A STUDY OF GROWTH, REPRODUCTION, AND COMPETITION IN POPULATIONS OF IRIDAEA CORDATA (TURNER) BORY (RHODOPHYTA) IN GEORGIA STRAIT, B.C.

by

ROBERT W. ADAMS

B.Sc., University of Victoria, 1971

A THESIS SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biology

ACCEPTED
FACULTY OF GRADUATE STUDIES
[redacted]
DEAN
DATE JUL 23 1979

We accept this thesis as conforming
to the required standard

[redacted]

© ROBERT W. ADAMS, 1979

UNIVERSITY OF VICTORIA

April 1979

All rights reserved. This thesis may not be reproduced in whole or in part, by mimeograph or other means, without the permission of the author.

QK569
R4A3

ABSTRACT

Supervisor: Dr. A.P. Austin

Observations were made on Iridaea cordata communities in northern Georgia Strait during a 15 month period to investigate the in situ population dynamics of this species.

The standing crop of I. cordata populations sampled at three locations where it dominated, ranged from lows of 0.00±0.000 to 0.03± 0.009 kg fresh/0.5 m^2 in December through February, to highs of 0.7±0.05 to 2.0±0.24 kg fresh/0.5 m^2 which occurred variably in May through August. Increase and decline in both water temperature and solar radiation were generally coincident with seasonal variation in I. cordata standing crop. Nitrate-nitrogen depletion may limit growth in some locations during summer. I. cordata standing crop may also be limited by competition for light with laminarian species and for space by Plocamium coccineum.

Standing crop and density of I. cordata life history phases varied differentially with season. Gametangial fronds were dominant in May and June and tetrasporangial fronds were dominant in August through December. There was no consistent relation between I. cordata population standing crop and life phase composition.

Patterns of macroscopic development of cystocarpic and tetrasporic soral cover on I. cordata fronds are described. Maximum potential spore production of cystocarpic fronds occurred in July and of tetrasporic fronds occurred in late August through September.

The growth rate of transplanted I. cordata fronds was highest at shallow depths, in mid rather than late summer and for cystocarpic rather than tetrasporangial fronds.

The settlement of spores was high on Plexiglas plates immersed for short periods adjacent to *I. cordata* populations. However the survival of spores and growth to upright fronds was very limited on the horizontal surfaces of plates attached to platforms in the *I. cordata* community. Nearly monotypic, dense stands of *I. cordata* did colonize the vertical surfaces (sides) of concrete blocks, 12 - 14 months after immersion in June through September. A greater biomass of *I. cordata* was achieved if substrate was immersed from mid rather than late summer of the previous year or was immersed for two or more years. Uprights of *I. cordata* juveniles were observed on blocks three months after immersion in June.

Artificial populations of *I. cordata* were constructed at various densities on natural cobble and rope substrates. Population growth rates were maximum at an optimum frond area index (FAI) which was less than that in naturally recruited dense populations in mid summer. Over a period of 45-60 days, high density artificial populations exhibited a loss of large fronds, while low density populations added large fronds which were generated from the numerous frond initials on the basal crust. Calculation of potential biomass production in one summer using growth rates obtained at an optimum FAI yielded estimates approximately 1.6-2.0 times the maximum standing crops attained in adjacent natural populations.

Some implications of these observations to macroalgal cultivation are discussed.

[redacted]

TABLE OF CONTENTS

Page

ABSTRACT.................................... ii

TABLE OF CONTENTS........................... iv

LIST OF TABLES.............................. vii

LIST OF FIGURES............................. viii

ACKNOWLEDGEMENTS............................ xii

INTRODUCTION................................ 1

PART I: IN SITU STUDIES ON THE POPULATION DYNAMICS OF IRIDAEA CORDATA IN GEORGIA STRAIT, B.C.......... 5

INTRODUCTION................................ 5

METHODS..................................... 9
- Seasonal Sampling of I. cordata Communities........... 9
- I. cordata Frond Growth Experiments.................... 16
- I. cordata Spore Settlement and Growth Studies......... 23
  - (a) spore dispersal.................................. 24
  - (b) spore settlement and survival.................... 27
- Substrate Colonization Studies......................... 32

RESULTS..................................... 34
- Environmental Observations.............................. 34
- Seasonal Variation in I. cordata Density and Standing Crop compared to Community Standing Crop.......... 46
- Periodicity of I. cordata Life Phases................... 57
  - (a) standing crop.................................... 57
  - (b) densities.. 60
  - (c) population size structure........................ 63
  - (d) frond initials................................... 69
  - (e) reproductive maturation.......................... 71
- Growth Rates of Gametophyte and Tetrasporophyte I. cordata Fronds.......... 77
- Colonization of Artificial Substrate in the I. cordata Community.......... 89
  - (a) I. cordata spore settlement and growth........... 89
  - (b) macroscopic colonization......................... 97

Page

DISCUSSION.. 111
Seasonal Standing Crop of the Algal Community.......... 111
Environmental Parameters and Seasonal Abundance of *I. cordata*... 112
Stability of the Algal Community Components............ 118
Seasonal *I. cordata* Population Structure............... 122
Frond Maturation.. 128
Frond Growth Rate and Population Biomass Production.... 131
Spore Settlement and Substrate Colonization............ 134

CONCLUSIONS AND SUMMARY.. 143

PART II: POTENTIAL YIELDS OF *IRIDAEA CORDATA* IN NATURAL AND ARTIFICIAL POPULATIONS IN GEORGIA STRAIT, B.C...... 149

INTRODUCTION... 149

METHODS

Observation of Naturally Recruited Populations......... 151
(a) natural cobble substrate.......................... 151
(b) rope substrate...................................... 151
Construction and Observation of Artificial Populations. 152
(a) natural cobble substrate.......................... 152
(b) rope substrate...................................... 159

RESULTS.. 161
Maximum Density, Standing Crop and Frond Area of Natural Populations on Natural and Rope Substrate......... 161
(a) natural cobble substrate.......................... 161
(b) rope substrate...................................... 164
Growth Rate as a Function of Density in Artificial 168
Populations.. 168
(a) natural cobble substrate.......................... 169
(b) rope substrate...................................... 174

DISCUSSION... 180

CONCLUSIONS AND SUMMARY.. 184

LITERATURE CITED.. 186

APPENDIX I... 195

APENDIX II... 199

APPENDIX III... 200

APPENDIX IV.. 203

APPENDIX V... 209

Page

APPENDIX VI.. 213

APPENDIX VII... 215

APPENDIX VIII.. 218

APPENDIX IX.. 222

LIST OF TABLES

Table Page

I Seasonal frequency of *I. cordata* holdfasts, 0.5 - 5.0 cm long frond initials and fronds greater than 5 cm long on cobbles from Kye Bay.................... 70

II Fresh weight gain ± S.E. (g) of *I. cordata* fronds after 49 days, transplanted June 3, 1976............... 88

III Mean density of red algal spores per cm^2 adhering to settling plates immersed for four days at various distances from isolated *I. cordata* fronds............ 90

IV Mean density of red algal spores per cm^2 adhering to settling plates immersed for four days at varying heights above a dense *I. cordata* community........... 92

V Macroalgal species colonizing natural substrate and concrete blocks immersed for 3 - 36 months at Kye Bay, observed on August 29, 1976.......................... 98

VI Macroalgal species colonizing natural substrate and concrete blocks immersed for 8 - 14 months at Cape Mudge, observed on September 1, 1976................. 99

VII Abundance of *I. cordata* colonizing concrete blocks immersed for 7 - 36 months at Kye Bay, observed on August 30, 1976..................................... 108

VIII Abundance of *I. cordata* colonizing concrete blocks immersed for 7 - 14 months at Cape Mudge, observed on September 1, 1976................................. 109

IX Abundance of *I. cordata* colonizing polypropylene ropes immersed for various time periods.................... 165

LIST OF FIGURES

Figure — Page

1. Map of northern Georgia Strait with location of I. cordata sample plots.......................... 10

2. Diagram of I. cordata frond holding apparatus; fronds inserted into twine of 0.7 cm polypropylene rope stretched along a wood support, anchored at various depths.................................. 18

3. Basket used to contain unattached I. cordata for measurement of frond growth........................ 21

4. Diagram of distribution of Plexiglas settling plates attached to cement bricks around isolated I. cordata fronds in spore dispersal experiment....... 25

5. Diagram of Plexiglas settling plates attached to ropes in spore dispersal study above a dense I. cordata population............................. 28

6. Settling plate platform used in spore settlement and survival study................................ 30

7. Water temperature and salinity; May, 1975 to September, 1976.................................. 37

8. Dissolved nitrate (NO_3 - N) and orthophosphate (PO_3 - P); July, 1975 to September, 1976........... 39

9. Secchi depths; May, 1975 to September, 1976........ 42

10. Mean daily surface solar radiation; January, 1975 to September, 1976............................... 44

11. Standing crop of macroalgae in I. cordata communities; May, 1975 to September, 1976.......... 47

12. Standing crop of four most abundant macroalgal species associated with I. cordata at sample sites (mean ± examples of S.E., n=5); May, 1975.......... 50

13. Standing crop of I. cordata (mean ± S.E., n=5); May, 1975 to September, 1976...................... 52

14. Density of I. cordata fronds greater than 10 cm long (mean ± S.E., n=5); May, 1975 to September, 1976.. 55

Figure Page

15. Standing crop of *I. cordata* per life phase (mean ± examples of S.E., n=5); May, 1975 to September, 1976.................................... 58

16. Density of *I. cordata* fronds greater than 5 cm long per life phase (mean ± examples of S.E., n=5); May, 1975 to September, 1976............................ 62

17. Percent frequency of *I. cordata* fronds per life phase and size class, Kye Bay; May, 1975 to September, 1976.................................... 64

18. Percent frequency of *I. cordata* fronds per life phase and size class, Cape Mudge; May, 1975 to September, 1976.. 66

19. Male *I. cordata* frond distinguished by thin, filmy texture... 73

20. Very mature male *I. cordata* frond with distal end worn away.. 73

21. Immature cystocarpic *I. cordata* with sparse distribution of cystocarps (C) in localized areas of frond.. 73

22. Mature cystocarpic *I. cordata* with dense distribution of cystocarps over much of frond........... 73

23. Immature tetrasporangial *I. cordata* with 'rash' of sori (S) near sterile margin (M)................ 73

24. Very mature tetrasporangial *I. cordata* with very dense cover of sori and ragged edges............... 73

25. Percent reproductive maturity of cystocarpic and tetrasporangial *I. cordata* fronds expressed as frond area covered by sori divided by the total frond area in 0.5 m^2 samples (n=5); May, 1975 to September, 1976................................ 75

26. Reproductive potential of cystocarpic and tetrasporangial *I. cordata* fronds expressed as mean frond area covered by sori per 0.5 m^2 sample (n=5); May, 1975 to September, 1976................ 78

27. Growth curves for individual small, medium and large (by weight) *I. cordata* fronds transplanted on June 3, 1976.................................... 80

Figure Page

28. Mean growth rate of cystocarpic and tetrasporangial fronds in mid and late summer with depth (n=5 except where noted).................... 83

29. I. cordata frond with growing tip cut off before transplanting.............................. 86

30. I. cordata frond with excised tip, 50 days after transplanting.................................. 86

31. Settling plates attached to platform at Cape Mudge after 3 months immersion supporting mainly ephemeral chlorophyte species..................... 95

32. Concrete block set down at Cape Mudge in December, 1975 supporting laminarians after 8 months immersion to August, 1976.................................... 101

33. Concrete block set down at Kye Bay in June, 1975 supporting dense I. cordata population on vertical surfaces (sides) after 15 months immersion to August, 1976.. 104

34. Diagram of relative position of artificial I. cordata populations constructed along 15 m transect in Kye Bay.. 154

35. I. cordata fronds inserted in twine of polypropylene rope.................................... 158

36. Relation between density, biomass and surface area of I. cordata fronds in natural populations per 0.5 m^2 (lines placed by eye), June 20, 1975........ 162

37. Relation between the density and mean size of I. cordata fronds in natural populations per 0.5 m^2 (lines placed by eye), June 20, 1975............... 162

38. Dense population of I. cordata naturally recruited on rope substrate immersed for three years at Cape Mudge, July, 1977............................ 166

39. Relation of density of young I. cordata fronds to growth rate and final biomass in 0.5 m^2 frames after 45 and 65 days (lines placed by eye)......... 169

40. Relation of initial I. cordata frond density to frond loss or gain in 0.5 m^2 frames after 45 and 65 days (lines placed by eye)..................... 169

Figure Page

41. Frequency of I. cordata fronds per size class (length in cm) in artificial populations on cobbles, immediately after construction and after 45-60 days.................................. 172

42. Mean biomass of I. cordata per 0.5 linear meter (± sample values; n=2) in artificial populations constructed at various densities on rope substrate.. 175

43. Relation of initial I. cordata frond density to growth rate and final biomass in artificial populations on ropes after 50 days (lines placed by eye)........ 177

44. Relation of initial I. cordata frond density to the mean size of fronds in artificial populations after 50 days (line placed by eye)....................... 179

ACKNOWLEDGEMENTS

I wish to thank sincerely my supervisor Dr. A.P. Austin for providing continuous encouragement, a vast accumulation of experimental ideas and an appreciation for critical work to support my completion of this study. As well I would like to acknowledge the support and encouragement given by Drs. M.A. Bell, E.M. Hagmier, W.K. Hastings and P.R. Newroth.

I gratefully acknowledge and thank Mr. Ray Foucher who ably assisted throughout the sample program, particularly in designing field apparatus, assisting during the rigours of sampling with SCUBA during all seasons and in the sorting and measurement of numerous macroalgal specimens.

Many thanks are extended to Pat Mash who typed the manuscript.

With deepest gratitude and appreciation I thank my wife for her seemingly boundless support in providing essential field and laboratory assistance and for her enthusiasm and sacrifices during the difficult sample schedule and protracted period of data analysis and write-up.

This work was supported with funding from the Marine Resources Branch of the British Columbia Ministry of Environment and from the Department of Supply and Services of the Canadian Ministry of Environment.

INTRODUCTION

The red alga *Iridaea cordata* (Turner) Bory has an extensive geographical distribution around the Pacific rim, from northern Japan to northern Mexico (Abbott, 1972), and is the dominant species of certain benthic communities inhabiting the low intertidal and upper subtidal along the Pacific Coast of North America (Hansen, 1976; Fralick 1971; Austin and Adams, 1973, 1974, 1975). The species is valued commercially for its content of carrageenan, a stabilizing, emulsifying and thickening agent used in the preparation and processing of a wide variety of food, pharmaceutical and textile products.

Resource surveys in Georgia Strait, British Columbia delimited areas of abundance of this species which may provide the basis for a red seaweed industry in the Province (Austin and Adams, 1975). However, attempts in 1971 and 1972 to harvest the seaweed on a commercial basis (LITE Enterprises) in northern Washington, were frustrated by the lack of knowledge concerning seasonal changes in density and maturity of populations of this red seaweed in nature. Cultivation may prove to be more economical than harvest of the wild crop, but development of efficient cultivation techniques requires a background of data on reproduction, growth and the competitive nature of the species (Krishnamurthy, 1965).

Such biological information on carrageenophytes is just beginning to accumulate and studies have consisted of two, often combined, approaches: (1) monitoring the natural community to identify and describe population characteristics and (2) manipulative experiments to identify the ecological conditions which are most important in regulating population structure and to examine the interaction of community components.

Descriptive studies of Iridaea cordata include those on seasonal change in life phase abundance and size of I. cordata fronds (Fralick, 1971), and seasonal change in community similarity (Hruby, 1975), in northern Washington. The distribution of dense I. cordata populations in this area was related to high current velocities (0.06 - 0.38 m/sec at maximum) and substrates of non-friable rock larger than 35 mm (Hruby, 1974). Seasonal variation in I. cordata population structure and frond growth rates was observed in California waters by Hansen (in press a) and Hansen and Doyle (1976).

Experimental work has indicated that maximum growth of sporelings in laboratory culture is at temperatures of 10 - 14°C and light intensities of $8.9 - 16.0 \times 10^3$ erg/cm^2/sec. The alternation of haploid and diploid isomorphic generations has been followed through in culture (Kim, 1975) and developmental morphology of sporelings in culture was observed (Norris and Kim, 1972). Transplant experiments have determined the optimum depth for growth of fronds in the sea is 3-5 m below mean lower low water (Waaland, 1973). Field studies indicated that emersion of I. cordata at low tide inhibited growth (Hruby, 1974), and weeding experiments indicated that I. cordata was excluded from areas below its normal distribution by a competitive interaction with more rapidly growing kelps (Hruby, 1976). Fralick (1971) determined that harvest of I. cordata in the fall season would have the least effect on holdfasts.

Many such descriptive and experimental studies have been reviewed for the carrageenophyte *Chondrus crispus* Stackhouse (Harvey and McLachlan, 1973) which forms the basis of a major seaweed industry on the east coast of Canada. A comprehensive study of the biology of *Gigartina stellata* (Stackhouse) Batters was undertaken to assess potential for harvest in Great Britain (Marshall, Newton and Orr, 1949) and there have been more recent studies in New Hampshire (Burns and Mathieson, 1972). The carrageenophyte *Eucheuma* has recently been studied and species brought into cultivation (Dawes *et al.*, 1974; Doty, 1973; Doty and Alvarez, 1975; Parker, 1974).

The goal of the present study was to examine the population dynamics and biomass yields of dense stands of *I. cordata* in Georgia Strait, B.C., to characterize natural populations and to assess the potential for cultivating this species in the shallow subtidal. The study was partitioned into two sections: Part I included *in situ* studies of *I. cordata* population dynamics in relation to life history and major environmental parameters; Part II included experimental studies to investigate intraspecific competition in dense *I. cordata* populations and yields of *I. cordata* which could be produced in artificially enhanced populations.

Population biomass yield is typically the chief concern in the commercial utilization of biological resources (Watt, 1968). Fundamental to this concern is a knowledge of population dynamics and stability, determined by the interaction of the species life cycle and its environment. Observations of *in situ I. cordata* population structure and environmental parameters at sequential time intervals provide a means of correlating population dynamics with selected aspects of life history and environmental fluctuation. In this context, population structure includes density, standing crop, size composition and life phase composition. Measurements of growth and maturation rates of individual fronds provide a means to corroborate details of population dynamics obtained from analyses of population structure.

Stability and maintenance of algal populations are often neglected aspects of life history/environment interaction. It has been suggested that competitive dominance is exerted via the major common limiting resource(s), which in certain marine rocky shore communities is space (Dayton, 1971). The competition for space by dominant species may manifest itself in two strategies: (1) rapid colonization of vacant space or (2) the longevity of established individuals. In some algal species the spore to sporeling stage may be the "turnstile" in regulating population abundance (North, 1971). The role of these two mechanisms in macroalgal populations has been poorly studied.

The cultivation of I. cordata in the marine littoral would likely involve the maximization of one or both strategies in the competition for space: successful colonization, or population persistence, resulting in monotypic, high density populations typical of land crops. An important factor in such populations is intraspecific growth interference and an experimental approach was used to investigate this limiting factor in dense I. cordata populations in Georgia Strait. Potential yields of I. cordata in artificially dense populations were estimated with data on seasonal population dynamics and intraspecific competition.

PART I: IN SITU STUDIES ON THE POPULATION DYNAMICS OF IRIDAEA CORDATA IN GEORGIA STRAIT, B.C.

INTRODUCTION

The life history of Iridaea cordata (Turner) Bory was described in the detailed anatomical studies by Kylin (1928) and involves the alteration of isomorphic haploid (male and female gametophyte) and diploid (tetrasporophyte) generations. In recent culture studies, Kim (1975) confirmed this life history for I. cordata var. cordata, by following the growth of carpospores from female gametophytes into mature thalli, subsequently releasing tetraspores. No incidence of syngamy (fusion of spermatium with trichogyne) has even been visually observed in species of Gigartinaceae, but at least in the case of I. cordata var. cordata, all three life history phases, male and female gametangial and tetrasporangial thalli, are reported to occur abundantly at times in the field.

In the related species, Chondrus crispus, a modification of the basic triphasic life cycle has been speculated due to the rarity of male thalli in the field. Culture studies (Kim, 1975) also have suggested anomalies in the life history of Iridaea cordata var. splendens (Setchell and Gardner) Abbott, comb. nov., which produced tetrasporangial thalli directly from tetraspores with no intervening gametophyte life stage. Only recently this variety was reduced from a species by Abbott (1971).

The distinguishing morphological features of the two varieties of I. cordata overlap to some extent although it would appear that *I. cordata* var. *cordata* is the dominant variety in populations of Georgia Strait. *I. cordata* var. *splendens* is more common in California than variety *cordata*. Northward of Washington, var. *cordata* is more common than var. *splendens* (Abbott, 1971).

Based on observations on *Ceramium* (Svedelius 1927) as outlined by Hansen and Doyle (1976), it was speculated that many annual algae exhibit a seasonal alternation of generations. The seasonal abundance of different life phases may be attributed to their differential adaptation to environmental parameters. Boney (1966) suggested that seasonal behaviour of some species may be linked to photoperiodic factors. The implications of seasonal patterns of growth and maturation of life cycle phases on biomass yield in commercially harvested populations have been studied little.

The seasonal growth of *I. cordata* life phases was described by Fralich (1971) in northern Washington and by Austin and Adams (1975) in Georgia Strait, but neither of these studies compared the development of *I. cordata* life phases with population structure and biomass. Such comparisons undertaken in California waters (Hansen, 1976 and Hansen and Doyle, 1976) indicated a continuous dominance of tetrasporangial thalli, not apparent in northern populations.

It is suggested that the perennating base of many florideophycean algae will mask the alternation of generations of these forms. Thus "generations of perennial red algae are intermingled and develop syncronically, and therefore a seasonal alternation of generations is not apparent" (Svedelius, 1927). In species related to *Iridaea*, particularly *Chondrus crispus* and *Gigartina stellata*, perennating holdfasts have been observed to persist for many years and numerous successive seasons of annual vegetative growth were documented. The longevity of such holdfasts of *I. cordata* is not known and their importance, versus that of spores, in the maintenance and stability of populations is hitherto undocumented. Natural recruitment of *I. cordata* spores on cleared surfaces is reported to be rapid under some conditions (Lee, 1965; Northcraft, 1948), while the vegetative reproduction of upright fronds from perennating holdfasts suggests that space occupied by *I. cordata* may not be vacated rapidly.

Information on colonization by *I. cordata* is primarily derived from studies of succession in the low intertidal (Lee, 1976 and Dayton, 1971 in the north-east Pacific; Northcraft, 1948, in California) and from studies of colonization on netting in the subtidal in northern Washington (Mumford, 1978 and in press). Nylon line was colonized by *I. cordata* in tanks and developed dense stands of mature fronds when outplanted in Puget Sound (Waaland, in press). Such information is important for the commercial harvest of these populations to determine maximum yields and for the development of artificial enhancement techniques.

To investigate further these aspects of the population dynamics of *I. cordata* in natural communities in Georgia Strait, British Columbia, observations were made on:

1. the seasonal standing crop of algae in the *I. cordata* community;

2. major environmental parameters including water temperatures, salinity, incident radiation and macro-nutrients in relation to *I. cordata* seasonal abundance;
3. the interaction of algal components in the *I. cordata* community;
4. the seasonal population structure of *I. cordata*;
5. *I. cordata* frond maturation and season of maximum potential spore release;
6. the growth rate and longevity of individual tetrasporangial and gametangial fronds as they relate to the differential seasonal abundance of these forms and
7. the seasonal recruitment of *I. cordata* sporelings on artificial substrates in relation to frond maturation and colonization by other algal community components.

Some implications of these studies to macro-algal cultivation are discussed.

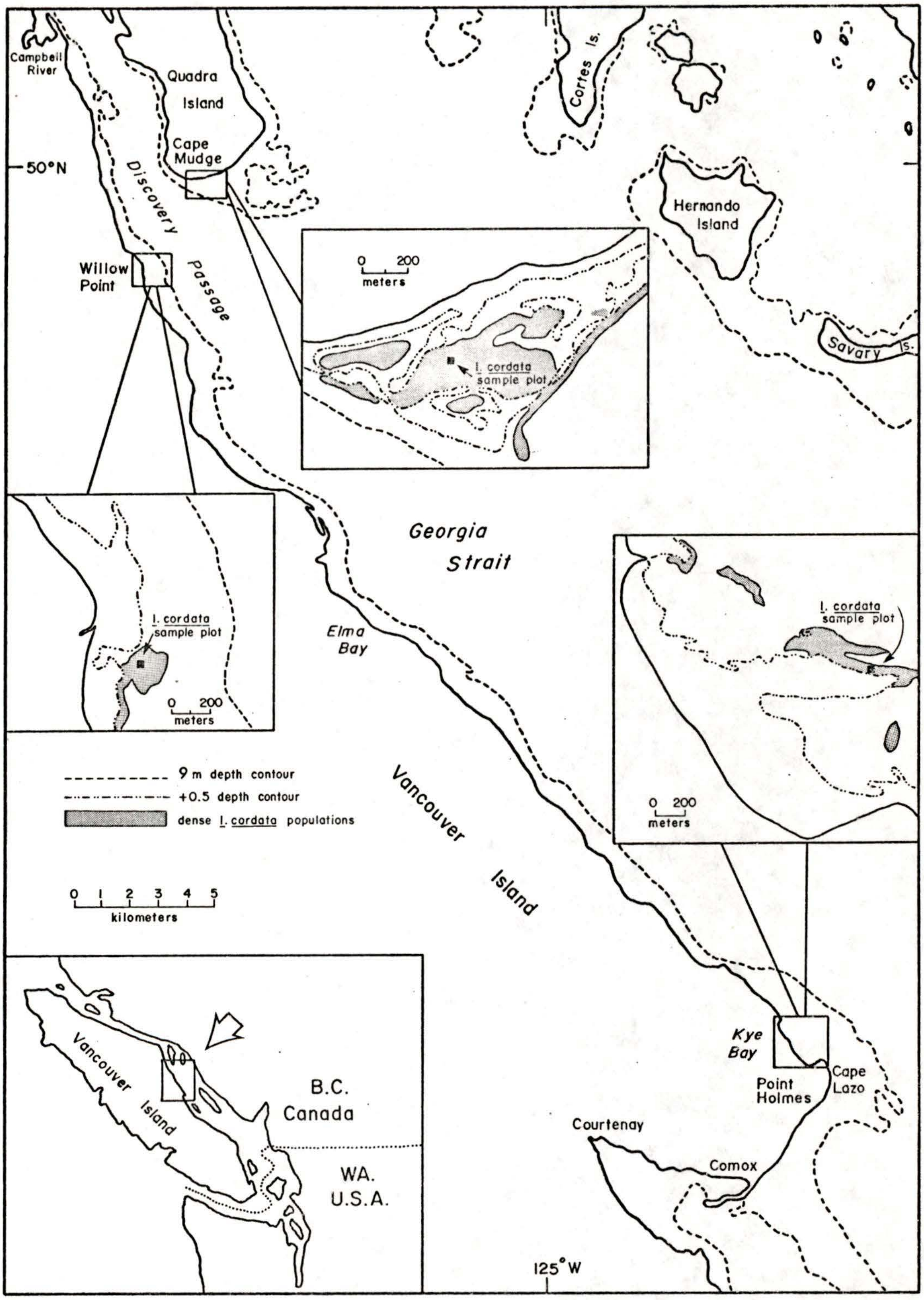
METHODS

Seasonal Sampling of I. cordata Communities

Three week to monthly sampling of I. cordata communities was conducted at three locations in Georgia Strait, from May, 1975 to September, 1976. Sample locations (Figure 1) were established within littoral regions where substrate, depth and community type were visually uniform over at least 0.1 hectares, and the mid-summer dominant alga was I. cordata. The two northerly sample areas represented two different I. cordata dominated habitats, an intertidal lagoon at Cape Mudge where current was strong and a subtidal area at Willow Point where current was moderate. The more southerly sample area, at Kye Bay, represented I. cordata populations subject to little current motion and less directly exposed to the well mixed water flowing into northern Georgia Strait through Discovery Passage. These sample areas contained some of the largest and most dense I. cordata populations observed during extensive aerial and ground surveys of I. cordata standing crop along this coast (Austin and Adams, 1973, 1974 and 1975).

At each sample area, a permanent 10 m x 20 m rectangular sample plot was staked out with 1 m x 1.4 cm iron rods driven into the cobble and sand substrate at each corner. These plots were positioned in the most dense portion of the I. cordata population in each area. At Kye Bay the sample plot was at -1.0 m relative to chart datum, at Willow Point the depth was -0.5 m and at Cape Mudge the depth was +1.0 m, but because it was located in an intertidal lagoon, it was covered by at least 0.25 m of water at low tide.

Figure 1. Map of northern Georgia Strait with location of *I. cordata* sample plots.


Campbell River
Quadra Island
Cape Mudge
50°N
Discovery Passage
Willow Point
Cortes Is.
Hernando Island
Savary Is.
0 200 meters
I. cordata sample plot
Georgia Strait
Elma Bay
I. cordata sample plot
0 200 meters
I. cordata sample plot
0 200 meters
9 m depth contour
+0.5 depth contour
dense I. cordata populations
0 1 2 3 4 5 kilometers
Vancouver Island
Kye Bay
Point Holmes
Cape Lazo
Courtenay
Comox
125°W
Vancouver Island
B.C. Canada
WA. U.S.A.

On each sample date, five to ten 0.5 m^2 quadrats were randomly positioned in the sample plots and all macroalgae greater than 5 cm in length were collected using SCUBA. Five 0.5 m^2 quadrats were determined to be adequate for sampling the species in an I. cordata community (Fralick, 1971). Care was taken to collect only fronds which had holdfasts within the quadrat frame, since collection of these fronds plus those with holdfasts outside the quadrat frame, but which flopped inside, would have yielded erroneously high biomass values per quadrat area. To prevent overlapping of samples on separate dates, the sample plots were divided into a grid. The grid position of each quadrat was established using a table of random numbers prior to SCUBA divers entering the water. The sampling procedure involved stretching two ropes, tagged at metre intervals, along the longest sides (20 m) of the sample plots and tying these to the corner pegs. A third rope (10 m long) was loosely tied between these ropes at the appropriate grid coordinate (a) and the quadrat frame was placed alongside the 10 m rope at the grid coordinate (b). Usually 10 quadrats were taken from each sample plot per sample date, but fewer quadrats were taken on some winter dates due to divers being subject to extreme cold and because biomass was lower and more uniform than in the summer. Most frequent (three week) sampling was done during the summer months when floristic changes were most marked.

Records of water temperature and water samples for nutrient and salinity analysis were taken at each of the three sample areas, at the surface and at 6 m below the surface. These two depths were considered to be the upper and lower limit of the water column impinging on the I. cordata community, as the tide fluctuated. Secchi depth was measured to determine water transparency. The water samples were packed in ice for 48 hours prior to analysis or were frozen at -10° C and analysed some weeks later. All samples were analysed for specific conductivity, nitrate-nitrogen, nitrite-nitrogen, ammonia-nitrogen, orthophosphate, and total phosphate, at the British Columbia Ministry of Environment, Water Chemistry Laboratory in Vancouver, B.C. (now Environmental Laboratory).

Specific conductance was determined using a Stebold ohm-meter and water bath at 22° C. Salinity was obtained using a conversion factor for specific conductance. Nitrogen and phosphorous were analysed using a Technicon Autoanalyser which measured concentrations greater than 0.02 mg/L NO_3, 0.005 mg/L NO_2, 0.01 mg/L NH_4 and 0.005 mg/L orthophosphate.

Surface radiation data were obtained from the Pacific Marine Biological Station at Nanaimo, B.C. The station is located 85 km south of Kye Bay sample site, but is within the same climatic regime. Radiation is measured in langleys per hour with an Eppley No. 2 pyranometer.

All algal samples were initially squeezed of excess water, weighed fresh, and then preserved in 23 kg plastic bags with 200 ml of 5% Formalin prior to examination and measurement. Preservation was best if as much air as possible was expelled from the plastic bag and the bag was well sealed, shielded from sunlight and kept in a cool area. Lots of five to ten samples collected from one plot on one date were put into large opaque plastic garbage bags to further seal the samples and shield them from sunlight.

Analysis of the 0.5 m^2 algal samples consisted of initially separating specimens into species piles then measuring damp weight and frond numbers for each species. I cordata was separated into four life phases: male gametangial, female (cystocarpic), tetrasporangial and vegetative (not macroscopically reproductive). The damp weight and frond abundance of each life phase was recorded. This procedure was performed on five samples from Kye Bay and Cape Mudge for each of 16 sample dates and from Willow Point for 11 sample dates. The I. cordata in samples from Kye Bay and Cape Mudge were analysed more completely including measurement of area, length, weight, percent cover of sori and frond condition for each I. cordata frond greater than 10 cm in length.

Data for each I. cordata frond were coded on computer cards and stored on tape. A program was written to tabulate the following information for each life phase and for all life phases combined: number of fronds and percent of total fronds per size class; number and percent of total ragged fronds per size class; mean percent cover of sori and total area covered by sori per size class; total surface area and percent of total surface area of fronds per size class; total and mean weight of fronds and percent of total weight of fronds per size class.

The identification of the two spore producing life phases of I. cordata (tetrasporangial and cystocarpic fronds) is accomplished easily with mature (highly reproductive) fronds, but this is not the case for immature fronds. Male gametangial fronds frequently have not been distinguished from vegetative fronds in previous studies (Fralick, 1971 and Hansen, 1976). Considerable emphasis was placed on the correct identification of these specimens in the present study, advocated by the seasonal nature of collections, permitting examination of maturation sequences in each life phase. With a knowledge of these sequences, macroscopic features of each life phase were selected at different development stages and used, with a large degree of assurance, for correct identification. Fronds were assigned to the vegetative category if no reproductive tissue was macroscopically visible.

