SEASONAL CHANGES IN THE

DIEL PRODUCTIVITY OF

MACROCYSTIS INTEGRIFOLIA BORY

UNDER NEAR-IN SITU CONDITIONS

by

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Title of Thesis/Project/Extended Essay

Seasonal changes in the diel productivity of Macrocystis integrifolia

Bory under near- in situ conditions

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ABSTRACT

Near-in situ experiments on enclosed entire specimens of
Macrocystis integrifolia of Barkley Sound, B. C. showed
seasonality in the kelp's net diel light-dependent carbon
fixation rates -- spring rates were the greatest, summer rates
were intermediate and fall rates were lowest. Low fall rates
coincided with low temperatures and low irradiances. The causes
of the observed summer decline are unknown, but nutrient
depletion is suspected. No seasonality was apparent in the
light-independent carbon fixation rates which ranged from 1.2 %
to 11.1 % of light-dependent carbon fixation rates, the range
paralleling the range of light-dependent fixation rates.

Results from the determination of exudation levels
indicated low dissolved organic carbon (DOC) exudation. Minimum
exudation, as measured by radiocarbon tracer techniques, was
generally less than 1 % and ranged up to 3.9 % of the plant's
carbon assimilation and appeared to be directly related to
irradiance and carbon fixation levels. Total exudation
measurements, determined by analysis of the water for total DOC
(including labelled and unlabelled DOC), generally did not
exceed the technique's minimum level of detection. Based on
current theories of causes of macroalgal exudation, the great
bulk of exudation should be detected by radiocarbon

tracer methodology and consequently, my minimum exudation levels
are probably close to realistic total exudation values.

ACKNOWLEDGEMENTS

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A. Introduction

The purpose of this study was to determine diel productivity of the lesser giant kelp, _Macrocystis integrifolia_ Bory (Order Laminariales) under near-_in situ_ conditions during different times of the year. It was necessary to modify some existing analytical techniques to achieve a higher level of precision than was previously possible.

The primary productivity of _M. integrifolia_ has been the focus of few quantitative studies. Previous studies can be divided into two categories -- the field approach and the laboratory approach. Field studies have provided information on wet weight gain for plants transplanted to a non-kelp bed location (Druehl, 1977), stipe elongation rates (Scagel, 1948; Sharp, 1975; Lobban, 1976, 1978) and blade elongation rates (Sharp, 1975). The laboratory approach involved observations on carbon fixation rates by excised blade discs under laboratory conditions (Willenbrink et al., 1979).

The giant relative of _M. integrifolia_, _M. pyrifera_ (L.) C. Ag. has been the subject of several productivity studies. Its productivity has been estimated by changes in standing crop (Aleem, 1956), changes in the dissolved oxygen content of the kelp bed waters (McFarland and Prescott, 1959), stipe elongation rates (Cribb, 1954; North, 1961; Neushul and Haxo, 1963), uptake of radiocarbon by individual attached blades (Towle and Pearse,

1973) and by oxygen production by excised sections of blades
enclosed in bottles (Sargent and Lantrip, 1952; Clendenning,
1964; Littler and Murray, 1974a,b).

All of the preceding studies fall short of accurately
determining the net primary productivity of an entire
Macrocystis plant. Changes in standing crop provide information
on harvestable biomass but, because of unmeasured loss of
biomass due to sloughing and grazing, fail to accurately measure
the primary productivity (Pomeroy, 1961). The McFarland and
Prescott (1959) study on changes in dissolved oxygen content of
kelp bed waters failed to account for metabolism by other
organisms in the community and changes in oxygen levels due to
diffusion and currents. The stipe elongation rates do not
translate directly into biomass increases due to the changing
lengths of internodes along the stipe (Lobban, 1978).

Extrapolations of whole plant productivity from
productivity measurements made on excised portions of the kelp
are difficult because of the kelp's spatial physiological
diversity. For example, translocation of assimilates from mature
blades to young blades and fronds has been demonstrated (Parker,
1963, 1965; Lobban, 1977, 1978). Varying levels of
photosynthesis along a blade (Clendenning, 1964; Towle and
Pearse, 1973) and with respect to the age and position of the
blade (Sargent and Lantrip, 1952; Towle and Pearse, 1973) have
been measured in M. pyrifera. Furthermore, estimates of an

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intact plant's productivity from tissue segments have been demonstrated to give unrealistic results. Hatcher's (1977) comparisons of photosynthesis and respiration rates of tissue segments versus whole thalli of _Laminaria_ demonstrated that the high initial respiratory rate of the tissue segment required 10 hours to return to the lower respiratory rate of the whole uninjured thallus and the tissue segment showed greater variability in photosynthesis and respiration rates.

In all of the above studies, an assessment of the plant's released dissolved organic carbon (DOC) was either impossible due to the methods used or it was not considered. There is some controversy on the importance or existence of extracellular release of DOC with respect to the primary production of marine macrophytes. Some studies indicate considerable release (Fogg and Boalch, 1958; Craigie and McLachlan, 1964; Khailov and Burlakova, 1969; Sieburth, 1969; Sieburth and Jensen, 1969; Kroes, 1970) whereas other studies report the release of organics to be low or non-existent (Majak et al., 1966; Moebus and Johnson, 1974; Harlin and Craigie, 1975; Brylinsky, 1977; Fankboner and deBurgh, 1977; Penhale and Smith, 1977; Ragan and Jensen, 1979).

An accurate assessment of a macrophyte's carbon uptake and release requires some form of containment. For measurement of the carbon flux of an entire plant and thus, the influence of the macrophyte on its surrounding environment, enclosure of the

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entire plant and monitoring of the water within the enclosure would seem a realistic approach. Guterstam (1977) and Hatcher (1977) have measured the primary productivity of the macrophytes, _Fucus_ and _Laminaria_ respectively _in situ_, by designing large 'bottles' to enclose the entire plant. Similarly, in this study, I have used an even larger 'bottle' to enclose an entire _M. integrifolia_ plant. This large 'bottle' was placed in the water column and productivity was measured by carbon tracer techniques.

Seasonality in the growth rates and photosynthesis of marine macrophytes has been demonstrated by various researchers (Parke, 1948; Lüning, 1971; Yokohama, 1971; Zavodnik, 1973; Buggeln, 1974; Mathieson and Norall, 1975; King and Schramm, 1976; Brinkhuis, 1977a,b,c; Chapman and Craigie, 1977; Hatcher et al., 1977; Lobban, 1977; Niemeck and Mathieson, 1978; Chock and Mathieson, 1979; Littler et al., 1979) and was also investigated in this study.

B. Materials and Methods

Experimental and collection sites

The experiments were conducted at Port Désiré, Grappler Inlet, in Barkley Sound, B. C., Canada (Fig. 1) during spring (April 26 to May 26), summer (July 19 to August 8) and fall (October 31 to December 6) in the years 1977 and 1978.

The plant for experiment 1 was collected at Mud Cove; the plants for all other experiments were collected at Kirby Pt. Cove (Fig. 1). Kirby Pt. Cove was chosen because of its accessibility during most weather conditions and the paucity of epiphytes on M. integrifolia at that site. Small (commonly < 2m in length) plants with at least one apical scimitar (growing tip) were collected using SCUBA. After collection, the fronds were wrapped in seawater-soaked paper towelling, placed into a plastic bucket and transported to Port Désiré where they were attached onto bricks and suspended in the water from the boat float awaiting experiment. The time out of water never exceeded 1.5 h.

Figure 1. Map of sampling and experimental sites in Barkley Sound, B. C.

Grappler Inlet

Port Désiré

Bamfield Inlet

48° 50'N

125° 10'W

N

Kirby Pt.
Cove

S. Dodger
Channel

Mud Cove

Cape Beale

1 Km
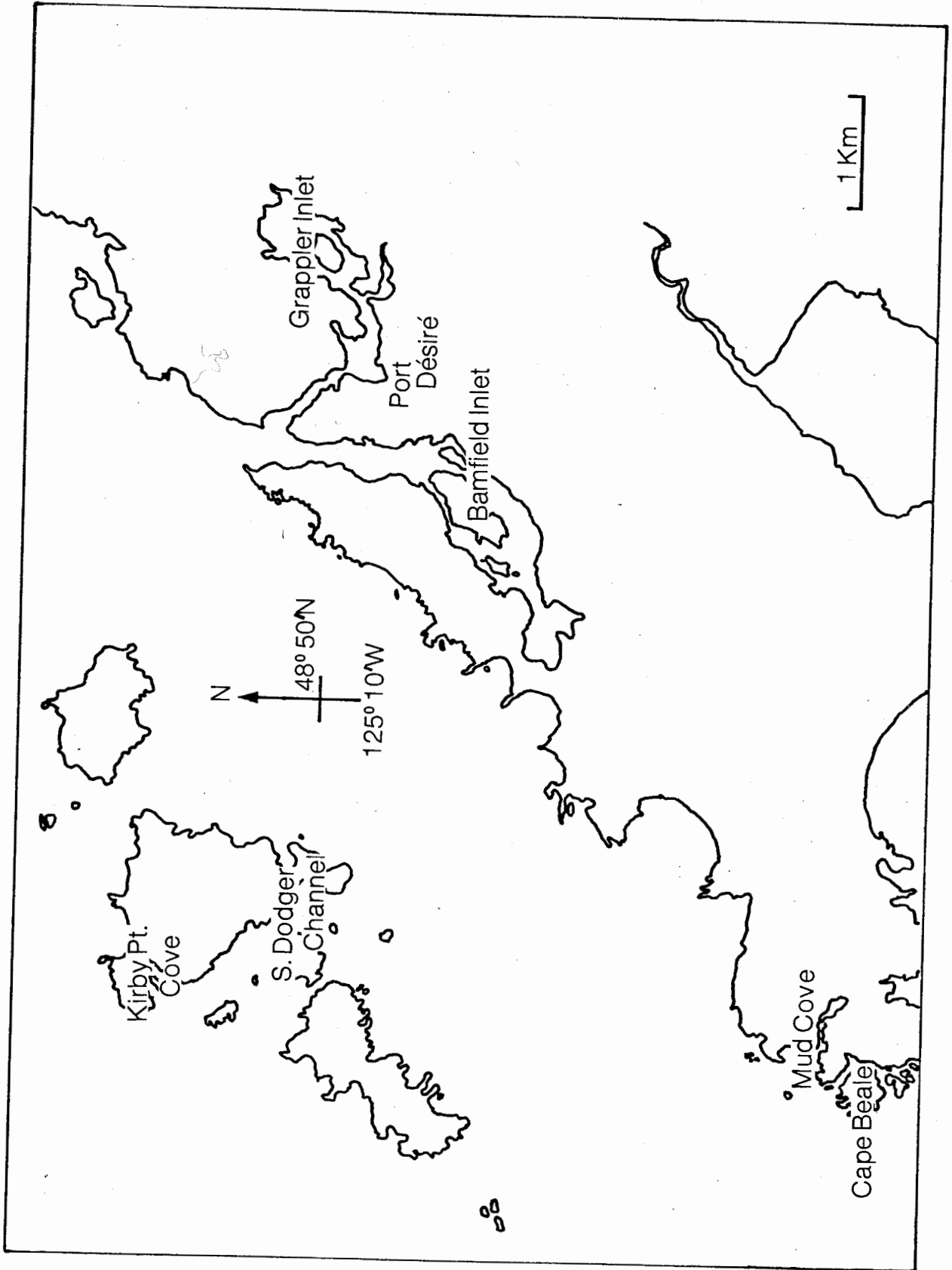
Experimental apparatus

Two submersible clear acrylic plastic cylinders connected
by a system of tubing to a separate carboy located above the
water were used for the experimental incubations (Fig. 2; Fig.
3). An entire M. integrifolia plant was placed into one cylinder
(experimental cylinder); the second control cylinder contained
no plant. The cylinders were 102 cm diameter x 214 cm height x
1.9 cm thickness with a capacity of 1750 l. The cylinders were
supported in the water by lines attached to a wooden boom at a
distance of 1.3 m from the float.

A 53 cm diameter hole located at the top of each cylinder
was covered by a 0.64 cm thick clear plexiglass lid bolted to
the cylinder and sealed by a neoprene rubber O-ring coated with
silicone stopcock grease. Each lid was equipped with one nipple
for a valve connection (for bleeding air during filling) (Fig
3., BV), two nipples for tubing connections and two holes for
the emergence of two electrical wires to two submersible pumps
(Fig. 3, PU) located within each cylinder. All nipple
attachments were water-tight and the holes for the electrical
wires were sealed with O-rings. The tubing (1.27 cm I.D.
nylon-reinforced polyvinylchloride (PVC) hose and tygon tubing
(Norton's R&D Laboratories, Akron, Ohio)) connected the cylinder

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Figure 2. Drawing of the cylinder-carboy system.

Key to symbols.

BV   bleed valve

CA   carboy

CF   coarse cotton batten filter

GFF   glass fibre filter disc

PU   submersible pump

RC   reservoir carboy

SS   serum stopper

SP   sampling port

V   valve

GFF

CF

RC

CA

CA

V V

SP

SS

SS

SP

PU

BV

BV

PU

PU

PU

CONTROL
CYLINDER

EXPERIMENTAL
CYLINDER

8b
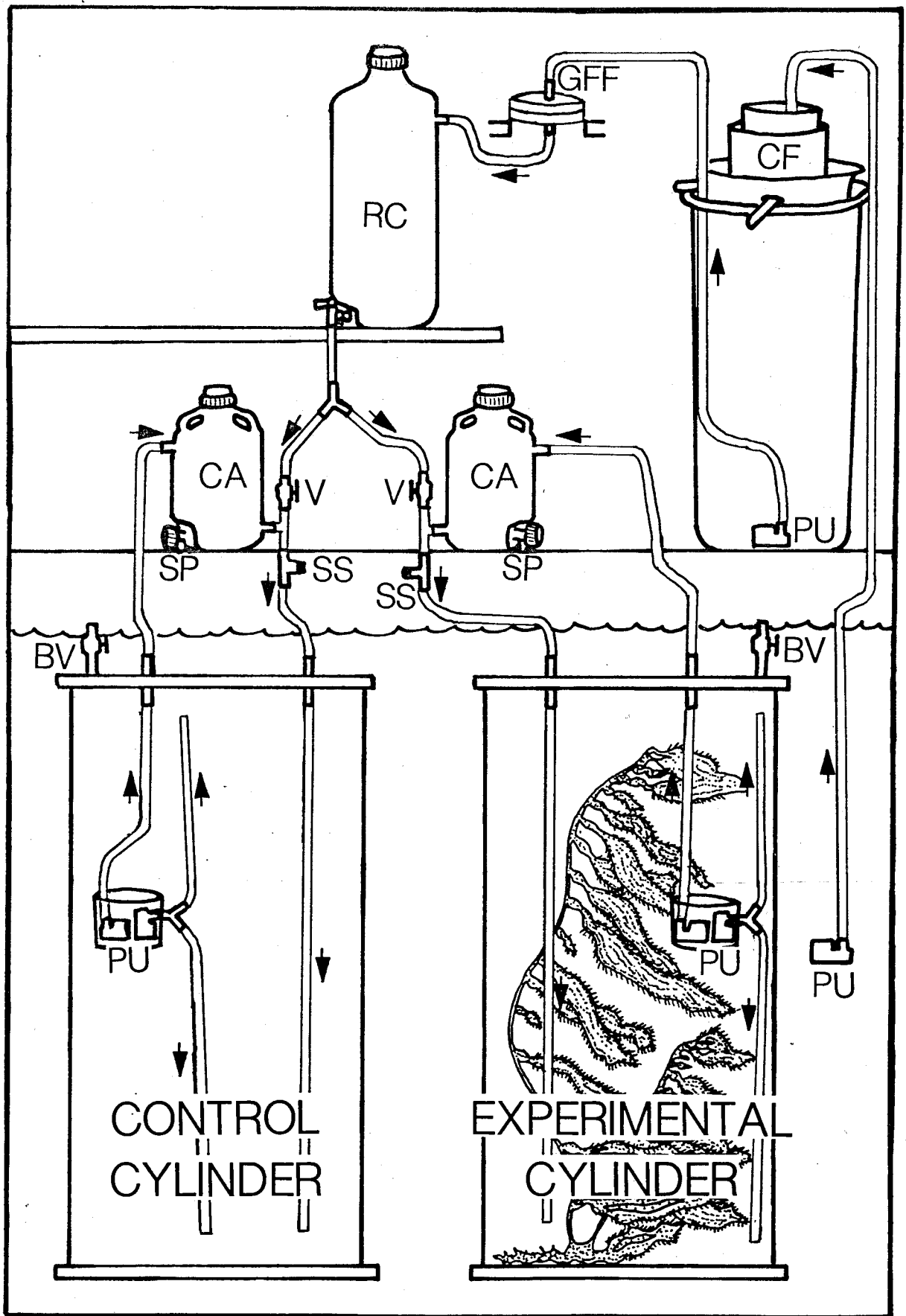
Figure 3.

