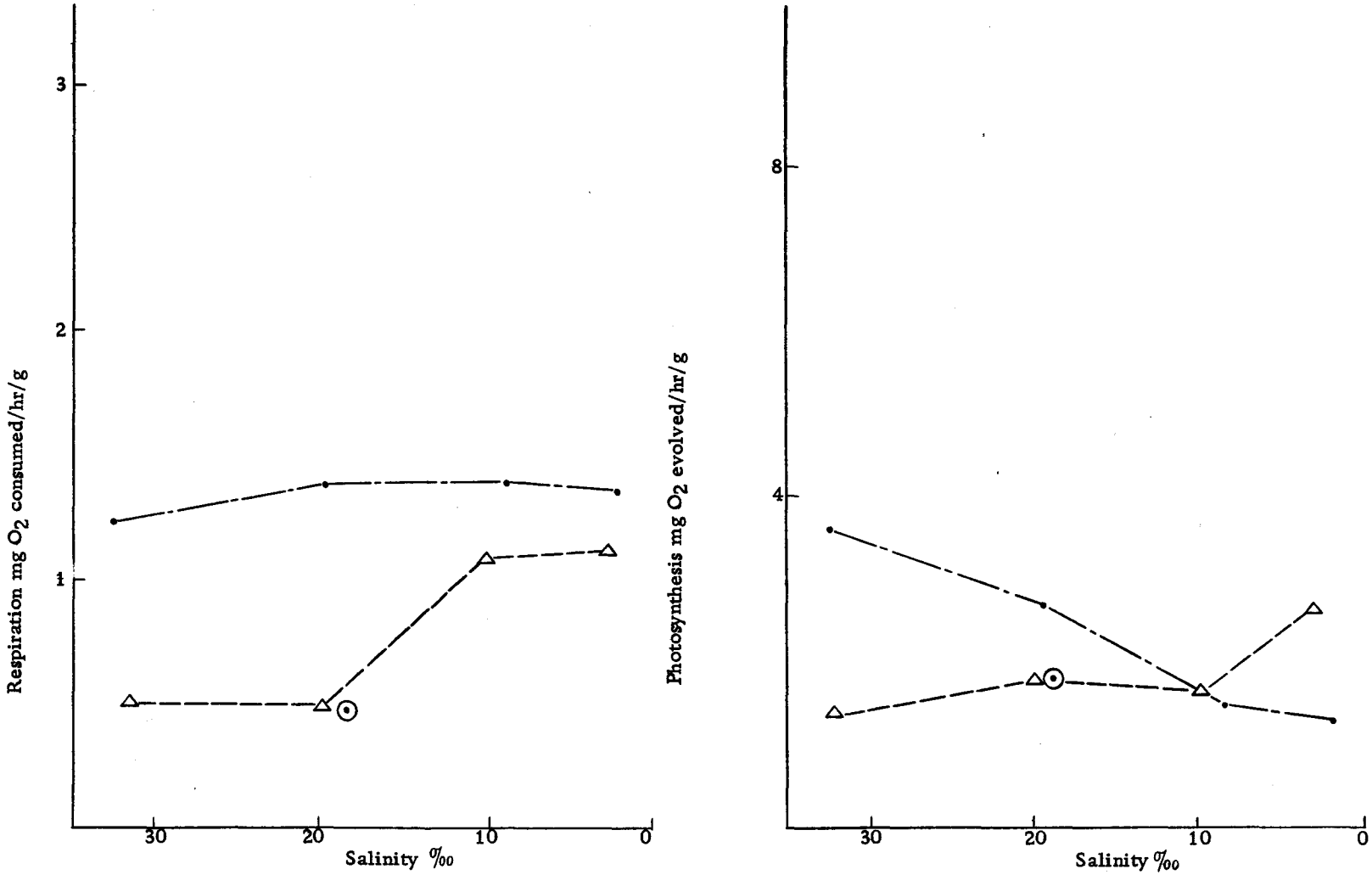


Figure 24. Comparison of the rates of respiration and photosynthesis at 15 C by adapted and non-adapted Alaria marginata.
△ Adapted rate • non-adapted rate ⊙ Rate and conditions of adaptation

rate for non-adapted plants ranged from 3.62 mg/hr/g in sea water to 1.28 mg/hr/g in fresh water.

Iridaea splendens (Figure 25). This species was adapted in water of 13‰ salinity at 15.5 C for a period of four days, and the rate of respiration under these conditions was 0.59 mg/hr/g. Respiration, in salinities ranging from sea water to fresh water, varied from 0.41 mg/hr/g in sea water to 0.69 mg/hr/g in fresh water for adapted plants, and from 0.29 mg/hr/g in sea water to 0.58 mg/hr/g in 11‰ salinity for non-adapted plants.

The rate of photosynthesis under the conditions of adaptation was 1.09 mg/hr/g. The rate of photosynthesis, in salinities ranging from sea water to fresh water, varied from 1.55 mg/hr/g in sea water to 0.34 mg/hr/g in fresh water for adapted plants, whereas the rate for non-adapted plants varied from 2.13 mg/hr/g in sea water to 0.24 mg/hr/g in fresh water.

In summary these studies showed that: a) rates of respiration of adapted plants when transferred to sea water were almost the same as under the conditions of adaptation; b) rates of respiration of adapted plants in salinities ranging from sea water to fresh water were lower than the non-adapted rate, except in the case of Iridaea in sea water and in the cases of Ulva and Iridaea in fresh water, c) rates of respiration in all cases were increased when the salinity was reduced below the salinity in which they were adapted; d) rates of

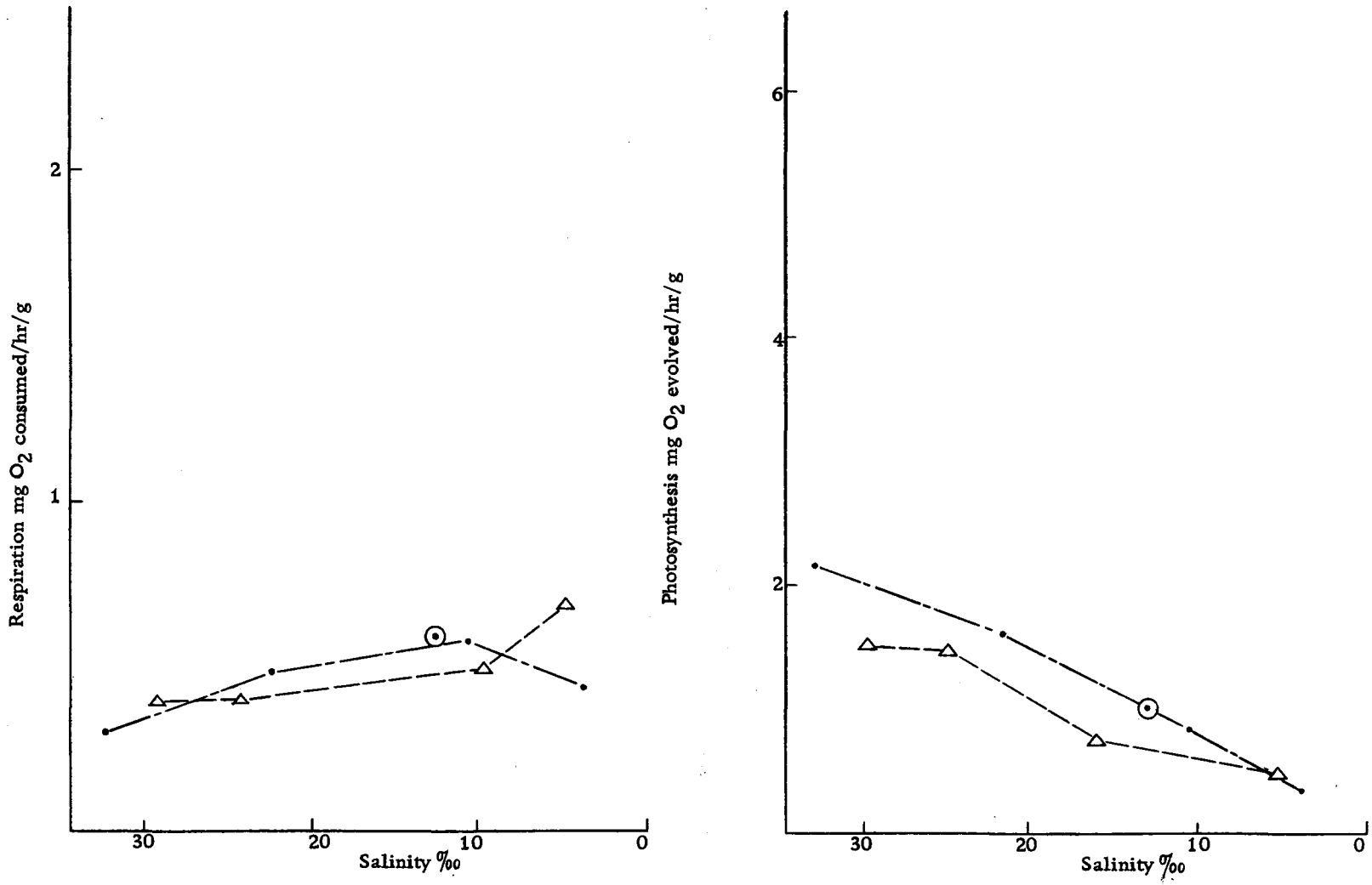


Figure 25. Comparison of the rates of respiration and photosynthesis at 15 C by adapted and non-adapted Iridaea splendens.
△ Adapted rate • non-adapted rate ⊙ Rate and conditions of adaptation

photosynthesis and respiration under the conditions of adaptation were lower than the rates of non-adapted plants under equivalent conditions; e) rates of photosynthesis of adapted plants when transferred to sea water approximated the rates under the conditions of adaptation; f) rates of photosynthesis of adapted plants in salinities ranging from sea water to fresh water were lower than rates for non-adapted plants, except in the cases of Ulva and Alaria in fresh water; and g) the rates of photosynthesis in Ulva, Sargassum and Alaria were increased in salinities lower than those in which the plants were adapted.

Field Studies

In Yaquina Bay and estuary three seasonal floras can be distinguished; 1) spring; 2) summer; 3) fall and winter. The largest number of species and the greatest biomass occurs during the spring and summer. From November to February the biomass is greatly diminished during peak occurrence of epiphytes and animal grazers, winter storms, low salinities, and short photoperiod. There is, however, a distinct winter flora. From visual observation it appears that there are two periods of decline and decay, one in the early summer of the spring vegetation, and another in the fall of the summer population. Evidence of this is seen in the windrows of debris that accumulate on the shores.

Information from the field collections and observations is presented under three topics: 1) the species present and their habitats, 2) spatial distribution and seasonal occurrence of species, and (3) tolerance of species toward variations of salinity and temperature.

Species Present and Their Habitats

Our knowledge of the algal species of the outer coast of Oregon is much more complete than our understanding of the flora of the estuaries. The marine algae of the Coasts of California, Oregon, and Washington have been studied by numerous workers in the field of marine phycology, but they have only incidentally considered estuarian forms. Doty (1947a, 1947b) and Sandborn and Doty (1944) have worked on the marine algae of Oregon.

The zones of vertical distribution of algae listed in Appendix B are in accordance with most phycological literature. The intertidal zone lies between high water and low water of the extreme spring tides. The sublittoral zone extends downward from the low water of the extreme low tides. Algae in the upper and mid-intertidal zones are usually exposed during low tides; those in the lower intertidal are only exposed occasionally; and those in the subtidal are never exposed. Depths in meters are determined from the mean low tide. The species present in Yaquina Bay, their habitat, and tidal zone are presented in Appendix B. A key to these species is

presented in Appendix C.

A very diverse flora exists in the Yaquina Bay and estuary. Some of the species common on the rocky outer coast of Oregon that are conspicuously lacking in Yaquina Bay include the following: Codium setchellii Gardner, Codium fragile (Suring) Hariot, Ralfsia sp., Coilodesme californica (Ruprecht) Kjellman, Desmarestia sp., Pleuorphycus gardneri Setchell and Saunders in Saunders, Costaria costata (Turner) Saunders, Macrocystis integrifolia Bory, Lessoniopsis litoralis (Farlow and Setchell) Reinke, Postelsia palmaeformis Ruprecht, Pterygophora californica Ruprecht, Cystoseira osmundacea (Menzies) C. Agardh, Endocladia muricata (Harvey) J Agardh, the coralline algae with three exceptions, Plocamium violaceum Farlow, Farlowia mollis (Harvey and Bailey) Farlow and Setchell, Ahnfeltia plicata (Hudson) Fries, Stenogramme californica Harvey, Botryoglossum farlowianum (J. Agardh) DeToni, and Odonthalia lyallii (Harvey) J. Agardh.

Among the algae collected in the Yaquina estuary the following are new records for the coast of Oregon: Chaetomorpha aerea, Haplospongidion gelatinosum, Halymenia californica, and Gracilaria verrucosa.

Distribution of Species and Seasonal Occurrence

Approximately 90% of the species of Yaquina Bay and estuary

are found in the area from the end of the jetties at the mouth of the estuary to the Yaquina Bay bridge. Most specis in this area are characteristic of the open coast and may be considered estuarine invaders. A few forms such as Ulva expansa, Laminaria saccharina, Sargassum muticum and Gracilariopsis sjoestedtii are found only in areas such as this. From the Yaquina Bay bridge to Marker 21, there is a transition zone containing both marine and brackish water species. Above Marker 21 to the Toledo bridge there is a brackish water flora.

The distribution of some species may be limited by the lack of suitable substrate. Most benthic plants require a firm surface for attachment, and the substrate must be free of silt for the sporlings to develop. In the estuary available substrates include large boulders on a shifting sandy bottom at the north and south jetties, a sandstone reef with tidepools between the north jetty and Yaquina Bay bridge, rock rubble of the fills along the estuary, and mud with some cobble and other debris from Marker 15 to Elk City. Shells, pilings, logs, and dock floats also provide common substrates. The log floats of docks along the estuary constitute a unique habitat, as the organisms colonizing them are never exposed by the tides and always remain near the surface where the light intensity is high and the problem of siltation is relatively minor. The general effect is of a sub-tidal habitat. Algae are absent, with a few exceptions, in the lower

intertidal zone along the main channel from Marker 15 to the Toledo bridge, probably because of lack of suitable substrate, constant exposure to currents, and the presence of moving silt. A rather lush flora of Fucus, Enteromorpha, Chaetomorpha, Gracilaria and Monostroma occurs, however, in protected locations in side channels and sloughs in this area.

Perennating vegetative structures were observed in a number of forms during the winter. The encrusting basal disks of Heterochordaria, Petalonia, and Corallina were common on the jetty during December, January, and February and resumed growth in the spring. Species of Iridaea and Gigartina persisted over the winter as basal holdfasts and resumed growth in the spring. Laminaria saccharina on the floats of the port docks died back to the stipe and resumed growth in the spring in competition with the young germlings. Laminaria setchellii and L. sinclarii showed similar responses. The holdfast and basal portions of the stipe of Egregia persisted through the winter, often in a battered and highly epiphytized state, resuming growth in the spring. Sargassum died back to its holdfast and a few basal branches and resumed growth in the spring. The greatest changes occurred in the upper and middle intertidal zone. Most of the forms were eaten or beaten back to their holdfasts during winter. Many other species, particularly some of the red algae in the lower intertidal and subtidal, were

not markedly affected by winter conditions and continued growth and reproduction throughout the year.

The spatial and seasonal distribution of the algal flora of Yaquina Bay are presented for each species in Table 2. The collecting stations in Table 2 are shown in Figure 26. The distance from the mouth of the estuary of these stations and other stations in the estuary is shown in Appendix D.

Temperature and Salinity Tolerance of the Macro-Algae of Yaquina Bay

Data concerning the temperature and salinity regimes in the estuary have been used together with data of collection of the algal inhabitants to determine their distribution with relation to temperature and salinity (Table 3). The results showed that the majority of the species were found in 35 to 30‰ salinity and of these 69 were red-algae, 33 brown-algae, and 23 green-algae. Analysis of the temperature data showed that the majority of the species were found in 10-12 C of these 70 were red-algae, 32 brown-algae, and 24 green-algae. Only eight species were found in salinities ranging from 35 to 5‰, and only 14 species were found in temperatures ranging from 20 to 10 C, all other species had narrower tolerance ranges.

Table 2. Spatial distribution and seasonal occurrence of the macro-algae in Yaquina Bay. The collection location and reference navigational markers are shown in Figure 26. By scanning these data vertically it is possible to appreciate the community composition at various points in the estuary. Sp = Spring, S = Summer, F = Fall, W = Winter. Lower case letters indicate presence of species but not in any abundance.