Thirty to fifty fronds of other dominant species (where individuals of the species weighed more than 10 g collectively) also were measured for length, and fronds of rhodophyte species examined for reproductive condition, in their random order of appearance in one or more samples from each date at Cape Mudge and Kye Bay.

Seasonal abundance of _I. cordata_ frond initials (fronds and sporelings less than 5 cm high) were examined on cobbles collected near Kye Bay sample plot in September, 1975 and December through May, 1976. Five cobbles supporting a visually representative stand of _I. cordata_ were collected on each of five sample dates, wetted with 5% formalin solution and deposited in plastic pails for examination in the laboratory. The number of _I. cordata_ fronds 0.25 - 5 cm long and greater than 5 cm long were counted for each holdfast on each cobble.

An estimate was made of the vacant space available on cobble substrate for algal colonization in late summer when _I. cordata_ spores were being released. The percent of bare rock surface (not covered by holdfasts or encrusting algae or animals) above the sand was visually estimated for 15 cobbles collected near the Kye Bay sample plot in September, 1975. The level of sand was marked on each cobble by scoring with a knife before removal.

I. cordata Frond Growth Experiments

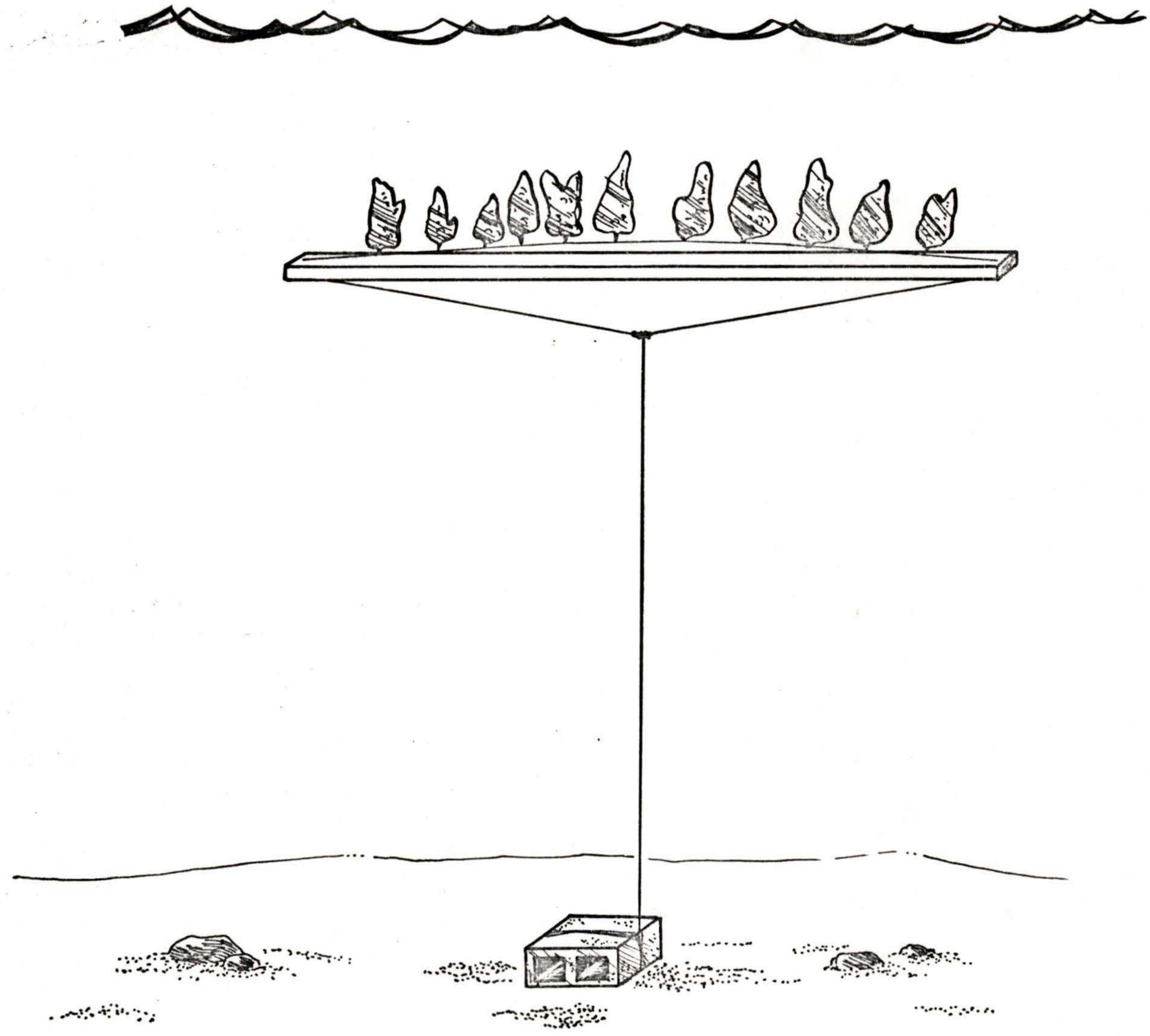
Observations on the growth rate of individual tetrasporangial and gametangial *I. cordata* fronds in different locations and in different seasons were required to assess seasonal differences in *I. cordata* population structure in mature stands.

Measurement of the growth of fronds attached to the natural substrate is extremely difficult. Length measurement has been used for some algal species (Austin, 1960; Prince, 1971; Fralick and Mathieson, 1973), but change in length is not an accurate measurement of growth of *I. cordata*. Tagging of fronds selected for measurement is difficult and often not effective as tags and plants may be dislodged by wave action or attractive to benthic invertebrates (Austin and Adams, 1970). Trials were made to explore the possibility of selecting fronds on portable cobble substrate which could be brought to the surface, weighed and then repositioned on the bottom in an ordered manner to facilitate retrieval. Hruby (1974) used this technique for observing the effect of exposure on *I. cordata*. However, the weight of the fronds was so much less than the weight of the cobbles that this method was determined to be too inaccurate for measuring changes in frond weights.

A more successful technique was used by Waaland (1973) who examined I. cordata and Gigartina exasperata growth in Puget Sound using a quick release apparatus consisting of plastic tubing which held individual fronds by crimping the frond stipe. The tubing was attached to polypropylene ropes which were anchored at one end and buoyed at the other. A technique similar to that of Waaland was employed in the present study except that the plastic holder was eliminated and frond stipes were inserted directly into the twine of polypropylene rope. This worked particularly well if fronds were used on which a portion of the holdfast had been retained to prevent the stipe from slipping out of the rope. Each rope holding fronds was 2 m long and was stretched along a timber support of equivalent length. Fronds were spaced at 20 cm intervals with five immature tetrasporangial and five immature cystocarpic fronds on each rope (Figure 2). Fronds were obtained by harvesting clumps of cystocarpic and tetrasporangial fronds growing at -1.0 m depth near the Kye Bay seasonal sample plot, and from this collection fresh undamaged individuals between 10 and 15 cm long (except where noted below) were selected. Although these small immature fronds initially bore no reproductive structures, their life phase type was assumed by selectively harvesting them from frond clumps that also contained some large mature fronds of only one life phase or the other. The identity of the 10 - 15 cm fronds was confirmed toward the end of the experiment when they had matured and sorus types were recorded.

Frond holding ropes were positioned on June 5 and on July 26, 1976 at -0.5, -2.0, -4.0 and -6.0 m below chart datum at Cape Lazo,

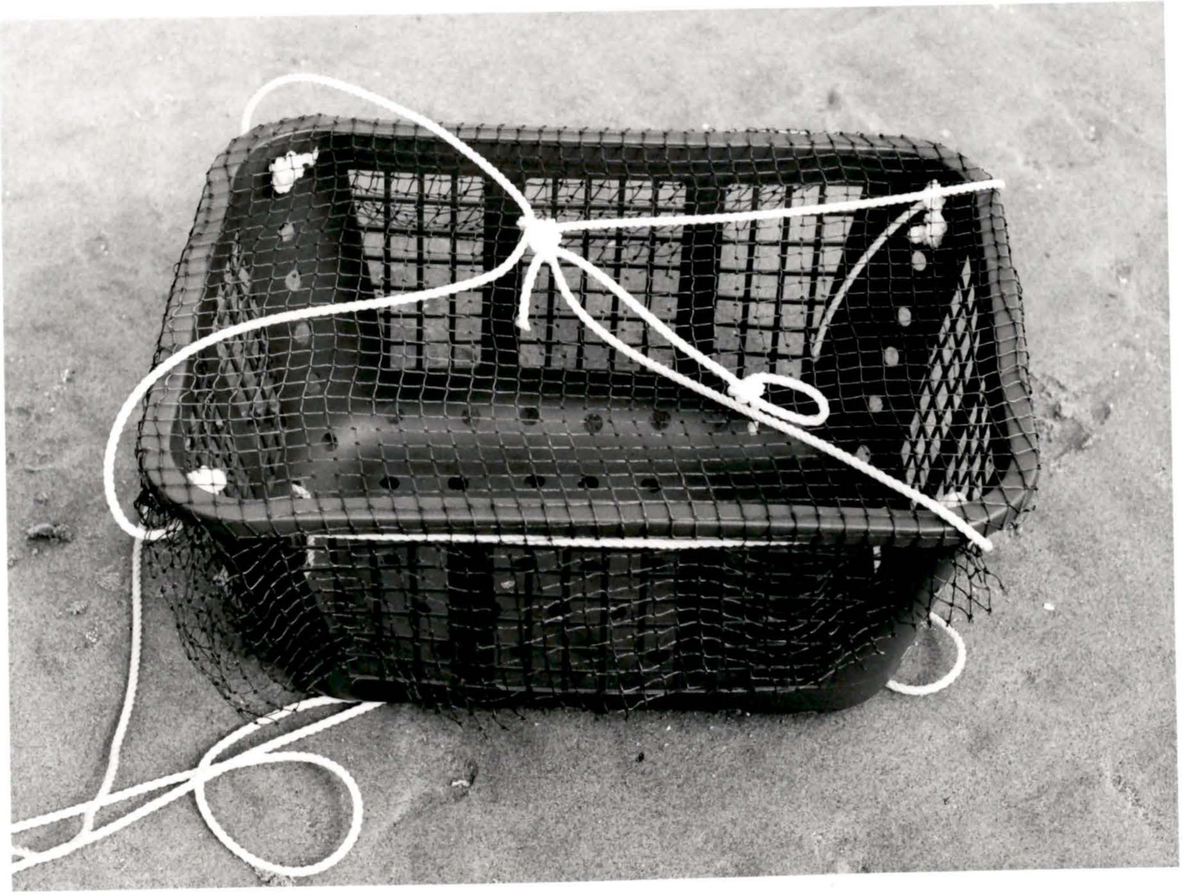
Figure 2. Diagram of _I_. _cordata_ frond holding apparatus; fronds inserted into twine of 0.7 cm polypropylene rope stretched along a wood support, anchored at various depths.



near Kye Bay. The latter two rope holders were below the depth at which I. cordata was found to occur naturally in dense beds. Two additional rope holders were positioned at Cape Lazo on June 5, 1976: one rope holder with cystocarpic fronds of two distinct sizes (5 - 10 cm and 20 - 25 cm long), and a second rope holder with cystocarpic fronds which had their growing tips cut off. These latter fronds were initially 15 - 20 cm long and were cut back to 10 cm in length before positioning in the sea to explore the regeneration capacity of these fronds. Photographs were taken before and after their 49 day growth period. Growth of fronds on holders suspended in the water column at Cape Lazo was compared with fronds inserted in rope and lying on the bottom and possibly competing with I. cordata in natural populations. One holder with five cystocarpic and five tetrasporangial fronds, 10 - 15 cm long, was weighted to the bottom in the I. cordata population near the seasonal sample plot in Kye Bay and a second near the seasonal sample plot at Cape Mudge on June 5 and 6, 1976.

A series of experiments were also undertaken to compare the growth rate of unattached (free-floating) I. cordata fronds with those attached to rope holders described above. Several large chambers (1.5 - 3m ^{3}) were constructed to utilize currents for circulating and suspending fronds (Appendix I) but no data on frond growth were obtained from these due to difficulties in anchoring the units. Locations where currents were sufficiently strong to suspend fronds in northern Georgia Strait were also exposed to considerable wave action. Plastic baskets, approximately 0.06 m^3 in size (Figure 3)

Figure 3. Basket used to contain unattached *I. cordata* for measurement of frond growth.



were finally used. These had only a small capacity for frond biomass but could be anchored easily. Five, 10 - 15 cm long I. cordata fronds were inserted in three baskets suspended at Cape Lazo at -0.5 m depth on June 3, 1976.

All fronds used in these growth experiments were measured initially for length, area, and damp weight (excess water shaken off), before inserting in the ropes and baskets, and the order of insertion of fronds in the rope holders was noted. On subsequent sample dates, fronds were collected from the baskets and the ropes bearing fronds were removed from their wood support and placed in buckets of water and taken to shore. Fronds were removed one at a time from the ropes and measured, then the fronds and holders were replaced in the sea. Fronds put down initially on June 5 - 6, 1976 were remeasured on July 5, July 25 and September 3, 1976 and fronds put down on July 26 were remeasured on September 3 only.

I. cordata Spore Settlement and Growth Studies

A series of experiments were undertaken to examine the dispersal of spores released from mature fronds, seasonal spore settlement on fresh substrate and the survival rate of newly settled spores and sporelings. In all of these experiments, 3 mm thick textured acrylic (Plexiglas with DP30 surface) settling plates, cut in 5.1 x 7.6 cm rectangles, were used to monitor settlement and survival of spores. Initial trials were undertaken to compare the settlement and resistance of I. cordata spores to current on glass and Plexiglas and no difference was found (qualitative observations only) indicating that Plexiglas material did not deter attachment

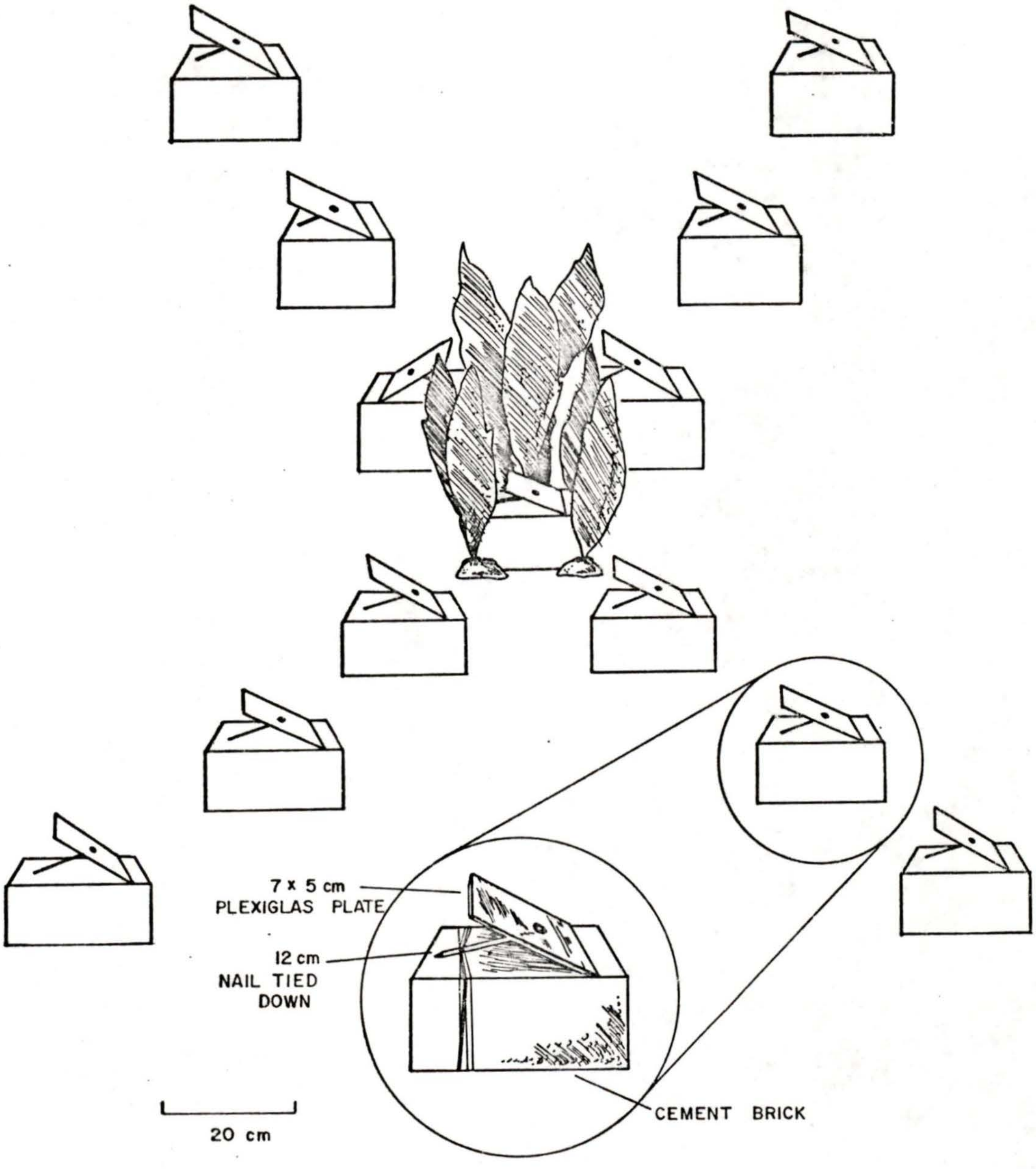
(a) spore dispersal

Two experiments were undertaken in September, 1975, to study *I. cordata* spore dispersal. The first of these was to investigate drift of spores over horizontal distances from a known number of reproductively mature *I. cordata* fronds.

A sandy bottom 2 - 3 m below low water and more than 200 m away from any *I. cordata* populations was selected at Point Holmes, near Kye Bay. In this sandy area, cobbles with varying numbers of fronds were positioned on the bottom to form three populations with three, six and twelve fronds. Each population was approximately 20 m apart. Surrounding each population, settling plates were positioned at distances of 1 m, 0.5 m, 0.2 m (touching the tip of fronds when extended) and at the base of the fronds in four perpendicular rows radiating outward from the populations (Figure 4). Each settling plate was fastened on the diagonal to a small cement brick (Figure 4) to prevent the plate being dislodged and/or being covered in a layer of sand. Earlier trials indicated that plates lying horizontally on the bottom became covered in sand.

After 96 hours immersion, all plates were removed, put in 285 ml jars and returned to the lab where they were examined with a microscope using a dipping lens. Red algal spores, 17 - 22 μm in diameter, were counted along 10 systematically spaced transects on each plate. A transect was 0.3 mm wide by 50.0 mm long with a total area of 0.15 cm^2. The total number of spores per cm^2 was calculated as the mean transect count (± standard error) divided by the transect area in cm^2.

Figure 4. Diagram of distribution of Plexiglas settling plates attached to cement bricks around isolated _I. cordata_ fronds in spore dispersal experiment.


7 x 5 cm
PLEXIGLAS PLATE
12 cm
NAIL TIED
DOWN
CEMENT BRICK
20 cm

The second experiment to examine drift was undertaken to assess the distribution of spores at varying heights in the water column above an I. cordata population. Settling plates were attached to ropes anchored to the bottom and with floats to hold them vertical (Figure 5). Plates were positioned at 0.3 and 1.0 m above the bottom and on the bottom at a depth of -1.5 m, adjacent to the Kye Bay seasonal sample plot. Spore density per plate was counted as above after 96 hours immersion. In both experiments the assumption was made that the number of non-I. cordata spores which settled on the plates and resembled I. cordata was very low. Coon et al. (1971) indicated that spore size for a species is relatively constant but varies between species.

(b) spore settlement and survival

Plexiglas settling plates, 5.1 x 7.6 x 0.3 cm in dimension, were also used to monitor temporal aspects of spore recruitment in I. cordata communities. Settling plate holding platforms (Figure 6) were constructed of wood and submerged within I. cordata communities near the seasonal sample plots at Kye Bay (-1.5 m depth) and Cape Mudge (0.25 m below surface of lagoon at low tide). A wooden box was filled with cobbles to weight it down, then the plywood and Plexiglas platform was bolted to the box. Settling plates were fastened to the Plexiglas sheet by means of nylon nuts and bolts and could be removed using SCUBA at high tide.

Plates were fastened and removed for two purposes: (1) to examine settlement between each three to nine week sample period from May, 1975 to September, 1976 and (2) to examine the accumulative settlement

Figure 5. Diagram of Plexiglas settling plates attached to ropes in spore dispersal study above a dense _I. cordata_ population.

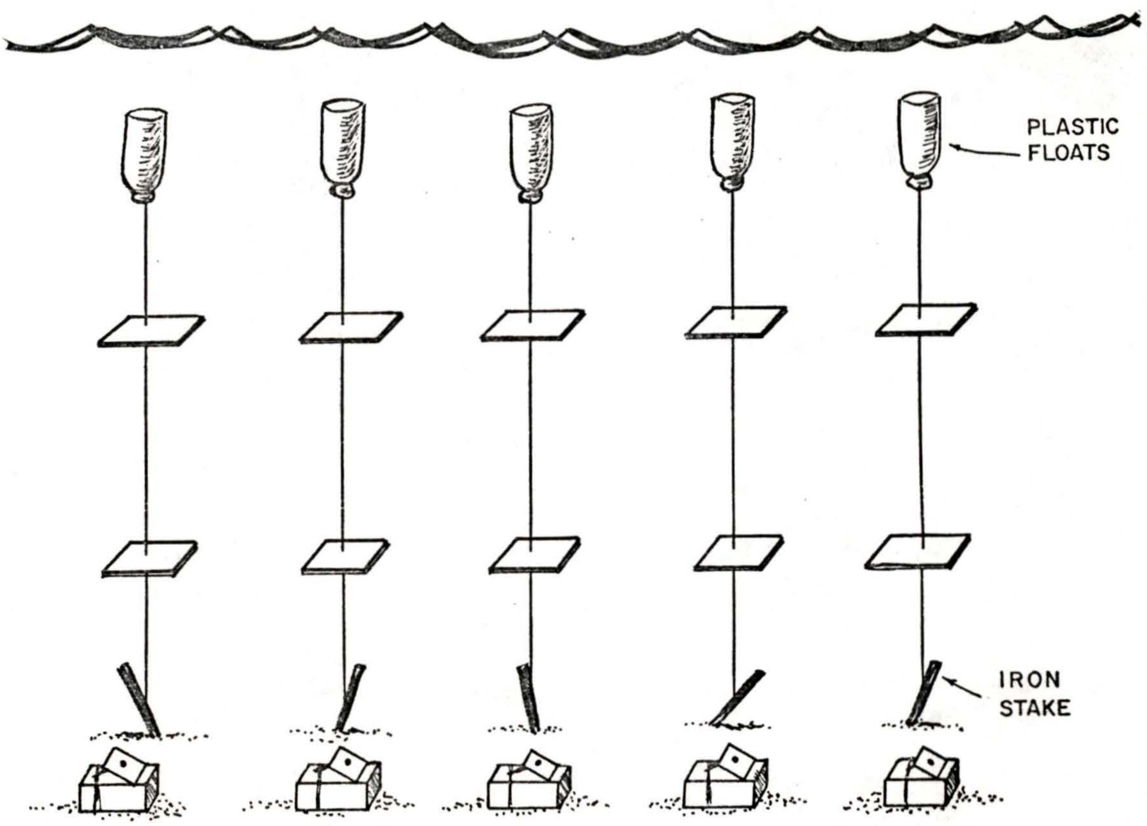
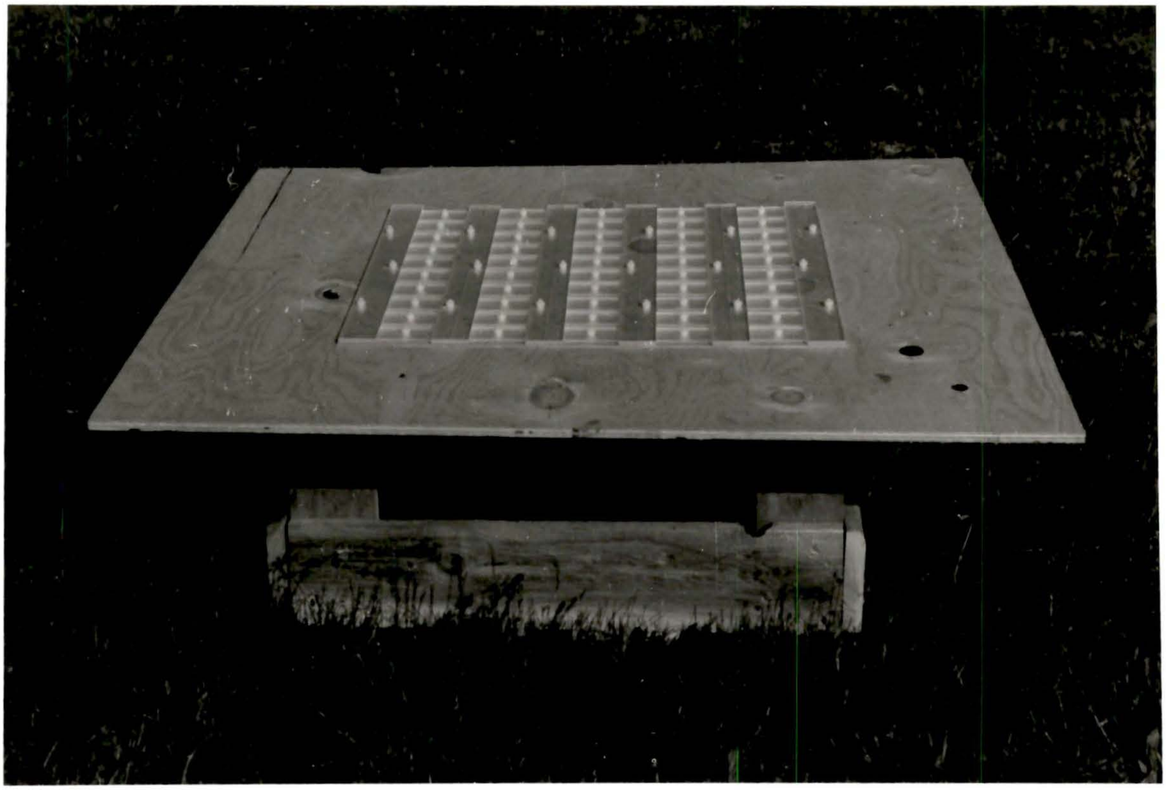

PLASTIC FLOATS
IRON STAKE

Figure 6. Settling plate platform used in spore settlement and survival study.



and development on plates submerged over two or more sample periods. In the latter case, series of approximately 20 plates were fastened to platforms in May, 1975, July, 1975, September, 1975 and December, 1975. One plate was removed on each three to nine week sample date from each series until September, 1976. All plates were pried loose with a knife and slipped into a 285 ml jar to minimize handling. On the surface a little seawater was decanted off and formalin added to make up a 5% solution and the plates were stored for later examination.

Plates were observed first macroscopically and notes made on the presence and number of young fronds of macroscopic algae. Observations were then made with a compound scope equipped with dipping cone objectives. The number of _I. cordata_-sized red algal spores and sporelings were counted along 10 transects crossing the width of the slides at equidistant intervals along their length. Each transect was 0.3 mm wide and 50.0 mm long, and the total area examined was therefore 1.5 cm^2. The abundance of non _I. cordata_-like sporelings and of diatoms was noted also.

Substrate Colonization Studies

The colonization of vacant substrate by _I. cordata_ and other possible competing species was observed within natural _I. cordata_ populations at three locations in Georgia Strait.

Concrete building blocks were used as a fresh substrate on which colonization could be examined. Two 10 kg blocks each measuring 20 x 20 x 40 cm were tied together to provide a mass which would not be rolled easily by winter storms. These units were dropped near the sample areas in I. cordata communities at Kye Bay, Cape Mudge and Willow Point. Blocks were put down first in June, 1975, and then at approximately monthly intervals until February, 1976. Several blocks had been put down on known dates in the same areas during prior studies (summer, 1973 and 1974) and these blocks were observed also.

Approximately monthly observations were made using SCUBA between July, 1975 and June, 1976 to ascertain the growth of algae on the previously immersed blocks. It quickly became apparent that tops and bottoms had different rates of colonization and observations were separated into these two areas. Colonizing species were identified to the most specific taxa possible, which varied according to the growth stage, and names and abundance were recorded on an underwater slate. Abundance was visually determined as the percent cover of a particular species on either the horizontal surface or vertical surfaces (sides) of the block units. In late August, 1976, all the blocks were pulled to the surface, photographed and then scraped to remove all algal growth. Material from the top and sides of each block were preserved separately in plastic bags with 5% formalin. In the laboratory, the material was separated into species and wet weight of each species was determined. In addition, I. cordata fronds were separated into each life phase and these were weighed and total fronds counted.

RESULTS

Environmental Observations

The three I. cordata communities sampled in Georgia Strait from May, 1975 to September, 1976 were sheltered from open Pacific waves, but were open to a considerable fetch (40 - 50 km) in the direction of the prevailing winds (Figure 1). The substrate consisted of glacially - derived cobbles and boulders imbedded in sand and marine clays in each sample area.

Both Willow Point and Cape Mudge sample sites were at the entrance to Discovery Passage, through which flow strong tidal currents. Cape Mudge, with intertidal flats over a kilometer in width, was particulally subject to strong currents (estimated at greater than 1.5 m/sec. during spring tide change). The Willow Point sample area was in a back-eddy where current changed direction often but was less severe (estimated to be 0.75 m/sec. maximum). Kye Bay, 40 km south of Willow Point, had current velocities considerably less than the former areas, and maximum velocity was estimated to be less than 0.5 m/sec.

At Cape Mudge, the total area covered by dense I. cordata populations in and surrounding the intertidal lagoons was estimated to be 21 ha (Austin and Adams, 1975). A layer of clam shells (primarily Tresus capax) covered the sand surrounding the cobbles and boulders. Dominant species associated with I. cordata were Prionitis lanceolata[1] and Constantinea subulifera. In portions

---

[1] A complete list of macroalgal taxa (with scientific authorities) observed in and immediately adjacent to the three sample plots and colonizing concrete blocks and settling plates is presented in Appendix II.

of the lagoons, usually where I. cordata was scarce, Sargassum muticum, Laminaria saccharina, and Alaria tenuifolia were abundant. Surrounding the lagoon at depths of -1 to -3 m was Nereocystis luetkeana. Below this depth the sea urchin Strongylocentrotus drobachiensis had denuded most algal vegetation.

At Willow Point, the I. cordata community was estimated to cover 7 ha and major species associated with I. cordata were Plocamium coccineum, Prionitis lanceolata and Botryoglossum farlowianum. The cobbles and boulders supporting these populations were imbedded more firmly in a clay/sand matrix than at Cape Mudge or Kye Bay. Plocamium coccineum predominated below the I. cordata population such that the lower limit of dense I. cordata was at -0.25 to -1.0 m relative to chart datum. A Nereocystis luetkeana bed grew to seaward in -2 to -5 m of water, and beyond this sea urchins were abundant.

At Kye Bay, I. cordata populations covered approximately 20 ha and were restricted to several discrete mounds of glacially deposited cobbles. Here the cobble substrate was imbedded in sand but did not appear to be vulnerable to constant overturning by wave action, but more to be covered and uncovered by sands. Cobbles were found buried to depths of 0.25 m bearing specimens of Iridaea cordata, Prionitis lanceolata and Lithothamnion species in an apparently living condition. The substrate was subject to disturbance by the occasional Pycnopodia helianthoides (sunflower star) which were observed to overturn numerous cobbles in large areas (up to 1 m^2) while digging for the clam Tresus capax. The I. cordata populations extended to

-3 m, below which sand predominated with scattered cobbles which supported laminarians. Dominant species associated with I. cordata were Plocamium coccineum, Constantinea subulifera, Botryoglossum farlowianum and Gigartina exasperata.

Both Kye Bay and Cape Mudge showed warm summer temperatures, attributed to the rapid heating of water in the tide pools at Cape Mudge and to warming over hectares of sun baked intertidal rocks and sand on incoming tides at Kye Bay. At these two areas, water temperatures reached a maximum of 15^{o} - 18^{o} C in mid-summer, while Willow Point reached 11^{o} - 14^{o} C (Figure 7). In 1976, water temperatures were considerably cooler than in 1975. Summer water temperature records in 1975 averaged for June 15 to August 30 were 15.0^{o}, 12.7^{o} and 14.0^{o} C for Kye Bay, Willow Point and Cape Mudge respectively, and in 1976 were 11.3^{o}, 12.0^{o} and 11.5^{o} for the respective areas. Winter temperatures at all sample areas were 4.5^{o} - 7.0^{o} C. Salinities reached a maximum of 28 ppt in February through May, 1976 and were not usually less than 23 ppt, except at the end of August 1976 when lows of 19 ppt and 16 ppt were recorded at Willow Point and Cape Mudge respectively (Figure 7).

The seasonal variation in nitrate nitrogen and orthophosphate sampled at Kye Bay, Willow Point and Cape Mudge (averaged for surface and -6 m depths) was typical for temperate near-shore waters. (Figure 8)

Nitrate nitrogen showed a high of 0.34 - 0.40 mg/L in winter and was reduced considerably in summer. At Kye Bay, in 1975, nitrate nitrogen was at less than detectable amounts (<0.02 mg/L) in July

Figure 7. Water temperature and salinity; May, 1975 to September, 1976.