Top. Photograph of the empty cylinders afloat.

Bottom. Photograph of the cylinders half full of seawater.

Figure 3 (cont.)

Top. Photograph of a cylinder full of seawater with the lid and tubing attached.

Bottom. Photograph of the two carboys (experimental and control) which are connected by tubing to the two cylinders.

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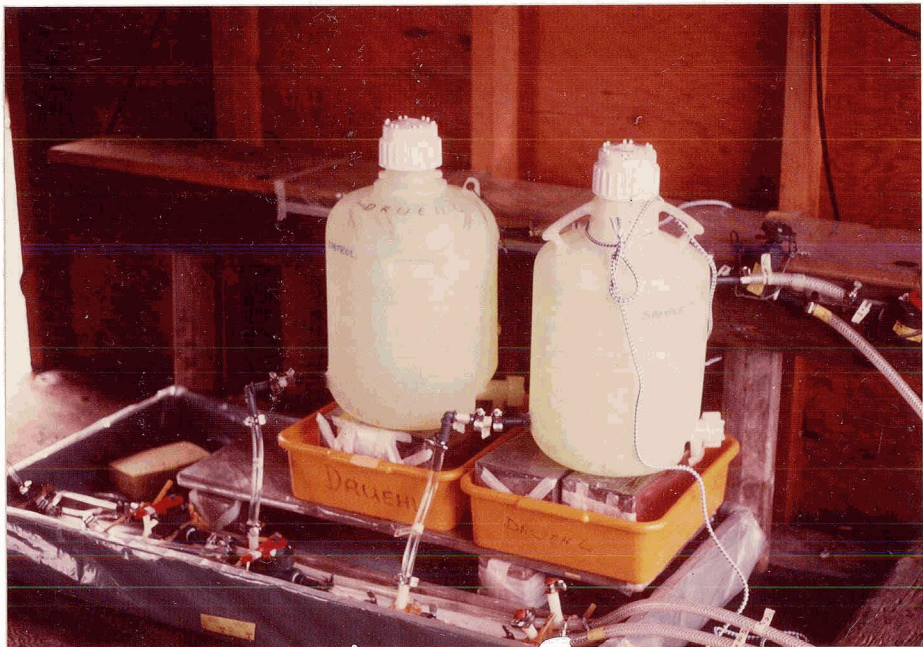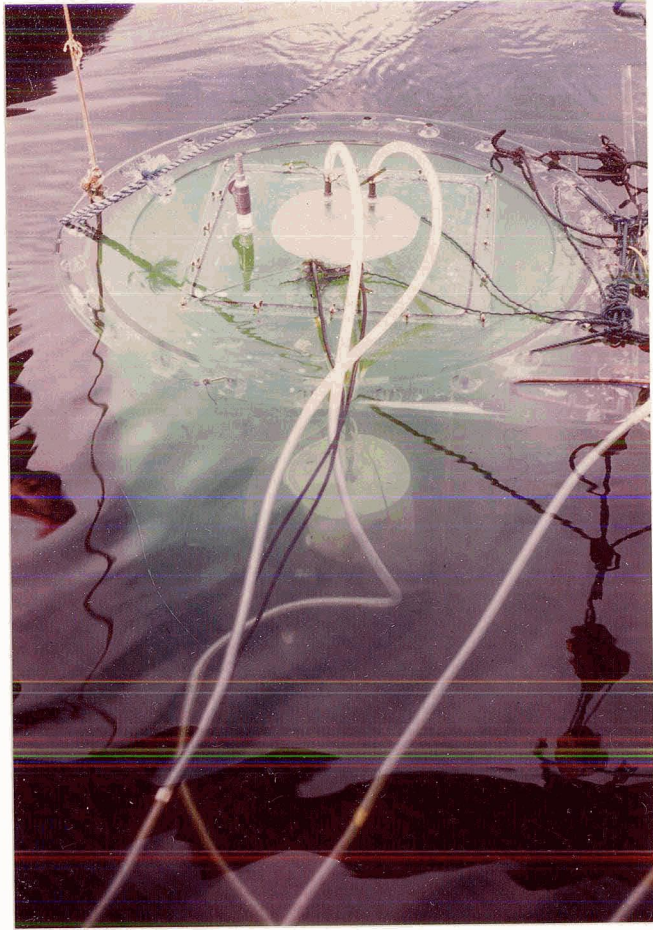
to a 18.9 l nalgene (Sybron Corp., Rochester, N. Y.)
polyethylene carboy (Fig. 3, CA) located on the float. One set
of tubing transported water from the cylinder to the carboy's
inlet located near the lid of the carboy and the other set of
tubing transported water from the carboy's outlet (located near
the bottom of the carboy) back to the cylinder. A spigot on the
carboy was used as a sampling port (Fig. 3, SP). Each carboy was
sealed with an O-ring placed under the lid.

The tubing transporting water from the carboy to the
cylinder was interrupted, just beyond the carboy outlet, by a
nylon 'T' connection which allowed for the insertion of a rubber
serum stopper (Fig. 3, SS). Radiocarbon-carbonate was introduced
through this serum stopper. The total volume of the
cylinder-carboy-tubing closed system was 1770 l.

Circulation within each cylinder-carboy closed system was
provided by one submersible pump (Model LC-2C-MC March
Epoxy-clad pump, March Mfg. Co., Glenview, Illinois). Further
circulation within the cylinder was provided by the second March
submersible pump. To prevent entanglement of the experimental
plant with the pumps, both pumps were enclosed in a perforated
plastic bucket. The exact rate of circulation was unknown;
however, when fluorescein dye was injected into the system at
the serum stopper, it took 3 min for the dye to circulate back
to the serum stopper.

Seawater for the two cylinder systems was provided by a common seawater filtering complex connected to each system by a separate valve (Fig. 3, V). The filtering complex consisted of a submersible pump which pumped seawater from a depth of 1.5 m to a series of four cotton batten filters, supported by perforated plastic buckets (Fig. 3, CF). The buckets were suspended, in a series, above a 190 l plastic bucket. A submersible pump within the 190 l bucket drove this 'coarsely' filtered water, through a 39 cm diameter positive pressure filter disc supporting a Whatman (Whatman Inc., Clifton, N. J.) GF/D glass fibre filter (retention diameter = 2.7 μm) (Fig. 3, GFF) to a 51 l nalgene polyethylene 'reservoir' carboy (Fig. 3, RC). The spigot at the bottom of the reservoir carboy was connected to tubing which led to a nylon 'Y' connector which divided the water for the experimental and control cylinders. Closing the connecting valves isolated each cylinder system from the reservoir carboy and the other cylinder system. Eight hours were required for filling both cylinder systems.

The above arrangement assured that background particulate matter larger than 2.7 μm diameter was filtered from the water and that both cylinder systems received similar water.

Johnston (1969) recommends a g dry weight of seaweed/l volume of incubation media ratio of 0.1 to 0.3 to prevent nutrient or carbon dioxide deficiencies in 24 h incubations. The plant in experiment 2, with a dry weight/volume ratio of 0.52

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exceeded these limits; all other 24 h or 48 h experiments
(ratios ranging from 0.03 to 0.22) were within the recommended
limits.

Experimental procedure

Pre-experiment preparation

Each experimental plant was hosed with filtered seawater
and visible epiphytes were removed before the plant was placed
in the cylinder. The plants were allowed to acclimatize to the
cylinder conditions for at least 12 h for 24 h and 48 h
experiments and approximately 24 h for dark experiments. During
this period filtered water was flushed through the cylinders.

Before dawn the next morning (for 24 h or 48 h experiments)
or at dusk the next day (for dark experiments), the cylinders
were sealed, converting the open flow-through system into a
closed circulation system. All lines, fittings, and containers
were inspected for trapped air which was always removed. The
cylinders were then lowered so that their tops were 0.3 m below
the water's surface.

Experiment

To start an experiment a ^{14}C carbonate solution was
injected with a syringe through the serum stopper. The $Na^{14}CO_3$
solution (Atomic Energy of Canada ltd., Chalk River, Ont.) was

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diluted prior to the experiment to a concentration of 1 mCi ml^{-1} with distilled water, at pH 10. The activity added to each cylinder was as follows: 10 mCi for experiments 1 through 104 and 7.5 mCi for experiments 105 through 125.

After the addition of the radioisotope, 7 min was allowed for its circulation in the system. Then the circulation pumps were shut off and 2 l of water was withdrawn via the carboy's sampling port into an erlenmyer flask and placed immediately into an ice-chest to await further processing. The carboy was then 'topped up' with filtered water and the pumps were started. The 'topping up' process following each sampling, resulted in a maximum total dilution of 0.8 %.

For all experiments, 2 l water samples were taken at dawn and at dusk.

At the termination of the experiment, the experimental cylinder's lid was opened, the plant was removed and, to minimize adhering 'non-fixed' radiocarbon, rinsed in the surrounding seawater. The plant was then placed into a plastic garbage can and transported to the laboratory for drying. The time of transport was approximately 10 min.

The following environmental conditions were monitored during experiments: water temperature, salinity, and secchi depth. Insolation values were obtained from pyreheliometer data (courtesy of C. Scrivener, Pacific Biological Station, Nanaimo, B. C.) recorded at Carnation Creek, Barkley Sound, 8 km from

Port Désiré. Comparison of Bamfield pyranometer charts with Carnation Creek pyreheliometer charts confirmed that the insolation levels were similar at these two locations.

Sample processing

Total carbon dioxide, nitrate, nitrite, ammonia and phosphorus contents of the water were estimated by the techniques described in Strickland and Parsons (1972).

Total particulate organic carbon (POC) content was sampled by filtration of 100 or 200 ml of water through pre-combusted (450 C, 4 h) Whatman GF/F glass fibre filters (retention diameter = 0.7μm) at a vacuum of 0.25 atm, and followed by a 5 sec exposure of the filter to concentrated HCl fumes to rid the filter of inorganic carbon. The filters were dried in an oven at 65 C and refrigerated until analysis with a Perkin-Elmer Model 240 Elemental Analyzer (Coleman Instr. Corp., Maywood, Ill.). The relative precision (2 x (standard error/mean) x 100) of this technique was 13.2 %, as calculated from 143 analyses.

Labelled POC ($PO^{14}C$) content was sampled by filtration, as described above. The HCl-fumed filter was placed in a glass scintillation vial, 2 ml of Protosol tissue and gel solubilizer (New England Nuclear, Lachine, Que.) was added, and the vial was refrigerated until processing. Processing involved incubation of the vials at 60 C (to ensure solubilization of all organic matter), the addition of two drops of glacial acetic acid (to

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neutralize the basic Protosol) and the addition of 15 ml of regular toluene cocktail (42 ml Liquifluor (New England Nuclear) per l toluene). The samples were then counted on a Beckman LS 8000 Scintillation Counter (Beckman Instr., Fullerton, Calif.) for 10 min or 1 % counting efficiency using the external standard method for quench correction. The relative precision of this technique was 24.8 % as calculated from 111 analyses.

The labelled dissolved organic carbon (DO^{14}C) content of the water was estimated by a concentration procedure developed for this study. Fifty ml of Whatman GF/F filtered water was dispensed with a glass syringe into each of three 272 ml glass bottles. Three drops of concentrated HCl was added to each bottle to bring the pH<2. The samples were bubbled with air for 1 h to rid the water of inorganic labelled carbon and then they were refrigerated until analysis. In preparation for analysis, the samples were evaporated at 45 C in a flash evaporator down to a volume of 1.5 to 3.0 ml. This salt 'brine' was poured into a scintillation vial containing 15 ml of Aquasol cocktail (New England Nuclear). The evaporation flask was then rinsed and sonicated with two or three small volumes of distilled water, which in turn were poured into the scintillation vial. The total volume of salt brine + rinse water added to the scintillation vial was 5 ml. The vial was then refrigerated and shaken until the contents formed into a homogeneous gel. The vials were counted in a refrigerated Packard Model B3003 Tri-Carb Liquid

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Scintillation Spectrometer (Packard Instr. Co., Downers, Ill.) using the channels ratio method for quench correction.

The above concentration procedure was necessary due to the great dilution of the $DO^{14}C$ in the large volume within the cylinders. Tests with ^{14}C-glycine showed a mean recovery of 100.8 % (standard error $(s/\sqrt{n})$ = 1.17, n = 6) following the acidification and bubbling step and a mean recovery of 97.9 % (standard error = 1.23, n = 5) following the evaporation step. The minimum detection level of the technique, as calculated from the precision $(2s/\sqrt{n})$ of 64 analyses, was 0.39 DPM ml^{-1} or 19.5 DPM (50ml)$^{-1}$. The relative standard error of this technique was 10.13 % as calculated from 127 analyses.

Total DOC (TDOC) was analyzed by a technique involving dry combustion in an oxygen stream followed by carbon detection with an infrared gas analyser (IRGA). This technique was adapted from the methods of Gordon and Sutcliffe (1973), who used a dry combustion technique but with the less sensitive Perkin-Elmer Elemental Analyzer for carbon detection, and the methods of Van Hall et al. (1963) and Sharp (1973), who developed elaborate liquid combustors with the IRGA for carbon detection. The technique used in this study was:

1. Sample preparation.

Fifty ml of filtered water was dispensed into 136 ml glass bottles; aluminum foil was placed between the bottle-cap and the bottle. The bottles were darkened and

refrigerated until freezing (1/2 h to 1 h later). Prior to freeze-drying, the samples were thawed and 10 ml sub-samples from each bottle were dispensed into weighed 50 ml erlenmyer flasks. To rid the sample of inorganic carbon, the water was acidified with two drops of 85 % phosphoric acid and bubbled for 5 min with nitrogen gas. The flasks were then covered with perforated aluminum foil caps and freeze-dried. Freeze-dried samples were stored in a dessicator until analysis. The weight of the sample's seasalts was the difference in the flask's weight before the introduction of the sample and after the freeze-drying. The nitrogen bubbling and freeze-drying steps probably purged the water of volatile organic compounds; this is a common shortcoming of most DOC analytical techniques (Wangersky, 1978; MacKinnon, 1979). MacKinnon (1979) has developed a technique for the measurement of volatile organic carbon and his results show that the volatiles compose 1.5 to 6 % of the total dissolved organic carbon content in ocean waters. Apparently, even his technique fails to detect the very volatile compounds (MacKinnon, 1979).

Calibration was accomplished with a standard salt/glucose solution which consisted of freeze-dried salt co-sublimated with a defined quantity of glucose. A 1 gC l^{-1} stock glucose solution was prepared by dissolving 1.25 g glucose in 500 ml distilled water. The standard salt

solution was made by adding 7.5 g of NaCl, which had been previously combusted for 12 h at 650 C, and 2.5 ml of the stock glucose solution into a 250 ml volumetric flask. The volume was brought to 250 ml with carbon-free-water, prepared as described in the DOC analytical technique in Strickland and Parsons (1972). This resulted in a 10 mgC l^{-1} solution with a salinity of 30 ‰. This standard solution then was processed as the seawater samples.

To prevent contamination of samples and standards, prior to use all glassware and metalware were combusted at 500 C for 4 h and pipettes were washed with carbon-free-water. To ensure homogeniety of the organic substances within the freeze-dried salts in the flasks, the salts were ground to a fine powder with a mortar and pestle. To prevent cross-contamination of samples, mortar and pestle were combusted intermittently and cleaned between samples by grinding with carbon-free-salt.

2. Equipment description

The combustor was constructed by the S.F.U. Machine, Electronics and Glass-blowing Shops and was based on the Perkin-Elmer Model 240 Elemental Analyser's combustor design. A difference is that my combustor required manual operation of the gas valves. A Beckman infrared gas analyser was used for the carbon detection.