Species	6th spur	3rd spur	1st spur N. J. flat Bridge	C. G. Dock #12 Port Docks	#15	#21	#25	#27	#32	#37	#47	Toledo Br.
Ulothrix implexa	Sp											
Monostroma fuscum			F									
Monostroma oxyspermum							Sp S W F					
Monostroma zostericola				SF								
Enteromorpha clathrata					Sp	S F W						
Enteromorpha compressa							S F W					
Enteromorpha intestinalis f. clavata						Sp	S F W					
Enteromorpha intestinalis f. cylindricea				Sp S								
Enteromorpha linza				Sp S F W								
Enteromorpha marginata							S					
Enteromorpha tubulosa						S F						
Ulva angusta				Sp	S F W							
Ulva expansa				Sp	S F W							
Ulva fenestrata		S F W										
Ulva lobata	Sp	S F										
Ulva rigida		S F W										
Ulva taeniata	Sp	S F W										
Rhizoclonium riparium							Sp	F W				
Urospora penicilliformis	S											
Chaetomorpha aerea								Sp S F W				
Chaetomorpha tortuosa	Sp	F W										
Cladophora gracilis					Sp							

Table 2. (Continued)

Species	6th spur	3rd spur	1st spur N. J. flat Bridge	C. G. dock #12 Port Docks	#15	#21	#25	#27	#32	#37	#47	Toledo Br.
Cladophora trichotoma	Sp S	F W										
Spongomorpha coalita		Sp	S F									
Spongomorpha spinescens		Sp										
Bryopsis corticulans			Sp S	F								
Pylaiella littoralis				Sp								
Ectocarpus acutus		Sp										
Ectocarpus confervoides		Sp										
Ectocarpus dimorphus			F W									
Ectocarpus granulosus			Sp W									
Ectocarpus granulosoides					W							
Ectocarpus mucronatus		Sp										
Ectocarpus oviger			W									
Streblonema pacificum	F	W										
Haplospongidiun gelatinosum	Sp S	F W										
Hecatonema variabile			W									
Elachistea fueciola					Sp	S F W						
Leathesia difformis		Sp	S									
Haplogloia andersonii			Sp									
Heterochordaria abietina	Sp	S F W										
Desmarestia munda				Sp S	F							
Soranthera ulvoidea	S											
Scytosiphon lomentaria			S	F								
Petalonia debilis		Sp S F W										
Dictyosiphon chordaria			Sp									
Laminaria saccharina				Sp S F w								
Laminaria setchellii	Sp	S F w										
Laminaria sinclairii	Sp	S F w										

Table 2. (Continued)

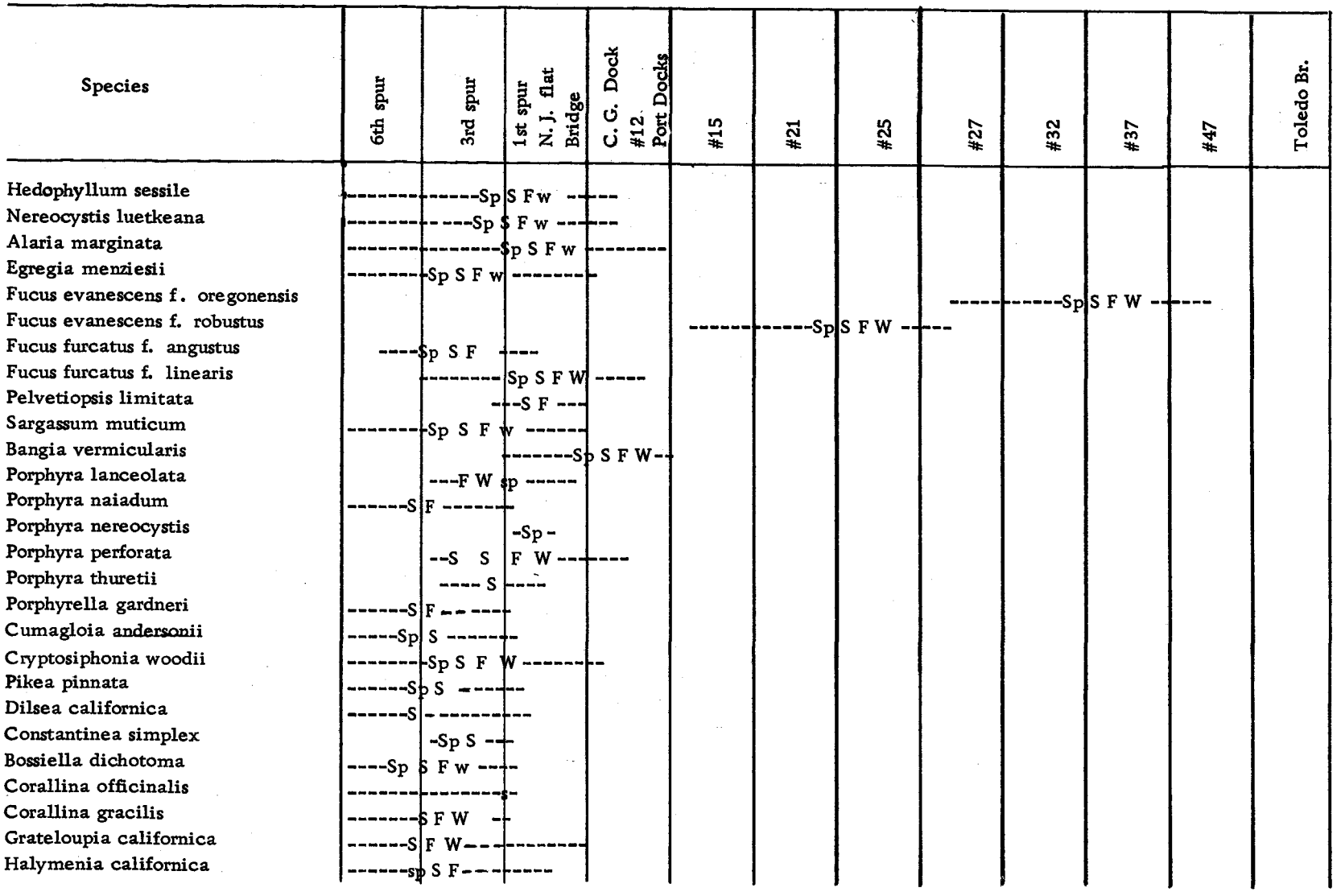


Table 2. (Continued)

Species	6th spur	3rd spur	1st spur N.J. flat Bridge	C.G. Dock #12 Port Docks	#15	#21	#25	#27	#32	#37	#47	Toledo Br.
Priontis andersonii		---Sp S F W --										
Prionitis lanceolata	-------Sp W	----										
Prionitis lyallii	-------Sp W ----											
Callophyllis megalocarpa	----Sp S F W----											
Callophyllis pinnata	-----Sp S F W ----											
Erythrophyllum delesserioides	---S----											
Schizymenia pacifica	-----S F W -----											
Opuntiella californica	-------Sp-------											
Plocamium pacificum	--F W ---											
Gracilariopsis sjoestedtii	-------Sp S F W -------											
Gracilaria verrucosa								-------Sp W		--------		
Ahnfeltia gigartinoides	-------Sp ------											
Gymnogongrus leptophyllus	--------Sp S F W ------											
Gymnogongrus linearis	-------Sp S F W ----											
Gigartina agardhii	-------Sp F W -------											
Gigartina canaliculata	-----Sp S F W --											
Gigartina californica	-----Sp S f w ------											
Gigartina cristata	-----Sp S F W ------											
Gigartina harveyana	-------F w ---											
Gigartina papillata	--------Sp S F W ------											
Gigartina spinosa	-------- S -------											
Gigartina volans	-------- Sp S F ---											
Iridaea coriacea	-------- S F W -----											
Iridaea flaccidam	-------- Sp S f w --------											
Iridaea heterocarpa	---------Sp S F W ------											
Iridaea splendens	----------Sp S f w ----------											
Halosaccion glandiforme												

Table 2. (Continued)

Species	6th spur	3rd spur	1st spur N. J. flat Bridge	C. G. Dock #12 Port Docks	#15	#21	#25	#27	#32	#37	#47	Toledo Br.
Rhodymenia pacifica	S	F										
Antithammion kylinii				S								
Antihammion pacificum			Sp	S								
Platythamnion pectinatum				Sp S F W								
Platythamnion villosum		Sp										
Callithammion pikeanum	Sp	S F W										
Ceramium californicum		Sp S F W										
Ceramium gardneri		Sp										
Ceramium eatonianum		w										
Ceramium pacificum		S										
Microcladia borealis	Sp	S F W										
Ptilota filicina	Sp	S F W										
Membranoptera multiramosa			Sp	S								
Delesseria decipiens			Sp									
Polyneura latissima			Sp	S f								
Hymenina flabelligera	W											
Hymenina multiloba	F W											
Polysiphonia collinsii		Sp										
Polysiphonia californica					Sp	S F W						
Polysiphonia decussata											S	
Polysiphonia pacificum							Sp	S F W				
Pterosiphonia dendroidea	Sp	S F W										
Pterosiphonia bipinnata		Sp S										
Laurencia spectabilis		Sp	S F	W								
Rhodomela larix	Sp	S F w										
Odonthalia floccosa	Sp	S F W										
Odonthalia washingtoniensis	Sp	S F W										

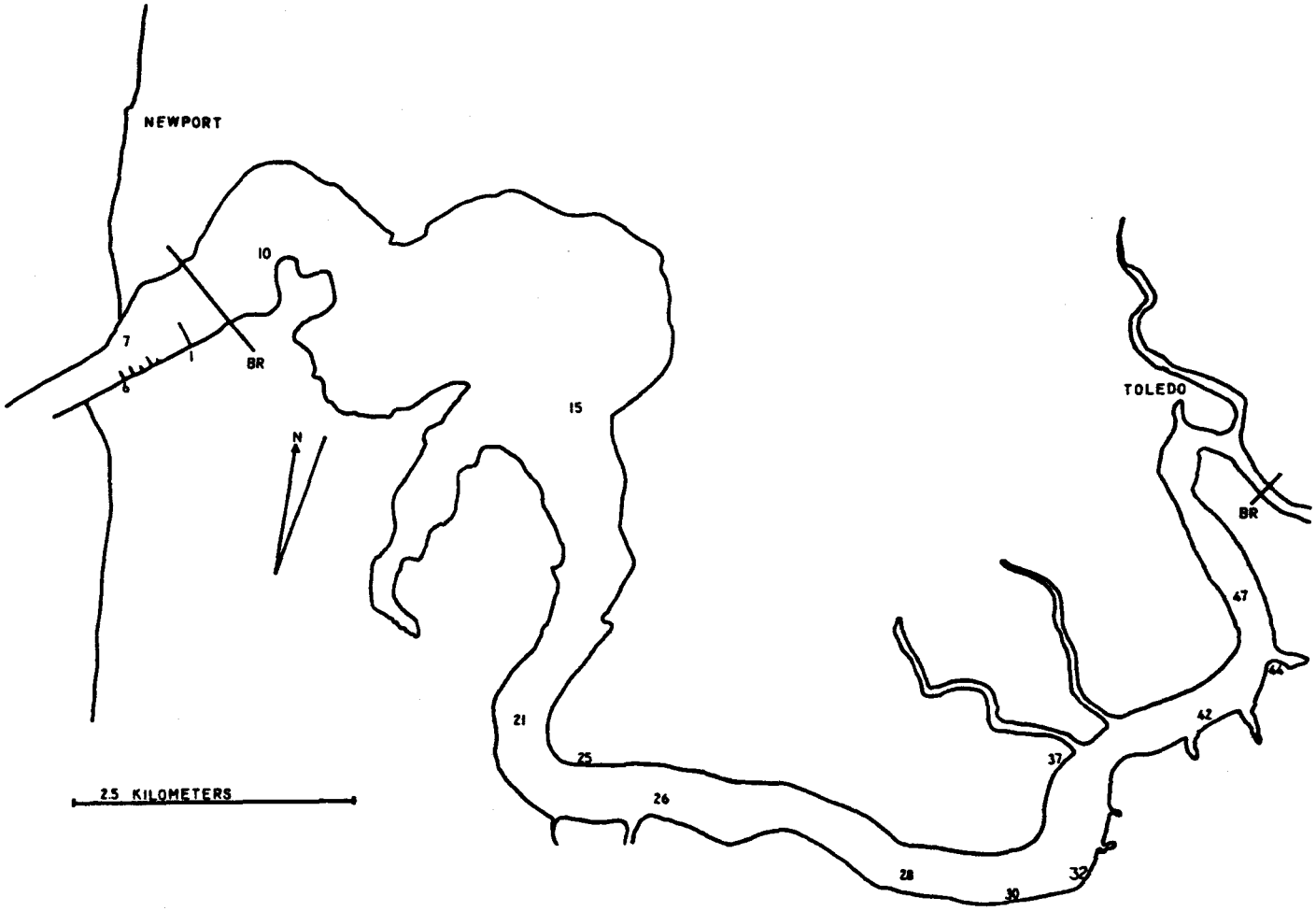
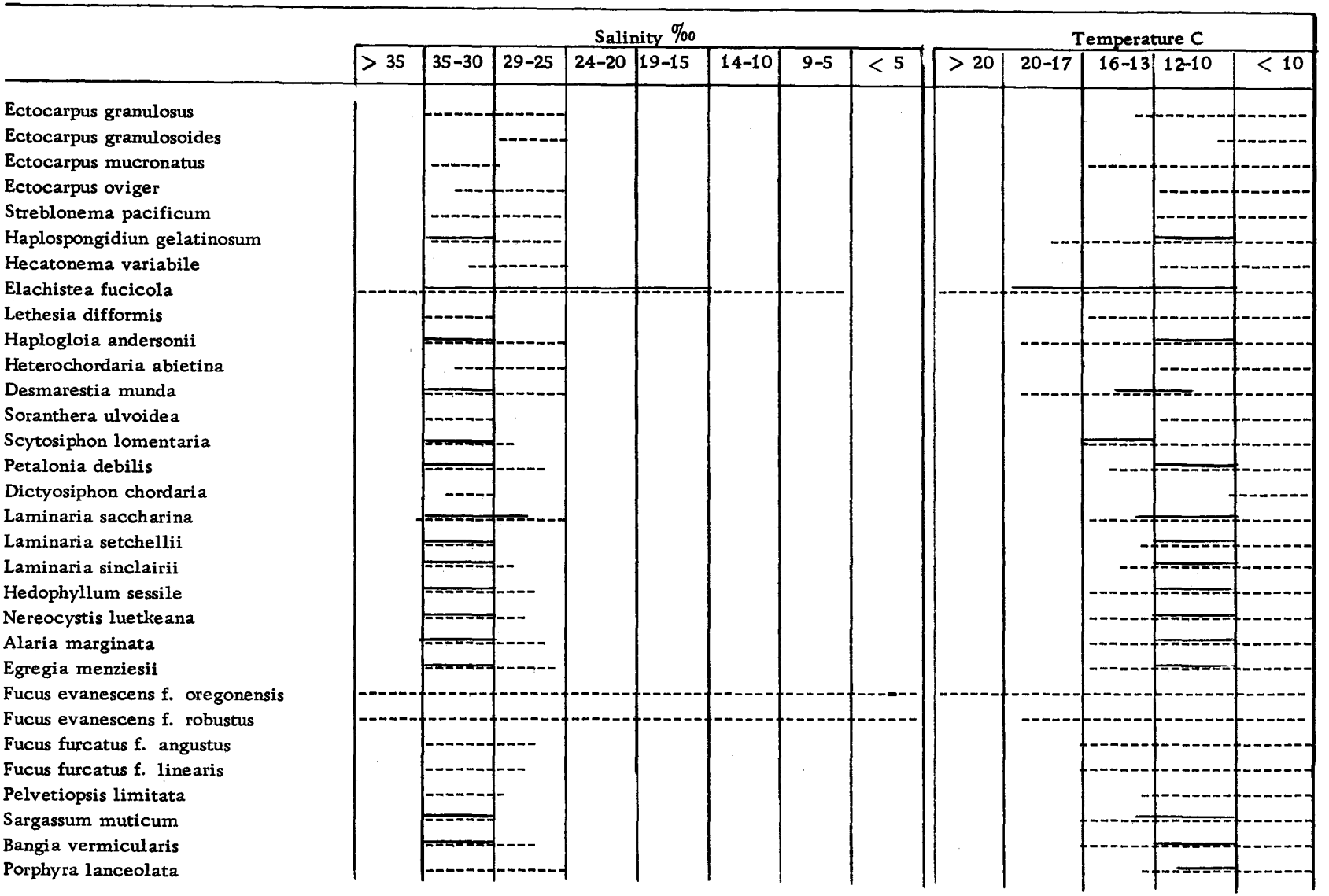


Figure 26. Map of the survey area showing collecting stations.

Table 3. The ranges of salinity and temperature tolerance and growth optima of the macro-algae of Yaquina Bay.

	Salinity ‰								Temperature C				
No. of species present	> 33 12	33-30 125	29-25 14	24-20 15	19-15 13	14-10 10	9-5 9	< 5 5	> 20 8	20-17 19	16-13 82	12-10 127	< 10 84
Ulothrix implexa													
Monostroma fuscum													
Monostroma oxyspermum				Optimum Growth									
Monontroma zostericola													
Enteromorpha clathrata													
Enteromorpha compressa													
Enteromorpha intestinalis													
Enteromorpha linza													
Enteromorpha marginata													
Enteromorpha tubulosa													
Ulva angusta													
Ulva expansa													
Ulva fenestrata													
Ulva lobata													
Ulva rigida													
Ulva taeniata													
Rhizoclonium riparium													
Urospora penicilliformis													
Chaetomorpha aerea													
Chaetomorpha tortuosa													
Cladophora gracilis													
Cladophora trichotoma													
Spongomorpha coalita													
Spongomorpha spinescens													
Bryopsis corticulans													
Pylaiella littoralis													
Ectocarpus acutus													
Ectocarpus confervoides													
Ectocarpus dimorphus													

Table 3. (Continued)