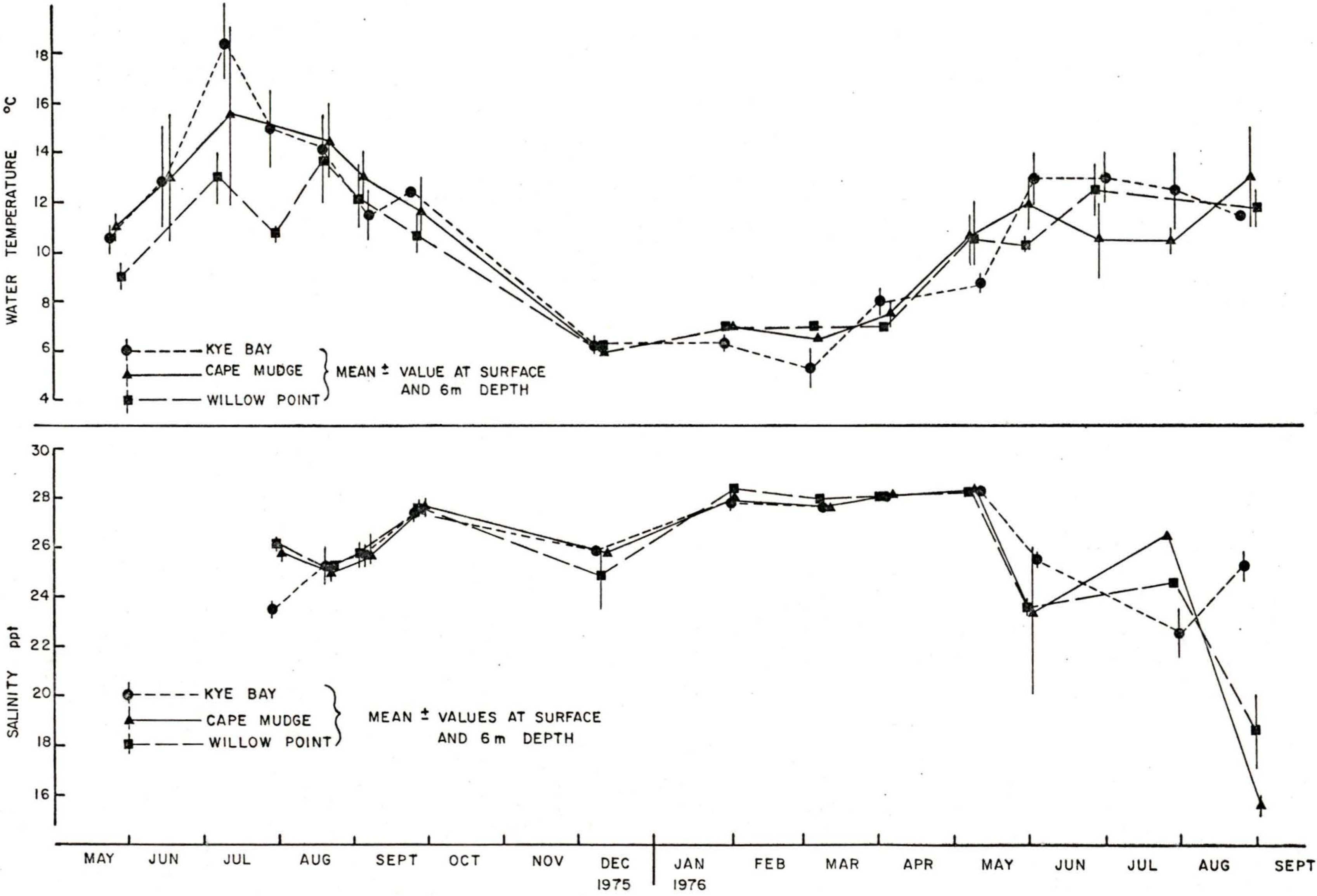
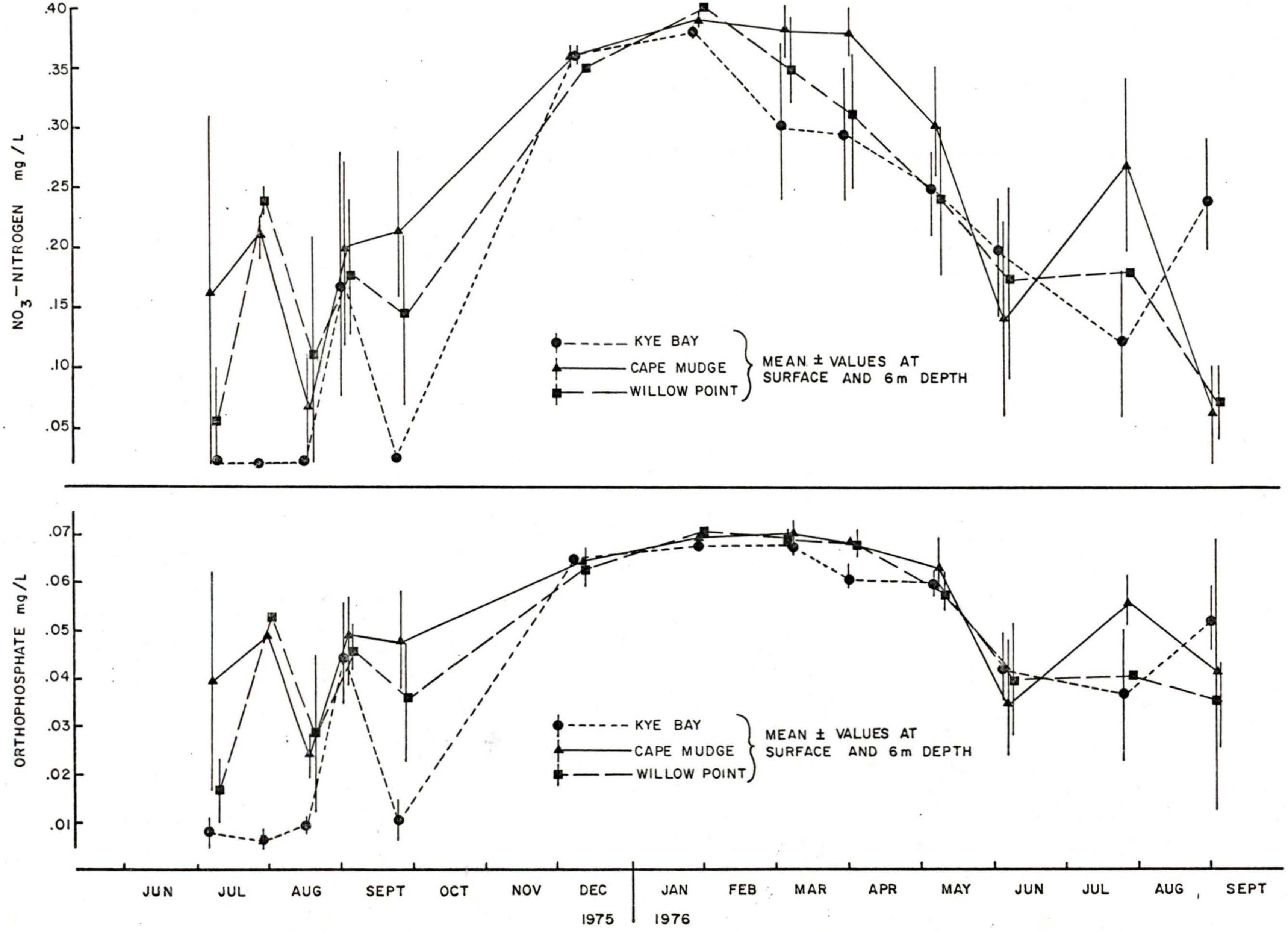

WATER TEMPERATURE °C
18
16
14
12
10
8
6
4
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUE AT SURFACE AND 6m DEPTH
SALINITY ppt
30
28
26
24
22
20
18
16
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUES AT SURFACE AND 6m DEPTH
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
JAN
1976
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT

Figure 8. Dissolved nitrate (NO_3 - N) and orthophosphate (PO_3 - P); July, 1975 to September, 1976.


.40
.35
.30
.25
.20
.15
.10
.05
NO_3–NITROGEN mg/L
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUES AT SURFACE AND 6m DEPTH
.07
.06
.05
.04
.03
.02
.01
ORTHOPHOSPHATE mg/L
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUES AT SURFACE AND 6m DEPTH
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
1976

and August, increasing to 0.16 mg/L in early September, then in late September was again less than 0.02 mg/L. At Cape Mudge and Willow Point, summer nitrate nitrogen concentration varied between 0.05 mg/L and 0.27 mg/L. Nitrite and ammonia nitrogen remained below detectable levels (0.005 mg/L NO_2 and 0.01 mg/L NH_3) for much of the year and seasonal changes in their concentrations could not be observed. A maximum value of 0.06 mg/L ammonia nitrogen was detected in July, 1975 at Kye Bay with traces in December, 1975 and August, 1976. Nitrite nitrogen values of 0.006 mg/L were recorded in September, 1975 and April, 1976 at Kye Bay.

Orthophosphate showed a seasonal trend similar to nitrate, with a high between 0.055 mg/L and 0.075 mg/L in the winter months, December through April, and lower concentrations in summer. Again at Kye Bay, in 1975, extreme lows of just above detectable amounts (0.007 - 0.009 mg/L) were recorded in July and August with an increase in early September (0.045 mg/L). At Cape Mudge and Willow Point, orthophosphate values were between 0.015 and 0.065 mg/L in summer.

Secchi depth observations (Figure 9) show the clarity of water in December through April (secchi depths of 12 - 18 m) compared to the high turbidity in summer (secchi depths of 3 - 10 m). Daily surface solar radiation taken at Nanaimo, B.C., graphed as fortnightly means (Figure 10) shows the gradual trend from a low mean daily radiation of 58 ± 8.9 langleys/day in January to a high of 631 ± 34.3 langleys/day reached in early July 1975. There was 11 percent less solar radiation during March through July 1976 than in the same period in 1975. Solar radiation was seen to increase rapidly during the month of March in both years.

RESULTS

Environmental Observations

The three I. cordata communities sampled in Georgia Strait from May, 1975 to September, 1976 were sheltered from open Pacific waves, but were open to a considerable fetch (40 - 50 km) in the direction of the prevailing winds (Figure 1). The substrate consisted of glacially - derived cobbles and boulders imbedded in sand and marine clays in each sample area.

Both Willow Point and Cape Mudge sample sites were at the entrance to Discovery Passage, through which flow strong tidal currents. Cape Mudge, with intertidal flats over a kilometer in width, was particulally subject to strong currents (estimated at greater than 1.5 m/sec. during spring tide change). The Willow Point sample area was in a back-eddy where current changed direction often but was less severe (estimated to be 0.75 m/sec. maximum). Kye Bay, 40 km south of Willow Point, had current velocities considerably less than the former areas, and maximum velocity was estimated to be less than 0.5 m/sec.

At Cape Mudge, the total area covered by dense I. cordata populations in and surrounding the intertidal lagoons was estimated to be 21 ha (Austin and Adams, 1975). A layer of clam shells (primarily Tresus capax) covered the sand surrounding the cobbles and boulders. Dominant species associated with I. cordata were Prionitis lanceolata[1] and Constantinea subulifera. In portions

---

[1] A complete list of macroalgal taxa (with scientific authorities) observed in and immediately adjacent to the three sample plots and colonizing concrete blocks and settling plates is presented in Appendix II.

of the lagoons, usually where *I. cordata* was scarce, *Sargassum muticum*, *Laminaria saccharina*, and *Alaria tenuifolia* were abundant. Surrounding the lagoon at depths of -1 to -3 m was *Nereocystis luetkeana*. Below this depth the sea urchin *Strongylocentrotus drobachiensis* had denuded most algal vegetation.

At Willow Point, the *I. cordata* community was estimated to cover 7 ha and major species associated with *I. cordata* were *Plocamium coccineum*, *Prionitis lanceolata* and *Botryoglossum farlowianum*. The cobbles and boulders supporting these populations were imbedded more firmly in a clay/sand matrix than at Cape Mudge or Kye Bay. *Plocamium coccineum* predominated below the *I. cordata* population such that the lower limit of dense *I. cordata* was at -0.25 to -1.0 m relative to chart datum. A *Nereocystis luetkeana* bed grew to seaward in -2 to -5 m of water, and beyond this sea urchins were abundant.

At Kye Bay, *I. cordata* populations covered approximately 20 ha and were restricted to several discrete mounds of glacially deposited cobbles. Here the cobble substrate was imbedded in sand but did not appear to be vulnerable to constant overturning by wave action, but more to be covered and uncovered by sands. Cobbles were found buried to depths of 0.25 m bearing specimens of *Iridaea cordata*, *Prionitis lanceolata* and *Lithothamnion* species in an apparently living condition. The substrate was subject to disturbance by the occasional *Pycnopodia helianthoides* (sunflower star) which were observed to overturn numerous cobbles in large areas (up to 1 m^2) while digging for the clam *Tresus capax*. The *I. cordata* populations extended to

-3 m, below which sand predominated with scattered cobbles which supported laminarians. Dominant species associated with I. cordata were Plocamium coccineum, Constantinea subulifera, Botryoglossum farlowianum and Gigartina exasperata.

Both Kye Bay and Cape Mudge showed warm summer temperatures, attributed to the rapid heating of water in the tide pools at Cape Mudge and to warming over hectares of sun baked intertidal rocks and sand on incoming tides at Kye Bay. At these two areas, water temperatures reached a maximum of 15^o - 18^o C in mid-summer, while Willow Point reached 11^o - 14^o C (Figure 7). In 1976, water temperatures were considerably cooler than in 1975. Summer water temperature records in 1975 averaged for June 15 to August 30 were 15.0^o, 12.7^o and 14.0^o C for Kye Bay, Willow Point and Cape Mudge respectively, and in 1976 were 11.3^o, 12.0^o and 11.5^o for the respective areas. Winter temperatures at all sample areas were 4.5^o - 7.0^o C. Salinities reached a maximum of 28 ppt in February through May, 1976 and were not usually less than 23 ppt, except at the end of August 1976 when lows of 19 ppt and 16 ppt were recorded at Willow Point and Cape Mudge respectively (Figure 7).

The seasonal variation in nitrate nitrogen and orthophosphate sampled at Kye Bay, Willow Point and Cape Mudge (averaged for surface and -6 m depths) was typical for temperate near-shore waters. (Figure 8)

Nitrate nitrogen showed a high of 0.34 - 0.40 mg/L in winter and was reduced considerably in summer. At Kye Bay, in 1975, nitrate nitrogen was at less than detectable amounts (<0.02 mg/L) in July

Figure 7. Water temperature and salinity; May, 1975 to September, 1976.

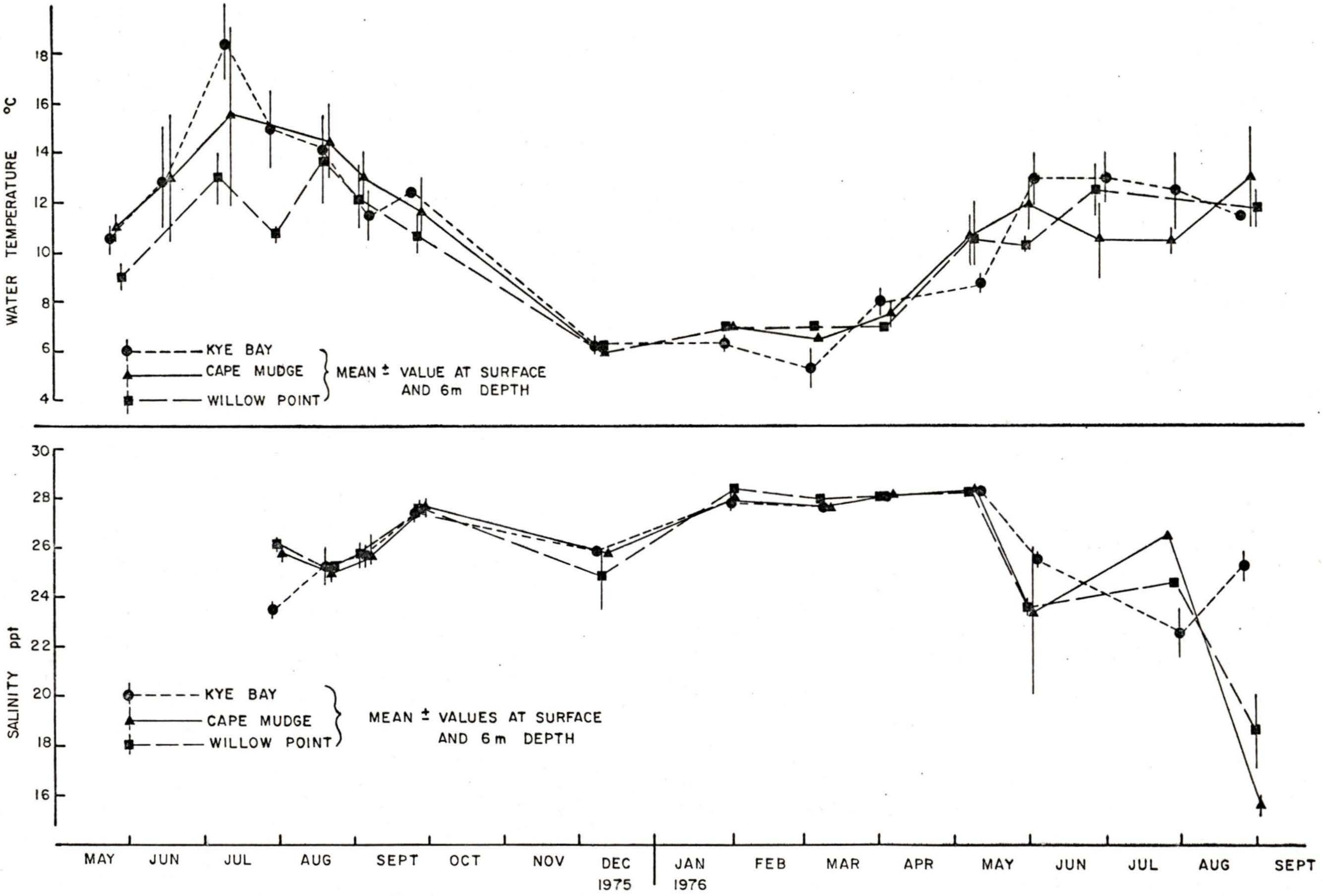
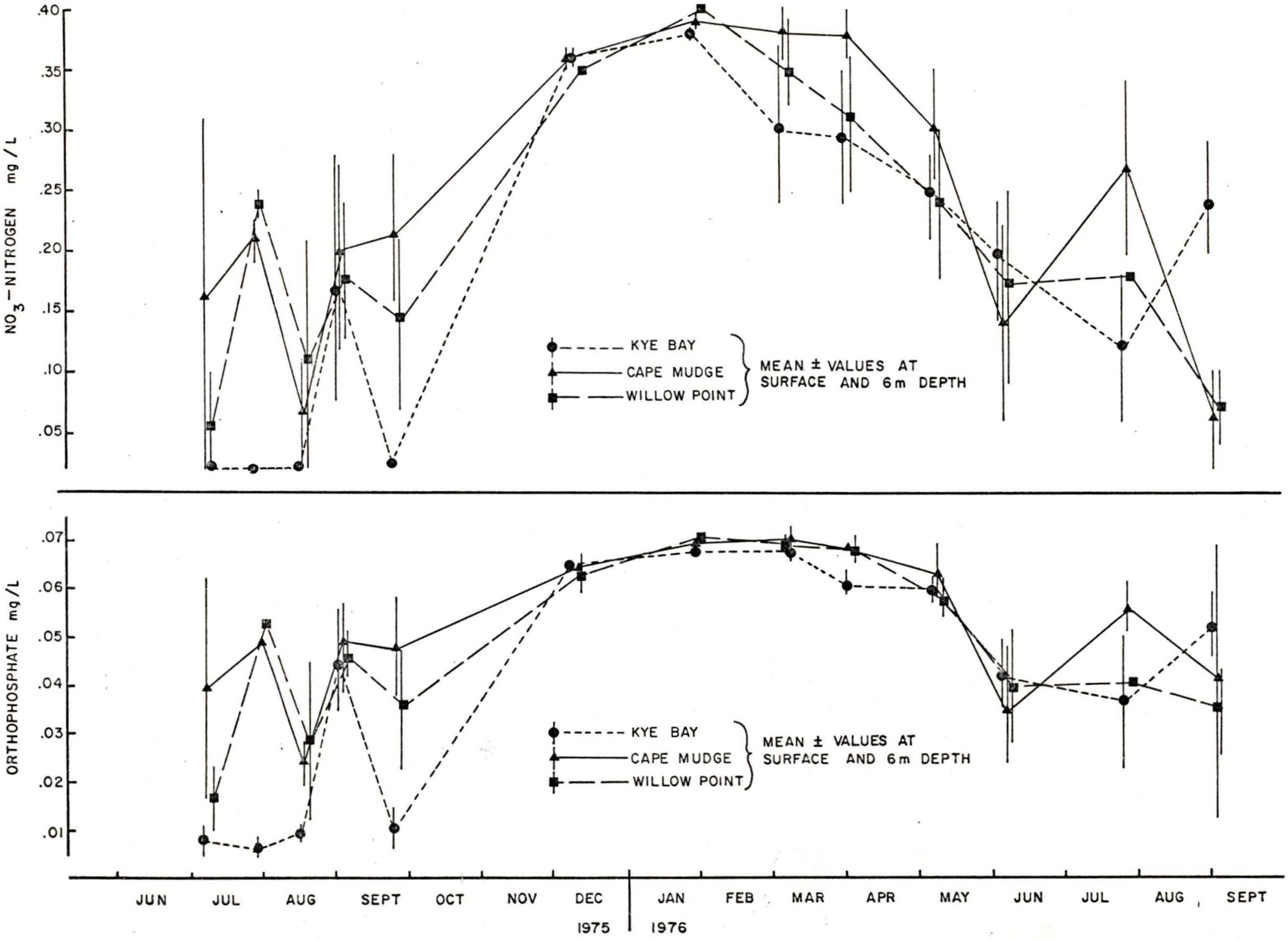

WATER TEMPERATURE °C
18
16
14
12
10
8
6
4
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUE AT SURFACE AND 6m DEPTH
SALINITY ppt
30
28
26
24
22
20
18
16
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUES AT SURFACE AND 6m DEPTH
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC 1975
JAN 1976
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT

Figure 8. Dissolved nitrate (NO_3 - N) and orthophosphate (PO_3 - P); July, 1975 to September, 1976.


.40
.35
.30
.25
.20
.15
.10
.05
NO_3-NITROGEN mg / L
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUES AT SURFACE AND 6 m DEPTH
.07
.06
.05
.04
.03
.02
.01
ORTHOPHOSPHATE mg/L
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± VALUES AT SURFACE AND 6 m DEPTH
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1976

and August, increasing to 0.16 mg/L in early September, then in late September was again less than 0.02 mg/L. At Cape Mudge and Willow Point, summer nitrate nitrogen concentration varied between 0.05 mg/L and 0.27 mg/L. Nitrite and ammonia nitrogen remained below detectable levels (0.005 mg/L NO_2 and 0.01 mg/L NH_3) for much of the year and seasonal changes in their concentrations could not be observed. A maximum value of 0.06 mg/L ammonia nitrogen was detected in July, 1975 at Kye Bay with traces in December, 1975 and August, 1976. Nitrite nitrogen values of 0.006 mg/L were recorded in September, 1975 and April, 1976 at Kye Bay.

Orthophosphate showed a seasonal trend similar to nitrate, with a high between 0.055 mg/L and 0.075 mg/L in the winter months, December through April, and lower concentrations in summer. Again at Kye Bay, in 1975, extreme lows of just above detectable amounts (0.007 - 0.009 mg/L) were recorded in July and August with an increase in early September (0.045 mg/L). At Cape Mudge and Willow Point, orthophosphate values were between 0.015 and 0.065 mg/L in summer.

Secchi depth observations (Figure 9) show the clarity of water in December through April (secchi depths of 12 - 18 m) compared to the high turbidity in summer (secchi depths of 3 - 10 m). Daily surface solar radiation taken at Nanaimo, B.C., graphed as fortnightly means (Figure 10) shows the gradual trend from a low mean daily radiation of 58 ± 8.9 langleys/day in January to a high of 631 ± 34.3 langleys/day reached in early July 1975. There was 11 percent less solar radiation during March through July 1976 than in the same period in 1975. Solar radiation was seen to increase rapidly during the month of March in both years.

Figure 9. Secchi depths; May, 1975 to September, 1976.

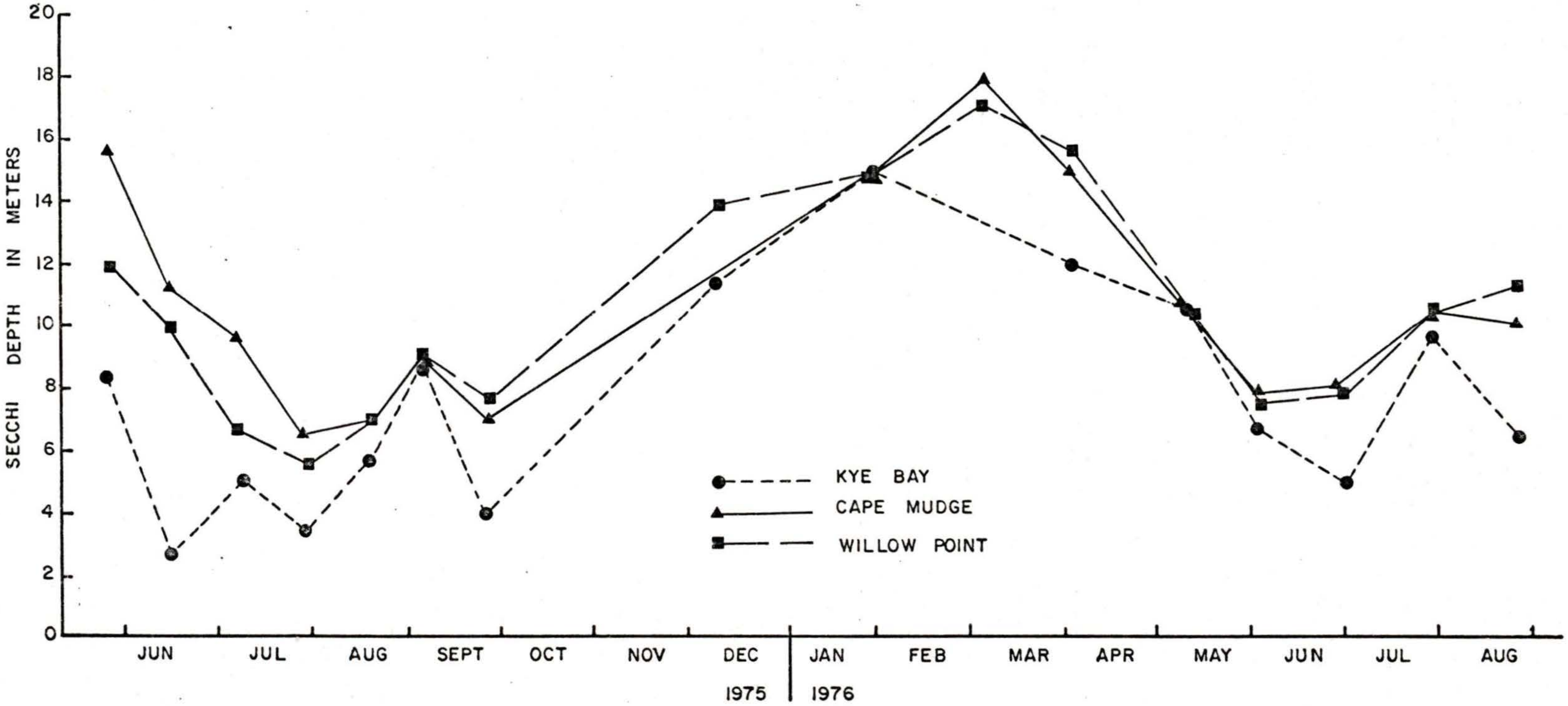
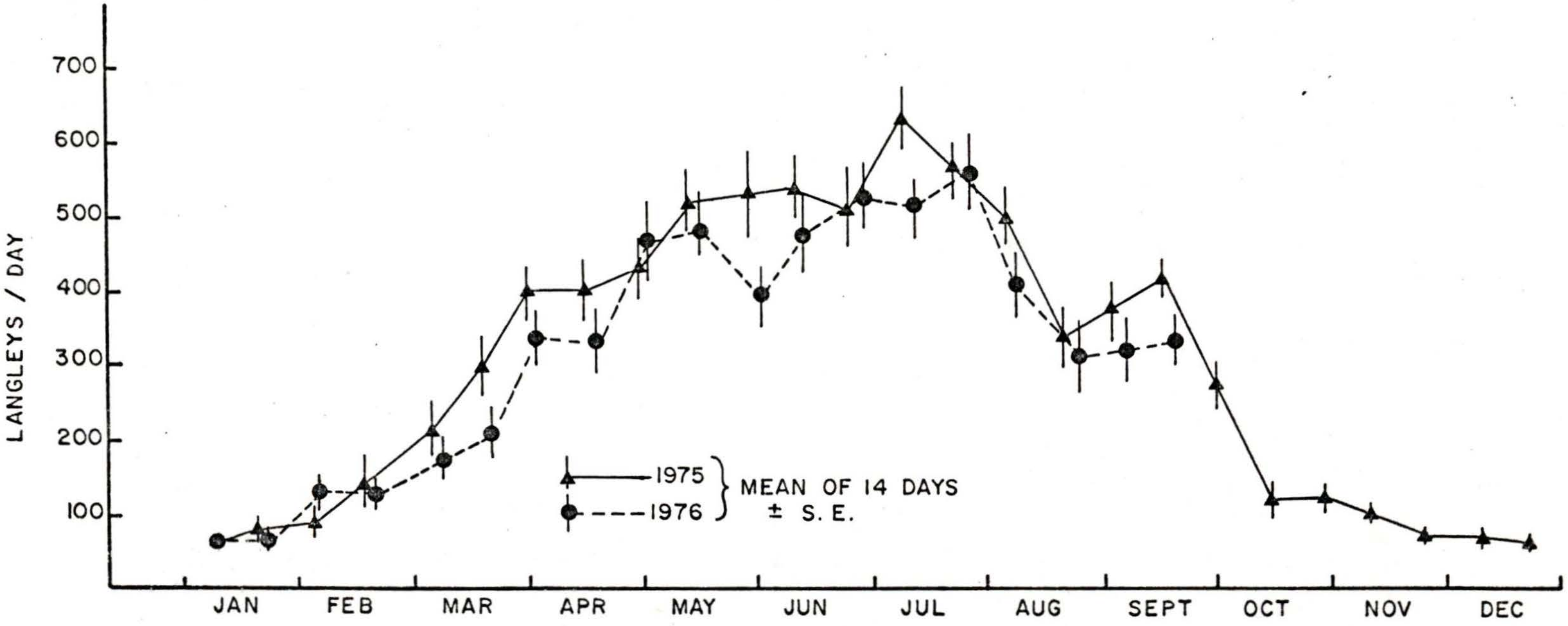

SECCHI DEPTH IN METERS
0
2
4
6
8
10
12
14
16
18
20
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
1975
1976
KYE BAY
CAPE MUDGE
WILLOW POINT

Figure 10. Mean daily surface solar radiation; January, 1975 to September, 1976.


LANGLEYS / DAY
700
600
500
400
300
200
100
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
1976
MEAN OF 14 DAYS
± S. E.

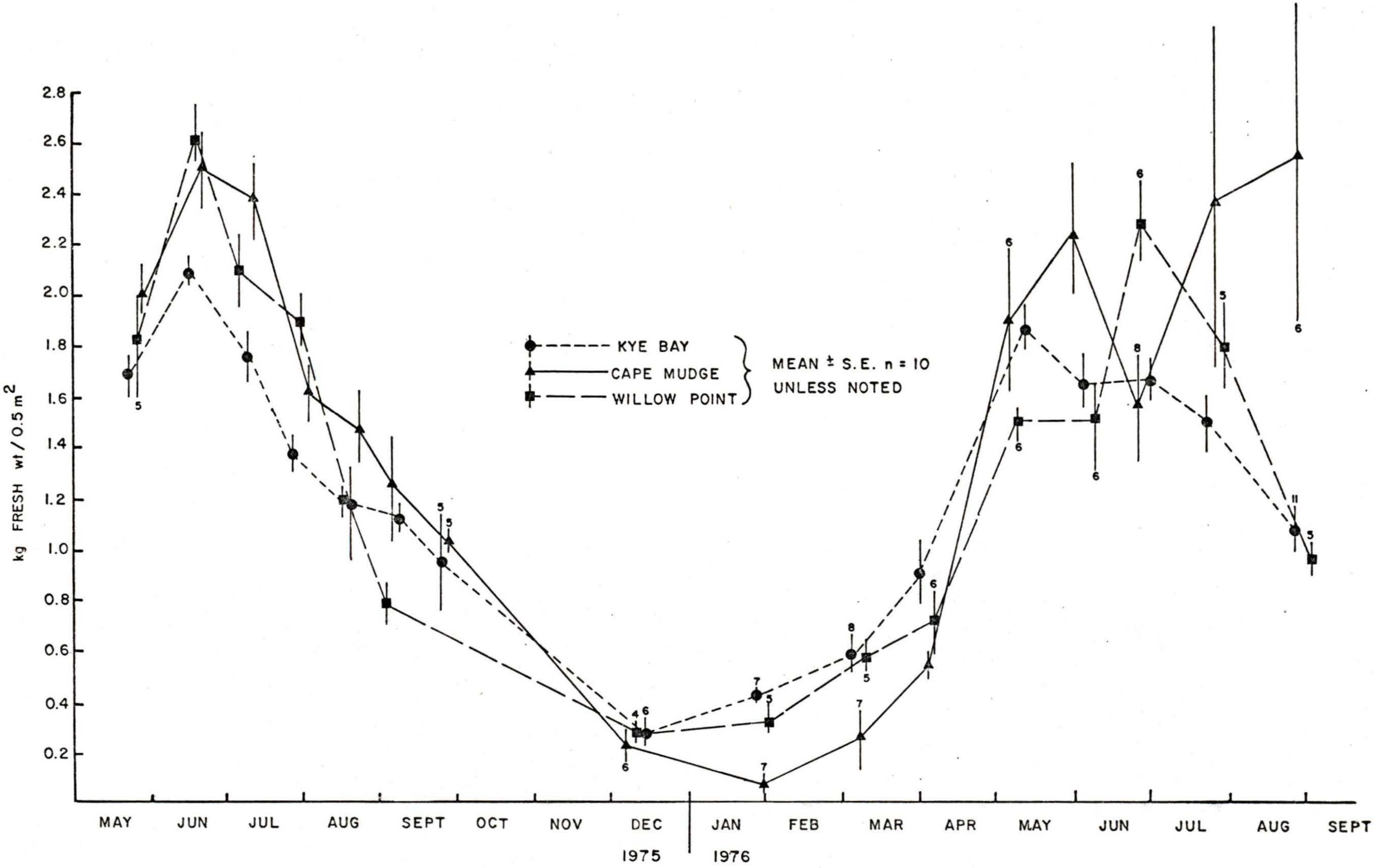
Several factors modify the surface solar radiation that reaches algal communities on the bottom. The rapid increase in surface solar radiation is countered by the increase in water turbidity in spring, but conversely, bottom light is increased by the switch in time of spring low tides (semi-diurnal) from night and late afternoon in February and March, to near noon in April through July. Theoretically it can be calculated that an algal community at -1 m below chart datum would receive 20 percent more radiation on a day with a spring low tide at noon, than on a day with a neap tide at noon (estimated with an extinction coefficient of 0.17 for a secchi depth of 10 m and a tidal range of 4.5 m; calculations in Appendix III).