Essentially, the combustor consisted of a 63 cm long hollow quartz tube sealed at either end with an O-ring and knurled bolt (Fig. 4, E). The first 30 cm of this tube was for sample insertion, followed by a 15 cm length encased in a furnace (Fig. 4, F) which, in turn, was followed by an 18 cm chemical trap. The combustion tube and chemical trap were identical to those of the Perkin-Elmer Elemental Analyser. Each end of the tube was connected, via a solenoid valve, to a gas line; oxygen entered via the valve at the sample insertion end of the tube (Fig. 4, G) and exited through the valve at the chemical trap end of the tube (Fig. 4, H). The exiting gas then flowed toward the IRGA unit. Inserted in the gas line, between the combustor unit and the IRGA, was a $Mg(ClO_4)_2$ water trap (Fig. 4, l) and a 'crumpled up' Kimwipe particle trap (Fig. 4, M). The flow rate was measured on a Gasmet flowmeter (Fig. 4, N) after the oxygen left the IRGA. The IRGA peaks were recorded on a Riken-Denshi X-Y recorder (Riken Denshi Co., Tokyo, Ja.)(Fig. 4, O).

The sample was introduced into the combustion tube by means of a quartz ladle equipped with a magnet in the handle.

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Figure 4. The total DOC analyser.

Key to components.

A   combustor

B   infra-red gas analyser (IRGA)

C   oxygen supply to reference IRGA cell

D   oxygen supply to combustor

E   quartz combustion tube

F   furnace

G   solenoid valve controlling oxygen flow into
    combustor

H   solenoid valve controlling oxygen flow exiting from
    combustor

I   combustion tube pressure gauge

J   furnace temperature control

K   gas line from combustor to IRGA

L $Mg(ClO_4)_2$ water trap

M   Kimwipe particle trap

N   flowmeter

O   recorder

From O$_2$ Supply

M

N

O

L

B

K

I

F

E

J

A

G

D

C

H

21b
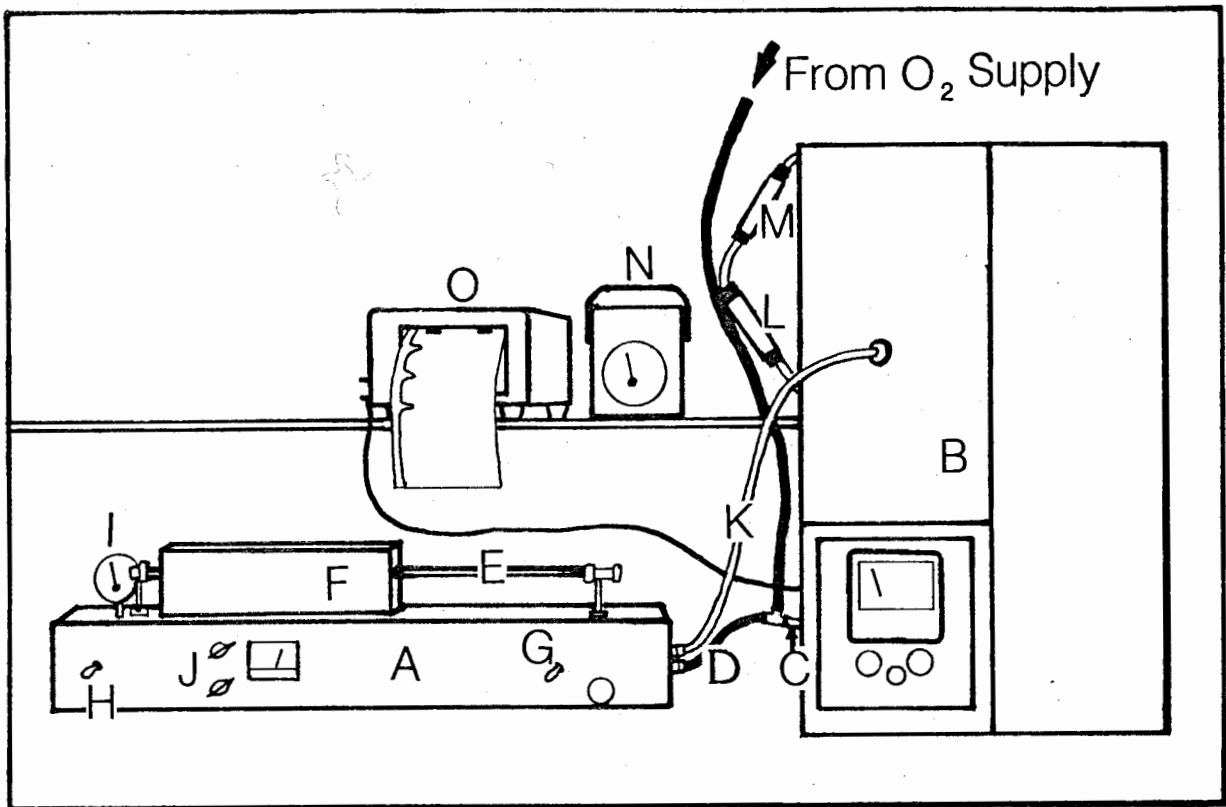
1. Analysis

The furnace was set to a temperature of 750 C and the oxygen flow rate through the combustion tube was set to 250 ml min^{-1}. The IRGA was standardized with oxygen gas for '0' setting and 350 ppm standard carbon dioxide gas. Using a Cahn electrobalance (Ventron Corp., Cerritos, Calif.) 10 to 20 mg of ground seasalts were weighed onto a previously combusted ladle, and inserted into the combustion tube. The combustion tube was sealed and allowed to purge for 30 sec to remove introduced carbon dioxide from the air. Then the exit valve was closed; the oxygen entrance valve remained open until a pressure of 0.4 kg cm^{-2} and then was closed. The sample was allowed to burn 45 sec. Tests showed that burning times of 30 sec to 3 min yielded identical carbon values.

When the combustion tube was opened and exposed to the atmosphere, the exit valve was closed and the entrance valve opened to create a positive internal pressure to prevent the entrance of atmospheric air.

2. Calculation

Calibration was achieved by combusting different weights of the standard glucose-salts and computing a regression of the IRGA peak heights against the amount of carbon present as determined by the weight of the combusted standard salts. Previously combusted NaCl crystals were

analyzed to determine the background '0' carbon level. For the quantities of carbon tested ($0 \mu g$ to $5 \mu g$) this resulted in a straight line function. A standard curve from one set of analyses is presented in the Appendix (Fig. A1). Tests showed that peak heights and peak areas produced similar results. The amount of carbon present in a sample was then calculated by comparison of the peak height to the corresponding carbon content. The relative standard error of this technique, based on 110 analyses, was 7.6 %.

Adenosine triphosphate (ATP) content of the water was estimated by the extraction and analytical technique of Holm-Hansen and Booth (1966), as modified by Hammerstedt (1973) and using Tobin et al's (1978) recommended pH's for the standard solutions. The ATP content was converted to an approximate carbon value by the ATP, carbon, and total cell weight interrelationships calculated by Holm-Hansen and Booth (1966).

Net carbon assimilated by the plant was estimated by the quantity of radiocarbon retained by the plant. After being hung to dry in a warm room for 2 h, the plant was placed into an oven at 65 C for three days to complete the drying process. After drying, the plant was pulverized with the 'kelp grinder'.

The 'kelp grinder' (Fig. 5) consisted of a cast iron hollow cylinder, 44.5 cm in length and 27 cm in diameter, into which was placed a solid iron cylinder (27 cm long, 10 cm diameter). The dried plant was placed into the cylinder with the roller.

The cylinder was sealed and rolled on the floor until the plant was pulverized.

Radiocarbon detection of samples of the fine powder was achieved by combustion. Plants from experiments 1 to 114 were combusted in a Searle Combustor Model 6550 (Searle Analytic Inc., Des Plaines, Ill.) and plants from experiments 121 to 125 were combusted in a Packard Model B306 Tri-Carb Sample Oxidizer. The released carbon dioxide was absorbed in Oxisorb-CO_2 (New England Nuclear) with ACS (Amersham Corp. Oakville, Ont.) as the scintillation cocktail. The scintillation vials were counted on a Beckman LS 8000 Scintillation Counter for 10 min or 1 % efficiency using the external standard method for quench correction. The relative standard error of this technique, as based on 26 analyses, was 2.4 %.

Total carbon and nitrogen content of the plant powder was determined with a Perkin-Elmer Model 240 Elemental Analyzer.

Figure 5.

Top. Photograph of the kelp grinder being rolled on the
floor.

Bottom. Photograph of oven-dried kelp being placed into the
kelp grinder.

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The light available to the plant at the mean incubation depth was estimated by a Lambert's Law form of relationship as described in Strickland (1958). The irradiance in the photosynthetically active radiation region (PAR = 400 nm to 700 nm wavelength range) was calculated by multiplying spring and summer pyreheliometer values by 0.48 and fall values by 0.45 (Szeicz, 1974). Transmission through the air/water interface was estimated as 85 % (Parsons and Takahashi, 1973).

The water's attenuation coefficient, k, was determined by the following relationship:

k = factor/D (Strickland, 1958)

= 2.13/D

D = secchi depth in m

2.13 = factor determined by regression analysis of irradiance readings of 0, 1, 2, 3, 4 and 5 m depths measured with the Li-Cor quantum radiometer (Lambda Instruments, Lincoln, Nebraska) weekly at midday for a period from March to July in the Bamfield area (data, courtesy of L. D. Druehl).

Light attenuation through the acrylic cylinders, in the PAR region was measured as 8 %. All values were converted to Einsteins m^{-2} h^{-1} by the following relationship:

1 langley h^{-1} (g cal cm^{-2} h^{-1}) = 0.191 E m^{-2} h^{-1}.

Calculations

Carbon assimilated by the plant, as determined by radiocarbon uptake, was calculated as follows:

mgC gdw^{-1} plant (where gdw = g dry weight)

   = $\dfrac{(plantDPM - bkgDPM) \times wt.of\ C\ in\ water(mgC)}{activity\ added\ to\ water(DPM) \times gdw\ plant} \times 1.05$

   DPM = disintegrations min^{-1}.

   bkg = background count.

   wt. of C in water = total amount of inorganic carbon
      in the entire cylinder system's water at the beginning
      of the experiment.

   1.05 = correction factor to account for the different

behaviour of ^{14}C as compared to ^{12}C (Strickland and Parsons, 1972).

In this study the DOC content of the water was defined as (DOC + POC). The reasons for this definition are presented in the Discussion.

1. Total DOC + POC was calculated as follows:

TDOC + TPOC as mgC gdw^{-1} plant

= $\underline{DOC(mgC\ l^{-1})\ x\ 17701}$ + $\underline{POC(mgC\ l^{-1})\ x\ 17701}$

   gdw plant   gdw plant

2.   For the estimation of the DOC content of the water from the
labelled DOC (DO^{14}C + PO^{14}C) results, the DPM values were
converted to mgC gdw^{-1} value using the same equation as for
calculating carbon assimilation by the plant, above,
including the volume correction from mgC l^{-1} to
mgC cylinder^{-1}.

The DOC and POC values were corrected for background
levels measured at the beginning of the experiment and for
levels in the control cylinder by subtracting the initial
and control values from the final experimental cylinder
value.

The DOC content (DOC + POC), as estimated from the
labelled DOC results, represented exudate that had been
organically fixed during the experimental period. Total DOC
(referred to as TDOC + TPOC to distinguish it from DOC
values obtained from the labelled DOC data) represented all
the organic carbon released during the experiment --
including the unlabelled carbon which was incorporated by
the plant prior to the experiment and the labelled and
unlabelled carbon which was incorporated by the plant during
the experiment.

The plant's radiocarbon uptake was considered an estimate of net carbon fixation. Phytoplankton productivity studies have shown that radiocarbon uptake, especially in experiments of greater than 6 h duration are equal to net particulate carbon increases (Antia et al., 1963; Ryther and Menzel, 1965; Eppley and Sharp, 1975).

The plant's carbon fixation was expressed in the following 3 forms:

1. Net carbon fixed = carbon assimilated and retained by the plant at the end of the experiment as determined by sampling the plant tissue for labelled carbon.

2. Total net carbon fixed = 'net carbon fixed' (as defined above) plus the carbon assimilated during the experiment, but released as exudate as determined by analysis of the incubation water for labelled dissolved organics.

3. Net growth = 'net carbon fixed' minus or plus the 'old' dissolved organic carbon released or taken up, respectively. The 'old' DOC in the water represented organic carbon which had been fixed by the plant prior to the experiment.

Twenty-four h light-independent carbon fixation (dark carbon fixation) was subtracted from the above three measurements of carbon fixation. Kremer (1979) and Willenbrink et al. (1979) reported that light experiments with brown algae, including M. integrifolia, resulted in carboxylation products of light-independent carbon fixation in addition to products of

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light-dependent carbon fixation.

DOC in natural kelp beds

DOC exudation by M. integrifolia was studied indirectly by
DOC and POC sampling in two Barkley Sound natural kelp beds at
Kirby Pt. Cove and south Dodger Channel (Fig. 1). Out-of-kelp
bed water samples were taken at a distance of 100 m seaward of
these kelp beds. The water samples were collected from just
below the water surface in 3.8 l glass jars. DOC and POC content
were analysed by the techniques described above. Samplings were
made at slack tide, to ensure minimal offshore to inshore (or
vice versa) water movement, on February 24, May 1, May 23,
July 27, and December 16,1978.

Statistics

Each experiment had a sample size of one plant; analytical
precision was estimated by intra-plant and intra-water sample
replication. For between season comparisons, the plants within
one season were treated as seasonal replicates; the seasonal
means were calculated according to the guidelines described in
Bliss (1967). The statistical tests are identified as they are
used. All are referenced to Sokol and Rohlf (1969). The overall
level of significance for multiple tests was set at $P \leq 0.10$.

C. Results

Environmental conditions

The dates and environmental conditions for each 24 h and 48 h experiment are tabulated in Table 1 and for the dark experiments in Table 2. Summer temperatures ranged from 14.5 to 18.2 C, spring temperatures ranged from 11.5 to 15.0 C and fall temperatures ranged from 7.5 to 11.2 C. Salinities ranged from 22.0 to 32.8‰ in fall, 30.0 to 31.8‰ in spring and 32.0 to 33.4‰ in summer. Inorganic carbon levels did not demonstrate marked seasonal trends; the levels ranged from 16.8 mgC l^{-1} (experiment 5 in fall) to 24.0 mgC l^{-1} (experiment 121 in fall). The mean inorganic carbon level per season was between 21.2 and 22.2 mgC l^{-1}. Nutrient levels were approximately an order of magnitude higher in fall than in spring and summer. There was insufficient data for a detailed comparison of summer and spring nutrient levels.

The hours of sunlight (from dawn to dusk) varied from 15.0 to 17.2 h in summer, 14.5 to 16.8 h in spring, and 9.3 to 10.0 h in fall. Secchi depth readings indicated greatest light penetration in fall, with secchi readings ranging from 4.8 to 10.8 m; the lowest readings were in summer, ranging from 3.0 to 3.4 m. The total quantum irradiance received at the mean

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Table 1. Environmental conditions present during 24 h and 48 h experiments. Experiments 108 and 109 were 48 h experiments.

— denotes analysis not performed.
* denotes that NH_4^+ content is not included in value.
** denotes that secchi depth was not taken on that date but was extrapolated from other summer readings.