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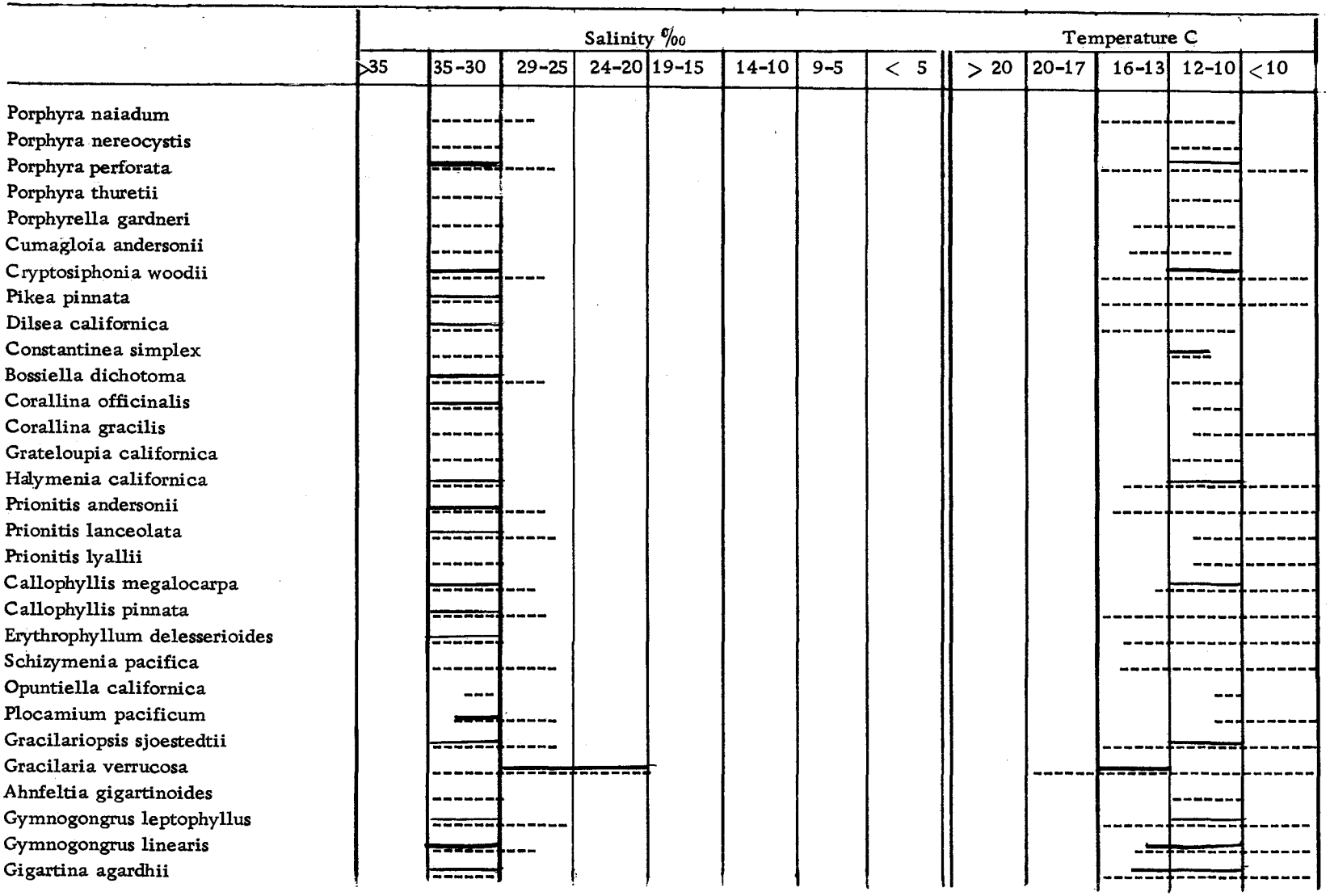

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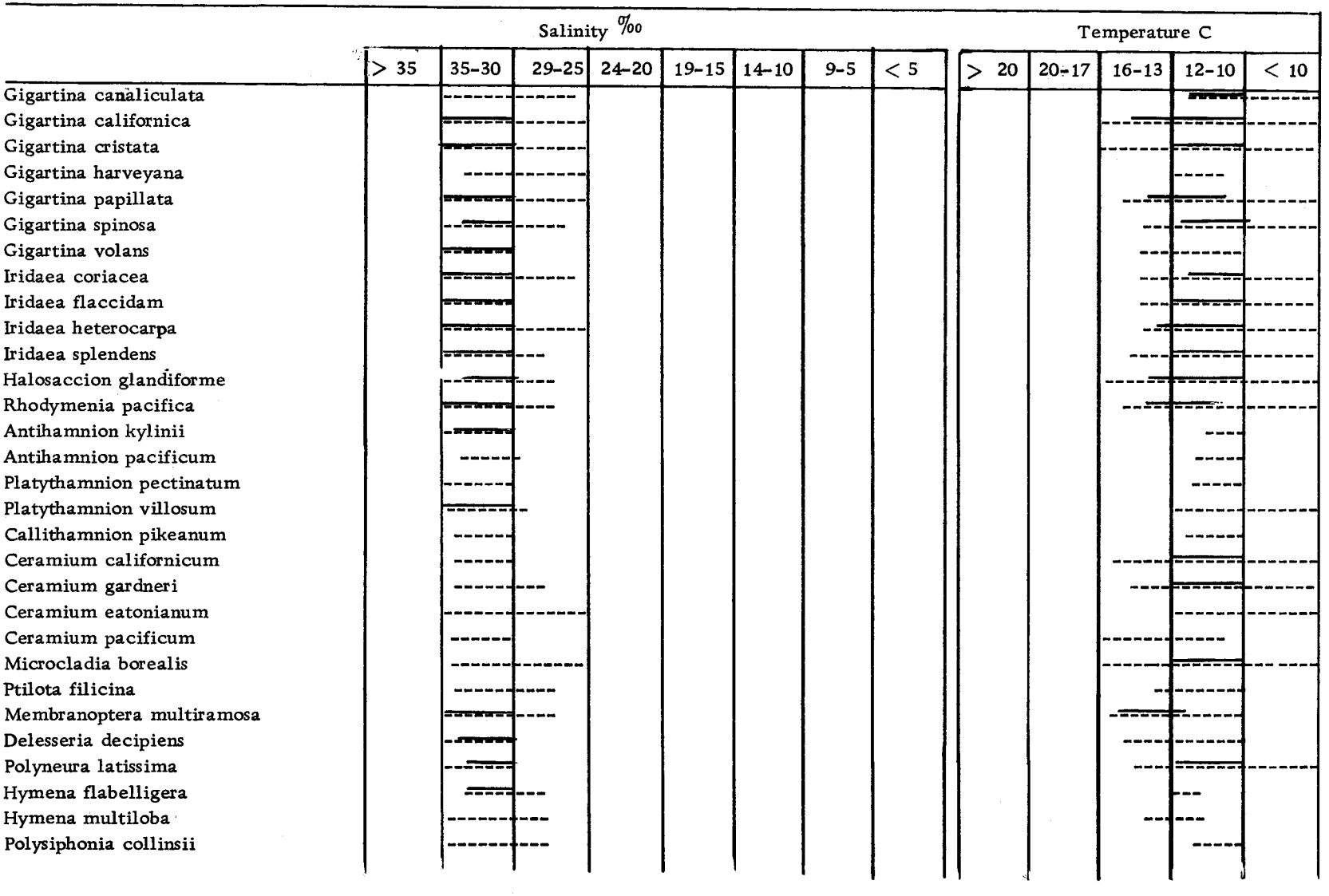

Table 3. (Continued)

	Salinity ‰								Temperature C				
	> 35	35-30	29-25	24-20	19-15	14-10	9-5	< 5	>20	20-17	16-13	12-10	< 10
Polysiphonia californica													
Polysiphonia decussata													
Polysiphonia pacificum													
Pterosiphonia dendriodea													
Pterosiphonia bipinnata													
Laurencia spectabilis													
Rhodemela larix													
Odonthalia floccosa													
Odonthalia washingtoniensis													

DISCUSSION

The distribution of the flora in an estuarian ecotone is controlled by salinity, temperature, light intensity, suitability of substrate, availability of nutrients, and biotic interrelations. Salinity, temperature, and silt are the chief physical and chemical factors determining the unique characteristics of an estuary. These factors are primarily controlled by the prevailing tides and climatological patterns. Tidal and seasonal variations of these factors is considerably greater than on the open coast. An understanding of the physiological influence of these variables is necessary for an appreciation of the significance of these factors in limiting the growth and distribution of the flora.

The extremes of the osmotic spectrum are encountered by fresh water species that are subjected to tidal inundation or are swept in an estuary by runoff and by marine species exposed to variations in salinity caused by fresh water entering the estuary from any source. Osterhout (1906) observed cases of tolerance to extremes in salinity by several genera of algae that made trips from salt to fresh water and back on the hulls of ships in San Francisco Bay and the San Joaquin River. Many studies, such as the early work by Munescher (1915), were concerned with death of algal species in hypotonic or hypertonic solutions or with resistance of the plants to dessication.

Biebl (1962) found that intertidal marine algae could be placed in three groups with respect to their salinity tolerance and the zone in which the occurred: (a) those species growing in deep water and never exposed that can only tolerate a range of approximately 13-50‰ salinity; (b) species growing at mean tide level that can tolerate from 7‰ to 66‰; and (c) species growing high in the intertidal that can tolerate from 7‰ to 99‰ salinity for 24 hours. These groups are ordered about a vertical transect. Questions still remain, however, concerning application of tolerance levels to plants along a horizontal transect through an estuary. Biebl's classification would apply at points along a horizontal transect near the mouth of an estuary like Yaquina Bay, but proceeding into the estuary, few algae are found below the intertidal zone and consequently only the last two cases of Biebl's classification are involved. One has to think also in terms of tolerance to variations in salinity for periods longer than 24 hours and this is further complicated by the effects of tides with resulting submergence, emergence, and drying.

Dissolved salts, according to Guillard (1962), have two kinds of effects on aquatic organisms. The first is related to the chemical nature of the ions in solution and their specific actions on living cells, and the second is the osmotic effect that depends upon the total number of dissolved particles. The tolerance marine algae show to variations in salinity increases with the calcium content of the

medium (Eppley and Cyrus, 1960). According to Eppley (1958) the degree of tolerance may be related to the loss of potassium from cells subjected to calcium deficiency. Kessler (1959, as reviewed by Guillard, 1962) feels that the ability of algae to maintain an osmotic pressure above that of their environment is lowered and finally destroyed by deficiencies in cations. The marine algae, however, vary considerably in their osmotic values, some are barely turgid, while others show values almost double sea water. Brackish water species tend to have osmotic values higher than that of their surrounding environment. Blinks (1951) and Guillard (1962) both feel that algae tend to maintain an internal concentration somewhat above that of their environment, and that the range of osmotic stress tolerated depends primarily on the ability of the protoplasm to function when its salt concentration is altered. Kessler (in Guillard, 1962) using a new "micro-cryoscopic" method, found that the turgor of Chaetomorpha linum was almost constant from fresh water to a salinity of 105‰ in a balanced artificial sea water. He also noted that turgors were relatively constant in nature. Eppley and Cyrus (1960) reported that in Porphyra perforata water contained in tissue, wet weight minus dry weight, increases with dilution and at the same time the free tissue space decreases.

Blinks (1951) showed that slow changes in salinity were tolerated more readily than rapid changes, presumably because normal

respiration can keep pace. Some algae, such as Monostroma, growing in estuaries are not influenced by sudden changes in salinity. According to Blinks their cells are probably permeable to salts rather than impermeable to water.

McLachlan (1960) found that the flagellate Dunaliella tertiolecta has clearly distinguishable osmotic and sodium requirements. In a medium having the ionic proportions of sea water, as the total salinity is decreased by dilution, the growth of D. tertiolecta is limited first by the osmotic requirement. If the osmotic value is maintained by the addition of other solutes, the first cation to become limiting on further dilution is sodium. Droop (1958 in Guillard, 1962) implied that certain other marine algae requiring a high salinity have a high non-osmotic sodium requirement. Sodium is involved in "ion pump" systems in a number of algae (Eppley, 1962). Ion transport systems and alterations of membrane permeability are the most obvious mechanisms by which the changes in ionic strength of the medium can influence the metabolism of marine algae (Guillard, 1962).

Many studies of the tolerances and metabolic responses of macro-algae to variations in salinity have involved measurements of respiratory rates. Inman (1921) was the first investigator to consider seriously variations in salinity as they influence respiratory rates. Hoffman (1929) and Schwenke (1960) have thoroughly reviewed the literature and made major contributions.

The first investigator to be concerned with variations in salinity as they influence photosynthesis was Legendre (1921). Only four subsequent papers have considered photosynthesis of the macro-algae with respect to salinity (Fromageot, 1923; Montfort, 1931; Gessner and Hammer, 1960; and Ogata and Matsui, 1965). None of these, however, has considered temperature effects at different salinities.

A complex relationship the "temperature-salinity relation" exists between the biological effects of temperature and salinity as noted by Kinne (1963). Temperature can modify the effect of salinity and enlarge, narrow, or shift the range of salinity tolerated by a species. Conversely, salinity can modify the effects of temperature. Despite its importance, information concerning the combined effects of temperature and salinity on living systems is rather limited. The lack of information is strange, since temperature and salinity are primary distributional factors for many aquatic organisms, and are easier to measure and control than many other environmental factors.

In the present study presentation of the photosynthetic data as net photosynthesis, as done by Ogata and Matsui (1965), would not give an understanding of the influence of variations of temperature and salinity on the algae, since omission of the increased rates of respiration when measuring net photosynthesis exaggerates the effects variations in the physical factors have on the process of photosynthesis. Consequently, gross photosynthesis was used because a

better understanding of the responses of the two metabolic systems could be gained.

Rates of respiration and photosynthesis obtained in the 50-liter P-R chamber using whole plants were compared with rates obtained manometrically from portions of plants in the 15-ml Warburg reaction vessels using the Gilson differential respirometer. Such comparisons were obtained by multiplying the rates obtained from the Gilson experiments, expressed as μl/hr/mg by the ratio 32/22.4; thus, a rate of 1 μ g/hr/mg was equivalent to 1 mg/hr/g in the P-R chamber. The values obtained are compared in Appendix A, Tables 3 to 8. In most cases the results agree remarkably well and show the same trends. Some of the deviations that occurred may have been the result of differences in the season of the experiments. Studies using the Gilson differential respirometer were conducted in the spring and early summer, whereas studies in the P-R chamber were conducted during the fall, consequently the plants may have been physiologically adapted to different conditions. Furthermore, the comparisons relate responses of whole plants to those of portions of plants. The deviations that occurred in the comparisons of photosynthesis are due to the different light quality and quantity in the two respirometers. With these limitations the two methods demonstrate the responses to hypotonic conditions at different temperatures, and from these responses an attempt can be made to

ascertain the significance of these variables in nature.

In order to relate the results obtained by the two methods the comparisons are presented in summary for each species.

Ulva expansa. The responses shown by this species in decreased salinities were: a) the rates of respiration were higher in the P-R chamber than in the Gilson; b) rates of respiration increased in dilutions of approximately 22‰ salinity; c) rates of respiration decreased in fresh water, with two exceptions; d) rates of photosynthesis at 10 C in all dilutions were higher in the Gilson, but at 20 C the rates were higher in the P-R chamber; f) rates of photosynthesis were stimulated in salinities near 22‰, except at 20 C in one experiment; and d) rates of photosynthesis decreased below the rate in sea water, in water of less than 5‰ salinity, except at 10 C in one experiment.

Enteromorpha linza. Rates of respiration and photosynthesis were measured only in the P-R chamber.

Laminaria saccharina. The following responses were shown by this species in decreased salinities: a) rates of respiration in both experiments were very close; b) rates of respiration at all temperatures were higher with decreasing salinity, except at 10 C in the P-R chamber; c) rates of photosynthesis were higher in the P-R chamber; and d) rates of photosynthesis, in dilutions of less than 11‰ salinity, were markedly lower than rates in sea water.

Alaria marginata. The metabolic response to salinity variation of this species was measured only in the P-R chamber.

Sargassum muticum. In summary, a) rates of respiration at 10 C were higher in the Gilson than in the P-R chamber, but at 15 and 20 C rates were higher in the P-R chamber, except in sea water at 15 C; b) rates of respiration increased with decreasing salinities; c) rates of photosynthesis were higher in the Gilson experiments at 10 and 20 C than in the P-R chamber, but at 15 C rates in the P-R chamber were higher than in the Gilson experiments; d) rates of photosynthesis, in all but one case, were higher at dilutions near 22‰ salinity; and e) photosynthesis, in dilutions of less than 12‰ salinity, was markedly depressed.

Odonthalia floccosa. Responses shown by this species in decreased salinities were: a) rates of respiration at 15 and 20 C were higher in the P-R chamber than in the Gilson experiments; b) in decreasing salinities rates of respiration increased above that in sea water, except at 20 C in the P-R chamber; c) rates of photosynthesis were higher in the P-R chamber than in the Gilson respirometer; d) rates of photosynthesis in salinities of less than 22‰ decreased markedly below rates in sea water.

Iridaea splendens. The responses this species showed were: a) rates of respiration at 15 C were similar in the two experiments, but at 20 C rates in the P-R chamber were considerably higher than

those in the Gilson experiments; b) rates of respiration increased above the rates in sea water with decreasing salinity, except at 20 C in the P-R chamber; c) rates of photosynthesis were measured only at 20 C by both methods and at this temperature rates were higher in the P-R chamber than in the Gilson respirometer; d) rates of photosynthesis decreased below the rates in sea water in dilutions of less than 30‰ salinity.

Gigartina californica. The responses of this species were: a) rates of respiration at 15 and 20 C were higher in the P-R chamber; b) rates of respiration at all temperatures in the Gilson experiments were increased to dilutions of 11‰; c) rates of respiration in the P-R chamber were not markedly altered in salinities greater than 11‰; d) rates of respiration in fresh water in all cases were higher than the rates in sea water; e) rates of photosynthesis at 15 and 20 C were higher in the P-R chamber than in the Gilson respirometer; f) in all cases rates of photosynthesis in salinities below 11‰ were less than rates in sea water; and g) in the Gilson respirometer photosynthesis increased with decreasing salinities to 11‰ at 10 and 20 C.

In studies by Fromageot (1923) and Hoffman (1929), many intertidal algae did not alter their respiratory rates at low salinities, but sublittoral algae exhibited temporarily increased rates of respiration. Nath (1955, in Schwenke, 1960) investigated respiratory rates

of tissue sections of Laminaria saccharina in varying salinities. He found that the rate of respiration increased approximately three times when the salinity decreased to 10‰. The present study used sublittoral algae, with the exception of Enteromorpha, and the results are in agreement with those of Fromageot, Hoffmann and Nath. In my experiments rates of respiration at most temperatures increased in salinities below sea water in the short-term experiments, but in adaptation experiments to decreased salinities, the rates were reduced.

There does not seem to be any satisfactory explanation for the enhancement of respiration in decreasing salinities. Dr. Harold J. Evans (verbal communication) thought it logical to look for some type of cellular damage, as many tissues respire at a higher rate when damaged, or if this is not a causal factor, consider enzymatic influences. Eppley and Cyrus (1960) found that Porphyra perforata in diluted sea water retained potassium and at the same time extruded sodium. Dr. Thomas C. Moore (verbal communication) proposed a possible explanation based on activation of respiratory enzymes by monovalent cations. Different rates may result from the change in ionic concentrations of sodium and potassium ions competing for cationic binding sites on potassium ion-activated respiratory enzymes, e.g. pyruvic kinase. As the salinity decreases, assuming the internal level of potassium ion was not altered, the decreased

sodium ion content would reduce cationic competition for enzyme binding sites and would permit a faster rate of turnover of the enzyme.