Seasonal Variation in *I. cordata* Density and Standing Crop Compared to Community Standing Crop

Seasonal standing crop (damp-dried weight) of all macrophytes in the *I. cordata* community exhibited similar trends at the three sample locations with a peak between 2.1 ± 0.05 and 2.6 ± 0.11 in June, July or August and a low equal to or less than 0.3 ± 0.04 kg/0.5 m^2 in December (Figure 11). The maximum standing crop sampled at Kye Bay was less than at Cape Mudge or Willow Point in summers of both 1975 and 1976. Within each area the peak standing crop was of similar magnitude in 1975 and 1976.

The extreme difference between summer and winter standing crop is characteristic of many temperate algal communities, attributed to seasonal change in temperature and light (Vadas, 1968; and Doty, 1971). In winter, the *I. cordata* community consisted of ragged remnants of luxuriant summer fronds, the perennating holdfasts of

Figure 11. Standing crop of macroalgae in I. cordata communities; May, 1975 to September, 1976.

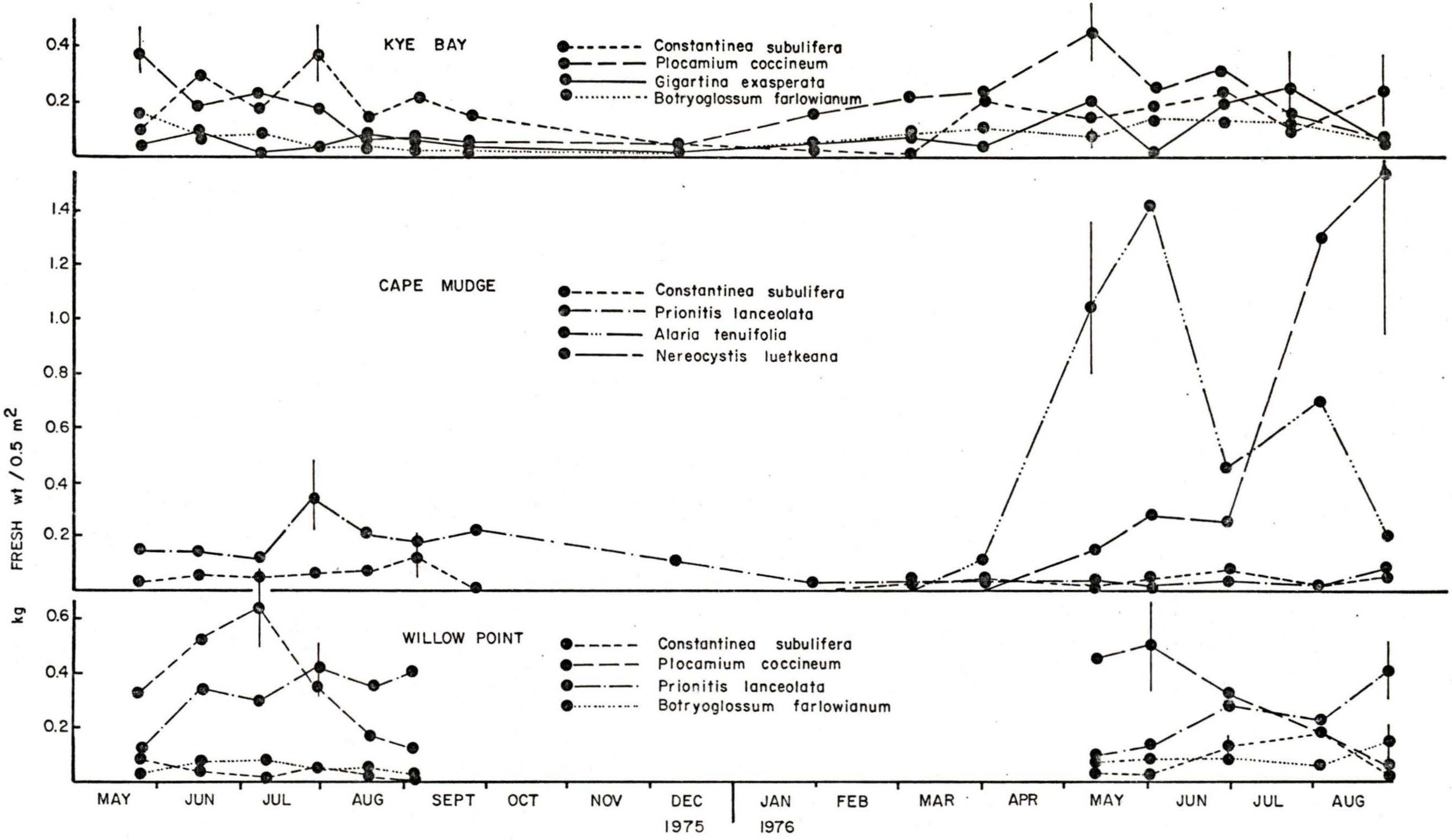


kg FRESH wt / 0.5 m²
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± S.E. n = 10
UNLESS NOTED
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
1975
1976

many red algal species, and encrusting species which became more conspicuous in the absence of the frond canopy. In summer, the frond canopy rose 20 to 50 cm above the substrate (except where kelps were present which attained a canopy depth of 1.0 - 3.0 m) and concealed the encrusting forms and substrate. The community was sufficiently dense that clumps of relatively flaccid algal species such as I. cordata, Rhodymenia pertusa, Rhodoglossum californicum and Gigartina exasperata were often supported in a nearly vertical position by neighbouring individuals.

Mean damp-dry biomass of algae which attained a biomass over 10 g/0.5 m^2 are listed for each sample date in Appendix IV. Seasonal presence of frondose algae which never exceeded 10 g/0.5 m damp-dry weight are listed in Appendix V. The total number of species collected in five, 0.5 m^2 quadrats per sample area and date ranged from 10 - 19 in summer and 11 - 17 in winter. A total of 56 species was collected from quadrats over the course of the study. However, in each sample area, four or less species co-occurred with I. cordata and attained a mean biomass over 0.1 kg/0.5 m^2 on any sample date. These species (Figure 12) were not similar in each of the three sample areas. Plocamium coccineum was one of the most abundant co-occurring species at Kye Bay and Willow Point, but was absent at Cape Mudge. Prionitis lanceolata was abundant at both Willow Point and Cape Mudge but not Kye Bay, and the phaeophyte species Alaria tenuifolia and Nereocystis luetkeana dominated at Cape Mudge in the summer of 1976, but were rare in samples at Willow Point and Kye Bay. Those species which persisted in greatest abundance through winter

Figure 12. Standing crop of four most abundant macroalgal species associated with I. cordata at sample sites (mean ± examples of S.E., n = 5); May, 1975.

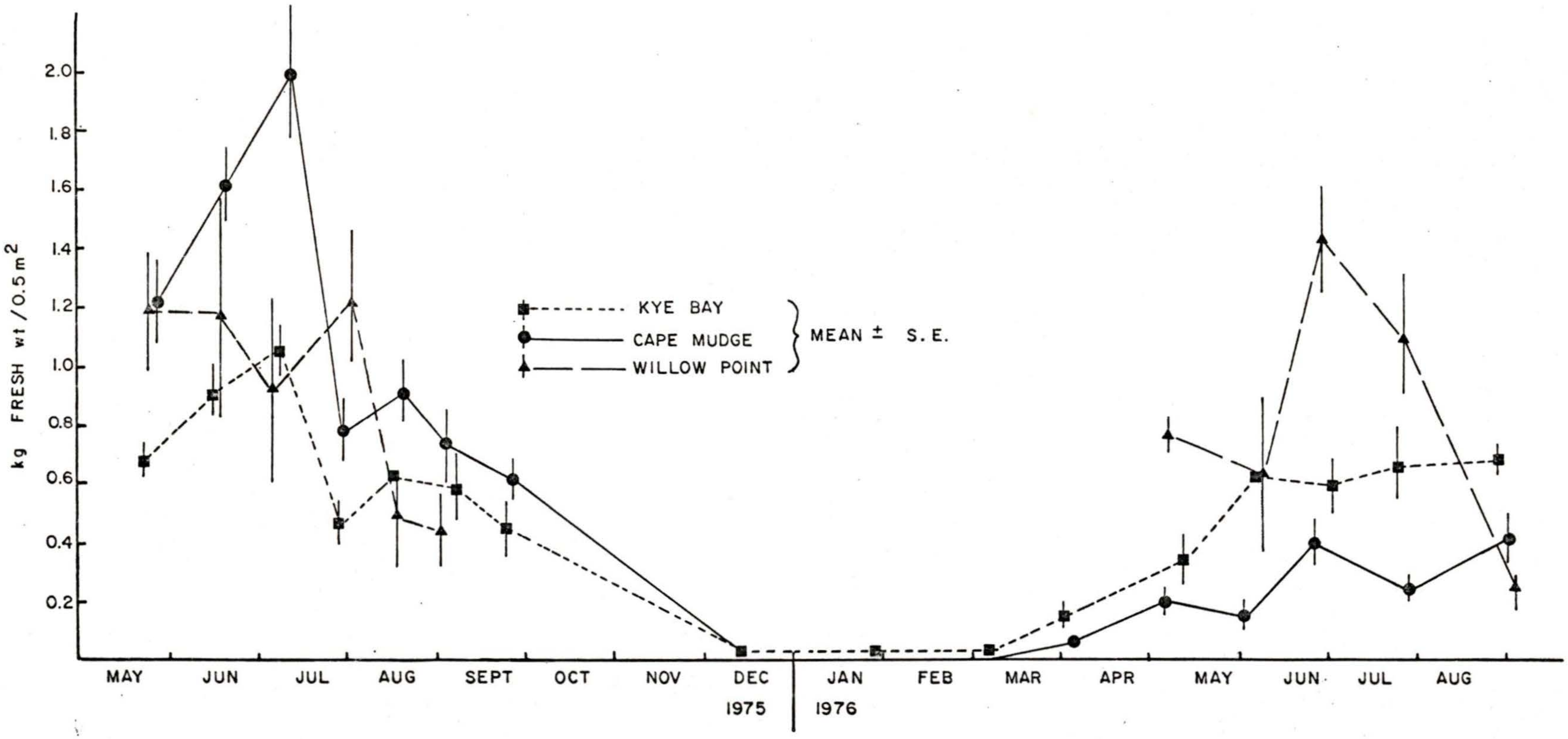

KYE BAY
Constantinea subulifera
Plocamium coccineum
Gigartina exasperata
Botryoglossum farlowianum
CAPE MUDGE
Constantinea subulifera
Prionitis lanceolata
Alaria tenuifolia
Nereocystis luetkeana
WILLOW POINT
Constantinea subulifera
Plocamium coccineum
Prionitis lanceolata
Botryoglossum farlowianum
kg FRESH wt / 0.5 m^2
0.4
0.2
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.6
0.4
0.2
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
1975
1976

were Plocamium coccineum, Prionitis lanceolata and Constantinea subulifera, but even these can be considered only pseudoperennials since they pass through the adverse season in a reduced form (Sears and Wilce, 1975). Only one species, Delesseria decipiens was entirely a winter form. The low biomass, lack of winter annuals and absence of true perennating species in the winter I. cordata community may attest the severity of conditions including low light, increased wave action from storms and scouring action by sand which is present in these areas.

The I. cordata peak standing crops occurred at close to the same time as total community standing crops (June-July) in each sample area in 1975, and were reduced to less than 0.05 kg/0.5 m^2 from December to March (Figure 13). Peak standing crop was followed by a rapid decline at all three areas in the summer of 1975. There was a higher I. cordata peak standing crop at Cape Mudge (2.0 ± 0.23 kg/0.5 m^2) than at Kye Bay (1.1 ± 0.22 kg/0.5 m^2) with intermediate biomass at Willow Point (1.2 ± 0.22 kg/0.5 m^2) in 1975. In 1976 the I. cordata peak standing crop was reduced compared to 1975, by 40 percent at Kye Bay, and most strikingly by 80 percent at Cape Mudge. In the latter area, I. cordata constituted 47 - 82 percent of the total summer standing crop in 1975 but only 7 - 26 percent of the summer standing crop in 1976, the dominant species being Alaria tenuifolia and Nereocystis luetkeana in the latter year.

At Cape Mudge, A. tenuifolia showed considerably more rapid spring growth between March and April, 1976 than did I. cordata and during this period, A. tenuifolia formed a dense canopy above the

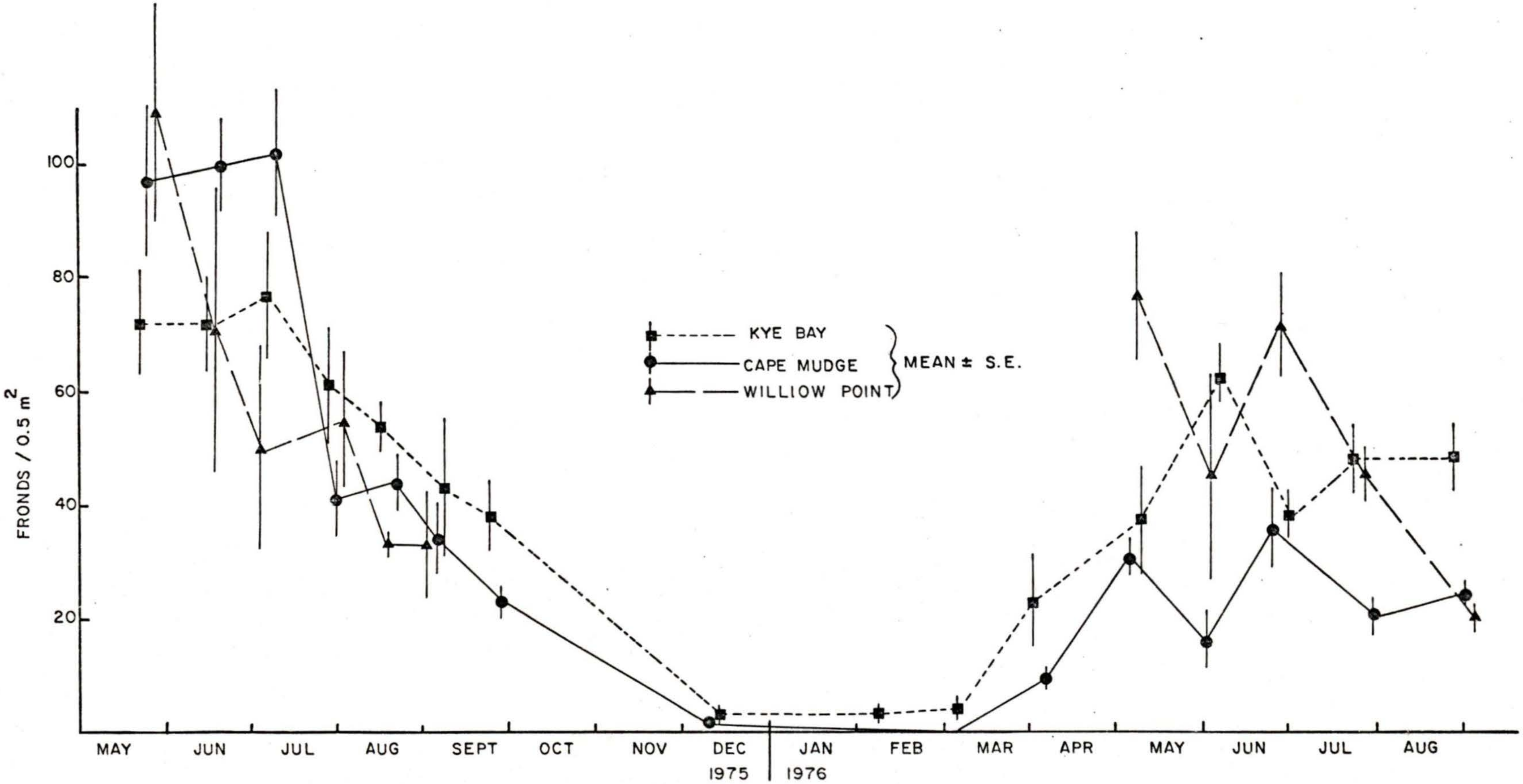
Figure 13. Standing crop of _I_. _cordata_ (mean ± S.E., n = 5); May, 1975 to September, 1976.


kg FRESH wt / 0.5 m2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
KYE BAY
CAPE MUDGE
WILLOW POINT
MEAN ± S. E.
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
1975
1976

smaller frondose algae. *A. tenuifolia* peak standing crop was in late May while *N. luetkeana* peaked three months later in August (Figure 12).

Mean seasonal densities of *I. cordata* fronds longer than 10 cm per 0.5 m^2 quadrat are graphed for each sample area in Figure 14. Density is a function of the size of fronds counted and increased enormously as smaller fronds were included. *I. cordata* fronds longer than 10 cm were examined here as they accounted for over 90 percent of the total *I. cordata* biomass but did not show the sample variability characteristic of smaller fronds. Densities varied considerably between sample areas but were consistent with their respective standing crops. Seasonal variation in density was large with a peak, in *I. cordata* dominated areas, of 60 - 100/0.5 m^2 in early summer, dropping to 20 - 40/0.5 m^2 in late summer and then to a low of 0 - 5/0.5 m^2 in winter. Highest mid-summer densities were observed at Cape Lazo in 1975 (102 ± 0.5 m^2), but in the following summer, this same area contained the lowest summer densities with a maximum of 36 ± 7/0.5 m^2, resulting from competition with *A. tenuifolia* and *N. luetkeana*. In addition to kelp fronds shading and outcompeting *I. cordata* for light, kelp holdfasts competed for space by growing over *I. cordata* basal crusts, thereby reducing the number of *I. cordata* sporelings producing large upright fronds. A parallel case was observed with *P. coccineum* which grew in dense clumps at Kye Bay and Willow Point and was observed to collect a layer of sand at its base. Underneath the sand, even most encrusting algae appeared to die back, and bare rock was commonly observed.

Figure 14. Density of _I_. _cordata_ fronds greater than 10 cm long (mean ± S.E., n = 5); May, 1975 to September, 1976.



FRONDS / 0.5 m²
100
80
60
40
20
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
JAN
1976
FEB
MAR
APR
MAY
JUN
JUL
AUG
KYE BAY
CAPE MUDGE
WILLIOW POINT
MEAN ± S.E.

Periodicity of I. cordata Life Phases

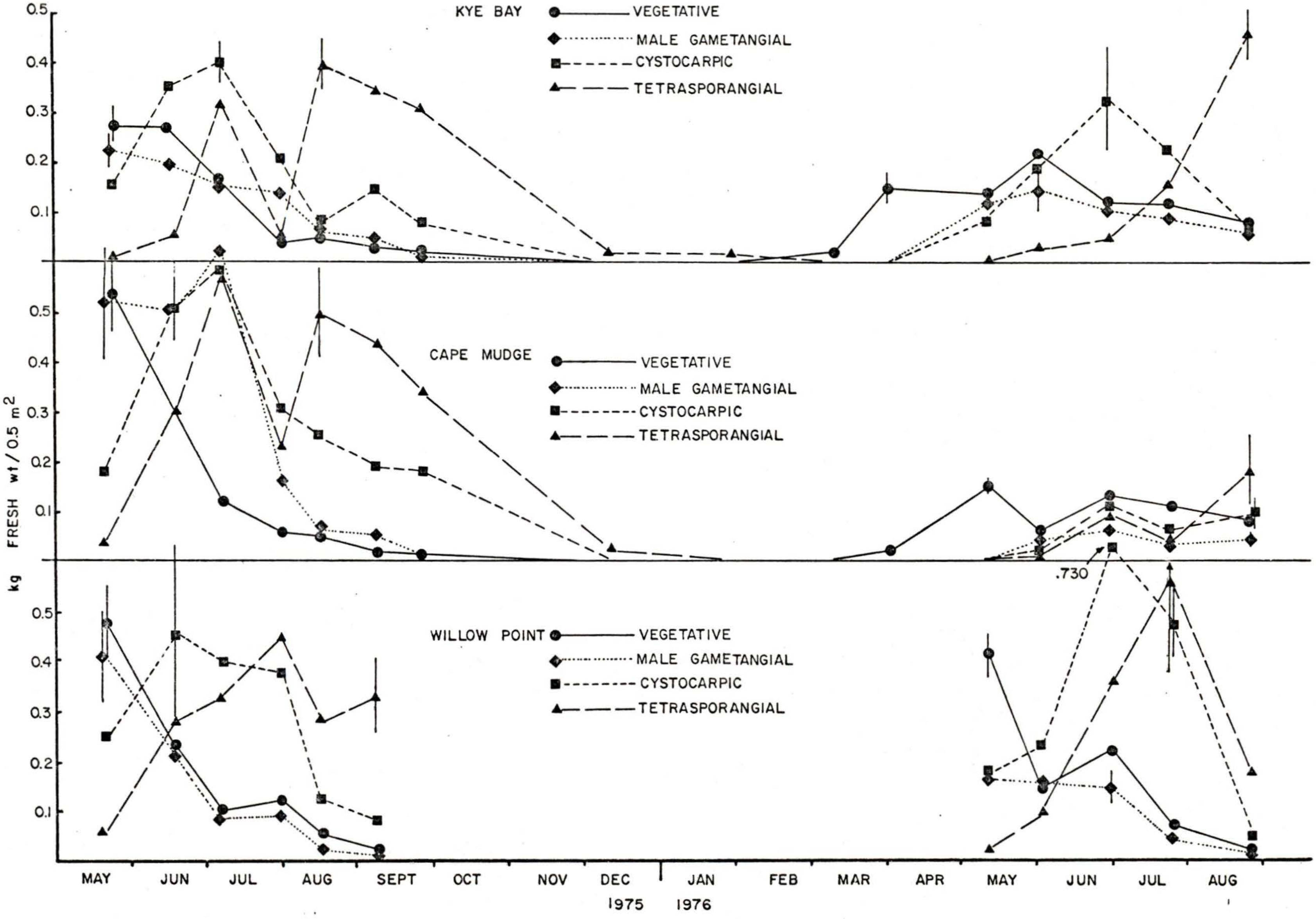
(a) standing crop

Mean biomass of the life phases of I. cordata sampled May, 1975, to August, 1976, at Kye Bay, Cape Mudge and Willow Point is graphed in Figure 15. The standard errors of these means (listed in Appendix IV) are large due to the variability in total I. cordata sample biomass and the small sample number (5), but significant trends were duplicated at all three sample areas.

The standing crop of all life phases was higher during the spring and summer months (March through August) than in fall and winter. Vegetative plants which had no macroscopically visible reproductive structures increased during Feburary through May and declined to a low in December. After July, vegetative frond standing crop was low as almost all large fronds were reproductive. Male gametophyte fronds increased in April and May, declining to near zero by the end of September. Standing crop of cystocarpic fronds increased from the beginning of April and was at first smaller than, but eventually surpassed the standing crop of male gametophyte fronds. At all three sample areas, cystocarpic fronds showed a sharp peak in standing crop at the end of June, then declined to near zero by December. Tetrasporangial fronds increased from mid May to a peak standing crop in late August, then declining through the fall with a few fronds remaining until February and March.

In the summer of 1975 an interesting phenomenon occurred at Kye Bay and Cape Mudge where tetrasporangial fronds showed a peak in mid July, coincident with and similar in size to the cystocarpic

Figure 15. Standing crop of _I_. _cordata_ per life phase (mean ± examples of S.E., n = 5); May, 1975 to September, 1976.


KYE BAY
VEGETATIVE
MALE GAMETANGIAL
CYSTOCARPIC
TETRASPORANGIAL
CAPE MUDGE
VEGETATIVE
MALE GAMETANGIAL
CYSTOCARPIC
TETRASPORANGIAL
WILLOW POINT
VEGETATIVE
MALE GAMETANGIAL
CYSTOCARPIC
TETRASPORANGIAL
.730
kg FRESH wt / 0.5 m^2
0.5
0.4
0.3
0.2
0.1
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
1975
1976

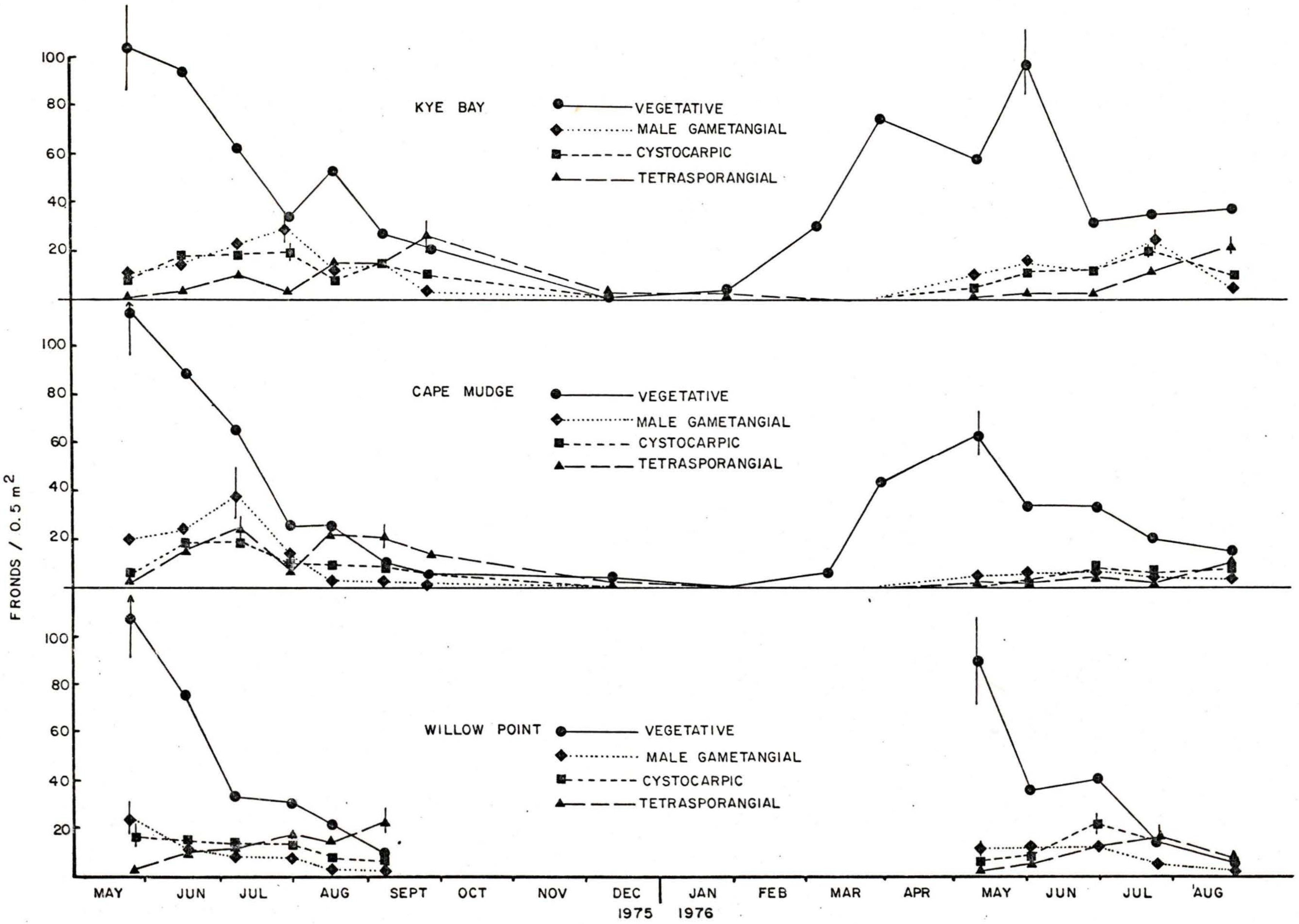
standing crop, but on the following sample date at the end of July the standing crop of both had been reduced by more than 40 percent. By the end of August, tetrasporangial fronds had regrown to their previous abundance, while cystocarpic fronds continued to decline in abundance. The coincidence of the peaks in standing crops of cystocarpic and tetrasporangial fronds in mid-summer, 1975 corresponded with the sharp peak in total I. cordata standing crop achieved in this year at Cape Mudge and Kye Bay. The separated peaks of these two life phases in 1976 corresponded with a flattened peak in I. cordata standing crop.

Where I. cordata was in competition with laminarians at Cape Mudge in 1976, neither gametangial nor tetrasporangial fronds reached biomass levels achieved in 1975. The major difference in life phase abundance was the greater percentage of vegetative fronds remaining through the summer. But the percent abundance of reproductive life phases followed the trends where no competition existed (Figure 15). Gametangial fronds were more abundant in early summer, followed by tetrasporangial fronds in August. Thus the suppressed growth of I. cordata caused by the development of a laminarian canopy resulted in a smaller percentage of fronds developing reproductive tissue, but did not disrupt the sequence in development of the three reproductive generations.

(b) densities

The density of fronds (longer than 5 cm) in each life history phase is graphed in Figure 16. The inclusion of fronds in the 5 -

Figure 16. Density of I. cordata fronds greater than 5 cm long per life phase (mean ± examples of S.E., n = 5) May; 1975 to September, 1976.


KYE BAY
CAPE MUDGE
WILLOW POINT
VEGETATIVE
MALE GAMETANGIAL
CYSTOCARPIC
TETRASPORANGIAL
FRONDS / 0.5 m²
100
80
60
40
20
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
JAN
1976
FEB
MAR
APR
MAY
JUN
JUL
AUG

10 cm size category permitted examination of the stock of juveniles from which the larger reproductive fronds develop. Vegetative fronds (mainly 5 - 10 cm in size) were numerically dominant throughout the spring and early summer, with mean peak densities in the I. cordata dominated sample areas over 90/0.5 m^2. Vegetative frond densities fell rapidly in July and August however, to an extreme low of 0 - 1/0.5 m^2 in December.

The mean density of male gametophyte fronds per sample area (maximum = 39 ± 10.0/0.5m^2) at times exceeded cystocarpic fronds (maximum 22 ± 2.7/0.5 m^2) during the summer. However, cystocarpic fronds eventually surpassed the male fronds in total standing crop because of the greater individual cystocarpic frond size. Mean fresh weight of male fronds in five, 0.5 m^2 samples at Cape Mudge in July, 1975 was 15 ± 1.4 g (n = 196) while cystocarpic fronds averaged 30 ± 2.9 g (n = 98) (some cystocarpic fronds reached 100 g fresh weight). The number of both male and cystocarpic fronds was similar to, or greater than tetrasporangial fronds from May until August, when the latter became dominant due to a decline in gametophyte density. Maximum density of tetrasporangial fronds was 22.0 ± 7.3/0.5 m^2. All densities were depressed at Cape Mudge, in 1976, when laminarians dominated.

(c) population size structure

Size structure was examined to obtain information on the dynamics of population growth. Area of fronds was used as an index of growth and a total of 5,752 fronds from Kye Bay and Cape Mudge were measured. Figures 17 and 18 show the frequency of fronds in

Figure 17. Percent frequency of I. *cordata* fronds per life phase and size class, Kye Bay; May, 1975 to September, 1976.