Season	Expt.	Date	Range in Water Temp. (C)	Salinity (‰)	Total Quantum Irradiance (E m⁻² day⁻¹)	Secchi Depth (m)	Hours of Light	Initial Inorganic Carbon Level (mgC L⁻¹)	Initial NO_3^- + NO_2 + NH_4^+ Level (μg-at L⁻¹)	Initial PO_4^{3-} Level (μg-at L⁻¹)
Spring	101	Apr. 26–27, 1978	11.5–12.0	31.2	6.9	7.5	14.5	23.2	—	—
	103	May 2–3, 1978	11.5–13.0	30.6	28.4	8.1	15.5	21.4	—	—
	105	May 13–14, 1978	12.0–12.5	31.8	8.9	4.6	15.3	22.6	0.83*	1.49
(48 h)	108	May 20–22, 1978	13.0–15.0	31.8	23.2 + 19.4 = 42.6	4.2 3.5	32.0	22.9	—	—
(48 h)	109	May 24–26, 1978	13.4–14.8	31.1	26.5 + 8.0 = 34.5	4.5 4.7	33.5	21.4	0.44*	0.39
Summer	110	July 19–20, 1978	14.5–17.0	33.1	19.7	3.4	16.8	22.4	1.89*	0.43
	111	July 22–23, 1978	15.0–17.0	33.1	17.2	3.0	17.0	22.3	—	—
	112	July 25–26, 1978	15.5–17.5	33.1	17.2	3.1	17.2	21.4	0.40*	0.20
	1	Aug. 7–8, 1978	15.5–18.2	32.0	15.1	3.2**	15.0	21.7	—	—
Fall	2	Oct. 31–Nov. 1, 1978	8.6–11.2	29.6	3.7	4.8	10.0	21.7	—	—
	3	Nov. 6–7, 1978	9.5–10.5	27.7	0.6	5.7	10.0	20.8	—	—
	4	Nov. 19–20, 1978	8.5–9.6	30.0	4.8	8.0	10.0	23.0	—	—
	121	Nov. 29–30, 1978	7.8–9.0	32.8	1.6	10.8	9.8	24.0	17.31	1.75
	122	Dec. 2–3, 1978	7.5–9.0	31.8	2.0	10.8	9.8	21.6	16.11	1.64
	123	Dec. 5–6, 1978	7.5	31.8	4.6	8.0	9.3	21.8	17.49	1.78

Table 2. Environmental conditions present during 'dark' experiments.

Season	Expt.	Date	Range in water temp. (C)	Salinity (‰)	Duration of expt. (h)	Initial inorganic C level (mgC l^{-1})
Spring	102	Apr.27-28/78	13.2	31.2	8.0	22.4
	104	May 3-4/78	13.0	30.0	8.5	21.6
	106	May 14-15/78	13.0	31.8	7.0	23.0
	107	May 17-18/78	13.8	30.6	8.0	21.0
Summer	113	July 28-29/78	15.5-16.0	33.4	6.7	21.6
	114	Aug.1-2/78	15.0-15.2	32.8	6.7	21.8
Fall	2'	Nov.1-2/77	10.5	29.0	13.0	21.2
	3'	Nov.7-8/77	10.1-10.5	28.0	13.0	21.8
	5	Nov.16-17/77	8.8-9.7	22.0	13.0	16.8
	124	Dec.10-11/78	8.0-8.2	31.8	13.5	18.0
	125	Dec.13-14/78	7.5-8.0	31.8	13.0	22.7

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incubation depth was a function of the daylength, the sun's elevation in the sky, and the clarity of the sky and water. Fall daily quantum irradiance levels were the lowest, ranging from 0.6 to 4.8 E m^{-2} day^{-1}, summer values ranged from 15.1 to 19.7 E m^{-2} day^{-1}, and the highest levels were received in spring, ranging from 6.9 to 28.4 E m^{-2} day^{-1}. Within a season, low irradiance levels corresponded to dull days and high irradiance levels corresponded to bright, sunnny days. Although summer experiments 110, 111 and 112 had longer daylengths than the spring experiments, total quantum irradiance values were lower in summer because of summer sea fog and greater light attenuation in the water column as indicated by the secchi depth readings.

Carbon fixation results

Light carbon fixation results

Figure 6 displays histograms of the carbon fixation results expressed as net carbon fixed, total net carbon fixed and net growth for the entire incubation period for each 24 h and 48 h experiment. Each experiment represented one plant. Also presented are histograms of total daily quantum irradiance received at the mean incubation depth.

Greater carbon fixation values corresponded to higher daily

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Figure 6. Histograms of net carbon fixed, total net carbon
   fixed and net growth in spring, summer and fall 24 h
   and 48 h (*) experiments. The histograms represent the
   total carbon fixed during the entire experiment.
   Histograms of total daily irradiance for each
   experiment are also presented.
   Vertical bars at top of histograms denote intra-plant
   precision ($2s/\sqrt{n}$; n = intra-plant replication = 8 - 12).
   'S' denotes that at least one of the three carbon
   fixation values is significantly different from the
   other two values ($P \leq 0.1$)..

35 a

Quantum Irradiance (E m⁻²)

Total Quantum Irradiance
Net C Fixed
Total Net C Fixed
Net Growth

FALL

SUMMER

SPRING

Expt. 101 103 105 108 109 110 111 112 1 2 3 4 121 122 123

Carbon Fixed (mg C gdw⁻¹)

35b
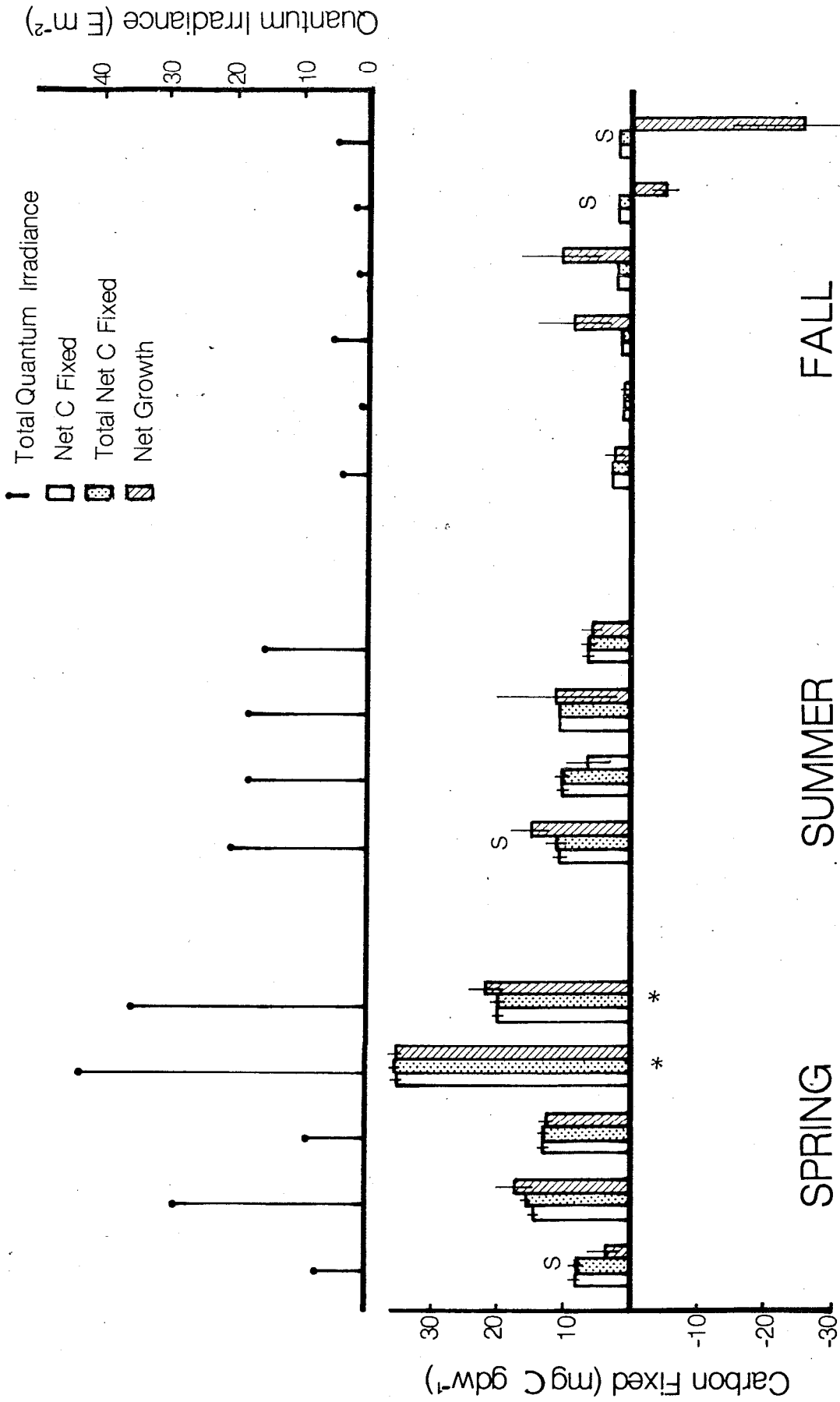
irradiance levels. Spring had a wide range of light conditions
and a correspondingly wide range in the plant's response. Summer
carbon fixation levels were intermediate between spring and
fall; summer carbon fixation values were lower than spring
values at comparable irradiance levels (for example, summer
experiments 110, 111, and 112 versus spring experiment 105).
Carbon fixation was lowest in fall, as were the irradiance
levels.

Some net growth values appeared to vary from the other two
fixation values (net carbon fixed and total net carbon fixed).
However, when tested with respect to the precision of the values
(using the intra-plant means and variances), only experiments
101, 110, 122 and 123 showed the net growth value to be
significantly different ($P \leq 0.1$) from the other two carbon
fixation values (Table 3).

Comparison of carbon fixation and irradiance levels between
seasons is given in Fig. 7, where mean hourly total net carbon
fixation values were graphed against the hourly quantum
irradiance levels. In general, spring hourly fixation levels
were higher than summer or fall levels at similar irradiances.
The one exception being the spring 48 h experiment, 109, which
displayed an hourly carbon fixation rate similar to the summer
rates.

Seasonal differences in the efficiency of M.integrifolia in
fixing carbon are indicated in Fig. 7 and Table 3. Spring

Table 3.   Carbon fixation results expressed as mgC gdw⁻¹ for 24 h period (* = 48 h period) and as mgC gdw⁻¹·h light⁻¹. Experiment 1 (Summer 1977) was excluded from the summer seasonal mean. ± 2S/√n; n = intra-plant replication for individual experiments; n = number of experiments in season for seasonal means.

The 'Test of Equality of Means When Variances Are Heterogeneous' was used to test if the three carbon fixation values within an experiment were significantly different (S) or not different (NS). (P≤0.10).

Season	Expt.	Net C Fixed in 24 h	Total Net C Fixed in 24 h	Net Growth in 24 h	Net C Fixed per h	Seasonal Mean	Total Net C Fixed per h	Seasonal Mean	Net Growth per h	Seasonal Mean	Results of Significance Test
Spring 1978	101(n=9)	7.9±0.23	7.9±0.23	3.5± 1.90	0.55±0.016		0.55±0.016		0.24±0.131		S
	103(n=11)	14.3±0.23	14.9±0.23	16.4± 3.51	0.92±0.014	0.78 ±0.203	0.96±0.015	0.79 ±0.212	1.06±0.226	0.76 ±0.327	NS
	105(n=10)	12.2±0.26	12.2±0.27	11.9± 0.80	0.80±0.017		0.80±0.017		0.78±0.053		NS
	108(n=11)	34.4±0.45*	34.9±0.43*	34.2± 1.16*	1.07±0.013		1.09±0.013		1.07±0.036		NS
	109(n=11)	19.0±0.28*	19.0±0.29*	21.1± 3.85*	0.57±0.009		0.57±0.009		0.63±0.115		NS
Summer 1978	110(n=11)	10.2±0.15	10.4±0.15	14.3± 3.26	0.61±0.009		0.62±0.009		0.85±0.194		S
	111(n=8)	9.7±0.24	9.7±0.25	6.1± 3.64	0.57±0.014	0.59 ±0.024	0.58±0.015	0.59 ±0.027	0.36±0.214	0.61 ±0.670	NS
	112(n=11)	10.0±0.14	10.0±0.16	10.6± 8.61	0.58±0.008		0.58±0.009		0.62±0.502		NS
Summer 1977	1(n=12)	6.1±0.50	6.1±0.50	5.8± 1.77	0.41±0.033		0.41±0.033		0.39±0.119		NS
Fall 1977	2(n=12)	2.6±0.10	2.6±0.10	1.9± 1.69	0.26±0.009	0.16 ±0.103	0.26±0.009	0.16 ±0.103	0.19±0.169	0.36 ±0.663	NS
	3(n=11)	0.9±0.05	0.9±0.05	0.5± 0.39	0.09±0.004		0.09±0.004		0.05±0.039		NS
	4(n=12)	1.3±0.05	1.3±0.05	8.3± 4.33	0.13±0.004		0.13±0.004		0.83±0.434		NS
Fall 1978	121(n=12)	1.9±0.06	1.9±0.06	9.9± 5.92	0.19±0.005	0.17 ±0.042	0.19±0.005	0.18 ±0.013	1.01±0.592	-0.82 ±2.466	NS
	122(n=12)	1.6±0.08	1.6±0.08	-6.0± 1.98	0.16±0.006		0.17±0.008		-0.61±0.202		S
	123(n=12)	1.6±0.07	1.6±0.08	-26.6±10.23	0.17±0.006		0.17±0.007		-2.86±1.02		S

Figure 7. Scattergram of hourly total net carbon fixation

   rates plotted against hourly quantum irradiance levels.

   The number adjacent to each point on the scattergram

   refers to the experiment number.
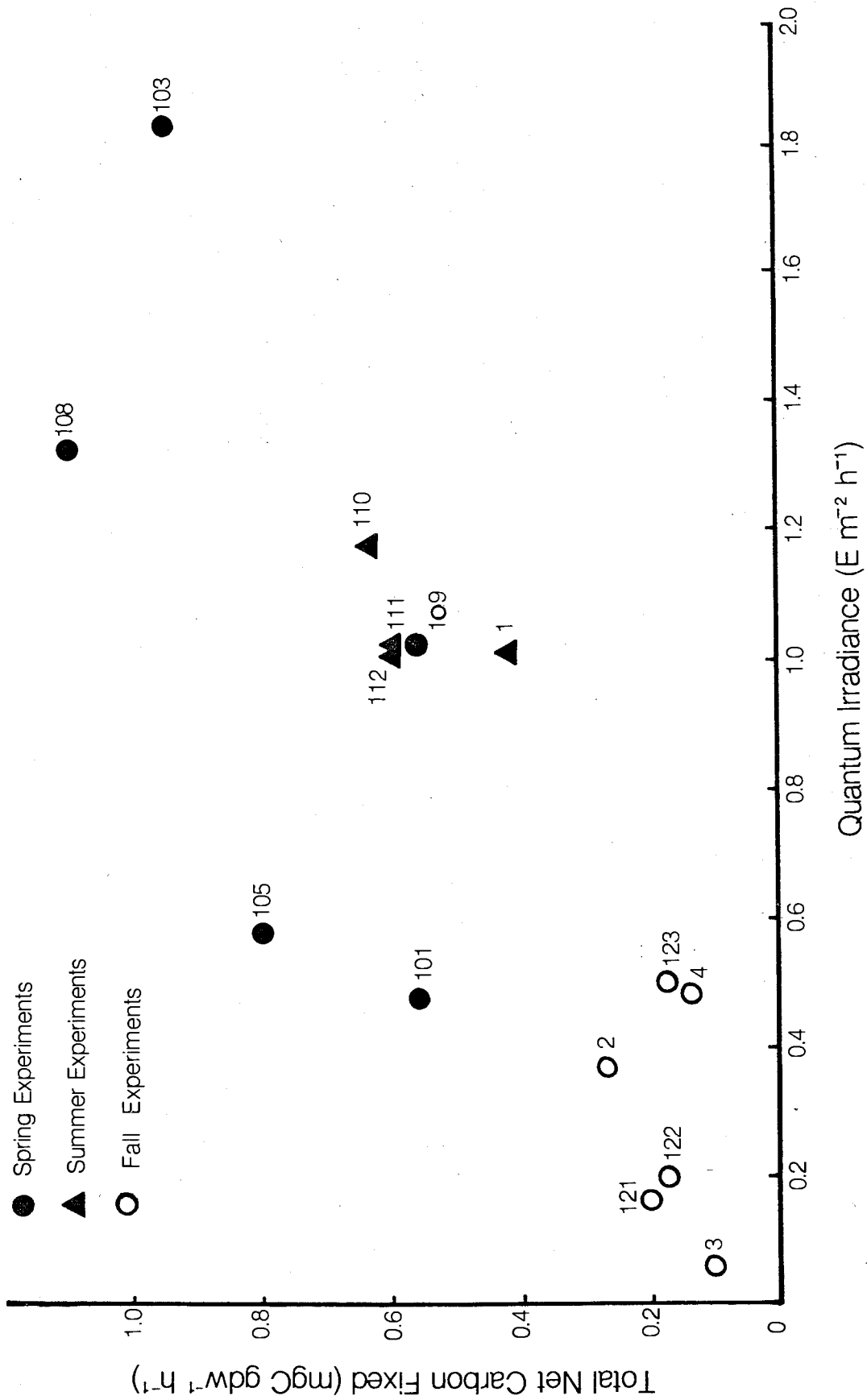
demonstrated the greatest carbon fixation rates, summer rates
were intermediate, and fall rates were the lowest.