Maximum rates of respiration of several species of marine algae in air saturated sea water at 20 C were listed by Gessner (1959), ranging from 0.13 to 2.80 mg oxygen consumed/hr/g dry weight of tissue. In the present study, rates in the Gilson respirometer in sea water at 20 C ranged from 0.21 to 0.87 μg/hr/mg dry weight of tissue, but in the P-R chamber much higher rates were obtained (1.80 to 7.44 mg oxygen/hr/g dry weight of tissue). The present results are certainly of the same order of magnitude as Gessner's and exhibit variation that could be encompassed by the variability of the species used.

Legendre (1921) found that, in a dilution of approximately 22‰ salinity, the rate of photosynthesis of Ulva lactuca and Fucus serratus gradually increased to more than double the rate in sea water. Fromageot (1923) noted that the highest rates of photosynthesis occurred in natural sea water and deviations in salinity in either direction caused a decline in the rate of photosynthesis. He also found that the algae retained a certain capacity for photosynthesis even in distilled water, but this was very weak. Ogata and Matsui (1965) conducted manometric studies of rates of photosynthesis of Ulva pertusa from the lower intertidal, Gelidium amansii from the

sublittoral, and Porhyra tenera from the upper intertidal in estuaries. Using hypotonic and hypertonic solutions they found the maximum rate of net photosynthesis occurred at dilutions of approximately 22‰. Similar results were obtained in the present study. Ulva, Enteromorpha, Sargassum, Gigartina and Odonthalia all developed maximum rates of photosynthesis at 22‰. Again, no proven explanation for this increased rate is available. Dr. Norman I. Bishop (verbal communication) has suggested the increase may result from either an osmotic effect on the chloroplast or a change in the concentration of some ion or ions involved in the process of photosynthesis.

Gessner and Hammer (1960) found that photosynthesis in Ulva lactuca decreased 77% when transferred to fresh water and Posidona oceanica showed a decrease in rate to zero under similar conditions. Ogata and Matsui (1965) found the rates of photosynthesis on transfer to fresh water were 0.5, 0.25, and 0.3 times the rates in sea water for Gelidium, Ulva and Porhyra respectively. In the present experiments the rate of photosynthesis was depressed from 0.7 to less than 0.1 times the rate in sea water at 10 C, 0.3 to less than 0.1 at 15 C, and 0.7 to 0.2 at 20 C.

Ogata and Matsui (1965) found that rates of net photosynthesis at temperatures above 20 C varied from 8.3 to 20.0 μl/hr/mg in sea water. Rates of net photosynthesis, in the present study at 20 C in

sea water ranged from 6.3 µl/hr/mg to 0.5 µl/hr/mg. The differences could be due to the different species used.

Ogata and Matsui (1965) have demonstrated, with studies in artificial sea water enriched with carbon dioxide, that the abrupt decrease in the rates of photosynthesis in salinities of less than 22‰ is due to a sudden decrease in the availability of carbon dioxide. This then may explain the decrease in rates of photosynthesis with decreasing salinity in the P-R chamber and Gilson experiments, but this explanation offers no clue as to why enhancement was encountered in some species at 22‰ salinity. Rabinowich (1945) notes that several workers have discussed the mechanisms by which ions may affect photosynthesis, and they feel, that they may either influence the colloidal properties of protoplasm or possibly the disposal of carbohydrates.

Gunter (1957) in his review of temperature and marine ecology stated "temperature is the most important single factor governing the occurrence and behavior of life, temperature changes affect protoplasm directly and changes the physical and biological environment as well." The relationship between temperature, salinity, and the rates of respiration were analysed using the data from the Gilson and P-R chamber studies. Temperature coefficients (Q_{10}) for five-degree temperature ranges were calculated from the equation

$$Q_{10} = \left(\frac{r_2}{r_1}\right)^{10/(t_2-t_1)}$$

where t_1 and t_2 were the lower and higher temperatures of the range under consideration, and r_1 and r_2 the corresponding rates of respiration (Tables 4 and 5). The values for the Gilson experiments were calculated from the mean of three replications. The comparison of temperature coefficients are based on data from different plants, and the time lapse between determination of rates of the two particular temperatures varied from one day to several weeks. It was not possible to analyze the influence of temperature, under conditions of decreased salinity because the experimental plants in lower salinities would have been in dilute sea water for over six hours to complete a series of temperature curves. Prolonged exposure to reduced salinities in itself affects the rate of respiration, as demonstrated by the previous experiments. With such limitations in mind the Q_{10} data are presented to illustrate the effect of temperature on tolerance to variations in salinity.

The Q_{10} values of respiration, calculated from data obtained using the Gilson respirometer, at 10-15 C varied from 4.4 to 0.7 in sea water, 4.8 to 0.8 in 22‰, 2.6 to 0.9 in 11‰, and 2.7 to 0.4 in fresh water. In the P-R chamber at 10-15 C the values varied from 5.3 to 0.8 in sea water, 9.4 to 1.4 in 22‰, 23.2 to 2.4 in

Table 4. Temperature coefficients (Q_{10}) for respiration of algae in the Gilson experiments.

Species	Conditions	Temperature range (°C)			
		5-10	10-15	15-20	20-35
U. expansa	S.W.		2.3	1.4	
	22.0‰		4.8	9.3	
	11.6‰		1.1	13.8	
	F.W.		1.6	16.2	
L. saccharina	S.W.	22.4	1.3	1.0	0.2
	22.0‰	7.7	1.2	1.6	0.7
	11.6‰	2.8	1.1	1.2	0.5
	F.W.	1.5	0.4	1.1	1.0
S. muticum	S.W.		0.7	0.8	
	22.0‰		0.8	2.0	
	11.6‰		1.1	1.0	
	F.W.		0.6	1.5	
O. floccosa	S.W.		4.4	0.7	
	22.0‰		1.9	0.6	
	11.6‰		2.6	2.0	
	F.W.		0.6	3.4	
I. splendens	S.W.		1.8	0.7	
	22.0‰		1.1	0.6	
	11.6‰		1.0	2.4	
	F.W.		2.7	1.9	
G. californica	S.W.		1.2	1.1	
	22.0‰		1.0	1.6	
	11.6‰		0.9	1.5	
	F.W.		0.4	2.5	

Table 5. Temperature coefficients (Q_{10}) for respiration of algae in the P-R chamber experiments.

Species	Conditions	Temperature range (°C)	
		10-15	15-20
U. expansa	S.W.	1.1	3.8
	25.0-19.7	2.4	--
	12.2-11.5	2.8	0.6
	F.W.	0.2	4.8
L. saccharina	S.W.	4.8	1.4
	22.0-20.3	21.1	2.7
	12.0-10.3	12.9	2.0
	F.W.	36.0	1.7
S. muticum	S.W.	0.8	13.1
	24.3-22.6	6.8	1.4
	12.4-11.5	4.4	1.5
	F.W.	4.8	1.3
A. marginata	S.W.	5.3	16.0
	22.4-19.5	10.9	9.4
	11.2-8.5	5.2	7.3
	F.W.	2.0	6.8
O. floccosa	S.W.		4.0
	23.9-21.2		3.4
	11.9-9.2		4.8
	F.W.		1.9
I. splendens	S.W.		3.6
	23.0-22.9		7.0
	11.4-10.7		2.8
	F.W.		18.8
G. californica	S.W.		3.4
	23.8-22.6		3.1
	12.2-11.1		4.7
	F.W.		5.3

11‰, and 36.0 to 0.2 in fresh water. The values, of data from the Gilson, at 15-20 C varied from 1.4 to 0.7 in sea water, 9.3 to 0.6 in 22‰ salinity, 13.8 to 1.0 in 11‰, and 16.2 to 1.1 in fresh water. In the P-R chamber, at 15-20 C, the values varied from 43.6 to 3.8 in sea water, 9.4 to 1.4 in 22‰, 7.3 to 0.6 in 11‰ and 18.8 to 1.3 in fresh water.

Results obtained in both the Gilson respirometer and the P-R chamber indicate that the greatest influence of temperature at 10-15 C was in salinities above 11‰, with the exception of Laminaria (P-R chamber) and Iridaea (Gilson respirometer); but at 15-20 C, with the exception of Laminaria and Sargassum in both respirometers and Alaria in the P-R chamber, the greatest influence of variations in temperature occurred in salinities of 11‰ or lower. Boyle and Doty (1949) noted that in laboratory experiments some algae were killed more quickly in dilute sea water at high temperatures than were control plants. Conover (1958) also noted that several estuarine species were less tolerant of low salinities in warm water. The results of the present study confirm these observations if the high temperature coefficients in salinities of less than 11‰ at 15-20 C are interpreted as cellular damage.

In Laminaria the temperature ranges were extended and the lowest Q_{10} values occurred at 20-25 C. McIntire (in press) and others have found that some aquatic plants have lower Q_{10} values

at higher temperatures. Such low Q_{10} values appear to be related to deactivation of some metabolic enzymes at high temperatures.

Ehrke (1929, 1931 as reviewed by Biebl, 1962) studied the effect of variations of temperature on respiration of plants in sea water based on data determined by the Winkler method. In many algae there was very little change in rate from0 to 20 C or 25 C. Above 25 C respiration increased very rapidly. Fucus serratus showed a sharp increase above 30 C, Plocamium at 20 C, and Delesseria at 25 C. Enteromorpha had a gradual increase and tolerated high temperatures well. Ehrke's results are quite different from those obtained in the present experiments, and may be due to the different species used and to differences in their environmental temperature regimes.

In the present laboratory experiments, rhythmic respiratory activity as reported for Hydrodictyon and Fucus by Schone (1955, in Biebl, 1962) may be involved. Another factor to consider is the complex time course of the effects of temperature changes as noted by Montfort (1935, in Blinks, 1951). He found that Fucus when transferred from 5 to 21 C showed an increase in respiration from 1 to 3.1 times the base rate during the first day, and finally stabilized around 1.7. He also noted that changes from 5 to 15 C were less drastic, but the same tendency was shown. In my experiments, there were temperature transfers that may have slightly influenced

the results, but the transfers were never greater than 10 C and were usually less than 5 C.

Biebl (1962) has shown that, in general, tropical algae show ability to survive at temperatures exceeding 29 C, but do not survive at temperatures below 6 C. In contrast, temperate and polar species seem to be highly resistant to colder temperatures, but will not tolerate temperatures above 22 C. Several species studied in the present laboratory experiments exhibited an intolerance to high temperatures. Biebl also noted that sublittoral algae are less tolerant to temperature extremes than the intertidal inhabitants.

The relationship between temperature and the rate of photosynthesis at various salinities were further analysed by calculation of temperature coefficients using data from both the Gilson respirometer and P-R chamber. Temperature coefficients were calculated from the experimental temperatures using the same equation from which the respiratory coefficients were calculated (Tables 6 and 7). The Q_{10} values for photosynthesis from the data obtained using the Gilson respirometer at 10-15 C ranged from 2.8 to 0.6 in sea water 1.2 to 0.6 in 22‰, 1.2 to 0.3 in 11‰, and 1.0 to 0.1 in fresh water. The temperature coefficients in the P-R chamber at 10-15 C varied from 8.4 to 4.0 in sea water, 10.2 to 2.6 in 22‰, 10.2 to 3.2 in 11‰, and 3.6 to 4.0 in fresh water. The values at 15-20 C in the Gilson respirometer ranged from 1.7 to 1.0 in sea

Table 6. Temperature coefficients (Q_{10}) for photosynthesis of algae in the Gilson experiments.

Species	Conditions	Temperature range (°C)				
		5-10	10-15	10-20	15-20	20-25
U. expansa	S.W.			1.8		
	22.0‰			3.3		
	11.6‰			7.8		
	F.W.			6.0		
L. saccharina	S.W.	1.2		1.2		0.6
	22.0‰	1.4		1.4		2.0
	11.6‰	1.4		0.5		0.6
	F.W.	1.0		1.7		4.0
S. muticum	S.W.		2.8		1.7	
	22.0‰		1.2		3.0	
	11.6‰		1.2		1.7	
	F.W.		1.0		2.2	
O. floccosa	S.W.		0.6		1.7	
	22.0‰		0.6		2.6	
	11.6‰		0.4		3.6	
	F.W.		0.1		3.0	
L. splendens	S.W.			0.5		
	22.0‰			0.7		
	11.6‰			0.9		
	F.W.			1.3		
G. californica	S.W.		2.0		1.0	
	22.0‰		1.0		1.4	
	11.6‰		0.3		3.2	
	F.W.		0.4		1.4	

Table 7. Temperature coefficients (Q_{10}) for photosynthesis of algae in the P-R chamber experiments.

Species	Conditions	Temperature range (°C)	
		10-15	15-20
U. expansa	S.W.	4.0	1.0
	25-18‰	2.1	0.7
	12‰	3.2	0.8
	F.W.	0.4	1.7
E. linza	S.W.		2.0
	22-19‰		2.9
	11-10‰		2.3
	F.W.		3.6
L. saccharina	S.W.	8.4	1.1
	22-21‰	10.2	1.4
	12-10‰	7.8	2.0
	F.W.	3.6	0.7
S. muticum	S.W.	7.2	0.4
	24-23‰	6.3	0.5
	12‰	8.4	0.2
	F.W.	0.6	0.8
A. marginata	S.W.	7.8	5.3
	22-20‰	2.6	6.3
	11-9‰	10.2	6.8
	F.W.	2.6	2.9
O. floccosa	F.W.		2.8
	23-21‰		3.8
	10‰		170.0
	F.W.		66.5
L. splendens	S.W.		8.4
	23‰		3.6
	11‰		6.6
	F.W.		18.5
G. californica	S.W.		3.2
	24-23‰		2.6
	12-11‰		3.6
	F.W.		3.2

water, 3.0 to 1.4 in 22‰, 3.6 to 1.7 in 11‰, and 3.0 to 1.4 in fresh water. In the P-R chamber at 15-20 C the values ranged from 8.4 to 0.4 in sea water, 6.3 to 0.5 in 22‰, 170.0 to 0.2 in 11‰ and 66.5 to 0.7 in fresh water.

In summary, the following trends were shown concerning the influence of temperature on rates of photosynthesis in various salinities: at temperatures of 5-10 and 10-15 C the greatest influence of temperature occurred in salinities above 22‰ in all species except Sargassum and Alaria in the P-R chamber; at temperatures of 10-20, 15-20, and 20-25 C the greatest influence of temperature occurred in salinities lower than 22‰; and photosynthesis appeared to be much more sensitive to salinity changes than respiration, but respiration on the whole was more sensitive to temperature changes than photosynthesis. This shows that temperature changes near those encountered in nature have the greatest influence in sea water, but at temperatures higher than those usually encountered in nature the greatest influence of temperature variations occurred in lower salinities.

Ehrke (1929, 1931, as reviewed by Biebl, 1962) noted that net photosynthesis, in several algal species, was high at low temperatures but decreased to zero at 15-25 C. When Porphyra was transferred from 5 C to 21 C, Montfort (1935 in Blinks, 1951) found that the ratio of photosynthesis first increased but later decreased.

Although none of the temperature transfers in the present experiments were as drastic as those of Montfort, there is a possibility that rates of photosynthesis may have been slightly affected by this type of reaction.

Montfort (1931) examined the effect of salinity upon photosynthesis of nine species of marine algae by placing plants in diluted sea water and back again in sea water. He summarized his results by indicating four types of responses: 1) depression accompanied by irreversible suppression, 2) temporary stimulation followed by depression rapidly leading to irreversible suppression, 3) temporary stimulation followed by depression, gradually leading to suppression which is partially reversible, and 4) insensitivity to changes in salinity. He found that sublittoral algae were immediately and irreversibly damaged by diluted sea water or fresh water, but intertidal algae exhibited a reversible inhibition of their photosynthetic activity. Five of the species in the present study were exposed to long-term reduction in salinity, to determine the effect on their metabolism. These algae were considered to be sublittoral or lower intertidal, and to agree with Montfort's results should have been immediately and irreversibly damaged. However, in most cases, the algae survived long-term exposure to low salinities.

Rates of respiration of individuals adapted at a particular salinity, were considerably lower than those of non-adapted plants at

this same salinity, except in the case of Iridaea (Appendix A, Table 1). In all species, except Iridaea and Ulva, rates of adapted plants under the conditions of adaptation were lower than rates of these same individuals when returned to sea water and then placed in various dilutions. After a period of adaptation in lower salinities rates of respiration of Ulva, Sargassum, and Iridaea when returned to to sea water either approximated or were higher than those of non-adapted plants. In salinities higher than those in which plants had been adapted, rates of respiration were only slightly altered; but at lower salinities the rates increased in all but two cases. Thus, although short-term immersion in reduced salinities resulted in increased rates of respiration, long-term exposure (adaptation) resulted in rates approximating those in sea water.

Rates of photosynthesis of non-adapted plants in a given salinity were always higher than in plants adapted in that salinity (Appendix A, Table 2). Except in the case of Alaria, rates of photosynthesis of plants adapted to lower salinities were always lower upon return to sea water than rates of non-adapted plants. Photosynthetic rates of plants adapted in a given salinity after return to sea water and reversal back to the salinity of adaptation were essentially unchanged.

Thus short-term immersion as well as long-term exposure (adaptation) in reduced salinities, resulted in decreased rates of photosynthesis.

Changes in rates of photosynthesis appear to indicate that adaptation to salinities above 11‰ does not alter the general protoplasmic response, but does reduce the magnitude of the response. This is equivalent to Montfort's third category of temporary stimulation followed by depression, gradually leading to suppression that is partially reversible. Initial stimulation of metabolic rates was evident in the results of the short term experiments. Depression gradually leading to suppression is exhibited in all of the species subjected to adaptation. Ulva, Laminaria, Sargassum, and Iridaea demonstrated the reversibility of the process by showing increased rates of photosynthesis upon return to sea water. These forms did not perform as sublittoral algae, as described by Montfort, presumably because they were estuarine forms and more euryhaline than the coastal forms he studied.

The tendency for greater numbers of marine animals to exist in tropical estuaries is due to their greater salinity tolerance at high temperatures (Reid, 1961). "It is apparent," says Reid, "that temperature is important in delimiting the uptake of nutrients and utilization of light by plants." From the results of the present studies, it would appear that the estuarine algae of Yaquina Bay respond

differently, at temperatures above 15 C, than those described by Reid. These algae were less tolerant of low salinities at high temperatures than low salinities at low temperatures.