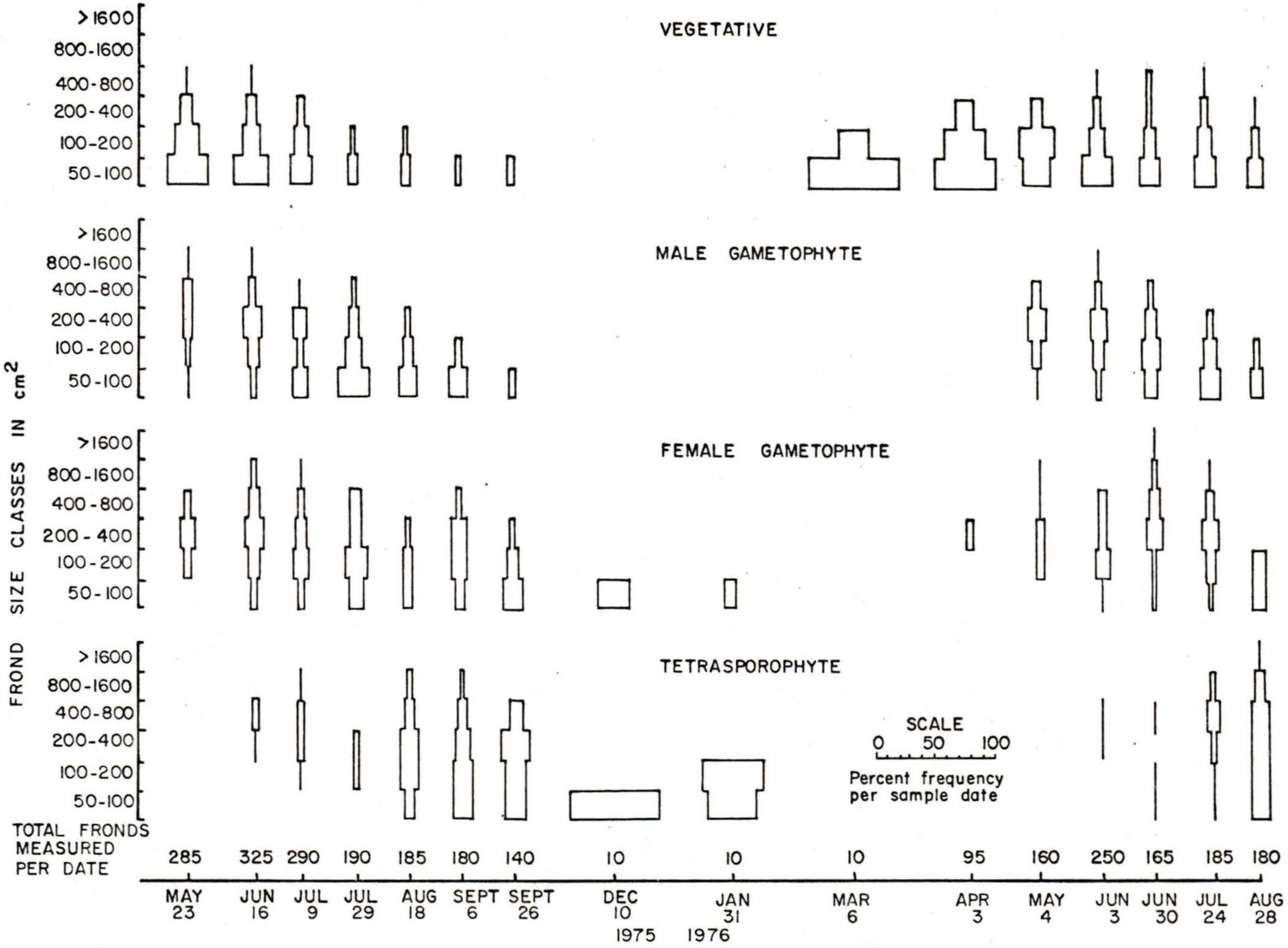
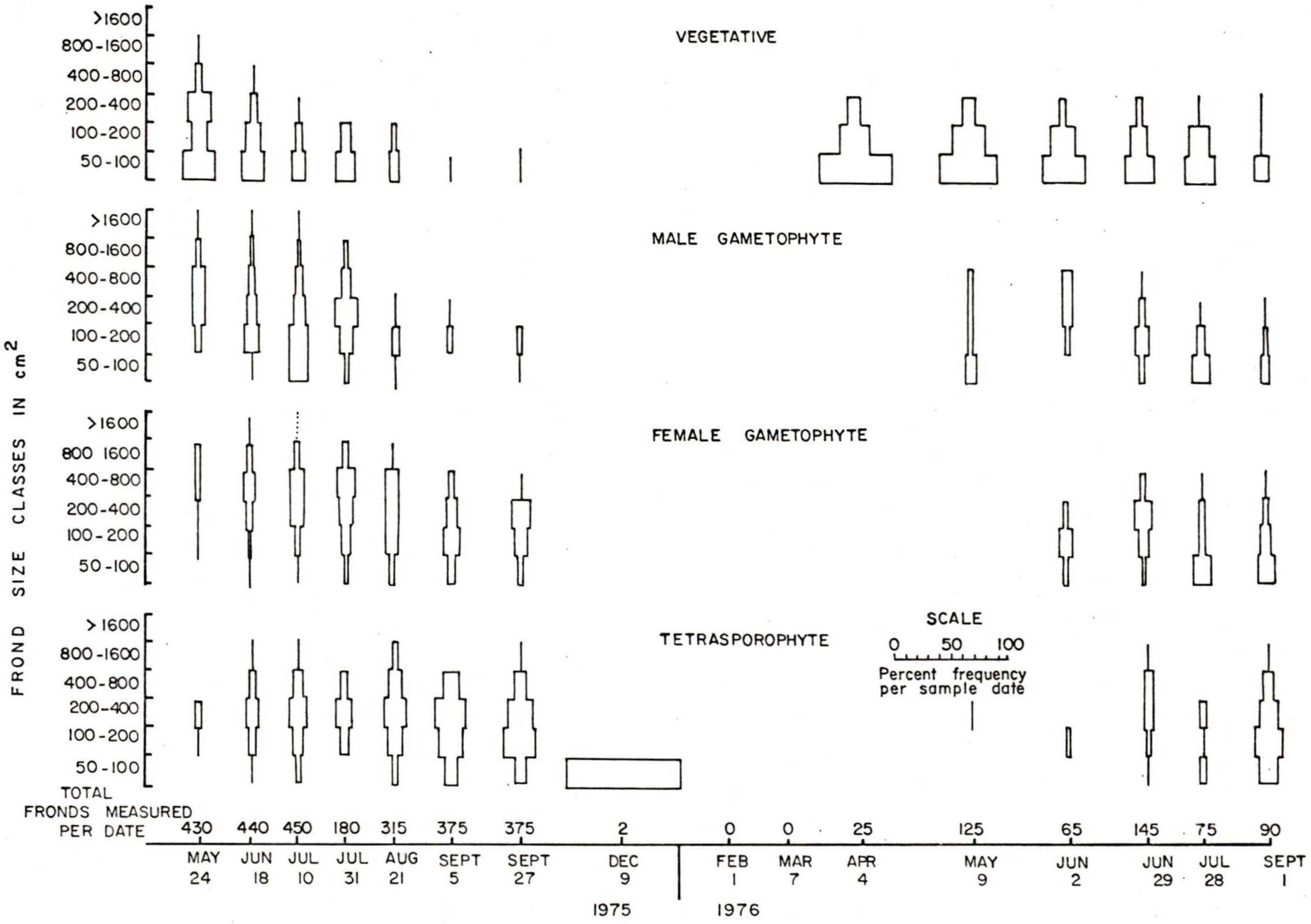

VEGETATIVE
MALE GAMETOPHYTE
FEMALE GAMETOPHYTE
TETRASPOROPHYTE
FROND SIZE CLASSES IN cm^2
>1600
800-1600
400-800
200-400
100-200
50-100
SCALE
0 50 100
Percent frequency per sample date
TOTAL FRONDS MEASURED PER DATE
285
325
290
190
185
180
140
10
10
10
95
160
250
165
185
180
MAY 23
JUN 16
JUL 9
JUL 29
AUG 18
SEPT 6
SEPT 26
DEC 10
JAN 31
MAR 6
APR 3
MAY 4
JUN 3
JUN 30
JUL 24
AUG 28
1975
1976

Figure 18. Percent frequency of I. *cordata* fronds per life phase and size class, Cape Mudge; May, 1975 to September, 1976.


VEGETATIVE
MALE GAMETOPHYTE
FEMALE GAMETOPHYTE
TETRASPOROPHYTE
FROND SIZE CLASSES IN cm^2
>1600
800-1600
400-800
200-400
100-200
50-100
SCALE
0 50 100
Percent frequency per sample date
TOTAL FRONDS MEASURED PER DATE
430 440 450 180 315 375 375 2 0 0 25 125 65 145 75 90
MAY 24
JUN 18
JUL 10
JUL 31
AUG 21
SEPT 5
SEPT 27
DEC 9
FEB 1
MAR 7
APR 4
MAY 9
JUN 2
JUN 29
JUL 28
SEPT 1
1975
1976

the six size classes: 50 - 100 cm^2, 100 - 200 cm^2, 200 - 400 cm^2, 400 - 800 cm^2, 800 - 1600 cm^2 and > 1600 cm^2.

Fronds less than 50 cm^2 and less than 5 cm long were not collected in regular sampling and their seasonal abundance is discussed below.

Fronds less than 50 cm^2 in area but greater than 5 cm long (usually 30 - 40 cm^2) were not diagrammed as they accounted for very little biomass but were disproportionately high in number, except in December and January. No fronds less than 50 cm^2 were reproductive at any time of the year. In spring the majority of less than 50 cm^2 fronds were thin and translucent with smooth edges. These immature fronds were present in March through September but disappeared by December and had apparently exfoliated along with mature fronds.

As diagrammed in Figures 17 and 18, small vegetative fronds 50 - 200 cm^2 formed the largest percentage of the total frond numbers (> 50 cm^2) in March and April. The successive reduction in percentage of vegetative fronds from May through September, correlated with, first an increase in percentage of male gametophyte fronds in May, secondly an increase in cystocarpic fronds in June, and thirdly an increase in tetrasporangial fronds in August. The successive appearance of reproductive phases suggests different growth rates of the reproductive fronds, gametophytes developing more quickly than sporophytes.

In early summer, most reproductive fronds (male, cystocarpic and tetrasporangial) were observed in the larger size classes, while as the summer progressed, the proportion of reproductive fronds increased in the small size classes. Evidently most vegetative fronds grew to a size of 200 - 400 cm^2 in early summer before reproductive tissue developed, but in later months, smaller and smaller fronds were observed to have reproductive sori. Some of the increase in number of reproductive fronds in small size classes was due to exfoliation of portions of mature large fronds, but in addition, small fronds developed sori in late summer and fall while only large fronds developed sori in early and mid summer.

Large male and cystocarpic fronds, over 800 cm^2, were present only in June through August. Large tetrasporangial fronds were present only in July through September. The life span of these large thalli was thus of short duration.

In the spring of 1975, tetrasporangial fronds developed earlier and more rapidly at Cape Mudge than at Kye Bay (Figures 17 and 18). Under favourable growth conditions, the difference in growth rates of cystocarpic and tetrasporangial fronds may be reduced. It was noted that fronds at Cape Mudge grew to a larger size than at Kye Bay in 1975 which could be attributed to enhanced growth rates as a result of high current velocity or higher nutrient concentrations at Cape Mudge.

(d) frond initials

_I_. _cordata_ frond initials (less than 5 cm long) were present in large numbers on cobble substrate in both winter and summer at Kye Bay (Table I). There were approximately 10 cobbles per 0.5 m^2 quadrat with _I_. _cordata_ holdfasts and the density of frond initials

Table I. Seasonal frequency of *I. cordata* holdfasts, 0.5-5.0 cm long frond initials and fronds greater than 5 cm long on cobbles from Kye Bay.

Date	Cobbles examined	Mean±S.E. holdfasts per cobble	Mean±S.E. fronds 0.5-5 cm/cobble	Mean±S.E. fronds >5 cm/cobble
Sept. 4, 1975	5	3.8±1.5	50±16.2	7.4±1.9
Dec. 11, 1975	5	3.4±0.7	57±12.6	0.0±0.0
Feb. 1, 1976	5	7.2±1.4	75±29.9	2.4±2.2
Mar. 6, 1976	5	8.8±1.7	62±15.9	9.6±1.5
May 10, 1976	5	6.8±1.8	31±9.0	3.8±1.4

(0.5 - 5 cm long) was estimated to be 310 - 750/0.5 m^2 during the winter to summer sample period. Variation in number of frond initials between cobbles was too large to detect significant seasonal variations with observations of five cobbles. It was observed that many frond initials elongated in March and by early May had grown longer than 5 cm.

Analysis of frond distribution on cobbles in May indicated that most fronds longer than 5 cm grew from holdfasts where there was a cluster of five or more frond initials. Holdfasts with less than five frond initials accounted for 25 ± 10 percent of the total frond initials present. Thus most frond initials developed from large holdfasts which were either several years old or were formed by the coalesence of many spores to produce a clump of uprights.

The area of bare rock (emergent from sand) which could be colonized by spores on cobbles collected from Kye Bay in September varied from less than 1 to 45 percent and the mean area was 13 ± 3 percent (n = 15). A relatively large percentage of the cobble surfaces was covered only by encrusting species but this area was not included in the estimate of bare rock as the degree of hindrance of encrusting species to spore settlement is not known.

(e) reproductive maturation

Male _I. cordata_ fronds were the first life phase to be macroscopically distinguished from vegetative fronds in spring. Male fronds were more transparent and thinner than other life phases of the same size, and could be identified first by a mottled coloration near the periphery of the base of the frond. The mottling consisted of lightly pigmented areas interspersed with slightly darker pigmented tan to purple regions and corresponded with the production of spermatia in broad patches on the frond surface (Figure 19). The entire surface of more mature fronds was usually a light tan color compared to the dark purple of most cystocarpic and tetrasporangial fronds. In very mature male fronds, endophytes and diatom epiphytes were numerous, often giving the frond a greenish hue. Large fronds were prone to tearing and eventually broke off leaving the more rigid apophysis region (area where stipe and blade converge) as a stub (Figure 20).

Cystocarpic and tetrasporangial reproductive structures develop in discrete sori, visible macroscopically. Maturation of these sori was distinct for each life phase.

Cystocarpic fronds were recognized initially in early summer by the macroscopic appearance of developing cystocarps which consisted of an opaque donut-shaped differentiation of tissue 0.5 - 1.0 mm in diameter. When these immature sori appeared, they were sparsely distributed (2 - 5/cm^2) over most of the frond surface, but were absent from fresh growing tips and the apophysis (Figure 21). Later in the summer as the cystocarps matured, they darkened to a red color and became swollen, to 2 mm in diameter, producing a prominent bulge on the surface of the frond, as well as becoming more dense in number and spreading to the rest of the frond (Figure 22). On older plants, all but the apophysis had mature sori extending to and abutting the frond margin.

Tetrasporangial sori were first noted on immature fronds as tiny red dots macroscopically visible as a reddish 'rash' along the lateral

Figure 19. Male _I. cordata_ frond distinguished by thin, filmy texture.

Figure 20. Very mature male _I. cordata_ frond with distal end worn away.

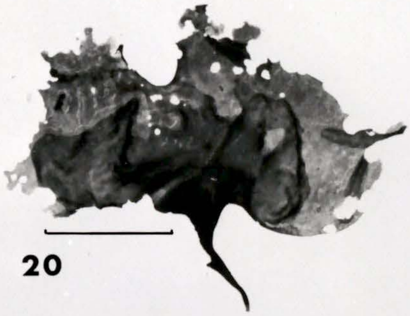
Figure 21. Immature cystocarpic _I. cordata_ with sparse distribution of cystocarps (C) in localized areas of frond.

Figure 22. Mature cystocarpic _I. cordata_ with dense distribution of cystocarps over much of frond.

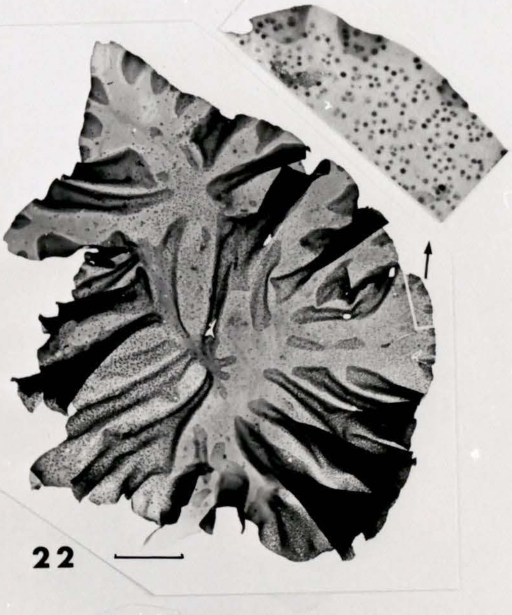
Figure 23. Immature tetrasporangial _I. cordata_ with 'rash' of sori (S) near sterile margin (M).

Figure 24. Very mature tetrasporangial _I. cordata_ with very dense cover of sori and ragged edges.

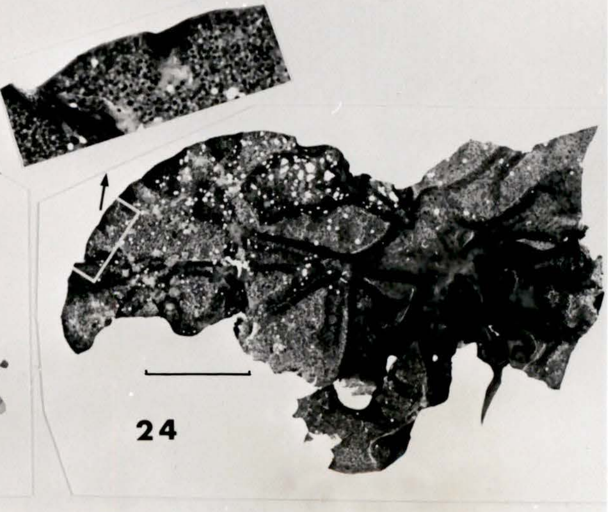

19


20


21


22


23

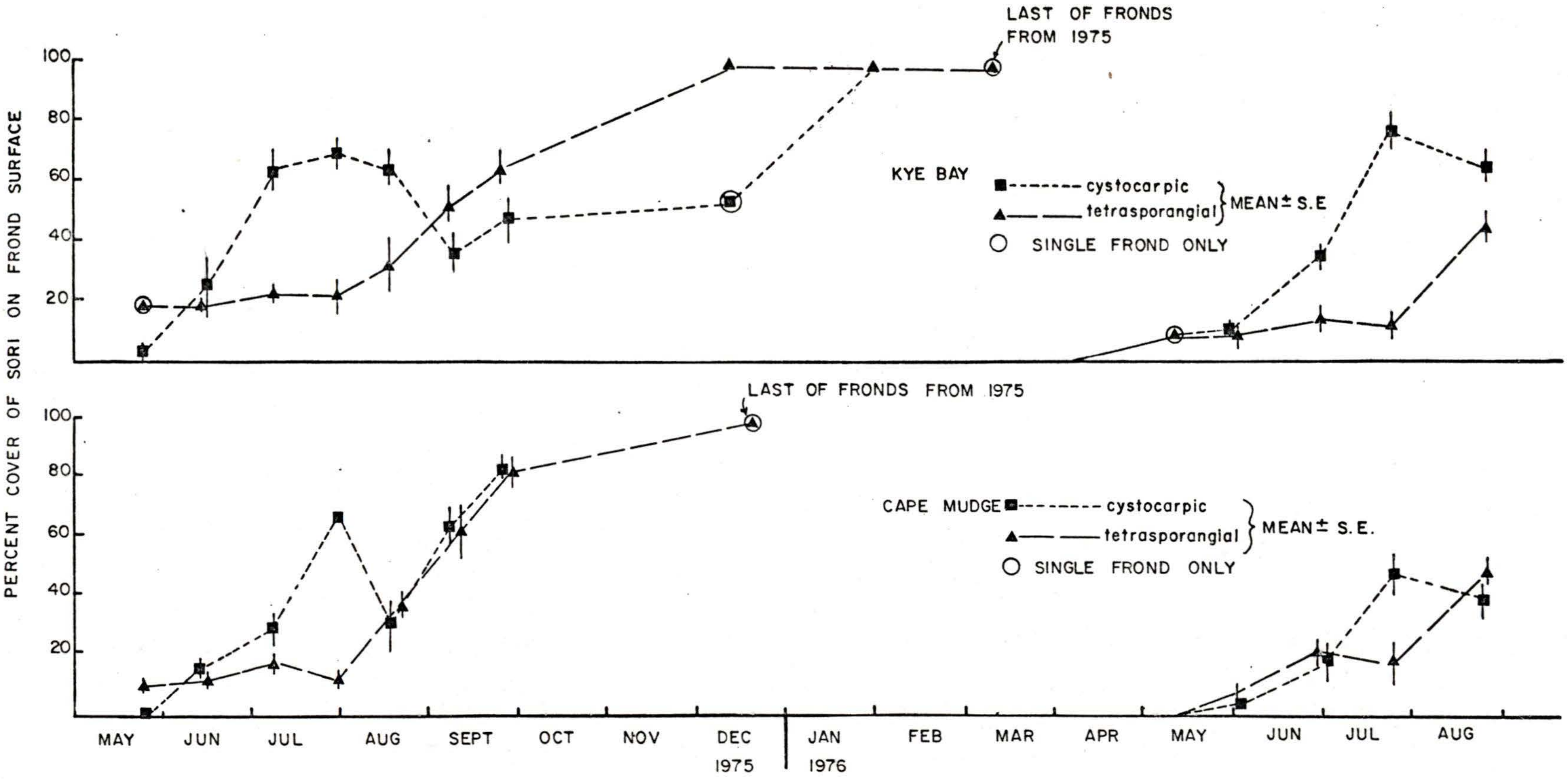

24

edges of the blade. There was always a narrow 0.5 - 1.5 mm margin of frond with no sori between this rash and the distal edge of the frond (Figure 23). As the season progressed, the tetrasporangial sori became larger to 1 mm in diameter (often irregular in shape) and dispersed over the entire lower half of the frond, excluding the apophysis and 0.5 to 1.5 mm margin. At first the growing tips had no sori but finally in late summer fronds were observed with even the tips of the blade bearing sori (Figure 24). Eventually as the frond deteriorated, the 0.5 to 1.5 mm margin exfoliated leaving no vegetative margin and presumably exposing soral cavities directly to the water. The apophysis bore no sori, even on very old and ragged fronds.

The percentages of total frond area covered by sori per sample date are illustrated for cystocarpic and tetrasporangial fronds at Kye Bay and Cape Mudge in Figure 25. Immature cystocarpic fronds were noted in May, but percent cover of sori quickly increased through June to a maximum sorus cover of 70 percent in mid-July. In August and September, fewer fronds were present but many of these had a lower cover of sori than in July suggesting that they were not of the same population that had reached full maturity in July. A very few cystocarpic fronds with 100 percent cover of sori were collected in early February, but none of these old fronds remained when the first immature cystocarpic fronds were observed in April and May.

Tetrasporangial fronds showed a different rate of maturation than cystocarpic fronds. Immature fronds with 10 - 20 percent cover of sori were first observed in May, but the mean percent cover of

Figure 25. Percent reproductive maturity of cystocarpic and tetrasporangial _I. cordata_ fronds expressed as frond area covered by sori divided by the total frond area in 0.5 m^2 samples (n = 5); May, 1975 to September, 1976.


LAST OF FRONDS FROM 1975
PERCENT COVER OF SORI ON FROND SURFACE
100
80
60
40
20
KYE BAY
■------- cystocarpic
▲—— —— tetrasporangial
MEAN ± S.E
○ SINGLE FROND ONLY
LAST OF FRONDS FROM 1975
100
80
60
40
20
CAPE MUDGE
■------- cystocarpic
▲—— —— tetrasporangial
MEAN ± S.E.
○ SINGLE FROND ONLY
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
JAN
1976
FEB
MAR
APR
MAY
JUN
JUL
AUG

tetrasporangial sori increased more slowly than cystocarpic sori to a maximum of 100 percent in mid-December. A few old ragged fronds with 100 percent cover remained through the winter until March of the following year.

The percent cover of cystocarpic and tetrasporangial sori times the total mean area of fronds per 0.5 m^2 of bottom is graphed in Figure 26 for Kye Bay and Cape Mudge per sample date. This measurement indicates the relative reproductive potential or spore output of the life history phase for each sample date. Cystocarpic fronds showed a peak in early July and tetrasporangial fronds showed a peak in early September at both Kye Bay and Cape Mudge in 1975 and 1976. The relative reproductive potential for both life phases at Cape Mudge in the summer of 1976 was much reduced over the previous summer due to the dominance of *Alaria tenuifolia* in the latter year.

Growth Rates of Gametophyte and Tetrasporophyte *I. cordata* Fronds

A total of 120 *I. cordata* fronds were transplanted and measured for weight and area during the summer of 1976 to investigate the growth of gametophyte and tetrasporophyte *I. cordata* fronds at different depths (-0.5, -2.0, -4.0 and -6.0 m) and in mid and late summer. Fronds which were obviously torn or ragged at the end of the experimental period were not measured for growth due to the variance they would introduce to the data.

The growth curves for several fronds at the shallowest depth (-0.5 m below chart datum) are shown in Figure 27. Large fronds, initially 15 - 30 g (20 - 25 cm long) when transplanted, reached a

Figure 26. Reproductive potential of cystocarpic and tetrasporangial I. cordata fronds expressed as mean frond area covered by sori per 0.5 m^2 sample ($n = 5$); May, 1975 to September, 1976.

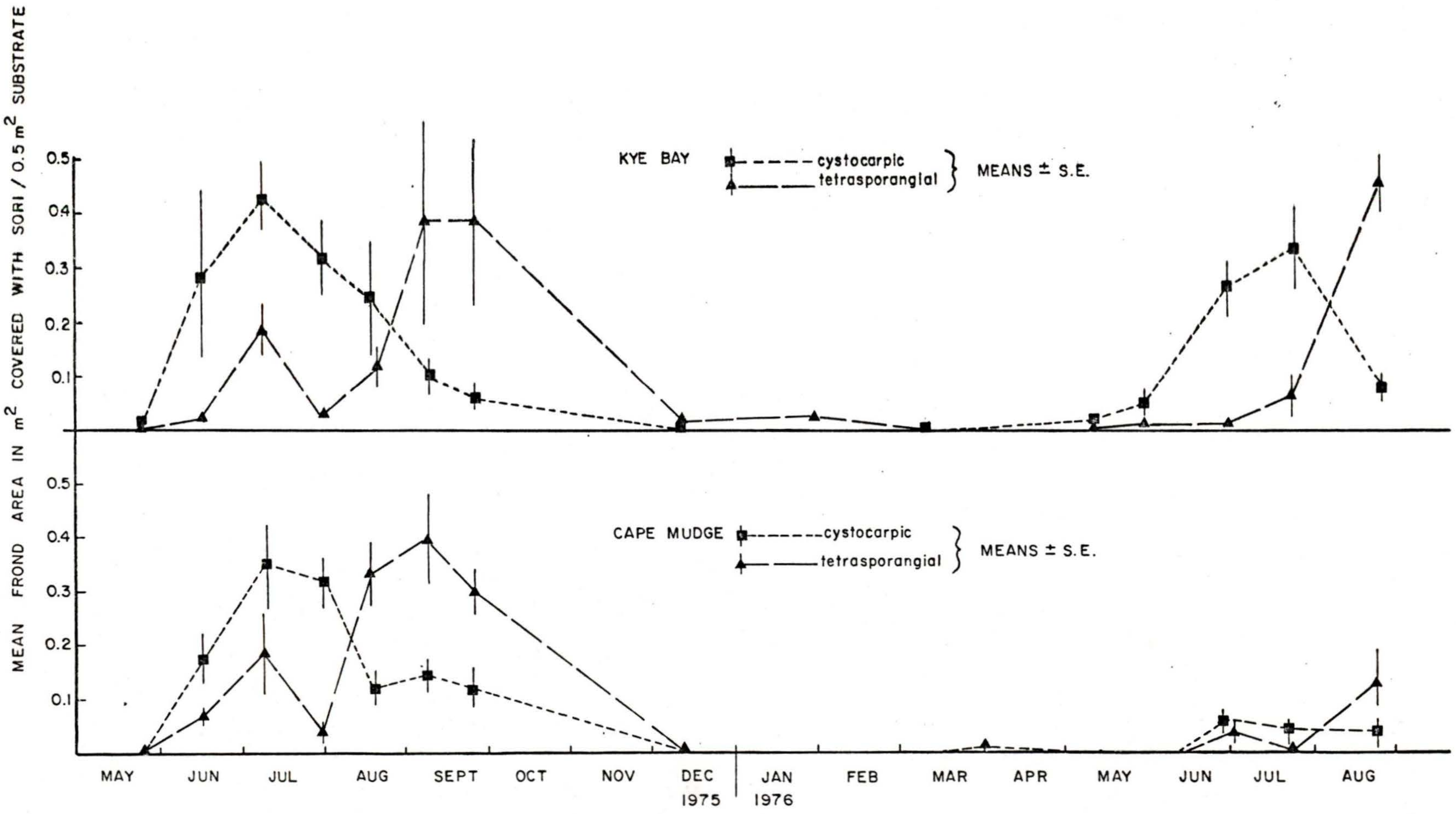
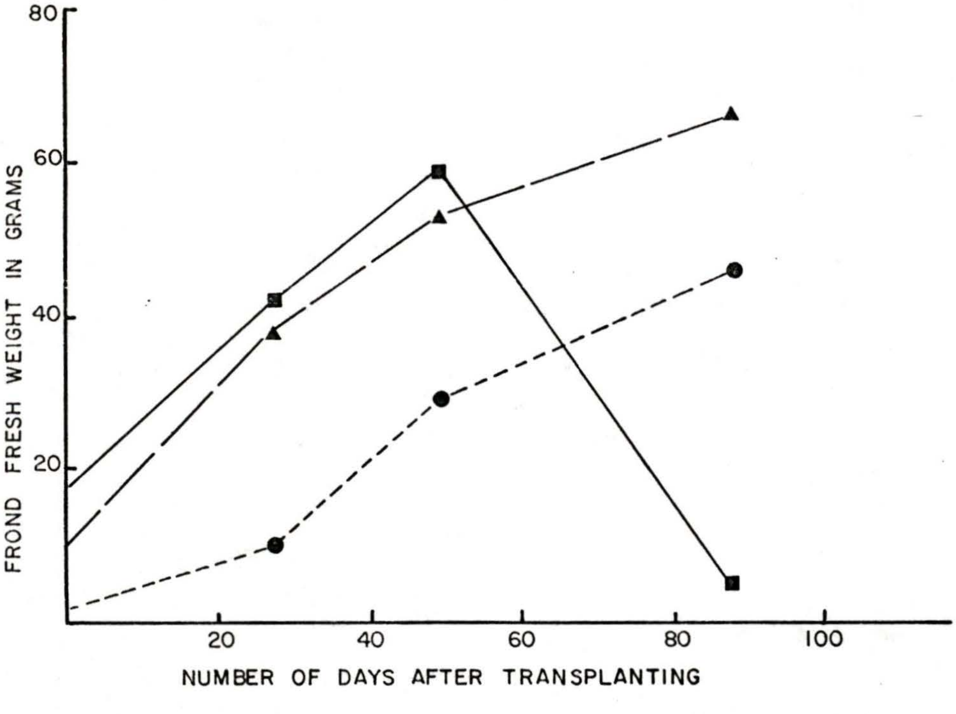

MEAN FROND AREA IN m^2 COVERED WITH SORI / 0.5 m^2 SUBSTRATE
0.5
0.4
0.3
0.2
0.1
KYE BAY
cystocarpic
tetrasporangial
MEANS ± S.E.
CAPE MUDGE
cystocarpic
tetrasporangial
MEANS ± S.E.
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
1975
JAN
1976
FEB
MAR
APR
MAY
JUN
JUL
AUG

Figure 27. Growth curves for individual small ● , medium ▲ and large ■ (by weight) I. cordata fronds transplanted on June 3, 1976.


FROND FRESH WEIGHT IN GRAMS
80
60
40
20
20
40
60
80
100
NUMBER OF DAYS AFTER TRANSPLANTING

peak weight of 50 - 100 g and were reduced to small stubs within 90 days. Medium size fronds, initially 5 to 15 g reached close to peak weight and were torn and ragged at the end of 90 days. The smallest fronds, initially less than 2 g (5 cm long) were still below peak weight and in apparently vigorous growing condition after 90 days. From these growth curves it was interpolated that a juvenile frond weighing 2 - 5 g in mid-May would reach maximum size in 90 - 125 days.