The seasonal ranges in the total net carbon fixed were the
following:

spring

7.9 to 17.5 mgC gdw^{-1} day^{-1} or 0.55 to 1.09 mgC gdw^{-1} h light^{-1}

summer

6.1 to 10.4 mgC gdw^{-1} day^{-1} or 0.41 to 0.62 mgC gdw^{-1} h light^{-1}

fall

0.9 to 2.6 mgC gdw^{-1} day^{-1} or 0.09 to 0.26 mgC gdw^{-1} h light^{-1}.

To examine seasonal differences in carbon fixation rates of
the Kirby Pt. Cove M. integrifolia population, the variances of
hourly rates within a season were compared to the variance of
hourly rates between seasons. The seasonal rates indicated M.
integrifolia's carbon fixation response to full seasonal ranges
in light conditions -- from overcast days to sunny days. The one
exception being summer, where all experiments were conducted in
at least partially sunny conditions.

The means for each season of each year are presented in
Table 3. Summer experiment 1 was excluded from these comparisons
because the plant was not collected from the Kirby Pt. Cove
site. Table 4 presents the results of the tests of significance.
Fall, 1977 (experiments 2, 3, 4) and fall 1978 (experiments 121,
122, 123) values were pooled because the Approximate Student's
T-test showed that they were not significantly different

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Table 4. Application of the 'Approximate Test of Equality of Means when Variances are Heterogeneous' to seasonal means of carbon fixation results (expressed as mgC gdw-1 h light-1). Experiment 1 (summer, 1977) was excluded from comparison tests. Fall 1977 and Fall 1978 were pooled when shown to be equal by the Approximate Student's T-test. The Approximate Student's T-test was used for multiple comparisons. A Common underline between means denotes no significant difference between those means. The over-all level of significance P, = 0.1. ($\pm 2s/\sqrt{n}$; n = no. of experiments in season.)

a) Comparisons of means within a season.

Season	Net C fixed	Total net C fixed	Net growth	Results of significance test s=sig. difference ns=no sig.
Spring (n=5)	0.78±0.203	0.79±0.212	0.76±0.327	ns
Summer (n=3)	0.59±0.024	0.59±0.027	0.61±0.670	ns
Fall (n=6)	0.17±0.047	0.17±0.047	-0.23±1.309	ns

b) Comparisons of means between seasons.

	Spring (n=5)	Summer (n=3)	Fall (n=6)	Result of sig. test
Net C fixed	0.78±0.203	0.59±0.024	0.17±0.047	s
Total net C fixed	0.79±0.212	0.59±0.027	0.17±0.047	s
Net growth	0.76±0.327	0.61±0.670	-0.23±1.309	ns

(P<0.05). Comparison of mean hourly fixation rates within a season (Table 4a) showed that there was no significant difference between net carbon fixed, total net carbon fixed, and net growth in either spring, summer, or fall. Table 4b shows that the hourly net carbon fixed and hourly total net carbon fixed levels of spring and summer were significantly greater (P=0.1) than fall levels, but were not different from each other.

Due to the great variance of the net growth levels within and between seasons, the 'Approximate Test of Equality of Means when Variances are Heterogeneous' indicated no significant seasonal difference in net growth rates. The inclusion of the TDOC + TPOC values with their high variances (low levels of precision), especially in fall experiments, in the calculation of net growth masked any seasonal trends and consequently decreased the significance of the net growth results. This effect can be visualized by observation of the histograms in Fig. 6.

The net change in the total inorganic carbon content of the experimental cylinder's water is tabulated in Table 5. Unfortunately, the pH technique used for the analysis of inorganic carbon lacked the precision of the radiocarbon methodology for precise detection of the small carbon changes occurring in many experiments, especially the fall experiments. Comparison of the changes in inorganic carbon expressed as

Table 5.   Net changes in the total inorganic carbon content
            of the experimental cylinder's water during
            24 h and 48 h (experiments 108 and 109)
            experiments.
            The net changes are expressed as mgC l^{-1} and as
            mgC gdw^{-1} plant.
            Negative values denote a decrease in the water's
            inorganic carbon content or net uptake of carbon
            by the plant. Positive values denote an increase
            in the water's inorganic carbon content, or a net
            release of carbon by the plant.
            $\pm 2s/\sqrt{n}$; n = intra-sample replication = 2.

Season	Expt.	Net Change in Inorganic Carbon	
		as mgC l^{-1}	as mgC gdw^{-1}
Spring	101	−2.0±0.51	−10.0± 2.48
	103	−1.4±0.76	−16.2± 8.68
	105	−1.0±0.60	−12.9± 7.59
	108	−2.4±0.61	−34.8± 8.88
	109	−1.0±0.17	−12.8± 2.26
Summer	110	−1.7±0.17	−11.4± 1.15
	111	−1.3±0.47	−12.0± 4.42
	112	−0.7±0.17	−11.2± 2.64
	1	−1.6±0.00	− 7.1± 0.00
Fall	2	−1.4±0.50	− 2.6± 0.94
	3	−0.1±0.99	− 0.5± 4.48
	4	−0.4±0.17	− 1.8± 0.87
	121	−0.7±1.10	−14.5±22.11
	122	−0.2±0.52	− 2.7± 7.92
	123	+0.2±0.24	+ 8.2± 8.17

mgC gdw^{-1} plant in Table 5 with the total net carbon fixation
results in Table 3, reveals that the radiocarbon results were,
generally close to and usually slightly less than the mean net
inorganic carbon change. This comparison indicates that the
radiocarbon uptake technique was measuring values that closely
approximated net productivity.

Light-independent carbon fixation results

Histograms of hourly net light-independent carbon
fixation, as evaluated by experiments conducted during the night
(from after dusk to before dawn the next morning), are presented
in Fig. 8. The duration of each experiment is recorded in Table
2. The mean seasonal hourly rates were as follows: 0.013
mgC gdw^{-1} h^{-1} in spring, 0.014 mgC gdw^{-1} h^{-1} in summer, and
0.010 mgC gdw^{-1} h^{-1} in fall. There was no significant seasonal
difference in these hourly rates when tested by the 'Test of
Equality of Means when Variances are Heterogeneous' ($P \leq 0.1$).
Table 6 presents the net light-independent carbon fixation
results as hourly rates and as percent of net light-dependent
carbon fixation rates. These percentages were 1.2 to 2.4%
(spring), 2.3 to 3.4 % (summer) and 3.8 to 11.1 % (fall) and
were a direct function of the variations in light-dependent
fixation rates.

Figure 8. Histograms of hourly net light-independent carbon

fixation rates in spring, summer and fall.

Vertical lines at top of histograms denote precision

$(2s/\sqrt{n}$; n = intra-plant replication = 8 - 12).

Net Light-independent Carbon Fixed (mg C gdw^{-1} h^{-1})

SPRING   SUMMER   FALL

Expt. 102 104 106 107   113 114   2' 3' 5 124 125

44b
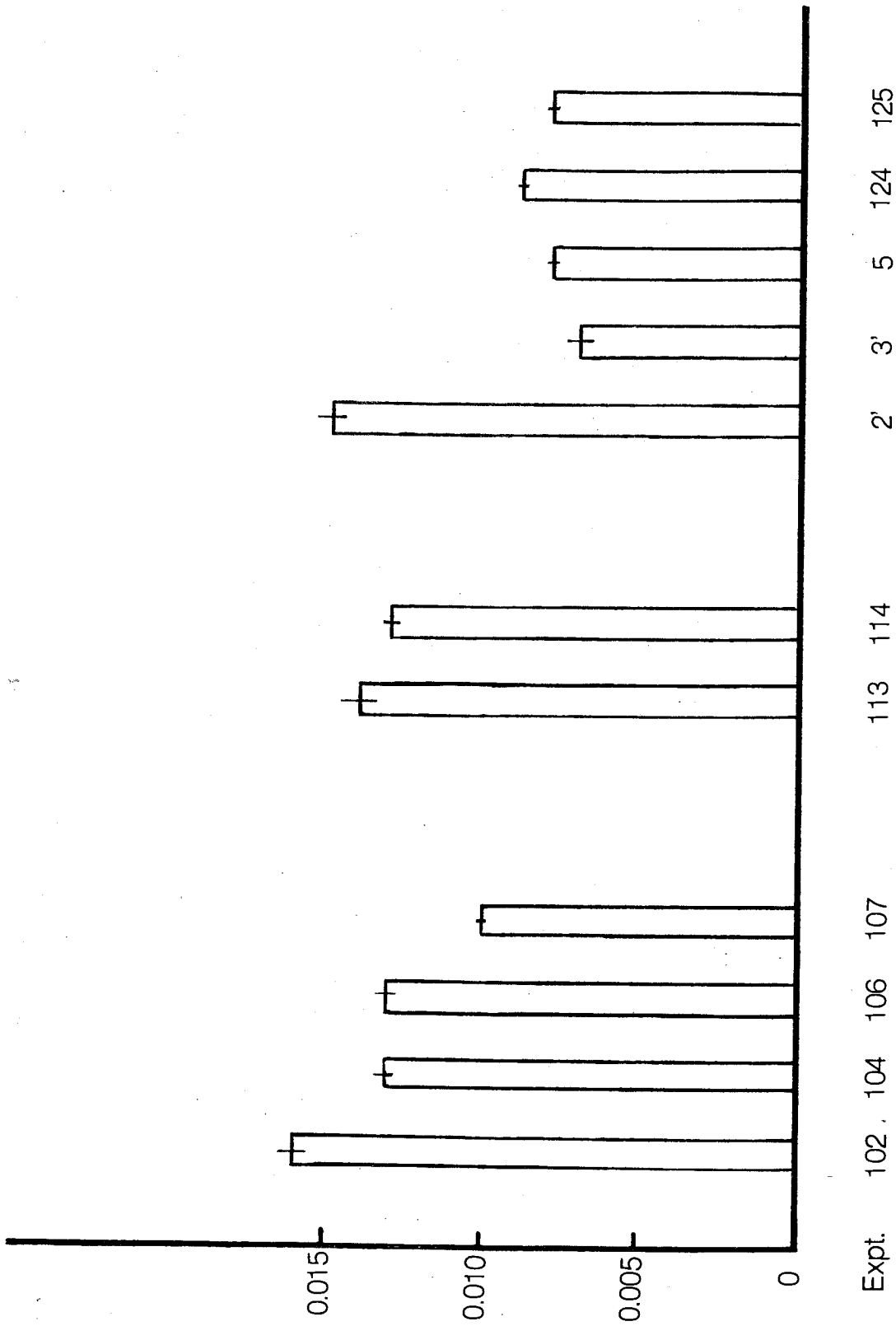
Table 6 .   Comparison of light-dependent and light-independent net carbon

fixation rates expressed as mgC gdw^{-1} h^{-1}.

($\pm 2s/\sqrt{n}$; n = intraplant replication = 8-12)

Season	Light C fixation		Dark C fixation		Mean seasonal dark rate	Mean dark rate x100 / light rate
	Expt.	rate	Expt.	rate		
Spring	101	0.55±0.016	102	0.016±0.0003	0.013±0.0028	2.4
	103	0.92±0.014	104	0.013±0.0002		1.4
	105	0.80±0.017	106	0.013±0.0002		1.6
	108	1.07±0.013	107	0.010±0.0001		1.2
	109	0.57±0.009				2.3
Summer	110	0.61±0.009	113	0.014±0.0006	0.014±0.0017	2.3
	111	0.57±0.014	114	0.013±0.0002		2.5
	112	0.58±0.008				2.4
	1	0.41±0.033				3.4
Fall	2	0.26±0.009	2'	0.015±0.0004	0.010±0.0029	3.8
	3	0.09±0.004	3'	0.007±0.0004		11.1
	4	0.13±0.004	5	0.008±0.0002		7.7
	121	0.19±0.005	124	0.009±0.0001		5.3
	122	0.16±0.006	125	0.008±0.0001		6.3
	123	0.17±0.006				5.9

Exudation of organic carbon

DOC exudation based on labelled DOC results

Figure 9 presents the levels of DOC + POC in the water, as calculated from the labelled DOC ($DO^{14}C$ + $PO^{14}C$) results and expressed as mgC gdw^{-1}. Presented are the levels at dusk and dawn in the experimental cylinder when the initial and control levels have been subtracted from the experimental levels. Dusk and dawn levels were similar when observed with respect to the intra-experiment precision of the values. When Fig. 9 is compared to Fig. 6, similar trends in 'ups' and 'downs' in irradiance, carbon fixation and DOC + POC levels are apparent.

The relationship between DOC exudation and irradiance levels was investigated in the scattergram, Fig. 10, where the DOC + POC released per hour light, as calculated from the dusk DOC + POC values, was graphed against the average hourly irradiance level in each experiment. Summer experiment 1 was excluded from this scattergram and the following scattergram (Fig. 11) because of reasons stated earlier; the dusk DOC + POC value for day 2, only, was included for 48 h experiments 108 and 109 in the scattergrams, Fig. 10 and 11. Seasonal differences in daylengths were cancelled by using hourly values. A positive

Figure 9. Histograms of DOC levels in the incubation water,

as estimated by the labelled DOC ($DO^{14}C$ + $PO^{14}C$)

results, at dusk and dawn samplings when compared to

initial and control levels.

Vertical lines at top of histograms denote precision

($2s/\sqrt{n}$; n = intra-sample replication = 2-3).

'ND' denotes that no data is available for the

experiment.

*
* denotes that value includes only $DO^{14}C$ data.

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Figure 10. Scattergram of dusk DOC (h light)$^{-1}$ released, as

estimated by the labelled DO^{14}C + PO^{14}C results,

plotted against average hourly quantum irradiances in

diel experiments.

Quantum Irradiance $\cdot$ h^{-1} (E m^{-2}h^{-1})

DOC+POC   released $\cdot$ h light^{-1} at dusk (mgC gdw^{-1}h^{-1})

● Spring Experiments

▲ Summer Experiments

○ Fall Experiments

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relationship between the DOC + POC and irradiance levels was indicated; an increase in DOC exudation corresponded to an increase in irradiance.

A similar relationship was indicated between DOC exudation and total net carbon fixed h light^{-1} in the scattergram, Fig. 11.

Table 7 tabulates the dusk and dawn DOC + POC levels based on the labelled organic carbon results. The final (dawn) exudation values ranged from < 0.01 mgC qdw^{-1} (experiment 4, fall) to 0.59 mgC qdw^{-1} (experiment 103, spring) representing approximately 0 % to 3.9 % of the plant's total net carbon fixed.

A net DOC uptake was indicated in some experiments, but the levels were below the level of precision and therefore not differing significantly from zero.