Species of benthic marine plants which are present along a salinity gradient have been listed in studies by Luther (1951, in Conover, 1958), Conover (1958, 1964), and Doty and Newhouse (1954). In Yaquina Bay the minimum plant biomass and numbers of species occurred during January and February. These minima were associated with minimal temperatures, salinities, and insolation, suggesting that these factors played the leading role in seasonal fluctuations in production.

Conover (1958) and Doty and Newhouse (1954) have observed, a greater salinity tolerance at low temperatures in the field, but this was not possible in Yaquina Bay, since there was much more precipitation in winter, consequently low temperatures in the upper portions of the estuary occurred concurrently with fluctuations in salinity. In general, one would have to conclude from the physical characteristics of the bay and estuary that most of the inhabitants must be stenohaline and stenothermic. The majority of the species were unable to tolerate annual or diurnal fluctuations in salinity greater than ± 3‰ and temperature variation greater than ± 6 C without noticeable effects. A few species, such as Enteromorpha clathrata, Enteromorpha tubulosa, Monostroma oxyspermum, Chaetomorpha

area, Garcilaria verrucosa, Polysiphonia californica, Polysiphonia pacifica, and Fucus, are very euryhaline and eurythermal, in that they can tolerate salinity changes at ± 15‰ and temperature variation at ± 10 C.

The estuary could be divided into four recognizable zones, each populated by a flora characteristic of the conditions existing in that zone. The first zone occupied an area extending from the outer ends of the jetties up to the Yaquina Bay bridge. In this zone the flora was strongly influenced by marine waters with their characteristic low temperatures and high salinities. The flora was considered a transitional open coast flora with the majority of the species being commonly found on the open coast, but with some species, such as Laminaria saccharina, Sargassum muticum, and Gracilariopsis sjosetedtii that are characteristic of more protected estuarine situations. The second zone extended ten kilometers into the estuary from the Yaquina Bay bridge to Marker 21. The flora of this zone was subjected to fluctuations in temperature of approximately ± 4 C and approximately ± 3‰ salinity during a 24 hour period. The flora was transitional, consisting of brackish water species and some of the species found in zone one (Bryopsis, Desmarestia, and Laminaria saccharina). Zone three extended from Marker 21 13-kilometers to the Toledo bridge. The flora here was exposed to fluctuations in temperature of ± 6 C and ± 7‰ salinity during a

24 hour period. The flora consists of typical brackish water species. Above the town of Toledo existed a fourth zone which was a transitional fresh water area influenced primarily by fresh water runoff.

Field studies have revealed the occurrence of 130 species of algae in Yaquina Bay. Of these 26 species were representatives of the Division Chlorophyta, 33 Phaeophyta, and 71 Rhodophyta. By relating the average monthly salinity of an area to the species occurring there, it was determined that 125 of the 130 species occurred in salinities of 30-35‰. Only 68 of these were limited to this range of salinities. Only 12 species were found to occur in salinities higher than 35‰, but this restriction in number may have been a result of the salinity regime and not necessarily indicative of the total number of species that might be tolerant of higher salinities. As salinities decreased below 30‰, the number of species decreased from 74 in 25-29‰ to five species in areas with an average monthly salinity of less than 5‰.

The absence of macro-algae in the lower intertidal areas of the upper estuary probably resulted from the load of suspended matter and fluctuation of salinity during the tidal cycle. Plants in the upper intertidal of this region may have escaped some of the variation in salinity by being submerged during only part of the cycle, but they would be exposed to additional short-term variations caused by rain.

A relationship also has been established between the distribution of species and the average monthly temperature ranges in the areas in which they occurred. Eight species occurred in waters with temperatures higher than 20 C, 19 species in 17-20 C, 82 in 13-16 C, 127 in 10-12, and 84 occurred in waters of less than 10 C. The majority of the species occurred in temperatures of 10-12 C, but only 18 were found at this temperature range.

Assessment of the relative importance of turbidity and the load of suspended matter on the distribution of the macro-algae in the estuary is difficult. Their influence may be manifested in several ways: 1) a higher coefficient of extinction of the water resulting from the absorption and scattering of light by suspended particles; 2) the deposition of silt and its continual movement over substrates available for attachment; 3) the covering of algae by silt, thus diminishing light penetration and the diffusion of dissolved substances. Conover (1965) measured light scattering under turbid conditions and found as much as 90 percent of the incident light was absorbed or scattered in the first 10 cm, but under calm conditions only 39 percent was absorbed or scattered. No experimental studies of the influence of silt and turbidity were conducted during the present study, but field observations and laboratory experience gave evidence of its significance as an ecological factor in the following ways: 1) with only three exceptions which were found in protected sloughs, all

macro-algae on the mud flats were growing on shell fragments or sticks; 2) there was a conspicuous absence of algae in the lower intertidal from Marker 15 to the Toledo bridge; 3) many of the species that did extend into the estuary were found only on dock floats which were specialized habitats; and 4) the rapid death and decay of portions of algae that were covered by silt in carboys in the laboratory.

Analysis of data concerning seasonal occurrence of macro-algae in Yaquina Bay showed that 90 species occurred in the spring, 93 in the summer, 84 in the fall, and 79 in the winter. Of these, 16 species were found only in the spring, 12 only in the summer, one only in the fall, and four only in the winter. When spring and summer are considered together 36 species were found only during this time of year, nine only during fall and winter, 19 only during summer and fall, and 21 only during winter and spring. There were 55 species that were present at all seasons.

Seasonal changes were found to influence the flora of the intertidal zone on the jetty. In the spring, by approximately the first of March, there was a lush growth of a wide variety of algae. The second major change in the intertidal zone was related to intense insolation, which apparently was detrimental to many forms as evidenced by bleaching and death of many algae in the upper intertidal during summer. Eppley and Cyrus (1960) indicated that drying was not the explanation but that bleaching and death was caused by excess heat

and possibly by photooxidation, since in many cases the underlying blades were not initially damaged. Changes also occurred in the lower portion of the intertidal zone. Platythamnion pectinatum was very common in the lower intertidal in the spring, but during summer and fall this species occupied sublittoral levels to a depth of five meters. Whether the migration resulted from increased insolation or competitive pressure from other species remains to be elucidated. A third change occurred in the fall when the macro-algae were gradually reduced in biomass and number of species by large numbers of grazers and epiphytes. The grazers included a wide variety of snails such as Lacuna, Littorina, and Tegula; other grazers included limpets, chitons, isopods, kelp crabs, and fish. Epiphytes consisted of other algae, particularly diatoms, a variety of hydroids such as Aglanophena, and Obelia, bryozoans such as Membranipora, and Tubulipora, barnacles, mussels, sponges, and several worms. Algae often grew on animals. It was observed by SCUBA diving that the gaper or horse neck clams often had algae growing on the horny plates at the tip of their siphons. The most common algae found on these clams was Polysiphonia californica, and Ulva expansa. The algae never reached a large size for portions of the thallus were torn off as the clam retracted its neck into the sand. The fourth change occurred in the winter with the appearance of winter species and recolonization of the upper part of the intertidal zone.

Recolonization of this area becomes possible at this time, probably because of cleaning of the substrate by wave action during storms, generally humid conditions, decreased insolation, and reduced numbers of grazers. Although comparative measurements were not made, it was apparent that the predominant Enteromorpha zone of the estuary extended above the intertidal zone during winter and early spring, but during spring and summer increased insolation reduces the extent of this zone.

Differences in the flora on the windward (ocean) and leeward (bay) sides of the spurs of the south jetty were also found. On the windward side there was an abundance of Alaria, Egregia, Nerocystis, Laminaria sinclairii, Laminaria setchellii, Prionitus, and Gymnogongrus linearis. On the leaward side, however, there was a conspicuous absence of these forms and an abundance of Sargassum muticum, Laminaria saccharina, and Ulva expansa. This distribution apparently resulted from differences in wave action on the different sides of the spurs. This may have been the factor causing the absence in the estuary of such surf forms as Lessoniopsis, Postelsia, Pterygophora, and Pleurophycus, but there appeared to be ample surf at the ends of the jetties, so their absence may have depended on some other factors.

Marked seasonal changes in the flora were observed in the estuary at Marker 21. Through the late spring and summer a lush

population of Laminaria saccharina, Ulva expansa, Bryopsis corticulans, Desmarestia munda, and Polysiphonia developed here and persisted through the fall to December. In late December their numbers were drastically reduced and those remaining were in poor condition, disappearing completely by January. The question remains to be answered whether this was due to decreased insolation, decreased temperatures and/or salinities, a combination of these physical-chemical factors, or the result of biotic factors. Opposite Marker 10, in this same zone, species such as Desmarestia and Bryopsis disappeared, but Laminaria and Ulva seemed to persist.

Observations of the colonization of wood, rocks, cement, and metal substrates near the mouth of the estuary showed that the pioneer invaders were a film of diatoms followed by barnacles, colonial diatoms, and Enteromorpha. At the Coast Guard dock, the pioneer invaders were followed by Spongomorpha, Laminaria saccharina, Desmarestia, Ulva angusta, Ulva expansa and Fucus.

The relationship of salinity and temperature to the ecology of benthic marine algae is closely integrated and complex. As indicated by the results of the laboratory studies these two factors are significant and, in some cases, may act as limiting factors in their distribution. If as has been demonstrated, decreased salinities result in a decrease in the rate of photosynthesis, the existence of an alga is endangered. However, as emphasized by Verduin (1965), in

natural aquatic habitats one must think not of a limiting factor, but in terms of limiting factors and, in an estuary, perhaps factors other than salinity may be more significant. For example, silt covers substrates otherwise available for attachment, limits light penetration, covers plants and limits diffusion between the cells and the medium. Biotic factors such as bacterial activity and grazing by animals also may limit the distribution of benthic algae.

If physiological laboratory studies, pertaining to the ecology organisms, are to be meaningful they should be related to the field. There was excellent agreement between the results of the laboratory and field studies of five of the species studied. In the field Ulva expansa was found in salinities ranging from 20 to 35‰ with optimum growth in water of 30-35‰ salinity and at temperatures from 10 to 16 C with optimum growth at 12-14 C. This species occurred in the field in areas where the tidal cycle caused variations of approximately 10‰ salinity and 7 C. In laboratory experiments, this species was tolerant of short term salinity dilutions to 11‰ at all temperatures, and at 15 C the greatest tolerance was shown: however, in the adaptation experiments the metabolic rates were markedly reduced after approximately a two-day exposure to reduced salinities. Comparing the laboratory results with field observations it appeared that this species was limited by the mean salinity of an area (approximately 22‰), which correlates with its distribution in the estuary.

Enteromorpha linza attained optimum growth in the estuary in salinities from 30-35‰ and in temperatures from 10-20 C. In laboratory experiments, this species was tolerant of dilutions to 11‰ salinity as was evident from the rates of respiration and photosynthesis at 15 and 20 C. Enteromorpha was found in areas where the tidal cycle cause variations of 5‰ salinity and 7 C. In comparing the laboratory results with field observations it appeared that this species was more tolerant to variations in salinity and temperature than its distribution would indicate and that some other factors limited its distribution.

Laminaria saccharina was found in nature in salinities ranging from 25-35‰ with optimum growth in the range of 30-35‰ and at temperatures from 16 C to less than 10 C with optimum growth occurring from approximately 10-13 C. During a tidal cycle variations of approximately 6‰ and 6 C were tolerated. In laboratory studies, dilution to 20‰ salinity only slightly affected rates of respiration and photosynthesis except at 25 C. Salinities below 20‰ produced a drastic reduction in the rate of photosynthesis. This species was very sensitive to high temperatures, rates of photosynthesis and respiration were reduced at temperatures above 20 C. When this species was adapted to salinities of less than 30‰ at 15 C the rate of photosynthesis was markedly reduced. Thus, in this species, both high temperatures and low salinities can be limiting

factors in its distribution and it appears from the field studies that the salinity and temperature tolerance of this species are exploited to their full extent in the estuary.

Sargassum muticum was distributed in salinities ranging from 27 to 35‰ with optimum growth at 30-35‰, and in water temperatures of less than 10 C to 16 C with optimum growth occurring from 10-13 C. Laboratory experiments showed slight enhancement of respiration and essentially no effect on photosynthesis in dilutions of 20‰ salinity, but with greater dilution both rates were markedly altered. Adaptation, at 15 C, to salinities of approximately 20‰ resulted in a marked depression of rates of both respiration and photosynthesis. At 20 C, the rates of respiration in both respirometers and the rate of photosynthesis, in the P-R chamber, were depressed below the rate at 15 C. Therefore, high temperatures or decreased salinities can act to control the distribution of this species, and it appears that this species has extended its distribution, in the estuary to its full range of tolerance.

Alaria marginata in the estuary, occurred in salinities of 27-35‰ with optimum growth at 30-35‰, and at temperatures from less than 10 to 16 C with optimum growth occurring at 10-12 C. Laboratory studies showed that the rates of respiration and photosynthesis in this species were only slightly altered at the lower temperatures by variations in salinity. Short-term variations in salinity did not

affect this species as much as they did the other species studied, but long term variations in salinity were significant, as demonstrated in the adaptation experiments. Adaptation at 15 C, in salinities of approximately 20‰, resulted in a sharp depression in the rate of respiration and photosynthesis. Therefore, decreased salinities would act as a limiting factor controlling the distribution of this species particularly at temperatures above 10 C, and it appears that this species is exploiting to its full extent its tolerance to the range of salinity in the estuary.

Odonthalia floccosa, in the estuary, was found occurring in salinities of 27-35‰ with optimum growth at 30-35‰, and in water of less than 10 C to 16 C with optimum growth at 10-12 C. The maximum variations of salinity and temperature tolerated during a tidal cycle was approximately 2‰ and 5 C. Experimental studies, at 20 C in the Gilson respirometer, showed a depression of metabolic rates below those at 15 C, and in both the Gilson and the P-R chamber rates of photosynthesis were markedly reduced in salinities of less than 22‰. Therefore the distribution of this species may be limited by high temperatures or low salinities but from the tolerance shown in the laboratory studies it appears that this species has not extended its range in the estuary to its full tolerance of variation in salinity and temperature, and some other factors may be acting to limit its distribution.

Iridaea splendens was found in the estuary distributed in salinities of 27-35‰ with optimum growth occurring in 30-35‰ and in water from less than 10 to 15 C with optimum growth at 10 to 12 C. The maximum variations in salinity and temperature tolerated during a tidal cycle were approximately 2‰ and 5 C. Laboratory experiments in the Gilson respirometer showed that the rates of photosynthesis and respiration in sea water at 15 and 20 C were below the rate at 10 C. With decreasing salinities the rates of photosynthesis determined in both instruments were markedly altered but variations in salinity above 11‰ did not significantly alter the rates of respiration. Long term adaptations did not significantly alter the rates of respiration and photosynthesis. Therefore high temperatures may act as a limiting factor, but decreasing salinities to approximately 11‰ did not markedly alter the rates of respiration and photosynthesis. It appears that this species was limited in its distribution in the estuary by some other factors since the tolerance range exceeds the range occupied.

Gigartina californica was found in the estuary in salinities from 26 to 35‰ with optimum growth occurring in 30-35‰, and in water from less than 10 to 16 C. The variation tolerated during a tidal cycle was approximately 3‰ salinity and 5 C. Laboratory studies showed a slight change in the rates of respiration and photosynthesis in dilutions of 22‰ salinity but with further dilution the rates were

markedly altered. Therefore, reduced salinities may act as a limiting factor in the distribution of this species. Temperatures above 15 C may also be a limiting factor since, in the Gilson respirometer experiments, the rate of photosynthesis in sea water, at 20 C was below the rate at 15 C. It appears that the distribution of this species in nature is extended to its full tolerance of variation in salinity and temperature and that salinity is perhaps a primary factor limiting its distribution.

As in almost any type of investigation questions are raised that suggest additional studies. Certainly the complete understanding of the complex influence of salinity and temperature on the metabolism of algae requires more physiological studies. Salinity tolerance should also be determined at different stages in the life cycle of the alga being studied. Animal investigations have shown that eggs and young of many species are less tolerant than the adults. As far as can be determined, except for some Japanese studies, there is a complete lack of this type of information for algae. Such a study could be approached in two ways. First, through culture techniques and secondly through field and laboratory studies similar to those used in the present study. These studies may prove salinity to be a significant factor limiting species such as Enteromorpha, Odonthalia, and Iridaea which as mature plants in the present study showed salinity tolerances in excess of variations they encountered

in nature. These studies might also shed some light on the sterility of many estuarine algae as noted by Munda (1964) and others. As mentioned earlier, silt is one of the major physical factors operating in an estuary such as Yaquina Bay and should be investigated thoroughly as to its significance in the ecology of estuarine algae. Studies of colonization of artificial substrates could be very valuable in understanding successional patterns, community development, and temperature and salinity tolerance at different stages of development. Cement blocks placed at various locations in Yaquina estuary failed because of rapid siltation. Perhaps, this would have been successful if the substrates had been suspended from the docks along the estuary where they would not be covered by silt or sand. This method would be advantageous in that it would be easier to maintain and one could easily establish a vertical gradient.

SUMMARY AND CONCLUSIONS

The causal analysis of growth and distribution of macro-algae requires a full understanding of the relationship between their metabolism and the environmental variables. The role of temperature and salinity as factors influencing the rates of respiration and photosynthesis were investigated in eight species of macro-algae by two laboratory methods. These methods were manometric measurements of changes in oxygen concentration in a Gilson differential respirometer, and Winkler titrations to determine changes in oxygen concentration in a 50-liter photosynthesis-respiration chamber. The species used in the laboratory studies were Ulva expansa, Enteromorpha linza, Laminaria saccharina, Sargassum muticum, Alaria marginata, Odonthalia floccosa, Iridaea splendens, and Gigartina californica.

Field studies of the 130 recognized algal inhabitants were undertaken to determine their distribution and growth in relation to tidal zone, spatial and seasonal occurrence, and tolerance to variations in salinity and temperature.