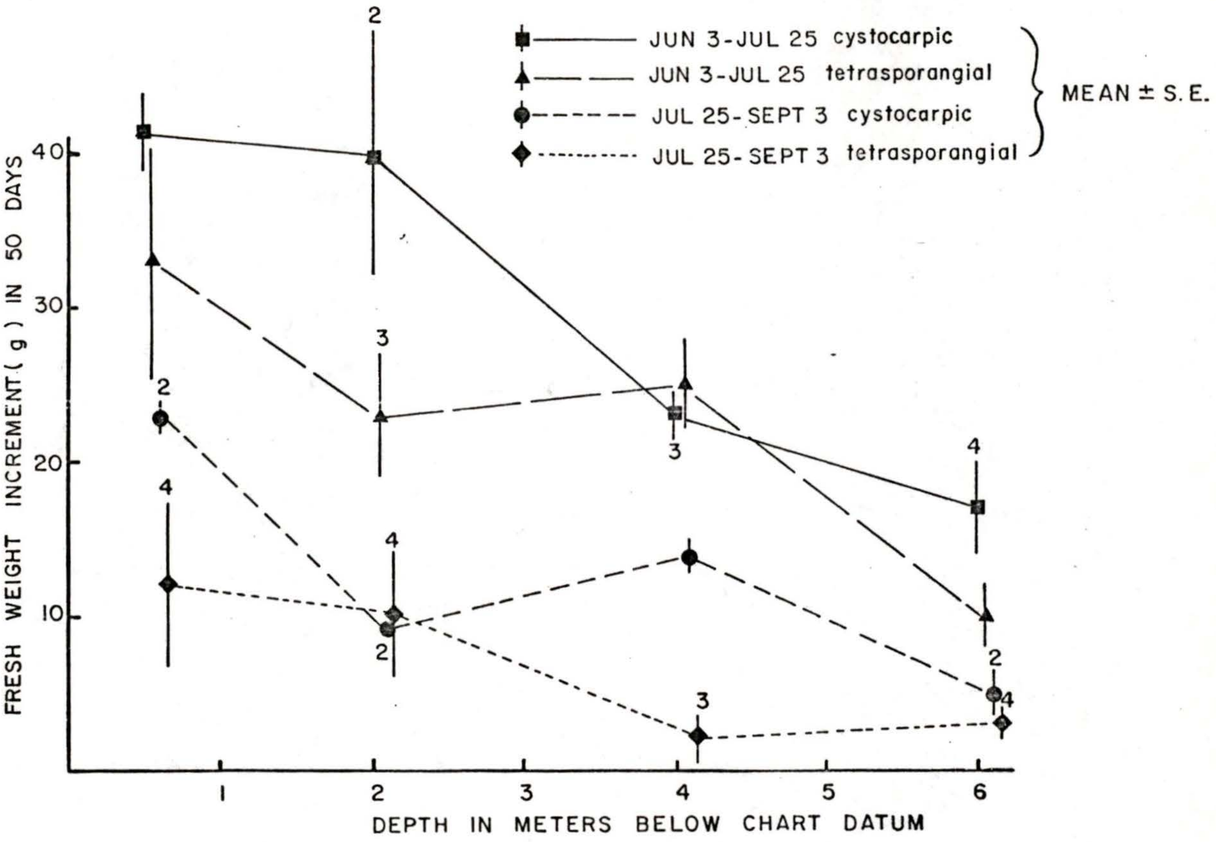
For comparison of growth rates with depth, time and life phase in Georgia Strait, the weight increments of medium size fronds (10 - 15 cm long) were examined. Computation of a three way analysis of variance[1] suggested that significant differences in growth rates were accounted for by all three variables: life phase, depth and time (ANOVA tables and additional information leading to this conclusion are presented in Appendix VI).

The mean growth rate of all fronds at any one depth was two to three times larger for the mid summer growth interval than late summer (Figure 28). These results were consistent with the senescence and die-back of old I. cordata fronds toward late summer with only limited growth of younger fronds, resulting in an overall decrease in standing crop. A comparison of growth with depth revealed the highest mean growth rate occurred nearest the surface (0.5 m below chart datum). Growth at 6.0 m below chart datum was 30 - 40 percent of that at -0.5 m in mid summer and 20 - 25 percent of that at -0.5 in late summer.

---

[1] Using a computer program for multivariate analysis of variance; program distributed by Clyde Computing Service, Box 166, Coconut Grove Station Miami, Florida 33133. Adapted for Ohio State University by David Poor and Lorne Rosenblood, Social Psychology Laboratory, 404C W. 17th Avenue, Columbus, Ohio 43210.

Figure 28. Mean growth rate of cystocarpic and tetrasporangial fronds in mid and late summer with depth (n = 5 except where noted).



JUN 3-JUL 25 cystocarpic
JUN 3-JUL 25 tetrasporangial
JUL 25-SEPT 3 cystocarpic
JUL 25-SEPT 3 tetrasporangial
MEAN ± S.E.
FRESH WEIGHT INCREMENT (g) IN 50 DAYS
40
30
20
10
1
2
3
4
5
6
DEPTH IN METERS BELOW CHART DATUM
2
3
2
4
4
2
3
3
4
2
4

A larger growth rate was observed for cystocarpic fronds in mid and late summer (Figure 28). Because of the large variability in weight increments between individual fronds, the difference in growth rates of these two life phases for any one depth was not significant, and only when all depths were considered and two dates combined were there sufficient data to indicate the high probability of such a difference. It is likely that a portion of the variability in frond growth rates was due to the handling of fronds during measurements and replacement in the sea, resulting in the tearing and subsequent loss of small portions of the fronds. Variability was also introduced because the initial weight of all fronds was not the same, varying between 5 to 20 g although the sizes selected for each test were random.

A comparison of mean weight increments of fronds at the shallower depths for Cape Lazo, Kye Bay and Cape Mudge, and for fronds with excized tips and in baskets (unattached) are listed in Table II. Mean cystocarpic frond increments were consistently larger than tetrasporophyte increments. Growth of fronds which had their tips cut back was very similar to that of uncut fronds suspended at -0.5 m at Cape Lazo. It was apparent that considerable damage to growing apices of _I. cordata_ did not impair frond growth. Figures 29 and 30 indicate how secondary growing tips developed with little growth occurring along the cut or damaged edges. Providing that damage is not too severe, tearing due to wave action or grazing would not result in the loss of the frond or termination of growth.

No growth inhibition due to possible nutrient or light limitation was detected for fronds transplanted to the natural _I. cordata_

Table II. Fresh weight gain±S.E. (g) of 5-30 cm long I. cordata fronds after 49 days, transplanted June 3, 1976.

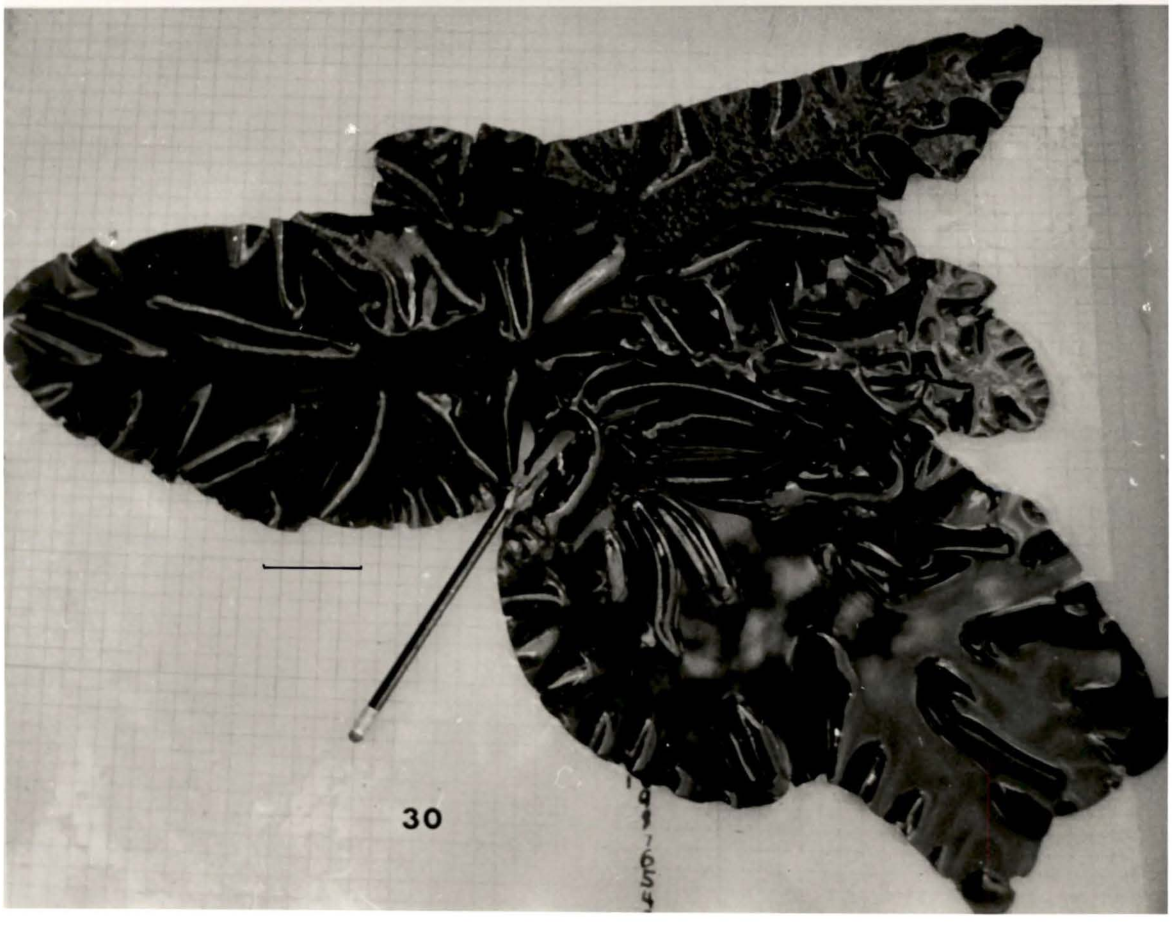
	Suspended at -0.5 m depth at Cape Lazo						
			10-15 cm fronds			Kye Bay on bottom -1.0 m depth	Cape Mudge under laminaria canopy +1.0 m depth
	25-30 cm fronds	5-10 cm fronds		tips removed	in basked unattached		
Female gametophyte	36±7.8 n = 4	29±6.3 n = 5	43±2.5 n = 3	50±8.3 n = 3	18±3.2 n = 6	57±10.2 n = 4	13±2.0 n = 10
Tetrasporophyte			33±7.6 n = 5	20±3.7 n = 3		41±7.8 n = 5	
Mean			38±4.1 n = 10	35±7.8 n = 6		49±6.6[a] n = 9	

[a] mean increase in surface area of fronds on bottom in Kye Bay after 49 days was 625±81 cm^2 (n=9) which equals 12.7 cm^2/day

Figure 29. *I. cordata* frond with growing tip cut off before transplanting.

Figure 30. *I. cordata* frond with excised tip, 50 days after transplanting.

29



30

population at Kye Bay (-1.0m). The transplanted I. cordata was not enveloped within the naturally growing fronds however, but rather lay on top, hence shading by other fronds likely did not occur.

I. cordata fronds in artificial enclosures suspended at Cape Lazo grew at one half the rate of fronds at the same (0.5 m) depth, but attached to rope supports. This slower growth of unattached fronds was attributed to the shading caused by the netting of the enclosure which became fouled quickly with diatoms and hydrozoans. The growth rate at Cape Mudge (+0.5 m) under the Alaria tenuifolia canopy also was considerably slower than at Cape Lazo (-0.5 m), again attributable to the shading from A. tenuifolia.

Colonization of Artificial Substrates in I. cordata Communities

(a) I. cordata spore settlement and growth

Results of spore dispersal studies indicated that considerable numbers of spores adhered within a period of four days to artificial substrate at the base of isolated I. cordata populations in the shallow subtidal (Table III). The highest density of spores (235 ± 29/cm^2) was observed on the settling plate positioned at the base of the largest population consisting of 12 tetrasporangial fronds. Plates 50 to 100 cm away from all three populations had over an order of magnitude smaller spore density (2 ± 0.7 - 7 ± 1.3/cm^2) than those at 0 to 20 cm. However, there was no apparent reduction in spore density at 100 cm compared to 50 cm. These plates may have been settled by spores present in the water column derived from the natural I. cordata populations approximately 200 m distant. Plates at 0 to 20 cm from the isolated populations were touched directly by

Table III. Mean density of red algal spores per cm^2 adhering to settling plates immersed for four days at various distances from isolated *I. cordata* fronds.

	Plate Distance from Fronds											
I. cordata	0 cm			20 cm			50 cm			100 cm		
Frond Numbers	$\bar{Y}$	S.E.	N	$\bar{Y}$	S.E.	N	$\bar{Y}$	S.E.	N	$\bar{Y}$	S.E.	N
3	97	21.3	10	49	6.0	40	2	1.7	40	7	1.3	40
6	49	5.3	10	26	4.0	30	3	0.6	40	4	0.6	40
12	235	29.3	10	99	19.3	40	6	1.3	40	7	1.3	40

I. cordata fronds as they swayed in the current. Frond contact with substrate may therefore be as important as substrate proximity to populations to obtain high spore recruitment.

However, observation of settlement on plates immersed for four days at varying heights above a natural, dense I. cordata population, indicated that spores were distributed throughout the water column (Table IV). It was surprising that a consistently higher density of spores (20 ± $3.7/cm^2$) were present on the plates at 1.0 m above the bottom than plates at 0.3 m (11 ± $2.2/cm^2$), or on the bottom under the I. cordata canopy (2 ± $0.5/cm^2$). One explanation for these results was the abundance of Lacuna sp. (snails) on the plates next to the bottom and near absence on the uppermost plates. Grazing by these snails may have resulted in differential survival of settling spores.

A total of 154 settling plates were retrieved at regular intervals during a 15 month period from platforms at Kye Bay and Cape Mudge sample areas and were examined for the presence of I. cordata red algal spores and sporelings, thalli of attached macro-algae and diatom cover (Appendix VII and VIII).

Settlement of I. cordata sized spores between the three to nine week sample periods over 15 months was abundant only on slides taken up in June and July, 1975, at Kye Bay. Densities were as high as $670/cm^2$. During the latter part of the summer and winter at Kye Bay and during May to December at Cape Mudge, thick diatom films obscured the surface of much of the plates, and spores could not be observed. Areas with no diatoms had apparently been grazed and had few spores

Table IV. Mean density of red algal spores per cm^2 adhering to settling plates immersed for four days at varying heights above a dense *I. cordata* community.

	Height Above Substrate								
	0 m			0.3 m			1.0 m		
Replica	$\bar{Y}$	S.E.	N	$\bar{Y}$	S.E.	N	$\bar{Y}$	S.E.	N
1	3	1.5	10	24	6.2	10	33	7.3	10
2	0	0.0	10	11	3.5	10	1	0.2	10
3	0	0.0	10	1	0.9	10	40	7.2	10
4	3	1.0	10	0	0.0	10	35	11.9	10
5	3	1.5	10	19	5.9	10	29	6.7	10
Mean	2	0.5	50	11	2.2	50	29	3.7	50

of any type. No I. cordata spores were observed between December and May, corresponding to the lack of reproductive fronds at this time of year.

Spore discs of I. cordata have been described by Fralick (1971) and Norris and Kim (1972). They develop from a single 17 - 25 μm diameter cell into 15-25 small cells by divisions perpendicular to the surface of attachment, to form a disc only slightly larger than the original spore. Further divisions increase the diameter and thickness of the spore disc to ultimately produce an erect shoot. Settling plates were observed in this study to include all of the stages of I. cordata development from spores.

The first I. cordata-like spore discs were observed at Kye Bay, 16 days after plates were first put down on May 30, 1975. Maximum disc size was 65 μm and such discs consisted of approximately 100 cells. By July 29, 60 days after immersion, plates supported I. cordata spore discs 200 μm in diameter with microscopic, erect shoots. On September 13, after 103 days immersion (commencing in May), a plate at Kye Bay had an I. cordata upright, 0.4 cm high. No erect shoots were observed at Cape Mudge before five months immersion, although the lack of sightings was likely due to the rarity of sporelings rather than a reduced growth rate.

At both Kye Bay and Cape Mudge, settling plates put down between May and December had erect I. cordata sporelings by the following spring or summer. Thus I. cordata spore settlement occurred over a prolonged period and sporeling growth continued through winter into the spring.

Sporelings commencing development in mid summer appeared to be more advanced by the next summer compared to those developing in late summer or fall. A settling plate immersed at Kye Bay in July, supported *I. cordata* frond initials 1 cm high in April, and another immersed in December had frond initials 1 cm high in August.

However, *I. cordata* sporelings were very sparsely distributed on all settling plates, if present at all, and it was apparent that few survived from one sample period to the next. *I. cordata* sporelings were too rare to quantify differential growth and survival during separate months. Sedimentation may have killed some sporelings as many of those surviving grew along the vertical edges of plates (10 percent of the horizontal surface area). Grazing by invertebrates also may have removed sporelings as portions of the horizontal surfaces were cleared of all algal growth.

Settling plates left submerged for the maximum period of 15 months did not develop populations typical of the natural substrate. The stage of colonization appeared to parallel that of the horizontal surfaces of the concrete blocks, discussed below and plates continued to support mainly ephemeral species of *Monostroma* and *Enteromorpha* (Figure 31) after 3 - 15 months.

Artificial seeding of Plexiglas settling plates with *I. cordata* spores released from mature fronds in laboratory trays resulted in many spores adhering to plates in less than one hour. Settling plates which were artificially seeded with a high density of *I. cordata* spores over a 24 hour period in laboratory trays quickly became fouled with diatoms after attachment to the Kye Bay platform in

Figure 31. Settling plates attached to platform at Cape Mudge after 3 months immersion supporting mainly ephemeral chlorophyte species.

September 1975. After three weeks no spores could be observed as the plate surfaces were obscured by the thick diatom film also present on non-seeded plates. In spite of high initial density of spores ($600 \pm 31/cm^2$; n = 12) on control plates (taken out to the platform with other seeded plates, but returned to lab for density count on same day), no increase in sporeling production was observed on the artificially seeded plates compared to naturally seeded plates collected in August 1976.

(b) macroscopic colonization

Algal species and visual estimates of species abundance on concrete blocks recorded while SCUBA diving are listed in Appendix IX for Kye Bay, Cape Mudge and Willow Point. The species list and fresh weight of each species recorded in the laboratory for concrete blocks harvested at the termination of these observations (August, 1976) are listed in Tables V and VI for Kye Bay and Cape Mudge. Final samples were not taken at Willow Point as storms had overturned many blocks which invalidated results.

Typical early sequences of colonization were observed on the concrete blocks at each area. The generalized sequence consisted of the establishment of a diatom mat, followed by a cover of rapidly growing ephemeral chlorophyte species (Enteromorpha linza, Monostroma fuscum and Ulva lactuca) and finally, encrusting and frondose rhodophyte species such as Iridaea cordata, Gigartina exasperata, Neoagardhiella baileyi, and Callophyllis violacea.

In addition to these stages, several phaeophyte species were

Table V. Macroalgal species colonizing natural substrate and concrete blocks immersed for 3 - 36 months at Kye Bay, observed on August 29, 1976.

Species	Abundance[a] per Dates and Period of Immersion																	
	3-7 months			8-14 months							24-36 months			Natural substrate (0.5 m^2 samples)				
	May 3, 1976	Apr. 3, 1976	Jan. 31, 1976	Dec. 10, 1975	Sept. 26, 1975	Sept. 6, 1975	Aug. 18, 1975	July 29, 1975	July 8, 1975	June 18, 1975	July, 1974	July, 1974	Aug., 1973	1	2	3	4	5
M. fuscum	A	A	A	A	A	A	A	A	A	A	A	A	R	A	R	R	R	R
E. linza	R	A															A	R
I. cordata				R	A	A	A	A	A	A		A	A	A	A	A	A	R
P. coccineum				R	R	R	R	R		R	R	R	R	A	A	A		A
G. exasperata						R	R	A	R	A	A	A					A	A
M. coulteri					R	R		R		R	A	A	R				A	A
N. baileyi							R	R	R	A	R							
C. violacea						R		A		R	R		R	A	A		A	A
L. saccharina				A					R									
C. woodii						R	R											
R. californicum									R									
P. dendroidea						R												
D. viridis					A	A				R		R						
P. latissina					R					R	R	R	R		A	A	A	A
S. pacifica												R						
R. palmata										R			R					
C. subulifera						R						R	R	A		A	A	A
R. roseum										R			R		A	A	A	A
R. pertusa									R				R	R	R	R	A	
U. lactuca										R	A					R	R	
P. lanceolata														A	A	A	R	A
B. farlowianum														A	A	R		A
A. gigartinoides				R														R
M. borealis																	R	
G. coulteri																		R
E. mollis																		R
Total No.	2	2		5	6	10	6	7	7	12	8	9	10	8	9	9	13	15

[a] R = Rare; A = Abundant

Table VI. Macroalgal species colonizing natural substrate and concrete blocks immersed for 8-14 months at Cape Mudge, observed on September 1, 1976.

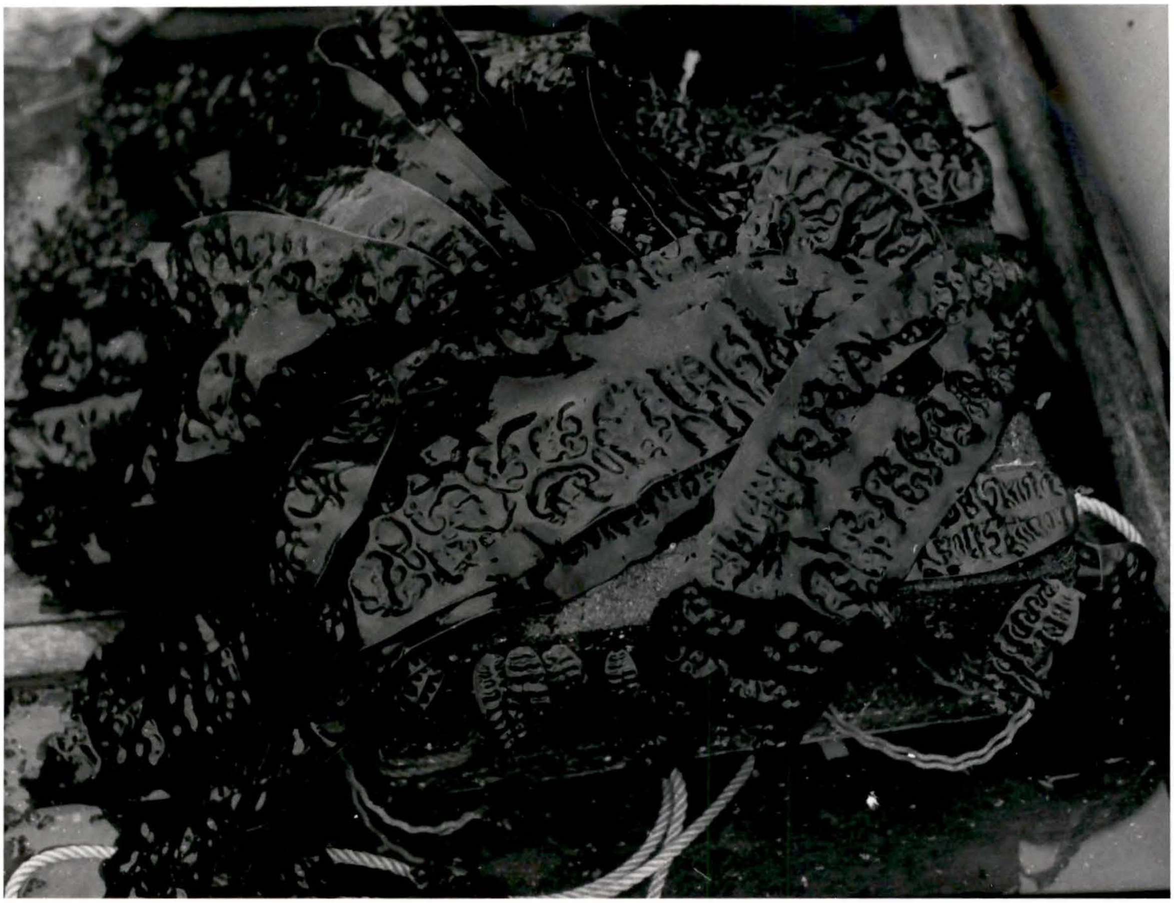
Species	Abundance[a] per Date and Period of Immersion											
	8-14 months											
	Dec. 10, 1975	Sept. 26, 1975	Sept. 5, 1975	Aug. 21, 1975	July 31, 1975	July 10, 1975	June 19, 1975	1	2	3	4	5
S. muticum	R			R								
D. aculeata	R											
D. decepiens				R		R						
R. affine				R		R						
G. exasperata				R		R						
O. lyallii				R								
G. stellata						A						
N. baileyi						R						
E. linza	R	R	R				R		R			
M. fuscum	A	A	A	A	A	A	A	A	R			R
I. cordata		R	R	R	R	A	R	A	A	A	A	A
L. saccharina	A	R			R	R	R	A	A	R	A	A
A. tenuifolia		R			R	R	R	A	A	A	A	R
P. lancealata		R		R				A	A	A	A	A
C. vidacea		R	R	R					A	A	A	
U. fenestrata			R							A		A
C. pacificum							R	A				
C. subulifera								A	A		A	A
R. roseum								A	A	R	R	R
C. regenerams									A	A	A	
B. farlowianum									R			A
G. leptophyllis									R			R
O. floccosa								R				
C. officinalis								R				
R. pertusa									A			
P. latissima										A		
S. pacifica											R	
Total No.	5	7	5	9	4	9	6	10	13	9	9	10

[a]R = Rate; A = Abundant.

observed to colonize the concrete blocks at particular times of the year, irrespective of the degree of prior colonization. *Desmarestia viridis* and *D. ligulata* were observed in April, 1976 on all concrete blocks put down in or before January, 1976 at Kye Bay. *Alaria tenuifolia* and *Nereocystis luetkeana* were noted in February and March on all concrete blocks put down in or before September, 1975 at Cape Mudge. Blocks put down in December, 1975 at Cape Mudge and Willow Point were colonized heavily by *Laminaria saccharina* and *Cymathere triplicata* (Figure 32), found infrequently on blocks immersed before or after this month.

The horizontal surfaces (tops) of all the concrete blocks developed differently from the sides. At Kye Bay the flora colonizing the horizontal surfaces did not go beyond the ephemeral, chlorophyte stage after three years. Apparently succession followed succession of the species *Enteromorpha linza*, *Monostroma fuscum* and *Ulva lactuca* but colonization by slower growing species was inhibited. Possible factors inhibiting growth of the perennial species were the accumulation of sand between barnacles and/or stipes of the chlorophyte species and the scouring action of starfish feeding on the barnacles which were more abundant on horizontal than vertical surfaces. Light would not appear to be a factor in deterring *I. cordata* from settlement on the horizontal surfaces since the highest density of sporelings was located on the corner separating the vertical from horizontal planes. Phaeophyte species including *Alaria tenuifolia*, *Laminaria groenlandica* and *Nereocystis luetkeana*, which were rare at Kye Bay, developed on both vertical and hor-

Figure 32. Concrete block set down at Cape Mudge in December, 1975 supporting laminarians after 8 months immersion to August, 1976.



izontal surfaces of the Cape Mudge and Willow Point blocks.

The slow growing, usually perennial species which followed the chlorophyte species on vertical surfaces, varied according to the time of year and location. On blocks put down in June and July, 1975 at Kye Bay, Neoagardhiella baileyi and I. cordata were among the first species to be noted, visible in December and January, 1976. By April, Gigartina exasperata, and Botryoglossum farlowianum, were noted and by May, Polyneura latissima and Rhodoglossum californica were observed. Eleven species were observed on blocks immersed since June, 1975 (15 months) although I. cordata was by far the dominant (Figure 33). Only two additional species were recorded on blocks immersed for two and three years. On blocks put down in August and September, 1975 Neoagardhiella baileyi and I. cordata were not observed until April, 1976. Eight species were observed by September, 1976. Blocks put down on or after December, 1975 had only one to two red perennial algal species by September, 1976.

At Cape Mudge, the first perennial species on blocks put down in June and July, 1975 were I. cordata and Prionitis sp., noted in December. In April and May, 1976, Rhodoglossum californica was noted on these blocks. The rhodophyte perennials were overshadowed by the rapid growing phaeophytes, Nereocystis luetkeana and Alaria tenuifolia in April and May. The holdfasts of these species covered at times 50 percent or more of the horizontal block surfaces. However, ten species were noted by September, 1976. Blocks put down in August and September, 1975, at Cape Mudge had visible I. cordata by April and May, 1976. Eight species were noted on these

Figure 33. Concrete block set down at Kye Bay in June, 1975 supporting dense _I_. _cordata_ population on vertical surfaces (sides) after 15 months immersion to August, 1976.

blocks by September, 1976. Again, blocks put down in December, 1975 or after, had only one or two perennial species by September, 1976.

On blocks immersed for even two and three years, macrophyte species composition remained unlike that on adjacent natural substrates (Tables V and VI). The species *I. cordata*, *Gigartina exasperata*, *Neoagardhiella baileyi* and *Callophyllis violacea* increased in abundance with age of substrate and approached natural abundance on the vertical but not horizontal surface of three year old blocks. *Monostroma fuscum* colonized rapidly and was very abundant on blocks immersed for one year or less, moderately abundant on two or three year old blocks and rare on natural substrates. Also restricted in abundance to the blocks were *Neoagardhiella baileyi* and *Desmarestia viridis*. Species observed on natural substrates but absent or rare on concrete blocks were *Plocamium coccineum*, *Constantinea subulifera*, *Rhodoglossum roseum*, *Prionitis lanceolata*, *Botryoglossum farlowianum* and *Polyneura latissima*. *Plocamium coccineum*, a major competitor of *I. cordata* at Kye Bay and Willow Point, was slow in colonizing the concrete blocks as frond recruitment occurred from secondary attachment of drifting fragments. No sporelings or fertile fronds of *P. coccineum* were ever observed. *Prionitis lanceolata*, *Botryoglossum farlowianum* and *Polyneura latissima*, which also were abundant and possible competitors of *I. cordata* on natural substrates, recruited from spores, but development of large frond clumps on vacant substrate was slow.

Although species composition, even on two and three year old blocks, was different than on natural substrate, species diversity of foliose algae was not very different. The most rapid increase in diversity took place during the first year, after which the loss in species was balanced by the gain (Tables V and VI).

The rapid speed of colonization by *I. cordata* was not surprising as the surrounding natural community was dominated by this species. A comparison was made of the abundance of *I. cordata* on blocks immersed for different time periods ending September, 1976 at Kye Bay and Cape Mudge (Tables VII and VIII). Blocks submerged for two and three years at Kye Bay had approximately twice as many (109-248) fronds longer than 5 cm and twice as many (565-665) fronds less than 5 cm long per block than blocks submerged only for one year since the previous summer (12-67 longer than 5 cm and 250-385 less than 5 cm long). Also, the mean weight of the fronds on the two to three year old blocks were nearly twice that of fronds on the one year old blocks. The maximum diameter of *I. cordata* holdfasts observed on the two and three year old blocks was 1.3 cm and only 0.7 cm on the one year old blocks.

Analysis of the distribution of the life phase classes of *I. cordata* fronds on the concrete blocks revealed an unusually high percentage of gametangial and low percentage of tetrasporangial fronds on the one year old blocks immersed at Kye Bay in August and September, compared to the two and three year old blocks, or the natural population (Table VII). The blocks immersed in August and September, 1976, were colonized primarily by tetraspores which developed into gametophyte plants. This dominance of tetraspores in August and September agrees with the higher reproductive

Table VII. Abundance of I. cordata colonizing concrete blocks immersed for 7 - 36 months at Kye Bay, observed on August 30, 1976

		Vertical sides (0.25 m^2)						Horizontal surface (0.16 m^2)	
		No. I. cordata fronds			Percent Composition[a]			No. I. cordata fronds	
Date blocks immersed	Time immersed in months	length >5 cm	length <5 cm	Total biomass (g)	V	G	T	length >5 cm	length <5 cm
Aug. 1973	36	109	665	1000	31	9	60	3	28
Aug. 1973	36	248	565	2120	28	17	54	10	183
July 1974	24	118	645	870	46	5	49	0	32
June 16, 1974	14	67	250	290	48	17	34	1	50
July 8, 1975	14	12	288	40	67	23	8	1	7
July 29, 1975	13	16	263	90	69	6	15	5	19
Aug. 18, 1975	12	46	365	100	22	71	7	2	9
Sept. 6, 1975	12	42	363	80	55	45	0	2	24
Sept. 26, 1975	11	15	384	50	73	20	7	0	2
Dec. 10, 1975	9	0	2	0	0	0	0	0	0
Jan. 31, 1975	7	0	0	0	0	0	0	0	0

---

[a] V = vegetative, G = gametangial, T = tetrasporangial

Table VIII. Abundance of *I. cordata* colonizing concrete blocks immersed for 7 - 14 months at Cape Mudge, observed on September 1, 1976.

		Vertical sides 0.25 m^2						Horizontal surface 0.16 m^2	
		No. *I. cordata* fronds			Percent Composition[a]			No. *I. cordata* fronds	
Date blocks immersed	Time immersed in months	length >5cm	length <5cm	Total biomass (g)	V	G	T	length >5cm	length <5cm
June 19, 1975	14	0	63	<10	0	0	0	0	45
July 10, 1975	14	2	101	30	0	50	50	1	165
July 31, 1975	13	0	60	<10	0	6	0	0	0
Aug. 21, 1975	12	0	95	<10	0	0	0	0	156
Sept. 5, 1975	12	6	8	<10	0	0	0	0	3
Sept. 26, 1975	11	2	39	<10	0	0	0	0	2
Dec. 11, 1975	9	0	0	0	0	0	0	0	0
Feb. 1, 1976	7	0	0	0	0	6	0	0	0

[a] V = vegetative, G = gametangial, T = tetrasporangial

NB: *I. cordata* was less abundant on blocks at Cape Mudge than at Kye Bay due to overstory of laminarians.

capacity of the tetrasporangial fronds recorded at this time of year (Figure 26).

The abundance of I. cordata fronds on blocks harvested at Cape Mudge in September, 1976 is compared in Table VIII. Very few fronds longer than 5 cm were present although a considerable number of juveniles (less than 5 cm long) were observed (8 - 101 per block). As described above, I. cordata appeared to be shaded and out-competed for light by Alaria tenuifolia and Nereocystis tenuifolia at Cape Mudge in the summer of 1976.

DISCUSSION

Seasonal Standing Crop of Algae in the *I. cordata* Community

Seasonal observations of *I. cordata* communities in Georgia Strait quantified the dramatic fluctuations in algal macrophyte standing crop and community structure which occur between summer and winter, typical of algal floras in temperate coastal waters.