DOC exudation based on total DOC (TDOC + TPOC) results

Histograms of TDOC + TPOC expressed as mgC qdw^{-1} are presented in Fig. 12; Table 8 tabulates these levels. Detection of significant changes in TDOC + TPOC levels in the cylinder was limited by the precision of the analytical techniques, in particular the DOC technique. The minimum amount of change that could be detected in the experimental cylinder's DOC + POC level was 0.53 mgC l^{-1}. This level translated into 1.0 to 17.9 mgC qdw^{-1} depending on the biomass of the plant being incubated.
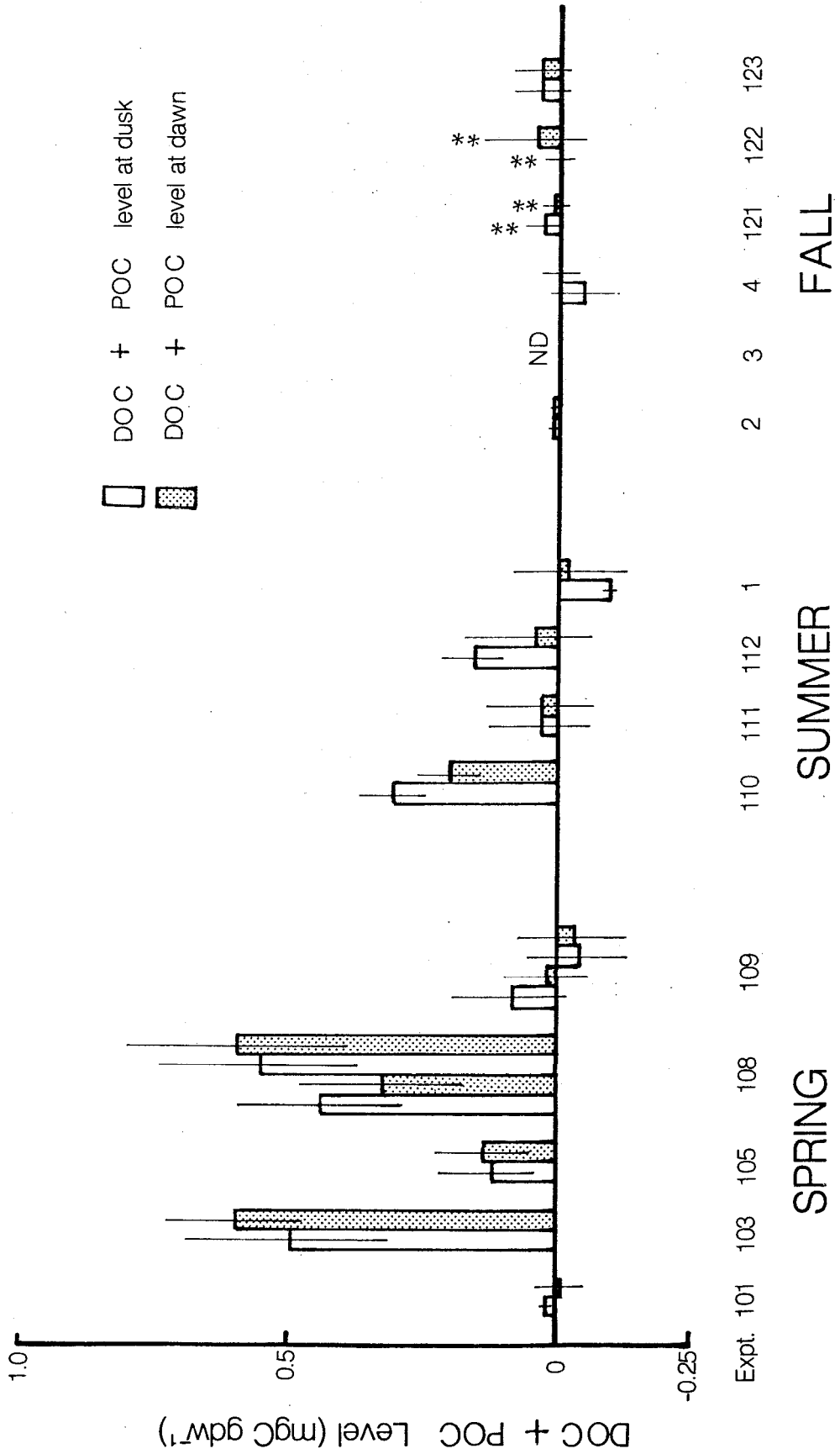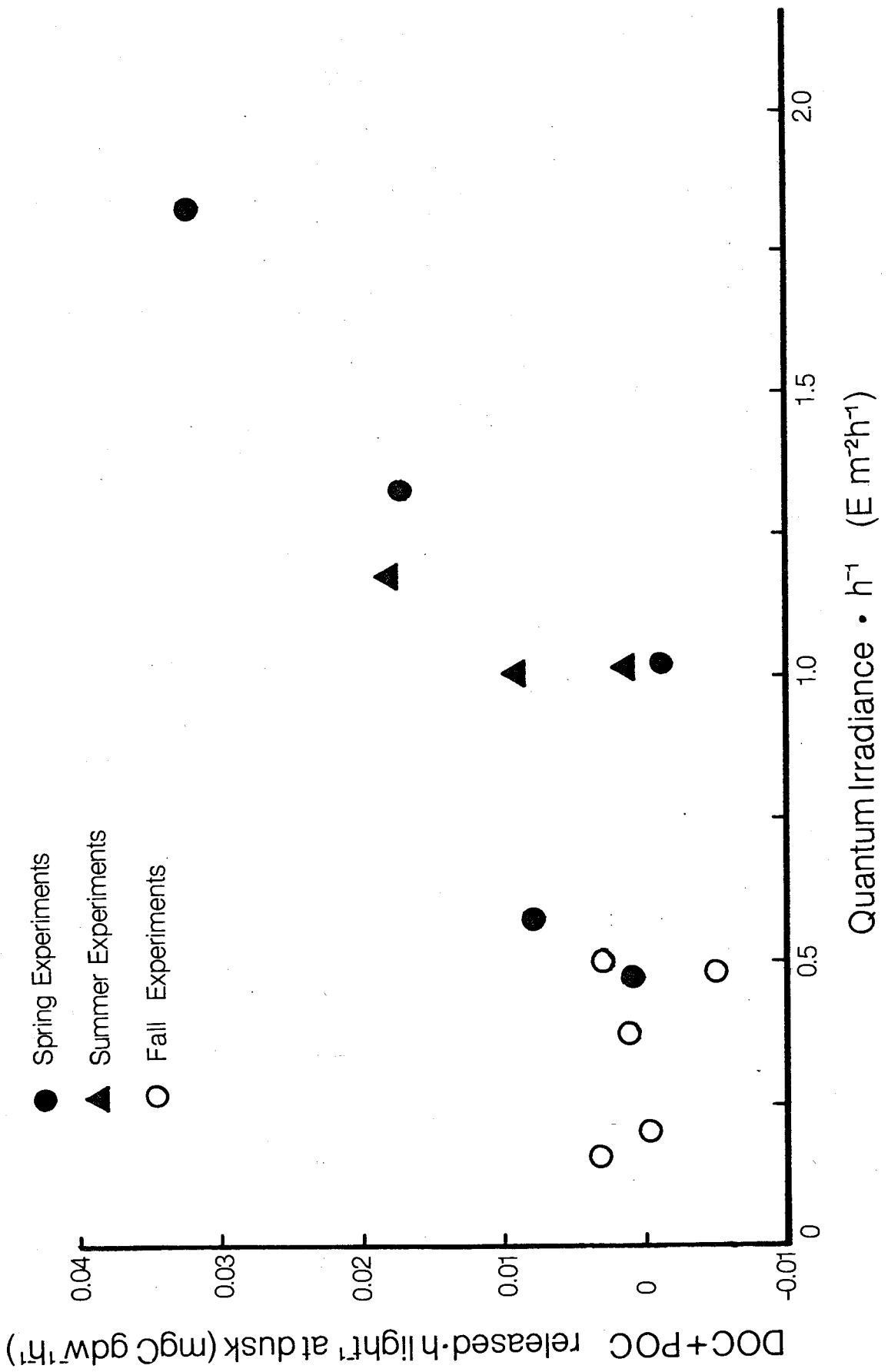
Figure 11. Scattergram of dusk DOC (h light)$^{-1}$ released, as
estimated by the labelled DO^{14}C + PO^{14}C results,
plotted against average hourly total net carbon fixed
in diel experiments.

Total Net C Fixed ·h light⁻¹ (mgC gdw⁻¹ h⁻¹)

DOC + POC released ·h light⁻¹ at dusk (mgC gdw⁻¹ h⁻¹)

● Spring Experiments
▲ Summer Experiments
○ Fall Experiments

Table 7 Levels of DOC as estimated by the labelled DOC
(DO-14C + PO-14C) data in the incubation
water at dusk and at dawn when compared to
initial and control levels.
Negative values denote apparent uptake of organics.
** = includes dissolved value only.
ND = no data available.
$\pm 2s/\sqrt{n}$; n = intra-sample replication = 2 to 3.

Season	Expt	DOC + POC level as mgC gdw^{-1}		Final level expressed as % of total net C fixed
		at dusk	at dawn	
Spring	101	0.02±0.012	-0.01±0.043	-0.1
	103	0.49±0.189	0.59±0.123	3.9
	105	0.12±0.089	0.13±0.083	1.0
(48h)	108	0.43±0.147 0.55±0.181	0.32±0.154 (day1) 0.59±0.213 (day2)	1.7
(48h)	109	0.08±0.096 -0.04±0.089	0.01±0.075 (day1) -0.03±0.096 (day2)	-0.1
Summer	110	0.30±0.065	0.20±0.062	1.9
	111	0.03±0.086	0.03±0.094	0.3
	112	0.16±0.061	0.04±0.131	0.3
	1	-0.10±0.015	-0.02±0.107	-0.3
Fall	2	0.01±0.010	0.01±0.007	0.3
	3	ND	ND	ND
	4	-0.05±0.066	0.00±0.030	0.0
	121	0.03±0.027**	0.01±0.025**	2.6
	122	0.00±0.027	0.04±0.088	2.0
	123	0.03±0.047**	0.03±0.049**	1.3

Figure 12. Histograms of DOC levels in the incubation

water, as estimated by the total DOC (TDOC + TPOC)

results, at dusk and at dawn when compared to initial

and control levels.

Vertical lines at top of histograms denote precision

$(2s/\sqrt{n};$ n = intra-sample precision = 2-9).

*   denotes that value includes only POC data.

*
*   denotes that value includes only DOC data.

Figure caption (rotated):

TDOC + TPOC Level (mgC gdw⁻¹)

Legend:
☐ TDOC + TPOC level at dusk
▨ TDOC + TPOC level at dawn

Y-axis: 40, 30, 20, 10, 0, -10

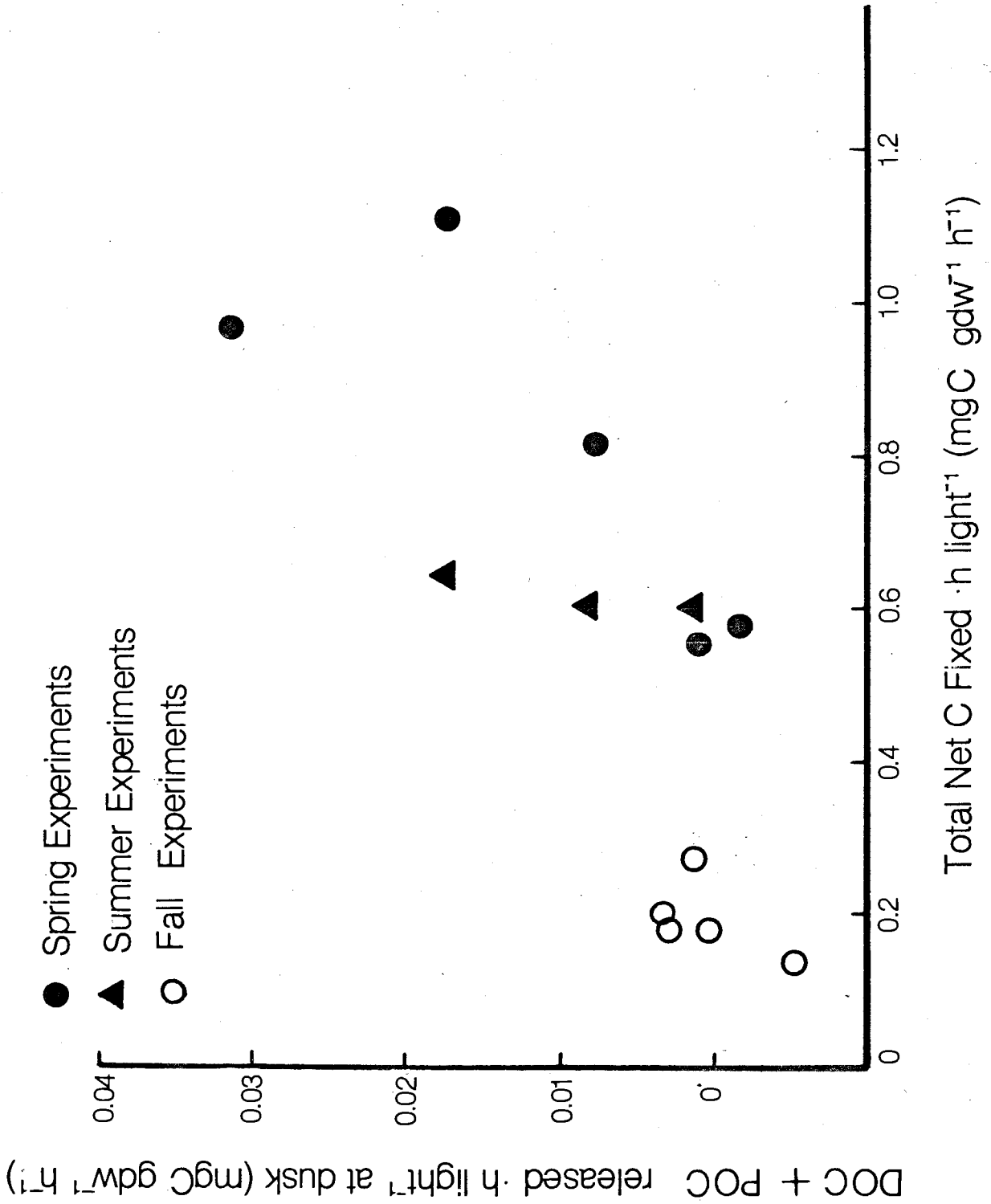X-axis: Expt. 101 103 105 108 109 110 111 112 1 2 3 4 121 122 123

SPRING   SUMMER   FALL

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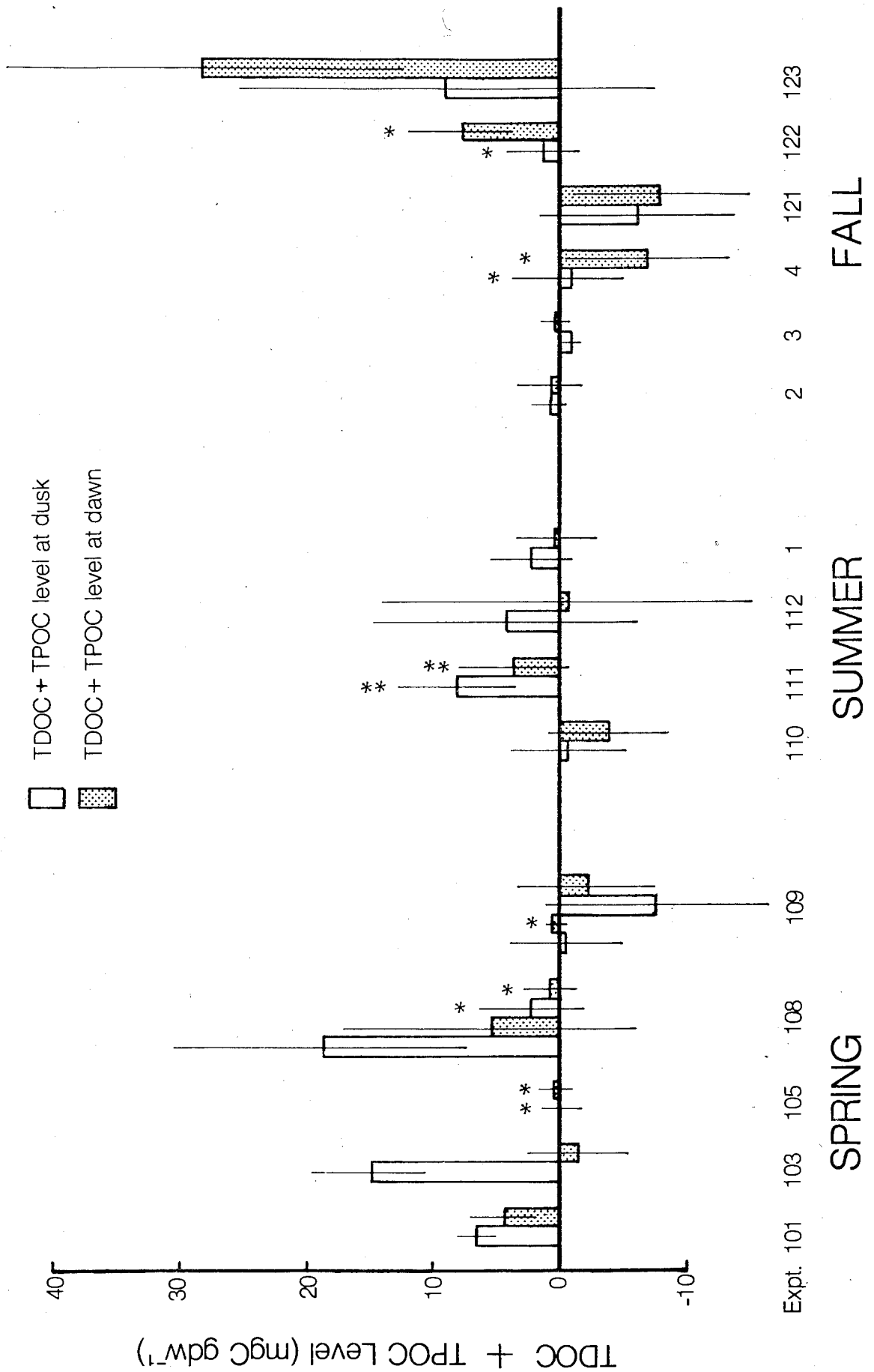
Table 8. Levels of DOC as estimated by the total DOC (TDOC+TPOC) data in the
incubation water at dusk and at dawn when compared to initial and
control levels. Minimum level of significant detection was determined
by the precision ($2s/\sqrt{n}$) of the techniques. Significance test =
Student's T-test; only levels exceeding minimum detection level
were tested. The overall level of significance P, =0.1.