Yaquina estuary can be divided into four zones, each populated by a flora characteristic of the conditions existing in that zone. Zone one, extending 1.5 kilometers into the estuary, supports a transitional open coast flora strongly influenced by marine waters with

their characteristic low temperatures and high salinities. Zone two, extending about eight kilometers into the estuary, is a transitional brackish water area occupied by by brackish water species and some of the more tolerant forms of zone one. Zone three, extending approximately 13 kilometers above zone two is a brackish water area with typical brackish water inhabitants. Zone four, above the town of Toledo, is essentially fresh water.

Of the 130 forms in the estuary 125 were found in salinities of 30-35‰, 73 in 25-29‰, 14 in 20-24‰, 12 in 15-19‰, 10 in 10-14‰, nine in 5-9‰ and five in salinities of less than 5‰. The distribution of species in relation to temperature by comparison of collection data with the patterns of temperature in the estuary revealed 84 species in temperatures of less than 10 C, 127 in 10-12 C, 82 in 13-16 C, 18 in 17-20 C, and eight species were found in water of a temperature above 20 C.

In the laboratory experiments the following general trends were shown: a) rates of respiration increased with decreasing salinity: b) rates of respiration increased with increasing temperatures; c) rates of respiration in some species were inhibited at 20 C; d) rates of photosynthesis in Ulva, Sargassum, Odonthalia, and Gigartina were, at some temperatures, increased by dilutions near 22‰ salinity, but usually with dilutions below 22‰, these and the other species studied showed lower rates of photosynthesis; e) rates of

photosynthesis were generally higher with increasing temperatures; f) rates of photosynthesis at 20 C in three cases were below the rates at 15 C; and g) rates of photosynthesis were influenced more than rates of respiration by extreme variations in salinity.

Temperature coefficients of respiration were highest at the 10-15 C range in sea water, but at 15-20 C the highest values were usually in water of less than 11‰ salinity. Temperature coefficients of photosynthesis at 10-15 C were generally highest in sea water, but at 15-20 C the greatest effect of temperature change occurred in salinities of less than 12‰. Thus, in the case of short term submergence, the response to variations in temperature and salinity is greatest in reduced salinities at high temperatures, but this response was so great that it was interpreted as cellular damage that will lead to death of the algae. Rates of photosynthesis were more responsive to extreme dilution than rates of respiration, but rates of respiration were more responsive to temperature variations than rates of photosynthesis.

The adaptation experiments showed that rates of respiration and photosynthesis were reduced when plants were adapted to salinities lower than sea water for a period of two days or longer. In salinities above those in which the algae were adapted, rates were only slightly altered from the rate under the conditions of adaptation, but in salinities below those of adaptation, rates tended to parallel

those shown by non-adapted plants.

Ulva expansa, Laminaria saccharina, Sargassum muticum, Alaria marginata, and Gigartina californica showed tolerance to variations in salinity and temperature in the laboratory experiments corresponding to their distribution in the estuary, and with its physical and chemical regime. In laboratory experiments, Enteromorpha linza, Odonthalia floccosa, and Iridaea splendens showed tolerance to variations of salinity and temperature exceeding the variations they encountered in nature and their distribution must be limited by some other factors.

The distance algae extend into an estuary is dependent upon their tolerance to the conditions therein. The magnitude of tidal and seasonal variations in temperature and salinity I consider to be of more importance than either mean annual salinity or temperature in contributing to the algal spatial and seasonal distribution. I also consider silt to be a very influential factor in determining the distribution of algae in an estuary.

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APPENDICES

APPENDIX A

Table 1. Comparison of rates of respiration by adapted and non-adapted plants.

Species	Cond. of adaptation	mg O_2 consumed/hr/g	Non-adapted plants mg O_2 consumed/hr/g		
U. expansa	40 hrs @ 8.9 ‰	2.81			salinity
Salinity	15.5 C		15.2 C		
31 ‰		2.72	2.81	33‰	
21 ‰		4.08	5.20	18‰	
11 ‰		2.72	5.22	12‰	
05 ‰		1.44	1.70	04‰	
L. saccharina	48 hrs @ 27.8‰	0.36			
	16.2 C		15.8 C		av of 2 runs
32‰		0.33	1.50	33‰	
21‰		1.14	1.85	21‰	
12‰		1.08	1.90	11‰	
05‰		1.49	2.09	05‰	
A. marginata	30 hrs @ 18.1‰	0.45			
	15.7 C		16.0 C		av of 2 runs
32‰		0.55	1.26	33‰	
21‰		0.52	1.41	20‰	
10‰		1.12	1.41	09‰	
03‰		1.16	1.35	02‰	
S. muticum	96 hrs @ 21.6‰	0.59			
	15.5 C		15.1 C		
32‰		0.50	0.49	33‰	
22‰		0.77	1.64	23‰	
10‰		1.82	2.06	12‰	
05‰		1.04	1.97	03‰	
L. splendens	96 hrs @ 13.3‰	0.59			
	15.5 C		15.5 C		
31 ‰		0.41	0.29	34‰	
25 ‰		0.41	0.48	23‰	
11 ‰		0.49	0.58	11‰	
05 ‰		0.69	0.43	04‰	

APPENDIX A (Continued)

Table 2. Comparison of rates of photosynthesis by adapted and non-adapted plants.

Species	Cond. of adaptation	mg O_2 evolved/hr/g	Non-adapted plants mg O_2 evolved/hr/g		
U. expansa	40 hrs @ 8.9 ‰	6.04	15.2 C		salinity
Salinity	15.5 C				
31 ‰		9.52	14.35	33‰	
21 ‰		8.84	14.35	18‰	
11 ‰		5.78	22.61	12‰	
05 ‰		4.66	6.96	04‰	
L. saccharina	48 hrs @ 27.8‰	2.75			
	16.2 C		15.8 C		av of 2 runs
32 ‰		2.79	6.05	33 ‰	
21 ‰		2.66	5.36	21 ‰	
12 ‰		1.74	1.07	11 ‰	
05 ‰		1.08	1.15	05 ‰	
A. marginata	30 hrs @ 18.1 ‰	1.79			
	15.7 C		16.0 C		av of 2 runs
32 ‰		1.29	3.62	33 ‰	
21 ‰		1.79	2.73	20 ‰	
10 ‰		1.64	1.52	09 ‰	
03 ‰		2.81	1.28	02 ‰	
S. muticum	96 hrs @ 21.6‰	2.86			
	15.5 C		15.1 C		
32 ‰		3.14	5.59	33 ‰	
22 ‰		3.13	5.51	23 ‰	
10 ‰		4.22	4.36	12 ‰	
05 ‰		1.63	0.90	03 ‰	
L. splendens	96 hrs @ 13.3 ‰	1.09			
	15.5 C		15.5 C		
31 ‰		1.55	2.13	34 ‰	
25 ‰		1.47	1.65	23 ‰	
11 ‰		0.87	0.91	11 ‰	
05 ‰		0.34	0.24	04 ‰	

Table 3. Comparison of respiratory rates at 10°C in the Gilson and P-R chamber.

Species	Gilson mean of 3 replicats @ 10°C μl O_2 uptake/hr./mg.	Conversion factor rate x 32/22.4 = rate in μg./hr/mg	P-R chamber mg O_2 uptake/ hr./g.	
U. expansa			(10.1°C)	
S.W.	0.33	0.47	2.61	31.2‰
22.0‰	0.48	0.69	3.35	25.0‰
11.6‰	0.41	0.59	3.10	12.2‰
F.W.	0.32	0.46	3.73	03.9‰
E. linza				
S.W.				
22.0 ‰				
11.6 ‰				
F.W.				
L. saccharina			(10.2°C)	
S.W.	0.49	0.70	0.51	29.8‰
22.0‰	0.50	0.71	0.32	22.0‰
11.6‰	0.72	1.20	0.44	10.3‰
F.W.	0.61	0.81	0.26	03.6‰
S. muticum			(09.8°C)	
S.W.	0.71	1.01	0.52	31.0‰
22.0‰	0.70	1.00	0.61	24.3‰
11.6‰	0.83	1.18	0.98	12.4‰
F.W.	1.00	1.43	0.90	5.2‰
A. marginata			(09.5°C)	
S.W.			0.26	31.4‰
22.0 ‰			0.25	22.1 ‰
11.6 ‰			0.46	10.7 ‰
F.W.			0.74	05.0 ‰
O. floccosa				
S.W.	0.32	0.46		
22.0 ‰	0.56	0.79		
11.6 ‰	0.35	0.50		
F.W.	0.97	1.38		
I. splendens				
S.W.	0.11 Av. of 2 runs	0.15		
22.0 ‰	0.19	0.27		
11.6 ‰	0.18	0.26		
F.W.	0.14	0.20		
C. californica				
S.W.	0.31	0.44		
22.0 ‰	0.42	0.60		
11.6 ‰	0.60	0.85		
F.W.	0.52	0.74		

Table 4. Comparison of respiratory rates at 15°C in the Gilson and P-R chamber.

Species	Gilson $\mu l\ O_2$/hr./mg.	Conversion to $\mu g\ O_2$/hr./mg.	P-R chamber mg./hr./g.	
U. expansa			(15.2°C)	
S.W.	0.51	0.72	2.81	33.3 ‰
22.0 ‰	0.55	0.78	5.20	17.9 ‰
11.6 ‰	0.44	0.63	5.22	12.0 ‰
F.W.	0.41	0.59	1.70	03.7 ‰
E. linza			(15.3°C)	
S.W.			1.49	32.9 ‰
22.0 ‰			3.73	19.2 ‰
11.6 ‰			3.73	11.1 ‰
F.W.			0.25	02.8 ‰
L. saccharina			(15.8°C)	
S.W.	0.55	0.78	1.50 Av. of 2 runs	33.0 ‰
22.0 ‰	0.54	0.77	1.85	20.5 ‰
11.6 ‰	0.75	1.07	1.90	10.5 ‰
F.W.	0.66	0.94	2.09	04.5 ‰
S. muticum			(15.1°C)	
S.W.	0.57	0.81	0.49	32.7 ‰
22.0 ‰	0.76	1.08	1.64	22.6 ‰
11.6 ‰	0.86	1.23	2.06	11.5 ‰
F.W.	0.78	1.11	1.97	02.5 ‰
A. marginata			(16.0°C)	
S.W.			1.26	32.5 ‰
22.0 ‰			1.41	19.5 ‰
11.6 ‰			1.41	08.5 ‰
F.W.			1.35	02.4 ‰
O. floccosa			(15.5°C)	
S.W.	0.67	0.95	3.71 Av. of 2 runs	32.2 ‰
22.0 ‰	0.77	1.10	3.34	23.2 ‰
11.6 ‰	0.57	0.81	3.25	10.5 ‰
F.W.	0.98	1.40	5.12	03.8 ‰
I. splendens			(15.9°C)	
S.W.	0.15	0.21	0.29	33.6 ‰
22.0 ‰	0.20	0.29	0.48	22.9 ‰
11.6 ‰	0.18	0.26	0.58	11.4 ‰
F.W.	0.23	0.33	0.43	03.9 ‰
G. californica			(17.4°C)	
S.W.	0.32	0.47	1.01	33.2 ‰
22.0 ‰	0.43	0.61	1.29	22.5 ‰
11.6 ‰	0.56	0.80	0.96	11.1 ‰
F.W.	0.33	0.48	1.35	04.8 ‰

Table 5. Comparison of respiratory rates at 20°C in the Gilson and P-R chamber.

Species	Gilson $\mu l\ O_2$/hr. / mg.	Conversion to $\mu g\ O_2$/hr. /mg.	P-R chamber mg. /hr. /g.	
U. expansa			(20.4°C)	
S.W.	0.61	0.87	5.46	32.7‰
22.0 ‰	1.68	2.40		22.2‰
11.6 ‰	1.64	2.34	4.17	11.5‰
F.W.	1.65	2.35	3.71	03.5‰
E. linza			(19.9°C)	
S.W.			7.04	33.6‰
22.0 ‰			11.74	22.2‰
11.6 ‰			9.86	10.5‰
F.W.			1.88	03.2‰
L. saccharina			(20.9°C)	
S.W.	0.54	0.77	1.80	33.0‰
22.0 ‰	0.69	0.98	3.04	21.7 ‰
11.6 ‰	0.81	1.16	2.72	12.0 ‰
F.W.	0.68	0.97	2.71	04.2 ‰
S. muticum			(20.9°C)	
S.W.	0.53	0.76	1.84	32.7‰
22.0 ‰	0.87	1.24	1.98	23.7 ‰
11.6 ‰	0.87	1.24	2.56	12.2 ‰
F.W.	0.97	1.38	2.25	05.2 ‰
A. marginata			(19.8°C)	
S.W.			2.86	33.2‰
22.0 ‰			3.05	22.4 ‰
11.6 ‰			3.24	10.8 ‰
F.W.			2.86	4.7 ‰
O. floccosa			(20.5°C)	
S.W.	0.55	0.78	7.44	33.4‰
22.0 ‰	0.58	0.82	6.15	21.2‰
11.6 ‰	0.81	1.15	7.12	10.8‰
F.W.	1.82	2.60	7.12	03.8‰
I. splendens			(20.7°C)	
S.W.	0.15	0.21	2.04	32.5‰
22.0 ‰	0.15	0.21	1.27	23.0‰
11.6 ‰	0.28	0.40	1.60	10.7‰
F.W.	0.32	0.45	1.87	04.5‰
G. californica			(19.8°C)	
S.W.	0.36	0.51	2.65	32.5‰
22.0 ‰	0.55	0.78	3.24	23.8‰
11.6 ‰	0.69	0.99	2.94	12.2‰
F.W.	0.51	0.72	4.41	03.5‰

Table 6. Comparison of photosynthetic rates at 10°C in the Gilson and P-R chamber.

Species	Gilson mean of 3 replicats @ 10°C μl O_2 evolved/hr./mg.	Conversion factor rate x 32/22.4 = rate in μg./hr./mg.	P-R chamber mg. O_2 evolved/ hr./g.	
U. expansa			(10.1°C)	
S.W.	3.55	5.07	7.08	31.2‰
22.0‰	3.64	5.20	13.05	25.0‰
11.6‰	1.07	1.53	12.48	12.2‰
F.W.	0.69	0.98	9.95	03.9‰
E. linza				
S.W.				
22.0‰				
11.6‰				
F.W.				
L. saccharina			(10.2°C)	
S.W.	2.03	2.97	2.32	29.8‰
22.0‰	1.76	2.52	1.64	22.0‰
11.6‰	2.07	2.95	0.87	10.3‰
F.W.	0.87	1.24	-.12	03.6‰
S. muticum			(09.8°C)	
S.W.	1.71	2.44	2.10	31.0‰
22.0‰	2.86	4.08	2.24	24.3‰
11.6‰	1.97	2.81	1.53	12.4‰
F.W.	0.98	1.40	1.09	05.2‰
A. marginata			(09.5°C)	
S.W.			1.28	34.4‰
22.0‰			1.74	22.1‰
11.6‰			0.51	10.7‰
F.W.			0.96	03.0‰
O. floccosa				
S.W.	3.57	5.10		
22.0‰	3.02	4.31		
11.6‰	1.99	2.84		
F.W.	0.59	0.84		
I. splendens				
S.W.	1.05 Av. of 2 runs	1.50		
22.0‰	0.93	1.33		
11.6‰	0.72	1.02		
F.W.	0.41	0.58		
G. californica				
S.W.	1.06	1.51		
22.0‰	1.41	2.01		
11.6‰	1.62	2.31		
F.W.	1.09	1.55		

Table 7. Comparison of photosynthetic rates at 15°C in the Gilson and P-R chamber.

Species	Gilson mean of 3 replicats @ 15°C μl O_2 evolved/hr./mg.	Conversion factor rate x 32/22.4 = rate in μg./hr./mg.	P-R chamber mg. O_2 evolved/ hr./g.		
U. expansa				(15.2°C)	
S.W.			14.35		33.0‰
22.0 ‰			14.35		17.9 ‰
11.6 ‰			22.61		12.0 ‰
F.W.			6.96		03.7 ‰
E. linza				(15.3°C)	
S.W.			10.95		32.9‰
22.0 ‰			10.45		19.2 ‰
11.6 ‰			9.70		11.1 ‰
F.W.			1.99		02.8 ‰
L. saccharina				(15.8°C)	
S.W.			6.05		32.7‰
22.0 ‰			5.36		21.2 ‰
11.6 ‰			1.07		10.5 ‰
F.W.			1.15		03.8 ‰
S. muticum				(15.1°C)	
S.W.	3.00	4.29	5.59		32.7‰
22.0 ‰	3.29	4.62	5.51		22.6 ‰
11.6 ‰	2.23	3.08	4.36		11.5 ‰
F.W.	1.00	1.43	0.90		02.5 ‰
A. marginata				(16.0°C)	Av. of 2 runs
S.W.			3.62		32.5‰
22.0 ‰			2.73		19.5 ‰
11.6 ‰			1.52		08.5 ‰
F.W.			1.28		02.4 ‰
O. floccosa				(15.5°C)	
S.W.	2.71	3.87	8.17		32.2‰
22.0 ‰	2.35	3.35	8.50		23.2 ‰
11.6 ‰	1.23	1.75	0.98		10.5 ‰
F.W.	-.19	-.27	0.65		03.8 ‰
I. splendens				(15.9°C)	
S.W.			2.13		33.6‰
22.0 ‰			1.65		22.9 ‰
11.6 ‰			0.91		11.4 ‰
F.W.			0.24		03.9 ‰
G. californica				(17.4°C)	
S.W.	1.50	2.14	4.04		33.2‰
22.0 ‰	1.36	1.94	3.99		22.5 ‰
11.6 ‰	0.92	1.31	2.19		11.1 ‰
F.W.	0.71	1.01	2.53		04.8 ‰

Table 8. Comparison of photosynthetic rates at 20°C in the Gilson and P-R chamber.