In other subtidal algal studies in the north-east Pacific, Neushul (1967) noted that late summer vegetation in Puget Sound was fully developed and showed a decline and defoliation during fall and winter months. Vadas (1968) remarked on the disappearance of the algal canopy in fall and appearance of exposed rock surfaces in winter contrasting with the maximum stages of algal growth and development in late summer. The cover of foliose species in two *I. cordata* dominated communities in northern Washington was reported to vary from less than 25 percent in winter to greater than 125 percent (including shading of small individuals by large) in summer, with most rapid changes in spring and fall. Winter species diversity was 36 percent of summer diversity (Hruby, 1974, 1975).

The seasonal distribution of algae has long been of interest to phycologists but primarily in terms of reproductive periodicity and species presence or absence (e.g. Sears and Wilce, 1975; Reynolds and Mathieson, 1975; Kapraun, 1974; Schneider, 1976). Only few investigations have been made of the quantitative variations in standing crop which illustrate the response of a particular flora to seasonal extremes in environmental conditions.

In contrast to the tropics where seasonal algal growth is less variable, seasonality is strongly influenced by light and temperature changes in polar and temperate latitudes (Doty, 1971). Maximum seasonal growth of benthic algae as measured by standing crop has been correlated with solar radiation maxima in Texas lagoons (Conover, 1964) while it was a function of temperature maxima in a New England estuary (Conover, 1958). In temperate latitudes, Taylor (1970) suggests that the period of maximum growth is no doubt correlated with both temperature and radiation maxima since water temperature is closely related to solar radiation input and meteorological conditions, although salinity and nutrients also may vary seasonally.

In Georgia Strait, the maximum standing crop of macroalgae in _I. cordata_ communities occurred between early May and early September at the three sample locations studied over a 15 month period. Maximum standing crop coincided within zero to two months of the maximum water temperatures (13-19° C) and within one to three months of the maximum incident light (560-640 langleys/day averaged over a two week period).

Environmental Parameters and Seasonal Abundance of _I. cordata_

The physical and chemical environmental variables measured adjacent to the _I. cordata_ communities in this study were generally consistent with those reported in the literature for surface waters of Georgia Strait (Pickard and McLeod, 1953; Tully and Dodemead, 1957; Waldichuk, 1957; Stephens _et al_., 1969). Maximum sea water temperatures were a few degrees higher at Kye Bay (19° C) than the range reported for Cape Mudge (4°-15° C) during 1948-57 (Anon. 1958) or for Texada Island (2^{o}-17^{o} C) during 1954-56 (Anon. 1957). The range in salinities reported for the same periods were 26 to 30 ppt at Cape Mudge and 24 - 30 ppt at Texada Island which were higher than those recorded for the I. cordata communities sampled in the present study, possibly due to their proximity to shore and the influence of run-off. A considerable depression in salinity to 15 ppt at the two communities sampled in northern Georgia Strait was below the range expected for this area, indicating exceptional run-off from the Homathko River system with major discharges into northern Georgia Strait in late summer (Herlinveaux and Giovando, 1969).

The annual range in near-shore water temperatures sampled in northern Georgia Strait (2 - 19^{o} C) is much greater than the range recorded for the coast exposed to the open Pacific (5 - 12^{o} C). Near shore salinities in northern Georgia Strait (usually 24 - 30 ppt) are also more brackish than the exposed coast (30 - 33 ppt).

The ranges in temperature and salinity in Georgia Strait appear to be well within the tolerance of I. cordata. Maximum growth of sporelings was achieved in culture at 16^{o} C, at optimum light intensities, but was considerably slower at 7^{o} C (Waaland, 1973). Warmer temperatures in the summer of 1975 may have increased the I. cordata growth rate in that year compared to 1976. Salinity is not considered to limit the growth of I. cordata in Puget Sound (Hruby, 1974), which shows similar variability to Georgia Strait. I. splendens S. and G, which was reduced to a subspecies of I. cordata (Abbott, 1971) was found to have maximum respiration and photosynthesis at 30 - 35 ppt salinity and at temperatures of 10 - 12° C. At these temperatures, decreasing the salinity to 11 ppt had little effect on respiration and photosynthesis (Kjeldsen and Phinney, 1972).

Seasonal variation of incident light in northern Georgia Strait of 58 langleys/day (average for two weeks) in winter to 631 langleys/day in summer was consistent with values reported for latitudes 48 - 60° N. (Edwards and Kapraun, 1973). Although water transparency was slightly reduced during spring, there would be a large increase in light reaching the subtidal I. cordata community during March, April and early May resulting from rapid increases in incident light and the change from night to daylight spring low tides. Laboratory and field productivity studies of individual I. cordata fronds in waters of California suggest that this species is light-limited during winter but not during spring and is limited by some other factor(s) during summer and fall (Hansen, in press b).

The seasonal range in the nutrients, nitrate nitrogen (<0.02 - 0.40 mg/L) and orthophosphate (<0.005 - 0.07 mg/L) sampled in I. cordata communities in northern Georgia Strait was consistent with values reported by Parsons (1965) and Tully and Dodimead (1957). Coastal values for nitrate nitrogen generally range between 0.00 - 0.01 mg/L in summer and 0.30 - 0.50 mg/L in winter. Nitrite nitrogen values, below detection in much of this study, are generally 0.001 - 0.002 mg/L in winter, increasing to a maximum of 0.004 - 0.008 mg/L in fall. Ammonium nitrogen also below detection in much of this study can reach a maximum of 0.03 mg/L in summer. Dissolved phosphate generally ranges from 0.06 - 0.09 mg/L in winter to near depletion (0.01 mg/L) during spring (Stephens *et al.*, 1969).

The large fluctuations in nutrient that were observed between *I. cordata* communities and between consecutive sample dates, particularly in summer, may reflect the variability in water mass present during different tidal states; stratified Georgia Strait water at ebb tide and well-mixed Discovery Passage entrance water at flood tide. The heterogeneity of the water mass is further increased in Georgia Strait by runoff from the major rivers which is variously dispersed over the tidal cycles (Tully and Dodimead, 1957).

The general reduction in nitrate nitrogen and dissolved phosphate in summer however, has been ascribed to their utilization by planktonic algae and it is suggested that under certain conditions nitrate nitrogen may become a growth limiting nutrient for planktonic algae in Georgia Strait (Parsons, 1965). Availability of this nutrient may also limit the growth of *I. cordata* populations in summer under certain tidal regimes and current velocities in northern Georgia Strait. Experiments with tank cultivation of *I. cordata* in northern Washington indicated that nutrient availability was particularly dependent on the tank water turnover rate and therefore related to current in the natural environment. Thus, at only one turnover rate per day, growth was reduced over that at four turnover rates per day. In the latter case, incoming inorganic nitrogen concentrations (from Puget Sound) of 0.21 to 0.28 mg/L (calculated here as 0.014 x μg at/L NO_3 - N) were reduced to 0.07 mg/L in outflowing water (Waaland, 1976). Additional studies have indicated that nitrate depletion was greatest with high plant density during periods of rapid growth. Phosphate was reduced to a much lesser extent than nitrate. In experiments conducted with Gigartina exasperata which has similar requirements to I. cordata, nitrate nitrogen was reduced in still water from 0.55 mg/L to 0.03 mg/L in five hours by fronds at a density of 6.55 kg fresh weight per m^3 (Waaland, 1978).

In northern Georgia Strait, highest I. cordata biomass at Cape Mudge was related to the strongest current, estimated to be 1.5 m/sec. at maximum during a large spring tide. Measurements of current velocities in I. cordata communities in northern Washington indicated maximum velocities between 0.06 and 0.38 m/sec. (0.12 to 0.74 knots) over a moderately large tidal cycle and no communities were present where currents remained less than 0.05 m/sec. (Hruby, 1974).

In subtidal red algal populations off Plymouth, Massachusetts, dominated by Chondrus crispus, nitrate nigrogen concentrations varied from 0.14 mg/L in winter to less than 0.05 mg/L in summer, but utilization of ammonia nitrogen by C. crispus was suggested since growth was most rapid during the period of nitrate depletion (Prince and Kingsbury, 1973). Hansen (1976) indicates possible use of ammonia nitrogen by I. cordata and reports that the most dense populations of I. cordata in California waters occurred in areas which are seasonally nutrient enriched by seal colonies. Values for ammonia nitrogen in Georgia Strait however, remained relatively low (generally < 0.01 mg/L).

Although the dramatic seasonal variation in I. cordata biomass has recently been reported, no other accounts have quantified this information in relation to environmental parameters in the north-east Pacific.

I. cordata blades were reported to be annual and to stop growing in late summer (Norris and Kim, 1972) while only the crustose holdfasts were noted to perennate (Waaland, 1976). In an I. cordata dominated community in northern Washington, bottom cover of this species varied from 6 percent in December to 74 percent in August (Hruby, 1974). Observations in the present study indicate lows of 0.00 ± 0.00 - 0.03 ± 0.009 kg fresh/0.5 m^2 I. cordata in December through February and highs of 0.7 ± 0.05 - 2.0 ± 0.24 kg fresh/0.5 m^2 in June through August in three communities dominated by this species. These values are considerably lower than those recorded for I. cordata populations of central California where values ranged from lows of approximately 0.6 kg fresh/0.5 m^2 in winter to highs of 3.4 kg/0.5 m^2 in summer (40 x kg dry/0.0625 m^2 reported by Hansen, 1976). The high winter biomass in waters off California may provide populations with a 'head start' on spring growth compared to those in the north-east Pacific. Comparison of standing crop values for these different areas must be tentative however, because those of Hansen (1976) have been converted from samples taken in 0.0625 m^2 quadrats rather than 0.5 m^2 as in the present work. Possible errors in such comparisons are discussed by Baardseth (1955).

In waters off California and in Georgia Strait, the rapid increase in I. cordata spring standing crop was correlated with increasing solar radiation. Although in California waters temperatures were not correlated with growth (Hansen, 1976), in Georgia Strait an increase in water temperature above the growth limiting 7 to 8° C (Waaland, 1973), did correspond to increasing I. cordata standing crop in spring. In fall, the decline in I. cordata standing crop in Georgia Strait was related to declines in both solar radiation and water temperatures.

In other rhodophyte populations, Prince (1971) noted that spring growth of Chondrus crispus off Plymouth, Massachusetts was closely related to water temperature and the reduced fall growth was due to a decline in temperatures, not solar radiation. The spring growth of C. crispus off New Hampshire was also initiated during March and April when water temperatures increased from 6 to 9° C, but fall decrease was attributed to a decline in solar radiation since fall water temperatures are higher than those of spring when active growth is initiated (Mathieson and Burns, 1975).

Several studies of phaeophyte populations have implicated light as a major factor limiting growth. Vadas (1972) suggests that adverse light conditions for short periods in spring may prevent successful competition of Nereocystis luetkeana with certain laminarians. Chapman and Burrows (1970) and Kain (1966, 1971) calculated available light energy seasonally at various depths. The data confirmed the limiting nature of light and the importance of competition for light in benthic algal communities

Stability of the Algal Community Components

Several macroalgal species, in addition to the dominant I. cordata, were abundant at times in the communities sampled in Georgia

Strait. Seasonal peaks in biomass and maturation of these community components did not necessarily coincide with the maximum biomass of *I. cordata* or the total community. It is plain that variation in environmental factors differentially affects each species, regulating their abundance and ultimately diversity in the community. Environmental processes however are only one of a number which may affect community structure.

Five kinds of processes that cause pattern in a subtidal marine community have been described (Fager, 1971 after Hutchinson, 1953), at least four of which are important in the seasonal dynamics of the *I. cordata* community: "*vectoral*", produced by physical and chemical factors in the environment; "*reproductive*", relating to the dispersal of propagules from the parent; "*social*", involving intraspecific signalling between individuals; "*coactive*", interspecific actions such as competition, predation and parasitism, and "*stochastic*", resulting from random processes. Certainly vectoral processes are most important in this subtidal algal community, but reproductive processes, including the seasonal spore release and vegetative propagation of algal fronds from perennial crusts, are also important. Coactive processes are manifest in the replacement of one species by another in competition for the limited resources, space and light. Several authors have described the importance of stochastic or random processes in development of pattern (Fager, 1971; Dayton, 1971). Substrate upheaval by *Pycnopodia helianthoides*, releasing space for colonization by seasonally changing spore and larval settlement is a good example of this latter process in the *I. cordata* community.

These processes are continually modified in the I. cordata community which prevents monopolization of the primary limited resource, space, by any one potential dominant. Such inconstancy is also characteristic of intertidal populations (Dayton, 1971).

In 1976, a shift in conditions favoured the development of laminarian species Alaria tenuifolia and Nereocystis luetkeana which overshadowed I. cordata, the dominant in 1974 and 1975. Subsequent observations in 1977 indicated reestablishment of I. cordata as the dominant. The exclusion of dense I. cordata populations from depths below 1.0 to 1.5 m below mean lower low water in northern Washington was attributed to competition with laminarians and appears to be a dynamic process which occurs every year (Hruby, 1976). The depth of the boundary between the two communities may vary from year to year depending on the conditions limiting the growth of laminarians to the deeper zone. Druehl (1967) suggested that the overwintering gametophyte may be a limiting stage for many laminarian species. Although competition for light has usually been suggested as the causal factor for the competitive dominance of certain kelps (Kain 1971; Norton and Burrows, 1969), competition for primary space also was observed to be important in the present study. The large holdfasts of Alaria tenuifolia frequently were observed growing over the basal crusts and frond initials of I. cordata and other species.

Certain disturbances in the I. cordata community also may promote the dominance of this species. In the absence of laminarian species, stable substrate was associated with a monopolization of space in the subtidal by the red alga Plocamium coccineum.

Disturbance of substrate by waves which overturn cobbles and shift sand was less evident in the Willow Point and Kye Bay communities, where *P. coccineum* was abundant, than in the Cape Mudge community where it was absent. *P. coccineum* often dominated the biomass in deeper water (2 - 3 m below chart datum) where wave action is greatly reduced in northern Georgia Strait (Austin and Adams, 1974, 1975). In such areas *P. coccineum* grows in spring from its ragged winter form to a thick mat, 5 - 15 cm deep, with many points of attachment. Sand is trapped at the base of the holdfasts, preventing establishment or growth of juveniles of other species. Thus in the absence of natural disturbances which vacate space for the rapid colonizing *I. cordata*, dominance in this community may shift to the more slow growing *P. coccineum*.

Grazing of algal cover by herbivores was not conspicuous in this community except for dense populations of the snails *Lacuna variegata* and *Lirularia lirulata* which are suggested to cause extensive damage to *I. cordata* fronds in certain areas in late summer and fall (Mumford, 1978). Although macroalgae including *I. cordata* have been recognized in the gut of several chitons, *Tonicella lineata* (Demopulos, 1975) and *Mopalia* spp. (Fulton, 1975), found in *I. cordata* communities, little evidence was found of substrate cleared by their activities except the space occupied by the animals themselves. Dayton (1975) suggests that the molluscan herbivores had little effect on succession in the low intertidal and their densities seemed to be far below the carrying capacity of the environment.

A combination of factors including the disturbance of substrate, the large annual fluctuation in temperature, light and nutrients which may retard or prevent development to a climax community, and the fluctuations in overstory (laminarian) development appear to prevent complete monopolization of space in the *I. cordata* community by any one species.

Seasonal *I. cordata* Population Structure

Standing crop, density and cover are all measures of species importance, but these values may result from differential effects of biological and environmental processes on a species' life history phases. Each of the three isomorphic frond types of *I. cordata* can reproduce vegetatively from perennial basal crusts and the independence of these life phases increases the variable reaction of the species to the environment.

The dominance of the gametangial phases in May and June and dominance of the tetrasporangial phase in August through December in this Georgia Strait study was comparable to their seasonal abundance in more southerly British Columbia populations at Victoria (Austin and Adams, 1971). In the latter location, cystocarpic fronds were numerically dominant from June through September and tetrasporangial fronds were dominant from October through February. Male gametangial fronds were not separated from vegetative fronds. Collections in northern Washington (Fralick, 1971) during May and June were reported as "undetermined life phase" while tetrasporangial fronds were dominant during August through March. It is possible that many "undetermined fronds" in early summer were male or female gametangial fronds in northern Washington and seasonal abundance of life phases were similar to those around southern Vancouver Island and in Georgia Strait.

In contrast, California populations of *I. cordata* were reported to be dominated in biomass by tetrasporangial fronds in summer, autumn and winter and these fronds attained twice the estimated maximum density of combined male and cystocarpic fronds in spring (Hansen, 1976). Seasonal alternation in the abundances of these life phases in Georgia Strait may be attributed to their differential growth and maturation. The absence of such alternation and dominance of tetrasporangial fronds in California waters is suggested to result either from high mortality of tetraspores or development of tetrasporangial thalli from tetraspores through apomeiotic processes (Hansen and Doyle, 1976). This latter process has occurred in culture of the subspecies of *I. cordata* var. *splendens* (Kim, 1975). This variety predominates in California waters (Abbott, 1971).

Differential abundance of life phases in red algae has been reported by a number of authors. In other studies of the genus *Iridaea*, Hasegawa and Fukuhara (1952, 1955a, 1955b) examined seasonal occurrence of sporophyte, gametophyte and undetermined life phases of *Iridophycus cornucopiae* in Japanese waters. Peak numbers of gametophyte thalli occurred in May through July and in two of four localities studied did not coincide with the peak in sporophyte thalli. *C. crispus* in New Hampshire was reported to be dominated by cystocarpic thalli during most of the year in the intertidal (Mathieson and Burns, 1975). Austin (1960) reported that *Furcellaria fastigiata* populations contained a slight predominance of asexual plants over sexual plants. *Eucheuma isoforme* and *Eucheuma* (Bahia Honda Form) were observed to have significant tetrasporangial dominance throughout most of the year (Dawes *et al.*, 1974). Such differential abundance is not restricted to comparison of cystocarpic and tetrasporangial forms, but also male and female gametangial thalli. Powell (1964) indicated that in many studies (collections) male plants were not found, had short fruiting periods, were ephemeral or inconspicuous. *Constantinea subulifera* was observed to have similar numbers of tetrasporangial and cystocarpic thalli at all depths, but there were a larger number of male plants at the shallow depths of its range and more females in deeper water. Powell suggested that males could be selected against because they lose their blades and have a slower growth in deeper water where they are shaded by larger algal species.

Temporal and spatial disproportionalities in life phases may be a unique adaptation of many species which extends their range beyond the optimum along such gradients as depth, northern and southern extent, or exposure to waves. Diploids may be better adapted to marginal habitats because they have a greater possible number of genotypes and a possible greater mean fitness. Within optimal habitats, reproductive processes favouring haploids may be more important (Barilotti, unpublished). Although differential survival or reproductive success of life phases could not be detected in *I. cordata* populations in Georgia Strait, differential growth and maturation were conspicuous. Thus the population dynamics of *I. cordata* is determined by the independent physiological characteristics of each life phase.

Seasonal data on density and size structure of life phases provided information on the pattern of I. cordata growth in Georgia Strait. Frond initials or juveniles of each life phase are abundant throughout the year at the base of adult fronds in summer or as the only upright on the perennating basal crust in winter. The number of these frond initials, arbitrarily defined as less than 5 cm long (300 - 800/0.5 m^2) was 2 - 200 times the number of immature or reproductive fronds greater than 5 cm long. Contrary to observations of populations in California (Hansen, 1976), no evidence was found in this study to indicate that frond initials were derived during winter. A large number of frond initials existed year round. In February a portion of these initials elongated and produced a considerable number of immature fronds which increased to a maximum of approximately 100/0.5 m^2 at the end of May. The abundance of these fronds dropped rapidly during the remainder of the summer as reproductive fronds increased and it was apparent that production of juveniles was greatly reduced after May. The reduced growth of juveniles during June and July, when temperature and light conditions remained optimal, can only be attributed to shading from larger fronds.

In experiments on the regrowth of I. cordata, immature fronds were produced after harvests in May and in June removed all fronds longer than 5 cm. Growth of fronds in both harvested areas continued until August, after which biomass declined as in the unharvested, natural populations. Harvests in late August and in October produced little growth of new fronds (Austin and Adams, 1975) presumably because light was reduced. Waaland (1976) observed that frequently a single *I. cordata* holdfast initiates several small blades but usually only one reaches full size, apparently 'out-competing' its smaller neighbours by shading them.

Commencing in April, the male thalli mature from juveniles to the point of macroscopic recognition and increase in size until June, after which there is a general deterioration of the largest fronds. A few new male fronds replace the old, but do not grow as large. By the end of August, only basal portions of old male fronds remain and few show signs of continued growth. Female gametophyte fronds are first recognized with developing cystocarpic sori commencing in April and reach maximum size in June and early July. Decline in size and relative abundance is observed through August and September. Some new cystocarpic fronds are observed during the latter part of this period but they remain smaller than mid-summer fronds. Tetrasporangial fronds are first recognized in May and June and maximum size is attained in late July and August, followed by a decline in size and number of new fronds and increase in proportion of ragged fronds through fall. It is possible that shading from male and female gametangial fronds in early summer is partly responsible for the slow development of tetrasporangial fronds until the former deteriorate in July and August.

A sharp peak in standing crop may be exhibited in *I. cordata* populations in mid-summer as a result of the growth of a proportionally small number of large fronds to maturity, followed by a rapid defoliation of these fronds and drop in standing crop as they become senile. Replacement growth from former small understory fronds becomes increasingly slow as the summer progresses until fall when nearly all large fronds are reduced to ragged stubs.

There did not appear to be a consistent relation between peak summer *I. cordata* standing crop and life phase composition. It is probable that in some years the growth of tetrasporangial fronds is more coincident with growth of gametangial fronds producing a higher and more pronounced peak population standing crop (e.g. Kye Bay and Cape Mudge, 1975). In other years their development may be separated in time, producing a lower and extended peak standing crop (e.g. Kye Bay, 1976).

The differential growth of these life phases may have application in the commercial harvest of this species. Waaland (1975) and McCandless *et al*. (1975) have determined that the life stages of *I. cordata* possess different types of carrageenan. The type is dependent on the ratio of fractions termed "kappa-" to "lambda-" carrageenan which possess differences in gel strength and viscosity. Kappa-carrageenan is characteristic of gametophytes and lambda carrageenan is characteristic of tetrasporophytes. Observations of seasonal population structure in northern Georgia Strait indicate that harvests before July would yield a high proportion of gametangial fronds and after July a high proportion of tetrasporangial fronds yielding a preponderance of kappa- and lambda-carrageenan respectively.

Frond Maturation

Using reproductive condition and frond appearance (ragged or fresh) as criteria for frond maturity, nearly all stages of maturity were observed in I. cordata populations between May and September inclusive. In spring only juveniles were represented, in fall only fully mature fronds and in late winter, only frond initials. During the summer growing season however, it was observed that maturation of sporophyte or gametophyte fronds did not occur synchronously. Female gametangial and tetrasporangial fronds with less than 10 percent cover of sori and fresh male fronds were observed from early May to late September, although the proportion of each life phase varied as previously discussed.

The variable timing of maturation indicates that it occurs as a result of the development sequence of each frond. However, during the rapid growth period in May and June, generally only large fronds (> 200 cm^2) were observed to develop sori, while toward late summer and fall, smaller fronds (50-100 cm^2) were reproductively mature, and maturation may be more a function of age of fronds than size. Thus fronds may take as long to grow to 100 cm^2 in late summer as to grow to 300 cm^2 in early summer, but each develop sori at approximately the same age. Dawes et al. (1974) suggest that a maturation sequence also is required before the production of reproductive structures in Eucheuma nudum, since the structures usually were on larger (older) fronds. In the absence of a maturation sequence one would expect a correspondence between optimum growth and reproduction. In many brown algal species for example, reproduction may be triggered by day length or light quality (Round, 1968; Smith, 1951).

It was apparent that cystocarpic I. cordata fronds matured more rapidly than tetrasporangial fronds. Immature fronds of undistinquished life phase were at a maximum size of 100 - 200 cm^2 in early March and by early May, the first cystocarpic and tetrasporangial sori were macroscopically visible. Cystocarpic fronds with over 60 percent cover of sori were observed by July, while mature tetrasporangial fronds with over 60 percent cover of sori were not observed until September. The more rapid rate of maturation of cystocarpic fronds is surprising as it involves two steps: development of female reproductive structures (procarp), followed by assumed fertilization and development of the diploid cystocarp and surrounding haploid nutritive tissue within which are produced the carpospores. In tetrasporangial fronds, tetraspores are produced after the development of spore mother cells.

It has been noted that growth of tetrasporangial and gametangial fronds ceases when they become fully reproductive (Waaland, 1976; Norris and Kim, 1972). Male fronds were noted to degenerate soon after they produce spermatia, not persisting as long as mature cystocarpic or tetrasporangial fronds.

The microscopic sequence of development of I. cordata reproductive structures has been followed in the laboratory through culture and anatomical studies (Kylin, 1928; more recently Kim, 1975). These studies indicate that the initial macroscopic distinguishing structure of the female gametophyte (opaque donut) is the enveloping tissue which surrounds the developing gonimoblast after fertilization. As the gonimoblast matures, spores are produced within the enveloping tissue which provides a dark red coloration to the structure and produces the swelling of the frond surface. Tetraspores are derived from accessory cells of the medullary filaments and ordinary cells of the medulla (Kim, 1975). The speckled, dark red tissue which is the first macroscopic distinguishing feature of tetrasporangial fronds is observed when spores become sufficiently dense to darken the frond.

The pattern of sorus development across cystocarpic and tetrasporangial fronds has not been reported previously. Results of this study pose certain development questions. For example, what initiates development of tetraspore mother cells along the basal margin of young fronds and how does further spread of sori relate to vegetative growth of the frond? Perhaps frond thickness is important as fresh, thin growing tips develop sori last. Do all cystocarps result from a fertilization event? Cystocarps often develop over most of the base of the frond and then expand distally to cover the frond tips. Such a sequence implies that either massive numbers of spermatia are present in the water column for fertilization as procarps develop, or a few fertilization events trigger development uniformly over the rest of the frond.

Reproductive potential of the I. cordata populations in Georgia Strait, calculated as the product of percent sorus cover times frond size (cm^2), was at a maximum in July for cystocarpic fronds and late August through September for tetrasporangial fronds. Although there was considerable sample variability in life phase reproductive potential (Fig. 26) the data suggest that differential production of spore types occur in early and late summer.

Prince (1971) also used presence or absence of sori as an indication of reproductive level of *Chondrus crispus* populations, however, he suggests a more accurate assessment would use additional criteria including 1) age and maturity of sori, 2) the presence and abundance of carpogonia, 3) the viability of the spores within the sori, 4) the amount of fungal infestation of the sori, 5) the number of sori capable of releasing spore masses in the laboratory and the amount of this release which was viable, 6) the frequency of empty and/or full sori and 7) the number of spores which settle on *in situ* settling plates. In this study only the lattermost criterion was compared with reproductive potential, and is discussed below (Spore Settlement and Substrate Colonization).

Frond Growth Rate and Population Biomass Production

Studies of the growth of individual (transplanted) *I. cordata* fronds confirmed several aspects of the seasonal population structure of this species, including abundance and longevity of cystocarpic and tetrasporangial fronds.

In terms of grams fresh weight per day, the growth of 5 - 20 g *I. cordata* fronds in Georgia Strait was highest at shallow depths (0.5 m below chart datum) and in mid-summer (June and July) rather than late summer (August and September).

The higher growth rate of cystocarpic fronds compared to tetrasporangial fronds recorded in this study may explain observations of the spring dominance of the former life phase. Thus in early spring, gametophyte fronds are first to attain a large size and mature due to their more rapid growth rate. Several authors have noted the persistence and growth of sporophyte fronds of various species in more adverse conditions than gametophyte fronds due to increased hardiness of the diploid plant. Such may be the reason for the persistence of tetrasporangial I. cordata fronds in the fall. There was no indication however, that tetrasporangial fronds grew more rapidly than cystocarpic fronds in late summer or at lower depths (less light) than cystocarpic fronds although growth rate may not be an indication of the hardiness of the frond during adverse conditions.

I. cordata frond growth rates in this study contrast somewhat with those of Waaland (1973) who observed that I. cordata growth in Puget Sound, Washington was maximal at -2.0 m below Canadian chart datum[1] (referred to as -3.0 m below mean lower low water by Waaland) and that there was a growth inhibition near the surface. Typical growth observed in northern Washington studies was approximately 110 g in 100 days compared to 45 g in 50 days in Georgia Strait. Longevity of transplanted fronds, initially 5 - 10 g was over 4.5 months in northern Washington and a maximum of 3 months in this study which may be due to the more sheltered waters or earlier date of transplanting (April) in the former study. Growth in deeper water (below -4.0 m) was similar in northern Washington and Georgia Strait with reductions to 25 percent of that above -2.0 m.

Growth rates of I. cordata in northern California were measured in terms of increase in frond surface area (cm^2) and reached a

---

[1] Canadian chart datum is defined as "a plane below which the water seldom goes" to which all depths in this study are referred and is approximately 1 m below mean lower low water on a 5 m tide range.

maximum of 5.7 ± 1.6 cm^2/day (Hansen, in press a). This growth rate was somewhat less than that recorded in the present study for cystocarpic and tetrasporangial fronds combined, initially 150 - 300 cm^2 located within a dense *I. cordata* population and measured over a 50 day period in mid-summer (12.7 ± 1.65 cm^2/day; n = 9 from Table 2). The lower growth rate reported for California was surprising in view of the higher standing crops reported there.

Growth of fronds that had 30 to 50 percent of the distal end removed was as rapid as similar sized non-cut fronds. Thus, damage by grazing, wave action, or commercial harvesting would not injure the diffuse meristematic region of young fronds.

While growth of individual *I. cordata* fronds can be quite accurately measured, the growth or biomass production of *I. cordata* populations is difficult to measure accurately because of frond losses due to senescence or wave action. Sequential sampling indicates that standing crop increased from near zero in January to a peak of 1.4 ± 0.28 kg/0.5 m^2 (mean ± S.E. of 3 sample locations, 1975) and an estimate of yearly *I. cordata* production would be the peak standing crop. However, *I. cordata* populations are comprised of three life phases which mature at different dates and a more accurate calculation of yearly production would be the sum of the standing crop increments between sample periods for each life phase. This calculation yielded a slightly higher mean value for production (1.6 ± 0.24 kg/0.5 m^2) for the 3 sample areas although the variance was too large to detect a significant difference between the means of the two calculations.

Spore Settlement and Substrate Colonization

Two processes are important to the maintenance of dense I. cordata populations: the long-term survival of perennating holdfast structures and the successful colonization of substrate by spores to replace lost holdfasts. Results of this study indicate that I. cordata is one of the most rapid perennial species to colonize vacant substrate in the I. cordata communities observed in Georgia Strait. However, colonization in the natural community is influenced by a variety of physical and temporal factors as well as the dynamic processes which govern available space.

It was apparent from this study that I. cordata spores would adhere to and develop on substrates of glass, Plexiglas, concrete or polypropylene rope. Variations in roughness may not be a factor in the initial settlement and attachment of spores. In explanation of spore adhesion to smooth surfaces, Charters et al. (1973) outline the contention that algal spores adhere to solid substrate by chemical bonding since smooth surfaces such as glass offer no opportunity for mechanical attachment. Spores are reported to attach by a "process of a liquid adhesive wetting the surface of the adherents (spore and substrate) and then changing phase to a solid by some chemical or physical process." Certain spores are ready to adhere immediately after shedding, while others are ready 3 - 4 hours after release (Suto, 1950). In laboratory experiments in this study I. cordata attached in less than one hour. Fukuhara (1958) reports that most spores shed from I. cornucopiae adhered firmly to substrate within 10 - 15 hours after shedding.

Neushul _et_ _al_. (1976) observed little difference in species diversity colonizing Plexiglas or concrete settling plates, but differences in abundance were noted and attributed to possible differences in water motion over the two substrate types. Possible toxicity of concrete substrates was suggested to inhibit colonization within the first season of immersion by Prince and Kingsbury (1973), but a time lag in colonization of concrete blocks was not observed in the present study, nor by Neushul _et_ _al_. (1976). _I_. _cordata_ biomass and sporeling density however, was much greater on the sides of concrete blocks and edges of Plexiglas plates, indicating that the orientation of the surface was probably more important than roughness. Foster (1975a) observed that variation in roughness of the order of millimeters had little effect on algal colonization, but topographic variation of the order of centimeters resulted in considerable differences in settlement. Thus on concrete plates, Foster noted significantly more sporelings of _Macrocystis_ _pyrifera_ near the upper horizontal edge than on the horizontal surface, and noted greater diversity and biomass on peaked triangular substrates rather than flat substrates. Such results were attributed to changes in water flow patterns causing increased turbulence near edges. Water speed is reduced in turbulent areas when the current hits a vertical obstruction and may enhance spore settlement.

Sedimentation may be another factor contributing to the disproportionate colonization of sloping rather than horizontal surfaces. Ephemeral species such as _Enteromorpha_ _linza_ and _Monostroma_ _fuscum_ were observed to entrap sand and sediment at their base on the horizontal surface of concrete blocks and Plexiglas settling plates. Neushul _et al_. (1976) also noted the abundance of sediment on horizontal surfaces of artificial substrates attached to the sea bottom in a kelp forest. On the mesh of preditor exclusion cages and edges of settling plates where no sediment accumulated, the settlement contrasted with that on horizontal surfaces, even where sediment was removed frequently. Prince and Kingsbury (1973) suggested that large accumulations of thick sediment can prevent development of _Chondrus crispus_ in cleared areas. Quantities of coarse sand sometimes accumulated at the base of tall _Ulva_ sp. or haptera of _Sacchoriza_. Prince and Kingsbury were however successful in obtaining _C. crispus_ sporeling survival on glass slides placed in dense populations of the same, in waters off Plymouth, Massachusetts. The lack of development on the Plexiglas plates in the present study may be partly attributed to the large surface area ($1m^2$) of the settling plate platforms. The settling plates were attached to the center of the platforms where they were distant from edges that create turbulence for sediment removal.