        S = level significantly different from 0.
        NS = level not   "   "   " "
        '-' denotes uptake of organics.
        * includes only dissolved value.
        ** includes only particulate value.
        $\pm 2s/\sqrt{n}$; n = intra-plant replication.

Season	Expt.	TDOC+TPOC levels as mgC gdw^{-1} at dusk	at dawn	Dawn level as % of total net C fixed	Minimum level of detection as mgC gdw^{-1}	as % of total net C fixed
Spring	101	6.5± 1.49 S	4.4± 2.31 S	53.6	2.5	31
1978	103	14.8± 4.52 S	-1.6± 3.87	-10.2	6.5	40
	105	-0.2± 1.47*	0.3± 1.38*	2.7	6.6	54
	108	18.4±11.56 NS	5.4±11.58			
	(48h)	2.2± 4.07*	0.8± 2.06*	2.1	7.6	21
	109	-0.4± 4.25	0.3± 0.80*			
	(48h)	-7.5± 9.09 NS	-2.1± 5.20	-10.8	7.0	36
Summer	110	-0.4± 4.50	-3.9± 4.41 NS	-35.8	3.6	33
1978	111	8.1± 4.52**NS	3.7± 4.14**	36.9	5.0	50
	112	4.3±10.28	-0.6±14.28	-5.6	8.2	79
1977	1	2.3± 2.99	0.3± 3.07	5.0	2.4	37
Fall	2	0.8± 1.14	0.7± 2.62	23.8	1.0	35
1977	3	-0.9± 0.58*	0.3± 0.92*	31.1	2.4	216
	4	-0.9± 4.67	-7.0± 6.13 NS	-455.1	2.7	174
1978	121	-6.1± 7.67	-8.0± 6.84	-379.1	10.6	499
	122	1.2± 2.82*	7.6± 3.95*	405.5	8.0	425
	123	8.9±16.53	28.2±15.85 NS	1530.6	17.9	972

This further translated into 21 % to 972 % of the plant's total

net carbon fixed, again depending on the plant's biomass in

addition to the plant's carbon fixation rate (refer to Table 8

for the minimum detection level of each experiment).

There were no obvious trends or correlations with

irradiance or carbon fixation levels in these results. The

levels were from two times to one or two magnitudes greater than

the DOC levels calculated from the labelled organic carbon

results. However, only experiments 101 and and 103 indicated

exudations significantly above the detection limitations and

experiment 103 did so only during the day. Experiment 103's low

DOC level the following dawn indicated night-time uptake of the

DOC released during the day. These results indicated no

excessive exudation of DOC by M. integrifolia, in spring or

summer. Fall exudation would have been undetectable by these

techniques.

ATP results

An analysis of ATP levels in the cylinders' waters

provided an estimate on the quantity of suspended microscopic

particulate organic carbon that was living matter. Table 9

presents a comparison of the experimental cylinder's net POC

levels based on total, labelled and living (= ATP) particulate

carbon results. The particulate carbon levels based on the

living and the labelled POC results were very low or below

Table 9. Levels of particulate carbon at dusk and at dawn as estimated by TPOC, PO-14C and ATP results. The initial and control levels were subtracted from each value. Data is presented only for experiments in which an ATP analysis was performed. Negative values denote decrease in level with respect to initial and control samplings. $\pm 2s/\sqrt{n}$; n = intra-sample replication. ND = no data available.

Season	Expt.	TPOC level (n=2-3) (mgC gdw^{-1})		PO-14C level (n=2-3) (mgC gdw^{-1})		ATP level (n=3-8) (mgC gdw^{-1})	
		at dusk	at dawn	at dusk	at dawn	at dusk	at dawn
Spring	101	1.3±0.67	1.8±0.72	0.00±0.006	-0.03±0.018	0.03±0.013	-0.03±0.030
	108(day1)	7.0±1.71	0.9±2.35	-0.09±0.060	-0.14±0.075	-0.04±0.045	0.00±0.024
	(day2)	2.2±1.39	0.7±1.03	-0.18±0.066	-0.16±0.130	ND	-0.06±0.077
Fall	2	0.1±0.30	0.3±0.32	0.01±0.006	-0.00±0.003	0.03±0.005	-0.02±0.027
	3	-0.9±0.31	0.3±0.46	ND	ND	0.12±0.036	0.23±0.032
	4	-2.3±0.35	-1.4±0.27	-0.05±0.033	0.00±0.003	-0.01±0.008	-0.00±0.054

precision limitations. The particulate carbon levels based on the total POC results were up to two magnitudes greater than the living particulate carbon levels.

DOC and POC levels in kelp beds

The exudation of organics by M. integrifolia was investigated indirectly by examination of DOC content in natural kelp bed waters from the Kirby Pt. Cove and S. Dodger Channel. Baseline DOC analyses were made on waters 100 m seaward from the kelp beds. The results of these analyses are presented in Table 10. The levels of DOC 'in' and 'out' of the kelp bed followed the same seasonal trend; levels were highest in mid-summer, fall, and early spring, at 4 to 5 mgC l^{-1} and lowest in mid-spring at 1 to 2 mgC l^{-1}. However, the 'in' kelp bed values were either greater than or equal to the 'out' of kelp bed values. The 'in' kelp bed levels were significantly (P=0.03) greater when tested by the Mann-Whitney U-test.

POC was also analysed and the results are presented in Table 10. The Mann-Whitney U-test showed that POC was significantly (P=0.008) greater 'in' the kelp bed than 'out' of the kelp bed.

Table 10. DOC and POC levels at Kirby Pt. Cove and S. Dodger Channel kelp beds at various times of the year. Also shown are the DOC and POC levels of waters 100 m seaward from the two kelp beds. ±2s/√n; n = 2 to 9. ND = sample not taken.

Date	Location	DOC levels (mgC l⁻¹) in kelp bed	DOC levels (mgC l⁻¹) 100m distant from kelp bed	POC levels (mgC l⁻¹) in kelp bed	POC levels (mgC l⁻¹) 100m distant from kelp bed
Feb.24/78	Kirby Pt.	4.8±0.46	4.8±0.58	ND	ND
	Dodger	5.0±0.48	4.1±0.19	ND	ND
May 1/78	Kirby Pt.	0.7±0.04	0.7±0.08	1.02±0.208	0.81±0.088
	Dodger	2.2±0.25	2.1±0.16	0.90±0.010	0.68±0.060
May 23/78	Kirby Pt.	2.4±0.23	1.9±0.32	0.88±0.057	1.04±0.010
	Dodger	2.4±0.24	1.6±0.07	1.20±0.030	0.97±0.020
July 27/78	Kirby Pt.	3.9±0.28	4.0±0.22	3.37±0.137	2.09±0.140
	Dodger	4.0±0.09	3.9±0.10	2.36±0.277	0.74±0.072
Dec.16/78	Kirby Pt.	5.1±0.11	4.8±0.08	1.12±0.070	0.67±0.163
	Dodger	5.3±0.17	4.2±0.23	0.43±0.035	0.92±0.164

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Carbon and nitrogen content of the Macrocystis

The seasonal change in the plant's nutritive state was investigated by measurements of internal carbon and nitrogen levels (Table 11). A one-way Analysis of Variance indicated significant seasonal differences ($P \leq 0.01$) in levels of carbon, nitrogen, and C/N ratios of the plants. The plant from experiment 1 was not included in these statistical comparisons for reasons stated earlier. The carbon content was highest in summer, $\overline{X}$ = 28.32 % dry wt, intermediate in fall, $\overline{X}$ = 26.55 % dry wt, and lowest in spring, $\overline{X}$ = 24.26 % dry wt. Conversely, the plant's nitrogen content was greatest in fall, $\overline{X}$ = 1.99 % dry wt, intermediate in spring, $\overline{X}$ = 1.60 % dry wt, and lowest in summer, $\overline{X}$ = 1.33 % dry wt. These resulted in a high summer C/N ratio, $\overline{X}$ = 25.0, and lower spring, $\overline{X}$ = 18.4, and fall, $\overline{X}$ = 15.6 C/N ratios. A multiple comparison test (Table 12) indicated that spring and fall ratios were not significantly different due to conflicting seasonal trends in carbon and nitrogen levels for these two seasons.

Table 11. Dry weights, carbon and nitrogen levels and C/N ratios of plants used for 24 h, 48 h and dark experiments. (±S.E.)
 * Plant from expt. 1 was not included in seasonal mean or seasonal comparisons.
 ** Fall 1977 and 1978 were combined when Student's T-test indicated they were not significantly different (P< 0.01).

Season	Expt.	Plant dry wt. (g)	C content as % dry wt.	Mean seasonal C content	N content as % dry wt.	Mean seasonal N content	C(moles)/N(moles)	Mean C/N ratio
Spring 1978	101	363	25.73	24.26 ±0.029	2.00	1.60 ±0.110	15.0	18.4±1.41
	102	324	24.03		1.94		14.5	
	103	155	23.66		1.88		14.7	
	104	339	23.28		1.74		15.6	
	105	140	24.83		1.67		17.4	
	106	309	25.48		1.48		20.1	
	107	109	23.83		1.37		20.3	
	108	122	23.80		1.00		27.5	
	109	133	23.70		1.34		20.6	
Summer 1978	110	261	29.40	28.32 ±0.541	1.07	1.33 ±0.094	32.1	25.0±2.03
	111	186	27.80		1.32		24.6	
	112	114	29.70		1.42		24.4	
	113	149	27.90		1.34		24.3	
	114	185	26.80		1.61		19.4	
1977	1*	391	25.26		2.18		13.5	
Fall ** 1977	2	929	26.84	26.55 ±0.329	2.14	1.99 ±0.045	14.6	15.6±0.35
	2'	549	25.76		2.30		13.1	
	3	391	27.65		2.16		14.9	
	3'	315	25.55		1.75		17.0	
	4	347	24.63		1.93		14.9	
	5	667	28.14		1.95		16.8	
1978	121	88	27.38		2.00		16.0	
	122	117	27.73		1.91		16.9	
	123	52	26.50		1.94		15.9	
	124	89	25.97		1.94		15.6	
	125	115	25.92		1.88		16.1	

Table 12a. Results of 1-way Analyses of Variance for carbon content, nitrogen content and C/N ratios of Macrocystis integrifolia with respect to season. Fall 1977 and fall 1978 values were pooled when the Student's T-test showed them not to be significantly different (P=0.01). Summer 1977 (expt. 1) was not included in the comparisons.

	Factor	df	F	P
C content	season	2	28.541	0.000
N content	"	2	13.514	0.000
C/N ratio	"	2	15.726	0.000

Table 12b. Results of multiple comparisons of seasonal C,N, and C/N contents of M. integrifolia using the Student-Newman-Keuls test. Common underline between means denotes no significant difference between the means. Values expressed as % of dry wt.

	Season			P
C content	summer > $\overline{X}$=28.32 (n=5)	fall > $\overline{X}$=26.55 (n=11)	spring $\overline{X}$=24.26 (n=9)	0.01
N content	fall > $\overline{X}$=1.99	spring > $\overline{X}$=1.60	summer $\overline{X}$=1.33	0.01
C/N ratio	summer > $\overline{X}$=25.0	spring > $\overline{X}$=18.4	fall $\overline{X}$=15.6	0.05

D. Discussion

Experimental Approach

The investigation of diel productivity of an entire $M.$ integrifolia plant was realized with the development of a system of sufficient dimensions to allow for the enclosure of an entire plant under conditions of low biomass/volume of water. The incubation cylinder's suspension in the water column at a near-in $situ$ location duplicated many of the environmental conditions normally experienced by the plant. Although $M.$ integrifolia does not grow naturally at Port Désiré, transplanted plants have survived there (Druehl, 1978). Druehl suggests that the persistence of $M.$ integrifolia at Port Désiré is prevented by sediment collecting on the gametophyte generation. Jackson (1977) maintains that, due to changes in environmental factors with depth, simulation of a giant kelp's natural conditions is impossible. Jackson, however, is referring to the California giant kelp, $M.$ pyrifera, which spans a much greater depth than $M.$ integrifolia. Further, these variances in conditions were probably not as pronounced in my experimental plants' natural environment because my plants were small, about 2 m in length.

The simultaneous monitoring of the control and experimental cylinders facilitated evaluation of background microbiotic activity. Continuous stirring provided by two submersible pumps, presumably restricted the formation of lamellar boundaries around the plant. Littler [?] (1979) and Buesa (1977) demonstrated that the absence of continuous stirring reduced photosynthetic rates up to 73 % and 34 %, respectively.

The low biomass/volume ratio in these diel experiments necessitated the development of DOC concentration procedures and improvements on existing analytical techniques in order to detect organics released by the plant. The flash evaporation technique for analysis of labelled DOC enabled detection of DOC levels down to $10 \mu g$ C 1^{-1} This is approximately 10 times more sensitive than would have been possible using the conventional methods (cf., Anderson and Zeutschel, 1970; Brylinsky, 1977; Fankboner and deBurgh, 1977; Penhale and Smith, 1977).

The total DOC technique involving freeze-drying followed by total combustion was relatively precise and quick to perform when compared to the standard Menzel and Vacarro (1964) wet oxidation technique, but not sufficiently sensitive for detection of low levels of exudation. Total DOC techniques are continuously being modified and improved; Salonen's (1979) technique measures DOC levels down to 0.5 mgC 1^{-1} and MacKinnon's (1978) technique is reputedly ten times more sensitive.

An advantage of the whole plant approach for the estimation of net daily productivity by a macrophyte is that any intra-plant photosynthetic differences, as have been demonstrated in M. pyrifera (Sargent and Lantrip, 1952; Towle and Pearse, 1973), can be circumvented.

The net daily carbon fixation was usually estimated by the uptake of radiocarbon during a 24 h incubation. A shortcoming of the radiocarbon productivity technique is the ambiguity of the measured uptake -- is it gross or net productivity? (Strickland, 1960). Net productivity could be measured in 24 h radiocarbon uptake experiments if newly synthesized labelled substrates are preferentially metabolised or respiration rates are minimal (Hobson et al., 1976). The similarity between my radiocarbon uptake results and the net change in inorganic carbon content of the experimental cylinder suggests that my radiocarbon uptake results estimated net carbon fixation. Quite often, the radiocarbon uptake results were less than the net inorganic carbon change in the cylinder. This discrepancy may have been caused by some ^{14}C losses due to respiration by the plant during the initial stages of the plant drying process following the experiment.

Experiments of a few hours duration, as opposed to 24 h experiments, may erroneously predict daily productivity because of possible diel rhythms in photosynthetic activity. Diel rhythms in macrcalgal productivity have been studied in few

species; <u>Porphyra</u> (Oohusa, 1980) and <u>Spatoglossum</u> (Kageyama <u>et al.</u>, 1979; Yamada <u>et al.</u>, 1979) have been demonstrated to possess such rhythms; whereas Blinks and Givan (1961) failed to find diurnal rhythms in the red, green, and brown algae that they tested.