Species	Gilson mean of 3 replicats @ 20°C μl O_2 evolved/hr./mg.	Conversion factor rate x 32/22.4 = rate in μg./hr./mg.	P-R chamber mg. O_2 evolved/ hr./g.	
U. expansa			(20.4°C)	
S.W.	6.25	9.83	14.63 Av. of 2 runs	32.7‰
22.0 ‰	12.14	17.35	12.36	22.2 ‰
11.6 ‰	10.0	14.29	10.28	11.5 ‰
F.W.	4.17	5.96	8.82	03.5 ‰
E. linza			(19.9°C)	
S.W.			15.26	33.6‰
22.5 ‰			17.37	22.2 ‰
11.6 ‰			14.79	10.5 ‰
F.W.			3.67	03.2 ‰
L. saccharina			(20.9°C)	
S.W.	2.19	3.13	6.31	33.0‰
22.0 ‰	2.16	3.09	5.74	21.7 ‰
11.6 ‰	1.97	2.81	3.36	12.0‰
F.W.	0.64	0.91	3.09	04.2 ‰
S. muticum			(20.9°C)	
S.W.	4.01	5.73	3.69	32.7‰
22.0 ‰	6.53	8.26	4.07	23.7 ‰
11.6 ‰	2.85	4.08	2.37	12.2‰
F.W.	1.50	2.14	1.46	05.2‰
A. marginata			(19.8°C)	
S.W.	3.63		8.69	33.2‰
22.0 ‰	3.63		6.67	22.4‰
11.6 ‰	2.31		4.19	10.8‰
F.W.	1.31		2.76	04.7‰
O. floccosa			(20.5°C)	
S.W.	3.56	5.18	13.59	33.4‰
22.0 ‰	3.63	5.18	16.80	21.2‰
11.6 ‰	2.31	3.30	12.94	10.8‰
F.W.	1.31	1.87	5.83	03.8‰
I. splendens			(20.7°C)	
S.W.	0.65	0.92	6.27	32.5‰
22.0 ‰	0.64	0.91	3.24	23.0‰
11.6 ‰	0.61	0.85	2.25	10.7‰
F.W.	0.54	0.77	1.32	04.5‰
G. californica			(19.8°C)	
S.W.	1.45	2.07	7.65	32.5‰
22.0‰	1.65	2.35	6.32	23.8‰
11.6‰	1.64	2.34	4.12	12.2‰
F.W.	0.86	1.22	4.55	03.5‰

APPENDIX B

SPECIES PRESENT IN YAQUINA BAY AND THEIR HABITAT

CHLOROPHYTA

Ulothrix implexa Kutzing. On rocks in the upper intertidal zone.

Monostroma fuscum (Postels and Ruprecht) Wittr. f. fuscum. On rocks in the mid-intertidal.

Monostroma oxyspermum (Kutzing) Doty. On rocks, logs, sticks, or entangled with other algae or salt grass in the upper and mid-intertidal.

Monostroma zostericola Tilden. Epiphytic on Zostera in the lower intertidal.

Enteromorpha clathrata (Roth) Greville. On rocks, logs, epiphytic, or free floating in the middle to lower intertidal.

Enteromorpha compressa (L) Greville. On rocks and logs in the upper intertidal.

Enteromorpha intestinalis f. clavata J. Agardh. On rocks, shells, logs, or epiphytic on Fucus in the upper intertidal. In January, February, and March a distinct and obvious green zone of this species appears on the rocks of the estuary in what would correspond to an extreme high intertidal or splash zone.

Enteromorpha intestinalis f. cylindricea J. Agardh. This may simply be a growth form of f. clavata. Free floating.

Enteromorpha linza (L) J. Agardh. On rocks, shells, or logs in the lower intertidal to mid-intertidal.

Enteromorpha marginata J. Agardh. Growing on pickle grass (Salicornia) of mud flats or in tide pools in marshes in the upper intertidal.

Enteromorpha tubulosa Kutzing. On logs or rocks in the upper intertidal.

Ulva angusta -- Enteromorpha angusta (Setchell and Gardner) Doty. On rocks, logs, or epiphytic in the lower intertidal to a depth of three meters.

Ulva expansa (Setchell) Setchell and Gardner. On rocks or logs in the lower intertidal to a depth of five meters.

Ulva fenestrata Postels and Ruprecht. On rocks or logs in the lower intertidal to a depth of four meters.

Ulva lobata (Kutzing) Setchell and Gardner. On rocks or epiphytic in the lower intertidal.

Ulva rigida C. Agardh. On rocks and wood or epiphytic in the intertidal and subtidal.

Ulva taeniata (Setchell) Setchell and Gardner. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Rhizoclonium riparium (Roth) Harvey. On rocks, mud, or logs in the lower intertidal.

Urospora penicilliformis (Roth) Areschoug. On rocks in the upper intertidal.

Chaetomorpha aerea (Dillwyn) Kuetzing. On mud flats in the middle intertidal.

Chaetomorpha tortuosa (Dillwyn) Kutzing. Entangled on other algae in the intertidal.

Cladophora gracilis (Griffiths) Kutzing. On mud flats, rocks or logs in the middle intertidal.

Cladophora trichotoma (C. Agardh) Kutzing. On rocks in the upper intertidal.

Spongomorpha coalita (Ruprecht) Collins. On rocks, logs, or epiphytic in the lower intertidal.

Spongomorpha spinescens Kutzing. Epiphytic in the lower intertidal.

Bryopsis corticulans Setchell in Collins, Holden and Setchell. On rocks or logs in the lower intertidal to a depth of three meters in the subtidal.

PHAEOPHYTA

Pylaiella littoralis (Lyngbye) Kjellman. On log floats.

Ectocarpus acutus Setchell and Gardner var. acutus. Epiphytic on Desmarestia and Alaria in the lower intertidal.

Ectocarpus confervoides (Roth) LeJolis f. confervoides. Epiphytic on larger brown algae in the lower intertidal.

Ectocarpus dimorphus Silva. Epiphytic on Desmarestia or Laminaria saccharina in the lower intertidal to subtidal.

Ectocarpus granulosus (J. E. Smith) C. Agardh. On rocks in the lower intertidal.

Ectocarpus granulosoides Setchell and Gardner. On log floats.

Ectocarpus mucronatus Saunders. On logs and epiphytic on L. sinclairii in the lower intertidal and subtidal.

Ectocarpus oviger Harvey. On rocks in the upper intertidal.

Streblonema pacificum Saunders. On Hedophyllum in the lower intertidal.

Haplospongidiun gelatinosum Saunders. On rocks in the upper intertidal.

Hecatonema variabile Setchell and Gardner. Epiphytic on the stipe of Nereocystis in the subtidal.

Elachistea fucicola (Velley) Areschoug. Epiphytic on Fucus in the upper intertidal.

Leathesia difformis (L) Areschoug. On rocks or epiphytic in the upper intertidal.

Haplogloia andersonii (Farlow) Levering. On rocks in the middle intertidal.

Heterochordaria abietina (Ruprecht) Setchell and Gardner. On rocks in the upper intertidal.

Desmarestia munda Setchell and Gardner. On rocks and logs in the lower intertidal to a depth of four meters.

Soranthera ulvoidea Postels and Ruprecht f. ulvoidea. Epiphytic on Rhodomela in the upper intertidal.

Scytosiphon lomentaria (Lyngbye) J. Agardh f. lomentaria. On rocks or logs in the lower intertidal.

Petalonia debilis (C. Agardh) Derbes and Solier f. debilis. On rocks, logs or Zostera in the upper to the lower intertidal.

Dictyosiphon chordaria Areschoug. On rocks, subtidal to a depth of two meters.

Laminaria saccharina Lamouroux f. saccharina. On rocks or log floats in the lower intertidal to a depth of three meters in the subtidal.

Laminaria setchellii Silva. On rocks in the lower intertidal or subtidal to a depth of one meter.

Laminaria sinclairii (Harvey ex Hooker f. et Harvey) Farlow, Anderson, and Eaton. On rocks in the lower intertidal to a depth of one meter in the subtidal.

Hedophyllum sessile (C. Agardh) Setchell, in Collins, Holden, and Setchell. On rocks in the middle intertidal.

Nereocystis luetkeana (Mertens) Postels and Ruprecht. On rocks in the subtidal to a depth of five meters. Dense stands develop each spring and persist until November on the spurs of the south jetty.

Alaria marginata Postels and Ruprecht. On rocks or logs lower intertidal to a dept of three meters in the subtidal.

Egregia menziesii (Turner) Areschoug subsp. menziesii. On rocks in the lower intertidal to a depth of three meters in the subtidal.

Fucus evanescens f. oregonensis Gardner. On rocks or mud flats in the middle intertidal. On the mud flats in some locations this species exists as sterile mats.

Fucus evanescens f. robustus Setchell and Gardner. On rocks or logs in the upper intertidal.

Fucus furcatus f. angustus Gardner. On rocks in the upper intertidal.

Fucus frucatus f. linearis Gardner. On rocks in the upper intertidal.

Pelvetiopsis limitata (Setchell Gardner) f. limitata. On rocks high in the upper intertidal.

Sargassum muticum (Yendo) Fensholt. On rocks subtidal to a depth of four meters. The most luxurious growth occurs on the leeward side of the spurs on the south jetty.

RHODOPHYTA

Bangia vermicularis Harvey. On piling or rocks in the upper intertidal.

Porphyra lanceolata (Setchell and Hudson) G. M. Smith in Smith and Hollenberg. On rocks in the upper intertidal.

Porphyra naiadum Anderson, in Blankinship and Keeler. Epiphytic on Zostera and Phyllospadix in the lower intertidal.

Porphyra nereocystis Anderson, in Blankinship and Keeler. Rare, found only on Nereocystis in wash.

Porphyra perforata J. Agardh f. perforata. On rocks in the upper intertidal.

Porphyra thuretii Setchell and Hudson. On rocks in the upper intertidal.

Porphyrella gardneri Smith and Hollenberg. On Phyllospadix or L. sinclairii in the lower intertidal to subtidal.

Cumagloia andersonii (Farlow) Setchell and Gardner, in Gardner. On rocks in the upper intertidal.

Cryptosiphonia woodii J. Agardh. On rocks in the upper to lower intertidal.

Pikea pinnata Setchell, in Collins, Holden and Setchell. On rocks in the lower intertidal.

Dilsea californica (J. Agardh) O. Kuntz. On rocks in the lower intertidal.

Constantinea simplex Setchell. Collected on several occasions only during the spring of 1964. On rocks in the lower intertidal.

Bossiella dichotoma (Manza) Silva. On rocks in the lower intertidal to a depth of two meters.

Corallina officinalis var. chilensis (Harvey) Kutzing. On rocks in the middle intertidal to a depth of three meters.

Corallina gracilis f. densa Collins. On rocks the encrusting basal portion present all year in the upper intertidal to a depth of three meters in the subtidal.

Grateloupia californica Kylin. On rocks in the lower intertidal.

Halymenia californica Smith and Hollenberg. On rocks in the lower intertidal.

Prionitis andersonii Eaton in Farlow. On rocks in the lower intertidal.

Prionitis lanceolata Harvey. On rocks in the upper intertidal.

Prionitis lyallii Harvey. On rocks in the middle intertidal.

Callophyllis megalocarpa Setchell and Swezy, in Setchell. Subtidal on rocks to a depth of five meters.

Callophyllis pinnata Setchell and Swezy in Setchell. Epiphytic on red algae in the lower intertidal to a depth of two meters in the subtidal.

Erythrophyllum delesserioides J. Agardh. On rocks in the subtidal to a depth of three meters.

Schizymenia pacifica Kylin. On rocks in the lower intertidal.

Opuntiella californica (Farlow) Kylin. On rocks in the lower intertidal.

Plocamium pacificum Kylin. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Gracilariopsis sjoestedtii (Kylin) Dawson. On rocks and shells in the lower intertidal to a depth of four meters in the subtidal.

Gracilaria verrucosa (Hudson) Papenfuss. Massive patches in protected mud flats in the mid-intertidal.

Ahnfeltia gigartinoides J. G. Agardh. On rocks in the lower intertidal.

Gymnogongrus leptophyllus J. G. Agardh. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Gymnogongrus linearis (Turner) J. G. Agardh. On rocks in the lower intertidal.

Gigartina agardhii Setchell and Gardner. On rocks in the upper intertidal.

Gigartina canaliculata Harvey. On rocks in the lower intertidal.

Gigartina californica J. G. Agardh. On rocks in the lower intertidal to a depth of three meters in the subtidal.

Gigartina cristata (Setchell) Setchell and Gardner. On rocks in the upper intertidal.

Gigartina harveyana (Kutzing) Setchell and Gardner. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Gigartina papillata (C. A. Agardh) J. G. Agardh. On rocks in the upper intertidal.

Gigartina spinosa (Kutzing) Harvey. On rocks in the lower intertidal to a depth of one meter in the subtidal.

Gigartina volans (C. A. Agardh) J. G. Agardh. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Iridaea coriacea (Setchell and Gardner) Scagel. On rocks lower intertidal to a depth of two meters in the subtidal.

Iridaea flaccidam (Setchell and Gardner) Papenfuss. On rocks lower intertidal to a depth of two meters in the subtidal.

Iridaea heterocarpa Postels and Ruprecht. On rocks upper to middle intertidal.

Iridaea splendens (Setchell and Gardner). Papenfuss. On rocks lower intertidal to a depth of three meters in the subtidal.

Halosaccion glandiforme (Gemlin) Ruprecht. On rocks in the upper intertidal.

Rhodymenia pacifica Kylin. On rocks in the subtidal to a depth of three meters.

Antithamnion kylinii Gardner. On log floats.

Antithamnion pacificum (Harvey) Kylin. On log floats.

Platythamnion pectinatum Kylin. On rocks or logs in the lower intertidal to a depth of five meters in the subtidal. In the early spring it is in the intertidal but is found only subtidally during the summer and fall.

Platythamnion villosum Kylin. On rocks in the lower intertidal and subtidally.

Callithamnion pikeanum Harvey. On rocks or epiphytic in the lower intertidal.

Ceramium californicum J. Agardh. Found only on Gracilariopsis as an epiphyte in the lower intertidal to a depth of three meters in the subtidal.

Ceramium gardneri Kylin. On rocks in the lower intertidal.

Ceramium eatonianum (Farlow) DeToni. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Ceramium pacificum (Collins) Kylin. On rocks in the lower intertidal.

Microcladia borealis Ruprecht. On rocks and epiphytic in the lower intertidal.

Ptilota filicina (Farlow) J. Agardh. On rocks in the lower intertidal.

Membranoptera multiramosa Gardner. On rocks in the lower intertidal or subtidal.

Delesseria decipiens J. Agardh. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Polyneura latissima (Harvey) Kylin. On rocks, logs or epiphytic in the lower intertidal to a depth of three meters. Common in the spring and summer of 1964 rare in the spring and summer of 1965, but common in the spring of 1966.

Hymenia flabelligera (J. G. Agardh) Kylin. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Hymenia multiloba (J. G. Agardh) Kylin. On rocks in the lower intertidal to a depth of two meters in the subtidal.

Polysiphonia collinsii Hollenberg. On rocks in the lower intertidal.

Polysiphonia californica Harvey. On rocks or logs in the lower intertidal to a depth of three meters.

Polysiphonia decussata Hollenberg. Epiphytic on Enteromorpha in the middle intertidal.

Polysiphonia pacificum Hollenberg. On rocks or logs in the lower intertidal to the subtidal.

Pterosiphonia dendroidea (Montagne) Falkenberg. Epiphytic and on rocks in the lower intertidal to subtidal.

Pterosiphonia bipinnata (Postels and Ruprecht) Falkenberg. On rocks in the lower intertidal to subtidal.

Laurencia spectabilis Postels and Ruprecht. On rocks in the lower intertidal to a depth of two meters.

Rhodomela larix (Turner) C. Agardh. On rocks in the upper intertidal.

Odonthalia floccosa (Esper) Falkenberg. On rocks in the lower intertidal to a depth of three meters in the subtidal.

Odonthalia washingtoniensis Kylin. On rocks in the lower intertidal to a depth of two meters in the subtidal.

APPENDIX C

KEY TO THE MACRO-ALGAE OF YAQUINA BAY

A. PLANTS BRIGHT GRASS GREEN OR DARK SPINACH GREEN . . . . . .CHLOROPHYTA
1. Thallus coenocytic . . . . . .Bryopsis corticulans
1. Thallus parenchymatous or filamentous in organization 2
2. Thallus filamentous 3
3. Filaments unbranched 4
4. Filaments free or entangled . . . . . Rhizoclonium riparium
4. Filaments attached 5
5. Filaments with enlarged basal attachment cell growing on mud flats . . . . . Chaetomorpha aerea
5. Filaments attached by rhizoids descending from several cells above . . . . the base 6
6. Cells 5 to 18 μ in diameter . . . . . .Ulothrix implexa
6. Filaments enlarged at tip 150 μ and narrower 30-60μ near the base . . . . . Urospora pencilliformis
3. Filaments branched 7
7. Filaments free or entangled never held together by specialized hooked branchlets 8
8. Plants low, densely matted, main filaments 120-250μ in diameter. . . . . Cladophora trichotoma
8. Plants fine, filaments usually less than 120 μ in diameter . . . . . Cladophora gracilis
7. Filaments held together in lower parts by specialized hooked branchlets or both 9
9. Hooked branchlets simple . . . . . Spongomorpha spinescens
9. Hooked branchlets compound or branched . . . . . Spongomorpha coalita
2. Thallus parenchymatous 10
10. Thallus membranous, flattened, and at maturity solid at the base 11
11. Thallus 1 cell thick 12
12. Epiphytic on Zostera or Phyllospadix . . . . .Monostroma zostericola
12. Thallus often becoming 40 cm in width, light green, estuarian in habitat . . . . . Monostroma oxyspermum
11. Thallus 2 cells thick 13
13. Thallus with numerous round perforations. . . . . .Ulva fenestrata
13. Not as above. 14
14. Cells approximately square in cross section . . . . . Ulva lobata
14. Cells elongate cross section 15
15. Thallus narrowly lancaolate many times longer than broad 16
16. Blades lobed or split into narrow segments with dentate margins . . . . . Ulva taeniata
16. Blades usually entire margin smooth . . . .Ulva angusta
15. Thallus broad in proportion to length 17
17. Thallus large, orbicular with deeply ruffled margins. . . . . .Ulva expansa
17. Thallus short ovate, plane, usually deeply split . . . . . Ulva rigida
10. Thallus hollow, tubular, upper parts sometimes expanded 18
18. Thallus expanded above tubular only at the base . . . .Enteromorpha linza

18. Thallus more or less tubular throughout 19
19. Cells arranged in longitudinal rows 20
20. Thallus simple, narrowly linear, not inflated ..... Enteromorpha marginata
20. Thallus branching 21
21. Thallus coarse with a few short proliferations near the base, sometimes occasional longer branches above, plainly tubular ..... Enteromorpha tubulosa
21. Thallus regularly branched the branches tapering from the base to apex ..... Enteromorpha clathrata
19. Cells not arranged in longitudinal rows 22
22. Thallus simple inflated ..... Enteromorpha intestinalis
22. Thallus with more or less plentiful branches that are constricted at the base ..... Enteromorpha compressa

B. PLANTS OLIVE GREEN, TAN, OR BROWN ..... PHAEOPHYTA
1. Thallus crustose on rock surfaces ..... Haplospongidiun gelatinosum
1. Not crustose on rock surfaces 2
2. Thallus consisting of uniseriate vegetative filaments, these free or partially endophytic or forming an epiphytic disc 3
3. Thalli almost wholly endophytic deeply penetrating the host, the free filaments only slightly above the surface 4
4. Creeping portion deeply penetrating the host, eruptive sori aecidiodid ..... Streblonema aecidioides
4. Attaching portion poorly developed, not deeply penetrating the host 5
5. Pleurilocular structures uniseriate, erect filaments to 75 μ high ..... Streblonema myrionematoides
5. Pleurilocular structures both uniseriate and pluriseriate erect filaments to 480 μ high ..... Streblonema variable
3. Plants epiphytic or on rocks at times partially endophytic 6
6. Thalli forming epiphytic crusts, discs or patches 7
7. Thallus with a diastromatic basal layer ..... Hecatonema variabile
7. Thallus with a monostromatic basal layer 8
8. Plurilocular reproductive organs pleuriseriate growing on Hedophyllum ..... Compsionema sessile
8. Plurilocular reproductive organs uniseriate 9
9. All erect filaments fertile (except hairs and marginal cells) ..... Myrionema foecundum
9. Some erect filaments sterile 10
10. Pleurilocular sporangia both terminal and lateral epiphytic on Hedophyllum ..... Myrionema differmans
10. Pleurilocular sporangia terminal 11
11. Sterile erect filaments longer than fertile filaments ..... Myrionema egregiophilum
11. Sterile erect filaments the same length as the fertile filaments ..... Myrionema corunnae
6. Thalli of free conspicuous filaments 12
12. Thallus consisting of a dense cushion of short and long filaments on Fucus ..... Elachistea fucicola
12. All external filaments similar 13

13. Reproductive organs seriate intercalary . . . . . Pylaiella littoralis
13. Reproductive organs terminal or lateral 14
14. Thalli gregarious, forming velvety layers, in cushions . . . . . Ectocarpus dimorphus
14. Thalli distinct, feathery at times in rope-like tufts 15
15. Plastids disc-shaped 16
16. Branching, loose, mostly secund 17
17. Gametangia 60-100 μ long . . . . . Ectocarpus granulosus
17. Gametangia 40-60 μ long . . . . . Ectocarpus granulosoides
16. Branching, mostly alternate or irregular 18
18. Main axis corticated . . . . . Ectocarpus oviger
18. Main axis uncorticated . . . Ectocarpus mucronatus
15. Plastids band-shaped 19
19. Filaments corticated below . . . . . Ectocarpus acutus
19. Filaments not corticated . . . . Ectocarpus confervoides

2. Thallus not of uniseriate filaments 20
20. Thallus hollow-vesicular, tubular, or with hollow stipe, floats or vesicles . . .21
21. Thallus hollow in major part, a sessile bubble-like form, or tubular except at the base 22
22. Thallus without a stipe, bubble-like . . . . . Lethesia difformis
22. Thallus stipitate or at least narrowed basally to a solid attachment . . .23
23. Thallus epiphytic on Odenthalia and Rhodemela . . . . . Sorantheria ulvoidea
23. Thallus growing on rocks, tubular . . . . . Scytosiphon lomentaria
21. Thallus not hollow in major part, but possessing floats or vesicles 24
24. Stipe terminating in a large vesicle from which blades arise . . . . . Nereocystis leutkeana
24. Plants with more than one air vesicle 25
25. Air vesicles not at blade tips 26
26. Air vesicles small (less than 1 cm) . . . . . Sargassum muticum
26. Air vesicles large (more than 2 cm) 27
27. Stipe and axes flat, vesicles and blades disticous . . . . . Egregia manziesii
27. Occasionally occurs in floating mats, stipe cylindrical vesicles and blades radial . . . . . Macrocystis integrifolia
25. Air vesicles at blade tips 28
28. Oogonia with one functional egg and one degenerate egg . . . . . Pelvetiopsis limitata
28. Oogonia with more than 2 eggs 29
29. Estuarian in habitat, few caecostomata 30
30. Average frond width less than 15 mm . . . . . Fucus evanescens f. organensis
30. Average frond width more than 15 mm . . . . . Fucus evanescens f. robustus
29. Restricted to oceanic influence, with abundant caecostomata. 31
31. Frond 4-7 mm wide, receptacles acute . . . . . Fucus furcatus f. angustus
31. Frond 8-12 mm wide, receptacles blunt . . . . . Fucus furcatus f. linearis

20. Thallus without hollow parts 32
32. Dominant parts cylindrical 33
33. Axis and branches clothed with hairs, particularly deciduous . . . . . .Haplogloia andersonnii
33. Axis and branches without hairs . . . . . Heterochordaria abietina
32. Dominant parts flattened or expanded 34
34. Branching dichotomus or subdicotomus - Back to Fucus 28
34. Branching not dichotomus 35
35. Thallus with ribs or veins in blade 36
36. Longitudinal ribs delicate with opposite lateral veins Branches 2-10 cm broad . . . . . .Desmarestia munda
36. Longitudinal ribs, thick lacking lateral veins . . . . . .Alaria marginata
35. Thallus without ribs or veins 37
37. Thallus with an evident heavy stipe 38
38. Thallus consisting of upright blades from a branched prostrate rhizome . . . . . .Laminaria sinclairii
38. Thallus consisting of single stipe and blade 39
39. Stipe thick blade, broad in relation to length . . . . . .Laminaria setchelli
39. Stipe rather thin,blade, narrow in relation to length . . . . . Laminaria saccharina
37. Thallus without an evident heavy stipe 40
40. Thallus sessile attached by coarse haptera . . . . . Hedophyllum sessile
40. Attached by a disc, blades linear lanceolate . . . . . Petalonia debilis

C. PLANTS RED, PURPLE,OR PINK . . . . . RHODOPHYTA
1. Thallus calcified 2
2. Conceptacles more than one on terminal and intercilary intergenicula . . . . . Bessiella dichotoma
2. Conceptacles only one on terminal intergenicula 3
3. Branches of erect shoots laterally appressed and all about the same length, tetrasporangial conceptacles antenniferous . . . . . .Corallina gracilis
3. Basal branches of erect shoots longer than upper branches,not antenniferous . . . . . Corallina officinalis
1. Thallus uncalcified 4
4. Thallus uniseriate, at least in part 5
5. Unbranched, uniseriated in younger lower parts, pluriseriate above . . . . . .Bangia fuscopurpurea
5. Uniseriate filaments branched, uncorticated at least in upper parts 6
6. Filaments heavily corticated in lower parts . . . . . Callithamnion pikeanum
6. Filaments uncorticated 7
7. Thallus with four or more pericentral cells 8
8. Thallus with four pericentral cells . . . . . Polysiphonia pacifica
8. Thallus with more than four pericentral cells 9
9. Trichoblast or scar cell on every segment and each 1/4 turn to the right of the one below . . . . . Polysiphonia californica

9. Trichoblasts not so regularly arranged . . . . . Polysiphonia collinsii
7. Thallus with a single large cell in the main axes 10
10. Branching with two opposite branches from each segment . . . . Antithamnion pacificum
10. Branching with four opposite branches from each segment 11
11. Branchlets with two filaments above and one below . . . . Platythamnion villosum
11. Branchlets with two filaments on upper side none below. . Platythamnion pectinatum
4. Thallus without free, uncorticated, uniseriate filamentous parts, except hairs. . . . 12
12. Vegetative portions of thallus cylindrical or if compressed, only at base of branches 13
13. Thallus hollow saccate . . . . . Halosaccion glandiforme
13. Thallus solid without hollow parts 14
14. Growing apices showing a single apical cell, may be obscured by trichoblasts or branches; a single axial filament 15
15. Axes corticated in bands 16
16. Growing on rocks . . . . . Ceramium gardneri
16. Epiphytic on Gracilariopsis . . . . . Ceramium californicum
15. Axes completely corticated 17
17. Thalli with typical externally visible pericentral cells . . Pterosiphonia bipinnata
17. Thalli without typical pericentral cells or if present obscured by cortication 18
18. Thallus showing a single cell filament of very large cells covered by a thin cortex 19
19. Older branches with many short lateral branchlets, cortical cells irregularly arranged . . . . . Ceramium pacificum
19. Lacking short lateral branchlets, cortical cells in longitudinal rows . . . . . Ceramium eatonianum
18. Axial filaments not as above, if present and evident born in medullary tissue 20
20. Branching unilateral . . . . . Microcladia borealis
20. Branching radial 21
21. Ultimate branchlets short, of similar length . . . . . Rhodomela larix
21. Branches all indeterminant 22
22. Medulla filamentous and without axial filaments . . . . . Gigartina canaliculata
22. Medulla of axial filaments and radiating filaments; branching radial, slimy in texture . . . . . Cumagloia andersonii
22. Medulla of compact, thick walled elongated cells interspersed with small rhizoial filaments 23
23. Thalli less than 5 cm tall . . . . . Gelidium sinicola
23. Thalli more than 5 cm tall . . . . . Cryptosiphonia woodii

14. Growing apices without a single cell, no single axial filament present 24
    24. Medulla with thick-walled, much elongated cells . . . . . Ahnfeltia gigartinoides
    24. Medulla of large, thin walled parenchymatous cells. 25
        25. Plants to 15 cm estuarian in habitat, cortex of 2-3 layers of small cells cystocarps with accessory nutritive filaments . . . . . Gracilaria verucosa
        25. Thallus large robust, cortex of 4-6 layers of small cells, cystocarps without accessory nutritive filaments . . . . . Gracilariopsis sjoestedtii
12. Vegetative portions of thallus dominantly compressed 26
    26. Thallus with ribs or veins 27
        27. Thallus with percurrent midrib 28
            28. Branching does not occur from the midrib . . . . . Erythrophyllum delesserioides
            28. Branching from the midrib 29
                29. With conspicuous parallel lateral veins . . . . . Membranoptera multiramosa
                29. Without conspicuous parallel lateral veins . . . . . Delesseria decipiens
        27. Thallus with veins but without a percurrent midrib 30
            30. Tetrasporangial sori at blade margins . . . . . Cryptopleura sp.
            30. Tetrasporangial sori scattered 31
                31. Thallus with a network or coarse veins . . . . . Polyneura latissima
                31. Veins delicate 32
                    32. Tetrasporangial sori transverse on the blade . . . . . Hymenena multiloba
                    32. Tetrasporangial sori in longitudinal rows . . . . . Hymenena flabelligera
    26. Thallus without distinct ribs or veins 33
        33. Thallus of round blade on a central stipe . . . . . Constantinea simplex
        33. Thallus not as above 34
            34. Apical cell sunken in a small depression at branch tips . . . . . Laurencia spectabilis
            34. Without a sunken apical cell 35
                35. Plants with regular tiers of paracentral cells . . . . . Pterosiphonia dendroidea
                35. Not as above 36
                    36. Branching opposite and with one of each pair much longer . . . . . Ptilota filicina
                    36. Not as above 37
                        37. Thalli membranous only 1 or 2 cells thick 38
                            38. Epiphytic on Zostera and Phyllospadix . . . . . Porphyra naiadum
                            38. On rocks or epiphytic on other algae 39
                                39. Plants dioecious longer than broad on rocks . . . . . Porphyra lanceolata
                                39. Plants monoecious usually broader than long 40

40. Epiphytic on Nereocystis and other browns 41
41. Epiphytic on Nereocystis . . . . . Porphyra nereocystis
41. Growing on Laminaria, purple in color . . . . . Porphyrella gardnerii
40. Growing on rocks shells or wood . . . 42
42. Carpospores in packets of 8 . . . . . Porphyra thuretti
42. Carpospores in packets of 32 . . . . . Porphyra perforata
37. Thalli more than two cells thick 43
43. Thallus branched 44
44. Branching dichotomus 45
45. Main branches more than 2.5 mm wide with short lateral branches . . . . . Prionitis australis
45. Main branches without short determinant branches 46
46. Blades smooth 47
47. Segments less than 2 mm broad . . . . . Gymnogongrus leptophyllus
47. Segments over 4 mm broad, thick robust plant . . . . . Gymnogongrus linearis
46. Blades covered with short papillae 48
48. Blades with elongated stipe and narrow above . . . . . Gigartina agardhii
48. Blades with short stipe expanded above. Gigartina papillata
44. Branching not dichotomus 49
49. Thalli with an evident percurrent axial filament . . . . . Pikea pinnata
49. Not as above 50
50. Branching sympodial . . . . . Plocamium pacificum
50. Not as above 51
51. Branching flabellate, medulla of large and small cells . . . 52
52. Thallus epiphytic, thin, and margins of segments with many stipitate proliferous outgrowths . . . Callophyllus pinnata
52. On rocks, thallus over 400 μ thick rounded segment tips . . . . . Callophyllus megalocarpa

51. Branching not flabellate, medulla filamentous 53
53. Thallus with branches on margins that are broadly orbicular . . . . . Opuntiella californica
53. Not as above 54
54. Main axes and branches subcylindical to compressed only the ultimate branches flattened . . . . . .Odonthalia floccosa
54. All branches flattened or compressed 55
55. Thallus profusely branched 56
56. Thallus robust dark in color over 15 cm . . . . . Odonthalia washingtoniensis
56. Thallus light red-pink under 15 cm high . . . . . Laurencia spectabilis
55. Thallus not profusely branched or if so blades expanded lingulate. . 57
57. Blades long-elliptical coarse, when mature with little branchlets on margin . . . . . Gigartina volans
57. Not as above 58
58. Thallus branched blades lingulate deep red, firm not slippery . . . . . Prionitis andersonii
58. Thallus branched, red-brown to olive soft and slippery . . . . . Prionitis lyallii

43. Thallus simple may be lobed or divided or split. 59
59. Thallus small to 10 cm tall from a branching rhizone, with a parenchymatous medulla . . . Rhodymenia pacifica
59. Not as above 60
60. Blades with papillae 61
61. Thallus less than 15 cm tall 62
62. Margins of thallus with thickened ridge and proliferous bladelets . . . . . Gigartina cristata
62. Margins not thickened few bladlets . . . . . Gigartina papillata
61. Thallus more than 15 cm tall 63
63. Blade branched or pinnately divided papillae large . . . . . Gigartina spinosa
63. Not as above 64
64. Blades broadly lanceolate . . . . . Gigartina californica
64. Blades narrowly lanceolate . . . . . Gigartina harveyana

60. Blades smooth 65
    65. Thallus with many medullary filaments running perpendicularly from cortex to cortex; plants when dry ox-blood red, adhering well to paper . . . . . Halymenia californica
    65. Not as above 66
    66. Blade split or torn into segments. 67
        67. Cortex with gland cells, slippery, brownish red, cystocarps deeply imbedded in medula . . . . . Schizymenia pacifica
        67. Cortex without gland cells, thallus usually split into asymetrical segments, narrow at base rounded at the apex, brownish black . . . . . .Delsea californica
    66. Blade entire 68
        68. Cystocarps large up to 3 mm, blade lobed or divided into several segments, usually less 20 cm tall. . . . . Iridaea heterocarpum
        68. Not as above 69
            69. Blades linear-lanceolate 3. 5 to 7 cm wide tetrasporangia scattered through the cortex . . . . Grateloupia californica
            69. Not as above 70
                70. Blades up to 1. 5 mm thick medullary filaments 25 μ in diameter, does not adhere well to the paper, black on drying . . . . . .Iridaea coriaceum
                70. Blades 500 to 700 μ thick, medullary filaments up to 10 μ in diameter, tends to adhere to paper, purple throughout . . . Iridaea splendens
                70. Blades less than 500 μ thick medullary cells less than 4 μ thick green above violet near the base of thallus . . . . . Iridaea flaccidum

APPENDIX D

Collecting areas in Yaquina Bay and distance from the mouth of the estuary.

Location	Distance from the mouth
North Jetty--during the time of study this was under repair	
South Jetty	
6th spur, finger, dolphin, groin, or lateral	less than 1 kilometer
5th	
4th	
3rd	
2nd--opposite Marker 7	1.0 kilometer
1st	1.5 kilometers
Sand reef on north side between Marker 7 and the Newport bridge	1.5 kilometers
Bolders between 1st spur and Newport bridge	1.6 kilometers
Newport bridge pilings and rubble	1.8 kilometers
Sand flat between bridge and O. S. U. M. S. C.	2.0 kilometers
Coast Guard docks	2.0 kilometers
Port docks #1 to 7	3.0 kilometers
O. S. U. M. S. C. point	3.0 kilometers
McLean Point, opposite Marker 12	4.0 kilometers
Hinton Point, opposite Marker 14	5.0 kilometers
Kings Slough, south of Marker 14	5.5 kilometers
Coquille Point, between Markers 15 and 17	6.0 kilometers
Old Yaquina Bay laboratory, Marker 17	6.5 kilometers
Yaquina Marina, between Markers 17 and 19	7.5 kilometers
Riverbend Marina, opposite Marker 21	8.5 kilometers
Marker 25	9.5 kilometers
Winant, Oregon Oyster Co., opposite Oysterville and Marker 26	11.0 kilometers
Marker 37	15.5 kilometers
Chrisiters Moorage, opposite Marker 44	17.0 kilometers
Jack's Sports Dock, opposite Marker 47	19.0 kilometers
Toledo Hill, 1/2 kilometer above Marker 47	19.5 kilometers
Toledo bridge, two kilometers above Marker 47	21.0 kilometers