<u>Experimental Results</u>

These results are discussed in reference to <u>M. integrifolia</u>, however, because the exclusion of its epiphytes was impossible, the results were actually due to the <u>M. integrifolia</u>-epiphyte system. Because relatively epiphyte-free plants were used for all experiments, the epiphytes' contribution to the results were probably small.

Carbon fixation results

Seasonality in the range of carbon fixation rates of <u>M. integrifolia</u> under near-<u>in situ</u> conditions has been demonstrated. The greatest total net carbon fixation rates were measured in spring, ranging from 0.55 to 1.09 mgC gdw^{-1} h^{-1}; summer rates ranged from 0.41 to 0.62 mgC gdw^{-1} h^{-1}; fall rates were the lowest at 0.09 to 0.26 mgC gdw^{-1} h^{-1}.

The experimental approach used here did not lend itself to the determination of photosynthesis versus light intensity curves. Experiments were performed at natural irradiance conditions. During each season some experiments were conducted

on clear bright days representing as bright an irradiance as the plant would normally experience in the season. Therefore, the highest carbon fixation rates in any season probably approximated the plant's maximum carbon fixation performance, in situ.

Macrocystis integrifolia's photosynthetic rates were determined by Willenbrink et al. (1979) as 2.28 mgC gdw^{-1} h^{-1} for old blades and 1.06 mgC gdw^{-1} h^{-1} for young blades under saturating light in September. Their experiments, however, were performed on blade discs with no consideration for less photosynthetically active tissue. Lobban (1976) summarized yearly growth rates in M. integrifolia, with respect to stipe elongation, as May/June rates being two times the rates of August/September and four times the rates of October/November. Lobban's relative seasonal rates agree with my relative carbon fixation rates.

Various factors may contribute to this seasonality. Irradiance levels showed a seasonality similar to that of the carbon assimilation rates. Fall irradiances, even on bright, sunny days, were considerably lower than irradiances of the other two seasons. Likewise, fall temperatures were 5 to 7 C lower than spring temperatures and 7 to 10 C lower than summer temperatures. Other studies on macroalgal seasonal productivity have shown greater photosynthetic rates to be coincident with seasons having longer daylengths (= greater cumulative

irradiances) and higher temperatures (Zavodnik, 1973; Brinkhuis, 1977a,b,c; Littler et al., 1979). Winter and fall light-saturated levels of photosynthesis were lower than summer and/or spring levels in Chondrus crispus (Kanwisher, 1966; Mathieson and Norall, 1975), in Ascophyllum nodosum (Kanwisher, 1966; Chock and Mathieson, 1979) and in Laminaria hyperborea (Lüning, 1971). These provide possible explanations for the lower fall fixation levels, but do not explain the lower summer levels with respect to spring fixation levels.

The water's nutrient content was highest in fall and an order of magnitude lower in spring and summer. Examination of the plant's nitrogen content further reflects this trend. The highest plant nitrogen content was in fall, followed by spring and then summer with the lowest content. Although spring carbon fixation rates were shown not to be significantly different from summer rates (partially a consequence of the small sample sizes), visual inspection of Fig. 7 indicates the spring rates, with the exception of experiment 109, were greater than summer rates at equivalent irradiances and with the summer temperatures equal or greater than spring temperatures. Possibly nutrient reserves accumulated during fall were being depleted by summer and, thereby, depressing the plant's summer carbon fixation rates. Translocation of nitrogenous compounds has been demonstrated in M. pyrifera (Jackson, 1977) in which the translocated fluid had a lower C/N ratio (C/N = 9) than the

canopy blades (C/N = 45). Jackson hypothesized the translocation
of nitrogen compounds taken up by lower blades occupying the
deeper, higher nutrient waters and nitrogenous storage products
to the canopy blades occupying nutrient-deficient surface
waters. Although M. pyrifera spans a greater depth range and
probably a greater nutrient differential than M. integrifolia, a
similar process might be occurring in M. integrifolia during
periods of spring and summer nutrient depressions until the
nitrogen reserves are diminished in summer. Further evidence on
translocation of nitrogenous compounds was provided by
translocation studies on M. integrifolia by Schmitz and
Srivastava (1979) which showed M. integrifolia's translocate to
have a higher amino acid content than the photosynthate of the
blades and some of the translocate movement was acropetal toward
the young tissue.

Similarly, studies by Chapman and Craigie (1977) on
Laminaria longicruris off Canada's East Coast showed the plant
to have a late fall and winter nitrogen reserve accumulation
which appeared to be exhausted by summer and was concurrent to a
summer growth rate depression. Summer nitrate fertilization of
the L. longicruris bed resulted in summer growth rates similar
to the higher spring growth rates, indicating nitrate depletion
as the cause of the growth depression.

My M. integrifolia carbon fixation values represented the
summed activity of the whole thallus. Any seasonal change in the

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structure of a plant would alter the final carbon fixation summation. Fall storms can remove many of the canopy blades and therefore reduce their contribution to the total carbon fixation. This could result in significantly reduced carbon fixation because the young mature canopy blades have been shown to have higher rates of photosynthesis than most other plant regions in $M.$ pyrifera (Clendenning, 1964; Towle and Pearse, 1973). This might contribute to seasonality in carbon fixation results.

Seasonal changes in macroalgal respiratory rates have not followed the expected Q_{10} (Lehninger, 1975) relationship to temperature increases in summer, resulting in greater summer net productivity (Kanwisher, 1966; Lüning, 1971; Mann and Chapman, 1975). Increases in chlorophyll content during winter have been shown to increase winter photosynthesis rates, thereby decreasing seasonal differences in net productivity (Zavodnik, 1973; Brinkhuis, 1977b). Such seasonal physiological changes have not been investigated in $M.$ integrifolia but might be important mechanisms in regulating seasonal growth patterns in the kelp.

Light-independent carbon fixation results did not show significant seasonal differences. The mean rate was 0.01 mgC gdw^{-1} h^{-1} with rates ranging from 0.008 to 0.016 mgC gdw^{-1} h^{-1}. When expressed as percent of light-dependent carbon fixation, the rates ranged from 1.2 % to 11.1 %,

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reflecting variations in light fixation rates. Willenbrink et al. (1979) observed greater levels of light-independent carbon fixation and correspondingly of the dark carboxylation enzyme, phosphenolpyruvate carboxykinase (PEP-CK), in young blades as opposed to older blades. They suggested that high light-independent carbon fixation activities might be important in the late winter and early spring periods of low irradiances for growth of young fronds. My April/May spring experiments were too late in spring to measure this early spring growth and, further, the whole plant approach would not detect the higher dark fixation rates in the young blades. This area of research benefits from studies on isolated blades.

Exudation Results

Exudation of organic carbon was defined as an increase in the dissolved plus particulate organic carbon levels of the water in the experimental cylinder when the initial and control cylinder's levels were subtracted from the experimental cylinder's level. A decrease in the dissolved + particulate level was interpreted as an uptake of organic carbon by the M. integrifolia system. The seawater in the experimental and control cylinders was the same at the start of the experiment; the only difference in these two systems being the presence of the plant in the experimental cylinder. Exudation of DOC by the microflora of the water should be similar in both cylinders.

Therefore, a net increase in the DOC level in the experimental cylinder, represented DOC exudation by the experimental plant system. Primary fixation of inorganic carbon into organic carbon by the water's microflora should also be similar in the two cylinders. Therefore, any changes in the net POC values of the experimental cylinder, when corrected for control values, must be due to the presence of M. integrifolia in the cylinder and through routes other than the direct primary fixation of inorganic carbon into particulate organic carbon by the water's microflora. The other possible routes include biological heterotrophic uptake of DOC by the microflora (Nalewajko et al., 1976; Williams and Yentsch, 1976), physical adsorption of DOC upon the pre-existing particulates (Chave and Suess, 1967; Riley, 1970) and molecular aggregrate formation of POC from DOC (Riley, 1963; Wangersky, 1972, 1978). The source of DOC for all these processes would be the plant system. The low net ATP values in the experimental cylinder, suggested very little difference in the living microscopic particulate carbon levels between the experimental and control cylinders. This, in turn, indicated that minimal microbial heterotrophic uptake of the kelp system's released DOC was occurring.

The above argument assumes that detrital particles are not being produced by the plant. Observation of the incubation water during an experiment confirmed the absence of visible plant particles. Due to these intimate DOC/POC relationships, it was

deemed artificial to set the arbitrary filter pore-size
(0.7 μ m) as a boundary between POC and DOC; and instead they
were combined as one measure.

The measurement of dissolved organic carbon poses
difficulties in interpretation and technique. First, the most
sensitive technique, and therefore, the technique most commonly
used in exudation studies is the radiocarbon tracer technique.
When the water's labelled DO^{14}C content is measured and compared
to the plant's carbon fixation rates, the common assumption is
that the exudate originated from an intracellular pool of
intermediate metabolites at isotopic equilibrium with the
inorganic carbon of the incubation medium. The validity of this
assumption has not been fully tested and consequently isotopic
measurements of DOC exudation perhaps should be interpreted as
minimum measurements -- there is the possibility of releases of
compounds from unlabelled cellular sources not at isotopic
equilibrium (ie., compounds that were synthesized prior to the
tracer experiment).

The exudation of organics fixed prior to the experiment was
investigated by Harlin and Craigie (1975). They labelled
Ascophyllum nodosum in radiocarbon for 24 h, placed the labelled
tissue into unlabelled seawater, and measured a total exudation
of 1.5 % of the initially fixed radiocarbon over a period of 1
week. This suggests a minimal exudation of previously fixed
organics.

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A solution to the ambiguity in the interpretation of radiocarbon DOC measurements, is the measurement of the total DOC content of the water by non-radioisotope tracer techniques. Unfortunately, these non-radioisotope tracer techniques lack the sensitivity for the detection of the apparent low levels of organic exudation.

It has been suggested that incubations under nonaxenic conditions underestimate exudations because of heterotrophic utilization of the exudates by the water's microflora (Nalewajko et al., 1976; Williams and Yentsch, 1976; Sharp, 1977). This should not have been a problem in my experiments because, as mentioned earlier, I included particulate carbon (corrected for primary particulate carbon production in the control cylinder) in my 'dissolved' organic carbon measurements. Heterotrophic activity by benthic microbes adhering to the plant was a possible interfering factor.

In this study, I investigated the exudation of organics by M. integrifolia by utilizing both of the above approaches; the radiocarbon tracer technique allowed for measurement of minimum exudation and the TDOC technique allowed for measurement of exudations exceeding the TDOC technique's detection limitations. Due to the length of the experiments, some cycling of exudate such as the uptake of previously released exudate could have occurred and was only detected if it occurred during the night (between the dusk and dawn samplings).

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The daily exudation levels as determined by the radiocarbon tracer results ranged from 0 to 0.59 mgC gdw^{-1} h^{-1} or 0 % to 3.9 % of the total net carbon fixed. This exudation appeared to be directly related to the level of irradiance and the rate of carbon fixation. There did not appear to be any seasonal exudation patterns that could not be explained by relationships to irradiance levels or carbon fixation rates. Penhale and Smith (1977) also reported a direct relationship between exudation and carbon fixation by the seagrass, Zostera marina.

The TDOC levels, in general, did not reach the TDOC technique's detection limitations. Only one spring experiment (101) significantly exceeded the TDOC detection limitation with a 24 h exudation of 53.6 % of the total net carbon fixation, but this was not shown in other experiments and therefore it would seem to be the exception rather than the norm. Excessive exudation did not occur in spring and summer; and fall exudations would have been undetectable by the TDOC technique.

Speculation on the cause of exudation has included the release of antibacterial and antialgal substances and releases of assimilatory surpluses during periods when environmental conditions prevented cell multiplication but not carbon fixation (see Hellebust, 1974; Wangersky, 1978). Within the yearly carbon budget of Laminaria longicruris and accounting for growth and storage, Hatcher et al. (1977) calculated, from their photosynthetic rate experiments' results, a spring and summer

35 % surplus in carbon assimilation and suggested exudation as the fate of this assimilatory surplus. They also suggested that high summer irradiances would encourage photosynthesis but nutrient depletions would inhibit cell division and growth. Jackson (1977) hypothesized exudation of assimilated carbon by M. pyrifera of California waters during nitrate depletion in the water, following depletion of stored nitrogen reserves.

The release of antibacterial and antialgal substances, especially in young tissue, would not be surprising because of the paucity of epiphytes on young growing blades of M. integrifolia (Roland, 1980). Further, antibacterial substances have been isolated from apical scimitars of this alga (A. Quek, pers. comm.). However, the release of such substances probably would be in small quantities and undetectable.

If assimilatory surpluses were being released during periods of high irradiances and nutrient depletion the exudate should be comprised mainly of the newly assimilated 'surplus' organics and, consequently, during a radiocarbon experiment should be close to isotopic equilibrium and detectable by the sensitive radiocarbon methodology. My radiocarbon exudation results for M. integrifolia did not exceed 3.9 % and, generally were less than 1 % of the carbon fixed. Further, during summer, when the C/N ratios were highest (C/N in summer = 25; C/N in fall = 15.6), no greater exudation was detected. Perhaps the nutrient limitation is not as severe in the M. integrifolia

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environment or the plant has developed a more conservative response to nutrient depletion.

Most other marine macrophyte exudation studies that attempt to employ gentle and 'close to natural' experimental conditions report exudations from less than 1 % to 4 % of the plant's carbon fixation (Moebus and Johnson, 1974; Harlin and Craigie, 1975; Pankboner and deBurgh, 1977; Penhale and Smith, 1977; Ragan and Jensen, 1979). Greater releases, up to 40 % of the plant's assimilation, have been reported, generally, under stressful conditions such as dessication (Sieburth, 1969; Kroes, 1970; Moebus et al., 1974). These studies indicate the possibility of greater exudation by M. integrifolia under stress, such as dessication during extremely low tides. My results indicate little release of organic compounds under near-normal, submerged conditions.

Uptake of previously-released DOC was indicated in experiment 103. Drew (1969) reported that many brown algae have slow mechanisms for uptake of exogenously supplied sugars and are unable to convert these sugars into their usual soluble carbohydrates. However, the exact chemical forms of macroalgal exudates are not known (cf., Hellebust, 1974) and may include chemical forms that are readily assimilated by the macroalgae. Possibly the apparent uptake in experiment 103 can be attributed to passive adsorption or uptake by the plant combined with epiphytic heterotrophic microbial uptake.

An indirect approach to the investigation of exudation by
M. integrifolia was the sampling of natural M. integrifolia bed
waters, with respect to waters 100 m distant from the kelp bed
for DOC content. The DOC content of the water demonstrated
seasonality at all sampling sites. Seasonal increases in the DOC
content of near-shore waters have been attributed to
autochthonous sources such as release of DOC by phytoplankton
during phytoplankton blooms (Parsons and Takahashi, 1973) and
allochthonous sources such as river freshets (Naiman and
Siebert, 1979). Possibly the summer (July 27) DOC peak was due
to phytoplankton exudation; with the summer POC peak
representing increased phytoplankton numbers. The fall DOC peak
possibly resulted from terrestial run-off during heavy fall
rains.

Of special interest, however, were the differences between
kelp bed and non-kelp bed DOC levels nested within the larger
universal seasonal DOC levels. When differing from the non-kelp
bed DOC levels, the kelp bed DOC levels were greater. These
results suggested that factors coincident to kelp bed locations
were responsible for increasing the baseline DOC content of the
waters. Macrocystis integrifolia was certainly the most
conspicuous biotic member of these locations and the
experimental results showed the occurrence of some exudation by
these plants. Other factors coincident to kelp bed locations
included other subtidal and intertidal macrophytes and

terrestial shoreline input. If terrestial organic input was an important source of the water's baseline DOC content, the lower non-kelp bed (offshore) DOC levels might merely be a reflection of a seaward DOC dilution. The particulate content also was greater in the kelp bed. Perhaps, kelp fragmentation and subsequent DOC leaching was one source of the POC and DOC in these nearshore waters.

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Appendix

Figure A1. A standard curve for the total DOC analysis
(IRGA peak height vs μgC of standard glucose-salt
powder). This curve was computed for the June 20, 1978
DOC analyses.

Y = 6.2 X + 5.0

IRGA Peak Height (in units of chart divisions)

Micrograms Carbon

88b