It was apparent that high numbers of _I. cordata_ spores could settle and adhere to Plexiglas plates immersed adjacent to _I. cordata_ fronds over a short period of time (three days). High settlement (up to 200 ± 29 spores/cm^2) was particularly evident on plates immediately under reproductive fronds but much lower settlement occurred on plates 0.5 - 1 m distant (up to 7 ± 1.3 spores/cm^2). Thus concentrations of spores may be reduced considerably at a distance of one or more meters from a single clump of fronds, but the density of spores at various distances from a population would no doubt be a function of population size and current velocity. For example, plates 1.0 m above a dense population were settled by numerous spores (29 ± 4 spores/cm^2) within three days of immersion. In other subtidal studies, Sundene (1962) suggests that spores of *Alaria esculenta* generally were distributed only 10 - 12 m from the parent plant and Anderson and North (1966) found that successful recruitment of *Macrocystis pyrifera* sporophytes was very low beyond 5 m from the parent plant.

Many Plexiglas plates immersed for three to eight weeks or longer within *I. cordata* populations developed dense populations of diatons which obliterated spores during microscopic examination and may have resulted in the smothering and death of spores and inhibited adherence of additional spores to the plate surface. Although large numbers of spores likely adhered over the first few days, very few survived to produce upright frond initials. Whereas these settling plates were raised off the sea bottom by 0.25 m and fully exposed to light reaching this depth, it is possible that diatom growth would be reduced considerably under the canopy of foliose algal species. Substrate uncovered by harvesting a dense *I. cordata* population was observed to develop a thick diatom film (Fralick, 1971).

Insufficient spores, sporelings and frond uprights developed on the settling plates on each sample date to determine if a particular growth stage was more vulnerable to losses than another. There can be no doubt however, that adhering spore mortality was high as laboratory enhancement of the density of spores on settling plates prior to immersion in the *I. cordata* community did not increase production of sporelings or frond uprights.

Although quantitative variation in *I. cordata* spore settlement could not be recorded due to poor survival between sample dates, it was apparent that spore release did take place over a considerable length of time, between the end of May and mid-December. Within this period, substrate orientation, sedimentation, grazing, diatom films and growth rate may be as important to colonization as the relative number of spores in the water column. However, on the vertical surfaces of the concrete blocks, *I. cordata* density the season following immersion was heaviest on those put down in June rather than later in the summer. On the June blocks spores could accumulate during the entire first season and some sporelings would have nearly two growing seasons to develop.

Dayton (1975) reported that many aspects of algal recruitment depend on the season in which the appropriate space becomes available and clearly the availability of disseminules at the opportune time. However, clearing experiments of Northcraft (1948), Lee (1965), Castenholtz (1967), Vadas (1968), and Dayton (1971) indicate that many algal species recruit over most of the summer and hence spores are released over a prolonged period. Dayton (1975) suggests that the availability of disseminules over a lengthy period permits colonization of the spatically and temporally unpredictable patches of bare substrate that may become available during the summer. *I. cordata* can be considered such a species. Other algal species in this community recruit during the winter such as the phaeophytes: *Cymathere triplicata*, *Alaria tenuifolia* and *Laminaria groenlandica* with the advantage of a greater abundance of vacant space during this period.

Colonization by *I. cordata* does not require a prior successional sequence nor the presence of a particular macrophyte algae and commenced within a few days of exposure during the summer, although growth to macroscopic size varied with date of immersion. One concrete block immersed in early July had macroscopic *I. cordata* sporelings by the end of September, other blocks immersed in June and July had macroscopic sporelings in December and January, while blocks immersed in August and September had macroscopic sporelings by April of the following year. Similar results were obtained for *Chondrus crispus* by Prince (1971), who reported that rate of colonization appeared to vary with season. Eight to nine months were required for *C. crispus* to recolonize (grow to visible size) on rock surfaces cleared in the fall, five to eight months were required to recolonize surfaces prepared in winter and spring and two months for surfaces prepared in late summer. The seasonal change in the rate of colonization by *C. crispus* was attributed to the seasonal growth rate of spores and the seasonal reproductive intensity of *C. crispus*. *I. cordata* developed most rapidly on substrate immersed in mid-summer when cystocarpic frond reproductive capacity and growth rate was maximal. In spite of winter die-back in the *I. cordata* community, substrate immersed in mid-summer had an advanced growth of *I. cordata* by the end of the following summer compared to substrate immersed in the fall. *I. cordata* colonizing blocks immersed in the fall were primarily gametophytic, corresponding to the high reproductive capacity of tetrasporic fronds and rarity of cystocarpic fronds in fall.

Colonization of the artificial substrate immersed in I. cordata communities passed through the sequence of macrophyte stages described by many (Lee, 1965; Northcraft, 1948; Castenholtz, 1967; and others): first a diatom film followed by ephemeral chlorophyte species followed by rapid then slower growing perennial red algal species. The order of appearance of colonizing species has been related to their speed of growth which is a function of their growth form (Lee, 1965). By this interpretation of succession, the communities which develop are not considered to be the result of any intrinsic process of development, but are contingent upon the morphology of the species and phenology of the various phases in the life history of the species. The interplay of these two factors and the all important factor of available space for colonization governs the abundance and distribution of populations. Foster (1975b) also found no evidence of succession in subtidal colonization in the sense that initial populations modify the environment for later populations. In fact, Foster suggested that established populations, whether early or late stages, seemed to inhibit further colonization and growth of new species.

The rapid colonization of vacant space during summer indicates that I. cordata is an early stage in the serial development on cleared surfaces. However the differences between the natural population and artificial substrate immersed for as long as four years suggests that the time required to reach a climax community is many years. Colonization by I. cordata requires at least two years to reach its maximum biomass. Individuals less than one year old are particularly fragile and easily lost, possibly due to grazing or wave action. Mature holdfasts over one year old may be long-lived and have been noted in the same location for 3.5 years (equals at least 4.5 years old). Gradually encrusting phaeophyte and rhodophyte species and slow establishing foliose reds such as *Prionitis* spp. and *Plocamium coccineum* begin to colonize amongst the *I. cordata* and reduce the bare rock surface in summer to roughly 15 percent of the total in undisturbed areas of the *I. cordata* community.

Although *I. cordata* is a rapid colonizer of artificial substrate, first year growth from spores in natural populations is not likely as important to summer biomass as growth from existing holdfasts for the following reasons: 1. the amount of bare rock surface for colonization during summer is little if the cover of encrusting species is considered. Unfortunately, little is known of the interference via cellular sloughing or allelopathic agents which these encrusting algae exert on recruitment of spores (Dayton, 1975); 2. fronds developing from spores in one year did not grow as large as fronds growing from two year or older holdfasts; 3. mature *I. cordata* holdfasts were observed to live for a considerable number of years; and 4. fronds and holdfasts one year or younger were observed to suffer a high mortality, possibly from grazing, scouring or shading.

The role of *I. cordata* however, in the shallow subtidal populations of Georgia Strait, would appear to be one of the first perennial species to colonize and dominate disturbed areas in the absence of phaeophyte species. It may be partly displaced by slower growing red algal species in the absence of disturbance or be out-competed for light and space when conditions shift to favour colonization by laminarians.

CONCLUSIONS AND SUMMARY

1. Standing crop of foliose algal species in subtidal I. cordata communities in Georgia Strait vary dramatically with season. Maximum summer standing crop of the I. cordata community (2.1±0.05 - 2.6±0.60 kg fresh/0.5 m^2) occurred between May - September inclusive, but within this period, the date and magnitude varied according to dominant species associated with I. cordata. Peak standing crops of dominant species were not necessarily coincident with one another. The near absence of any foliose algae in the I. cordata community in winter (0.08±0.01 - 0.27±0.02 kg fresh/0.5 m^2) attests the severity of winter conditions for algal growth. Artificial substrates for I. cordata cultivation in northern Georgia Strait may prove difficult to anchor in winter due to considerable wave action in the shallow subtidal.

2. Standing crop of I. cordata increased in relation to both incident light and water temperature in spring and similarly declined with both in fall. Lowered nitrate nitrogen concentrations in summer may limit I. cordata growth particularly where current velocities are low. Maximum summer standing crop of I. cordata in natural, uniformly dense, populations in northern Georgia Strait (0.7 - 2.0 kg fresh wt./ 0.5 m^2) appears to be considerably less than that reported for northern California (approximately 3.8 kg fresh/0.5 m^2), where seasonal incident light and water temperature are less variable.

3. Processes observed to affect I. cordata community structure included chemical and physical environmental factors, reproductive processes, competition for space and light and random disturbances. Environmental conditions may shift in certain I. cordata communities to favour dominance of laminarian species which may heavily colonize

natural and artificial substrates alike. In some locations, the overgrowth of _I. cordata_ by laminarians could interfere with cultivation in occasional years. A certain level of substrate disturbance which provides vacant rock surface, quickly colonized by _I. cordata_, may prevent dominance by slow growing species such as _Plocamium coccineum_ after a period of years. Thus limited substrate disturbance during commercial harvesting operations may enhance dominance of _I. cordata_, providing that colonization potential from spores is not diminished substantially.

4. Standing crop and density of _I. cordata_ life history phases varied differentially with season. Gametangial fronds were dominant in May and June and tetrasporangial fronds were dominant in July through December, in contrast to California waters dominated year round by tetrasporangial plants. _I. cordata_ frond initials were abundant year round though many commenced elongation in February to produce juvenile fronds. In April, juveniles matured into male gametangial fronds which exfoliated after June. Female gametangial (cystocarpic) fronds were noted in April and reached maximum size in June and early July. Tetrasporangial fronds were first noted in May and June and reached maximum size in late July and August.

Harvests before July would yield a high proportion of gametangial fronds and after July a high proportion of tetrasporangial fronds containing a preponderance of "kappa" and "lambda" carrageenan respectively.

There was no consistent relation between standing crop and life phase composition. Summer peak standing crop may be high and sharp if the growth of life phases tend to coincide or may be lower and extended if growth of the life phases are separated in time. Data suggest that maximum standing crop in a particular year would be obtained in an annual harvest timed just prior to exfoliation of mature cystocarpic fronds. Growth of tetrasporangial fronds in mid to late summer (after exfoliation of mature cystocarpic fronds) may not reach the same magnitude of standing crop. *I. cordata* life phases are subject to rapid growth followed by frond loss which provide a very short season for harvest of maximum population standing crop.

5. Production of reproductive structures on gametangial and tetrasporangial fronds appeared to be part of a maturation sequence. Cystocarpic fronds developed a cover of sori more rapidly than tetrasporangial fronds. Patterns of macroscopic development of cystocarpic and tetrasporangial frond cover are described. In late summer and fall when growth rates were slow, smaller fronds became mature, suggesting that age of fronds rather than size may be important in the maturation process which ultimately leads to the termination of frond growth and exfoliation. Reproductive fronds were abundant in June through September and rare in December through May. Maximum potential spore production of cystocarpic fronds occurred in July and of tetrasporangial fronds occurred in late August through September. Thus substrate immersed at these times would receive differential settlement of spore types.

6. The growth of 5 - 20 g *I. cordata* fronds was highest at shallow depths in mid rather than late summer, and for cystocarpic rather than tetrasporangial fronds. The higher growth rate of cystocarpic

fronds explains their spring dominance. Fronds with growing tips cut off continued to grow, indicating their capacity to grow even with possible injuries sustained from commercial harvesting. Fronds, 5 - 10 g transplanted in May reached a maximum size in 90 - 125 days.

7. Results of this study indicate that *I. cordata* is one of the most rapid perennial species to colonize vacant substrate submerged in the *I. cordata* community. Although spores are distributed throughout the water column above the *I. cordata* population, it appears that the highest settlement occurs near the base of adult fronds. Substrate orientation, sedimentation, grazing, diatom film and seasonal growth rate may be as important to colonization as the relative number of *I. cordata* spores in the water column. *I. cordata* spore recruitment occurred between May and December, which corresponded to the period when large numbers of *I. cordata* fronds were reproductive. However, growth was more advanced the following summer on substrate immersed in early rather than late summer. Data suggest that maximum colonization of artificial substrate by *I. cordata* is achieved by the following summer if substrate is immersed in June.

Several other perennial red algal species colonized artificial substrate within one to two years including *Gigartina exasperata*, *Neoagardhiella baileyi* and *Callophyllis violacea*, although less abundantly than *I. cordata*. Several species abundant in the natural community were slow to colonize artificial substrates including

Plocamium coccineum and *Prionitis lanceolata*. *Laminaria groenlandica* and *Alaria tenuifolia* colonized artificial substrates at one location and overgrew *I. cordata* fronds, severely reducing their summer abundance.

8. With respect to cultivation, the large numbers of spores released from *I. cordata* fronds, their poor survival rate and the low percent of vacant surface in the natural community suggest that enhancement of natural standing crop by dispersal of large numbers of spores would not be practical.

9. The rapid colonization by *I. cordata* may be an advantage in cultivating populations on artificial substrate as this species requires a short period to develop dense stands. Fully mature fronds can be obtained from spores in 12 months, although maximum standing crop was obtained after 24 months on concrete blocks and rope substrate in this study. Colonization of artificial substrates immersed in natural populations produced dense, nearly monotypic stands of *I. cordata*, but not consistently, and factors governing maximum *I. cordata* colonization must be researched further. Of particular concern is survival in the period between the spore to sporeling stage. Laboratory recruitment of spores on artificial substrate probably would not enhance colonization unless outplanting was delayed until *I. cordata* reached the upright sporeling stage.

10. Use of artificial enclosures to grow unattached *I. cordata* fronds from small "seed" fronds proved difficult in the high current

areas of northern Georgia Strait due to the exposed nature of the coastline. Further experiments with artificial enclosures should be conducted on land or in sheltered bays with the necessary current provided by air or water pump systems.

PART II POTENTIAL YIELDS OF IRIDAEA CORDATA IN NATURAL AND ARTIFICIAL POPULATIONS IN GEORGIA STRAIT, B.C.

INTRODUCTION

The red alga *Iridaea cordata* has been the focus of a number of resource-related studies including surveys of distribution and abundance (Austin and Adams, 1973, 1974, 1975) and growth rates of transplanted and cultured specimens (Waaland, 1973). Because natural populations presently are costly to harvest, attention has been paid to the *I. cordata* yields obtained from various methods of cultivation (Kemp and Mumford, 1976; Mumford, in press, 1978; Waaland, 1976, 1978).

Yields of annuals or pseudo-perennials (which die-back in winter; Sears and Wilce, 1975) in nature are sometimes equated with estimates of net production or the difference between maximum summer and winter standing crops (e. g. John, 1971; Niell, 1975). The accuracy of such measures of production is dependent on the mode of seasonal growth and maturation of the species (Katada and Satomi, 1975). Thus species subject to frond losses due to short life spans, non-synchronous life phases or grazing between sample periods will give erroneous measures of production. Furthermore, natural production may not always be equated directly with harvest yields. A number of harvests in one growth season have been shown to maintain high growth rates and increase the total yield of certain species of *Gracilaria*, *Gelidium* and *Porphyra* but not of *Hizikia* (Katada and Satomi, 1975) for example.

In terrestrial crops, theory predicts that maximum growth rates are obtained at an optimum leaf area index (leaf area per m^2 = LAI). Optimum LAI may be exceeded to a ceiling value with a corresponding reduction in growth rate until an equilibrium point is attained where non-photosynthesising parts consume as much as photosynthesising parts produce. At this point the instantaneous ceiling yield or maximum standing crop is reached (Donald, 1961), and any increase in mean leaf area per plant is accompanied by a decrease in population density in accordance with a self-thinning rule (Westoby, 1977). Sustained high growth rate may be obtained by frequent cropping, to maintain the LAI at its optimum. The relation of light penetration in plant communities to leaf arrangement and leaf area has been the subject of considerable research (e.g. Saeki, 1963; Black, 1963; Ikusima, 1966).

In this study, the frond area, density and standing crop of *I. cordata* were examined in populations growing on natural and rope substrates. Growth rate was measured as a function of these parameters in artificial populations on natural and rope substrates to determine relations between density, maximum seasonal standing crop, biomass production and potential harvest yields.

METHODS

Observation of Naturally Recruited Populations

(a) natural cobble substrate

Sample methods to assess the seasonal variation of I. cordata density, standing crop, size and life phase composition at three sites in Georgia Strait were described in Part I. Additional information on I. cordata population structure was obtained from a more intensive examination of I. cordata samples, collected at close to peak standing crop, from two of the seasonal sample plots. In this study, the ten random 0.5 m^2 samples from Kye Bay and Cape Mudge sample plots, collected on June 16 - 18, 1975 prior to mid-summer frond maturation and exfoliation, were examined. The frequency and total biomass of I. cordata fronds greater than 5 cm long were measured per 0.5 m^2 quadrat sample and the surface area of individual fronds greater than 15 cm long was recorded and summed per 0.5 m^2 sample to determine the relation between I. cordata frond density, biomass and frond surface area.

(b) rope substrate

Polypropylene ropes (0.7 cm diameter by 5 to 19 m long) were anchored to the bottom in dense I. cordata beds at Kye Bay, Willow Point and at Cape Mudge on a number of dates in the summers of 1973, 1974, and 1975. Each set of ropes was anchored by 20 kg concrete blocks at each end and the initial buoyancy of the ropes raised the centre of each 0.25 to 0.5 m off the bottom. When the mass of colonizing vegetation was sufficiently heavy, the ropes rested lightly on the bottom.

Rope samples were recovered by divers during the summers of 1975, 1976 and 1977 and were brought to the laboratory for analysis. Fresh weight, density and surface area of *I. cordata* fronds, and abundance of competing species were recorded per unit length of the ropes.

Construction and Observation of Artificial Populations

(a) natural cobble substrate

To examine *I. cordata* frond growth and loss as a function of density in monotypic stands, a series of artificial populations were constructed with frond densities ranging from well below to well above those found in natural populations. The cobble substrate of natural populations was amenable to transplant experiments, and cobbles 15 to 20 cm in diameter with 1 to 15 *I. cordata* fronds were easily located and transplanted by SCUBA divers to be arranged in artificial populations.

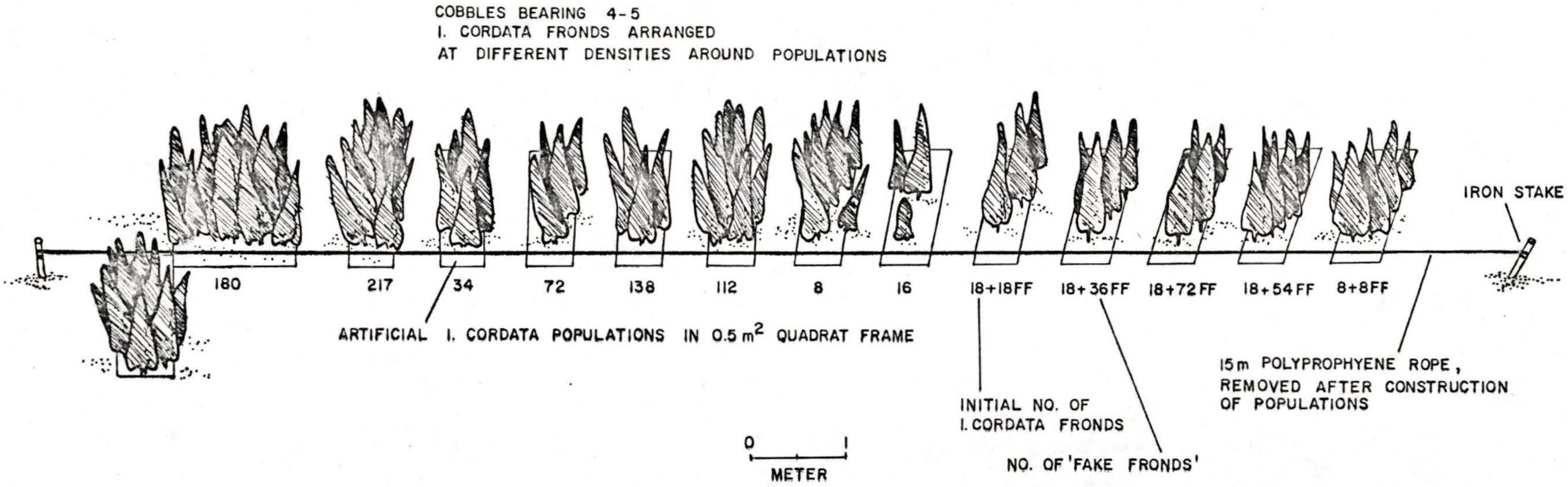
A total of 14 *I. cordata* populations were constructed at various densities in Kye Bay; two were completed by June 12 and the remainder by July 1, 1976. Each population was established within a 0.5 x 1.0 m quadrat frame. The quadrats were positioned at intervals along a 15 m transect line located at -1.0 m depth, near the Kye Bay sample plot.

To construct these populations, the bottom along the 15 m transect line was cleared of all cobbles supporting vegetation in a 2 m wide strip. SCUBA divers then selected neighbouring cobbles for their abundance of *I. cordata* fronds and these were lifted to a boat on the surface. Here all species other than *I. cordata* were removed from each cobble. In addition, all *I. cordata* fronds that were reproductively mature, in ragged condition or longer than 30 cm, were discarded to ensure that the larger fronds, contributing the most surface area, were not senescent and past their rapid growth phase. Finally the length of each *I. cordata* frond greater than 5 cm long was recorded for each cobble and a specific cobble was selected for the appropriate quadrat according to its number of fronds between 15 and 30 cm long. Each selected cobble was positioned in the appropriate quadrat to be equidistant from neighbouring cobbles and the edge of the 0.5 x 1.0 m quadrat frame. A row of cobbles bearing a similar number of *I. cordata* fronds to those inside the quadrat, were placed around the periphery to reduce the "edge effect". Figure 34 gives a diagramatic representation of the relative position of the artificial populations.

The initial length measurements of fronds in each population were listed as size-class frequencies. An approximation of the total weight and surface area of these fronds per population was obtained from observations on the relation between frond length, weight and surface area. A large number of these measurements were made in the life history study in Part I.

Of the 12 populations established on July 1, 1976, five were modified to test directly the hypothesis that frond growth rate was limited at high densities by shading from neighbouring fronds. This experiment required a synthetic material that would simulate the hydrodynamic characteristics and transparency of real *I. cordata* fronds. Although exact simulation of *I. cordata* frond habit was considered to be nearly impossible, materials were examined that

Figure 34. Diagram of relative position of artificial _I_. _cordata_ populations constructed along 15 m transect in Kye Bay.


COBBLES BEARING 4-5
I. CORDATA FRONDS ARRANGED
AT DIFFERENT DENSITIES AROUND POPULATIONS
IRON STAKE
180
217
34
72
138
112
8
16
18+18FF
18+36FF
18+72FF
18+54FF
8+8FF
ARTIFICIAL I. CORDATA POPULATIONS IN 0.5 m² QUADRAT FRAME
15m POLYPROPHYENE ROPE, REMOVED AFTER CONSTRUCTION OF POPULATIONS
INITIAL NO. OF I. CORDATA FRONDS
NO. OF 'FAKE FRONDS'
0
1
METER

would imitate the transparency, degree of rigidity and rate of sinking of real fronds.

After a number of trials, a 1 mil thick, semi-opaque, dark green plastic sheeting was selected as the most suitable material that was readily available. A template was made of cardboard in the shape of a typical *I. cordata* frond, 30 cm long by 20 cm wide, and roughly 500 synthetic *I. cordata* fronds were cut to the shape of the template. The positive buoyancy of the plastic was countered with 15 staples punched into the periphery of each plastic frond. The percent light transmittance of the plastic fronds was very close to an *I. cordata* frond of equal size. Twenty percent of the light (measured in foot candles) from a 60 watt incandescent light bulb passed through the plastic and real fronds held 0.2 m below the light.

Observations were made on the growth of real fronds interspersed between different densities of synthetic fronds. One to four of the plastic fronds were tied to cobbles which supported real *I. cordata* fronds, 15 - 30 cm long. These cobbles were placed equidistant in 0.5 x 1.0 m quadrat frames, and surrounded by a ring of similar cobbles to reduce "edge effects". Location of these populations along the 15 m transect in Kye Bay is diagrammed in Figure 34.

On August 14, 1976, all the artificial populations were harvested of fronds greater than 5 cm long. Two populations had been in place for 65 days and the remainder for 45 days. Biomass, density, frond area and size structure were determined for *I. cordata* fronds from each population.

(b) rope substrate

In order to examine the relation between growth rate, biomass, and density of I. cordata fronds on rope substrates, a series of I. cordata populations were assembled artificially on polypropylene ropes and anchored to the bottom within naturally occurring I. cordata communities.

One set of ropes was deployed on April 3, 1976; the second and principal set was deployed on June 3 - 4, while a third set was put out on July 3, 1976. All were located near the Kye Bay sample plot described in Part I.

To establish the rope populations, hundreds of I. cordata fronds were harvested by SCUBA divers and brought to shore where they were sorted. Divers attempted to obtain as much of the holdfast on the harvested fronds as possible. On shore, fronds between 10 and 15 cm long, with no ragged or torn edges, were selected for the April 3 rope series. These fronds were inserted into the twine of 0.7 cm diameter polypropylene line (Figure 35) at an approximate density of 50 per 0.5 m. Two ropes, each 2 m long were fashioned in this manner and were anchored to the bottom by concrete blocks at a depth of -1.5 m. The ropes were 2 - 3 m apart and rested lightly on the bottom. The various foliose red algal species attached to the natural substrate in close proximity to the ropes such as Constantinea subulifera, Gigartina exasperata, Rhodymenia pertusa, Plocamium coccineum, Rhodoglossum roseum and Iridaea cordata, were harvested to reduce competition with the growing I. cordata on the ropes.

Figure 35. I. cordata fronds inserted in twine of polypropylene rope.

The second set of ropes, completed on June 3-4 were inserted with slightly larger fronds, 15-20 cm long. Five different densities of fronds were established: 2.5/0.5 m, 12/0.5 m, 20/0.5 m, 38/0.5 m and 63/0.5 m. Two ropes with two meters of fronds were constructed at each density and anchored to the bottom near the first set.

The third set of ropes, deployed on July 3, was designed to test the differences in growth rates between plants suspended off the bottom and resting on the bottom. Four ropes were each inserted with 100 fronds over 1 m length. Two were anchored at each end while two buoys held the centre, frond bearing portion of the rope, at a height of 0.5 meters above the bottom. The other two ropes were anchored to lie on the bottom.

All ropes were weighed and total frond number recorded before being set out. Growth rate of *I. cordata* was measured as increase in fresh weight and observations were made at three week intervals. Ropes were brought to shore in coolers and carefully shaken, then held for five minutes to allow excess water to drain off before weighing. Little increase was observed in the biomass of the dense ropes between July 3 and July 29 and on the latter date, all ropes were collected and preserved for further analysis. In the laboratory, each rope was cut into 0.5 m sections, and each section was weighed separately. Ten fronds from each section were weighed individually, their area was measured and life phase and reproductive condition was determined.

RESULTS

Maximum Density, Standing Crop and Frond Area of Natural Populations on Cobble and Rope Substrates

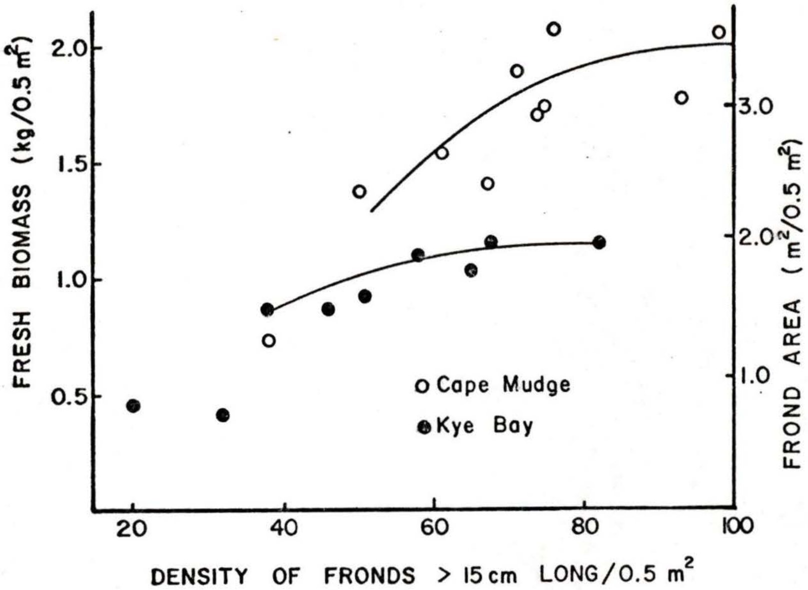
(a) cobble substrate

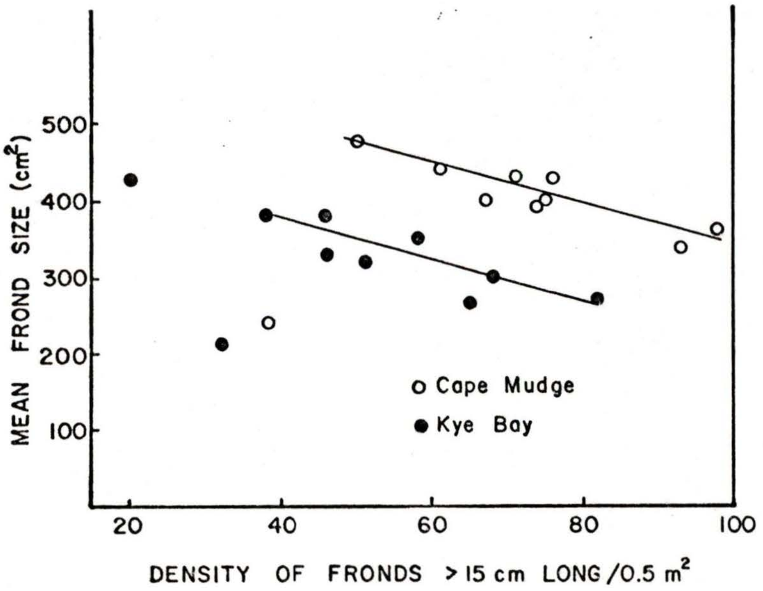
Standing crop of *I. cordata*, at three sample locations in Georgia Strait where this species was dominant, reached a mean sample peak in summers of 1975 and 1976 of 0.7 ± 0.05 to 2.0 ± 0.24 kg fresh/ 0.5 m^2 (Figure 13). Maximum biomass sampled in a single 0.5 m^2 quadrat was 1.34 kg at Kye Bay, 2.41 kg at Willow Point and 2.53 kg at Cape Mudge. Maximum frond area measured per 0.5 m^2 quadrat was 3.5 m^2 (FAI = 7.0). Maximum density of fronds greater than 15 cm in length (contributing 80 to 90 percent of the biomass) was 66 at Kye Bay and 97 at Cape Mudge in 0.5 m^2 samples. In 1975 peak summer standing crop at Kye Bay and Cape Mudge occurred in early July and was followed by a rapid decline in standing crop due to frond losses in all age classes.

The relation of *I. cordata* density to biomass and frond area per 0.5 m^2 quadrat at Kye Bay and Cape Mudge in mid-June is graphed in Figure 36. The data suggest that biomass and frond area did not continue to increase with increasing density, but these variables levelled off (varied independently) at high densities. Such a relation suggested that intraspecific competition interfered with growth of individual fronds at high densities. A graph of quadrat density and mean frond size (Figure 37) indicated that the mean size of *I. cordata* fronds was smaller in high density quadrats than some

Figure 36. Relation between density, biomass and surface area of *I. cordata* fronds in natural populations per 0.5 m^2 (lines placed by eye), June 20, 1975.

Figure 37. Relation between the density and mean size of *I. cordata* fronds in natural populations per 0.5 m (lines placed by eye), June 20, 1975.


FRESH BIOMASS (kg/0.5 m²)
2.0
1.5
1.0
0.5
FROND AREA (m²/0.5 m²)
3.0
2.0
1.0
20
40
60
80
100
DENSITY OF FRONDS > 15 cm LONG/0.5 m²
○ Cape Mudge
● Kye Bay


MEAN FROND SIZE (cm²)
500
400
300
200
100
20
40
60
80
100
DENSITY OF FRONDS > 15 cm LONG/0.5 m²
○ Cape Mudge
● Kye Bay

low density quadrats. Higher density, biomass and frond area values were observed at Cape Mudge and were attributed to higher current and concentrations of nutrients than present at Kye Bay.

In the summer of 1976, conditions at Kye Bay and Cape Mudge appeared more favourable for species competing with I. cordata. At Cape Mudge I. cordata no longer was dominant, while at Kye Bay, adjacent to the artificial populations the maximum I. cordata biomass sampled per 0.5 m^2 quadrat in the natural population was only 1.02 kg with a density of 39 fronds longer than 15 cm and frond area of 1.6 m^2 (FAI = 3.3).

(b) rope substrate

Observations of I. cordata biomass sampled from rope substrates laid down in summers of 1973 and 1974 are listed in Table IX. Maximum mean sample biomass was 0.42 ± 0.07 kg/0.5 linear m (maximum = 0.60 kg/0.5 m) sampled in mid-July, 1975 at Kye Bay on ropes immersed for two years. A section of the same rope measured in late July, 1976 had a similar mean standing crop of 0.41 ± 0.06 kg/0.5 m (maximum = 0.58 kg/0.5 m). Analysis of frond sizes in this latter rope indicated a mean density of 30 ± 6.8 (maximum 50) fronds greater than 15 cm long (90% of the biomass) per 0.5 m length of rope. Mean frond surface area (FA) was 0.66 ± 0.11 $m^2/0.5$ m (maximum = 0.93 m^2). Ropes immersed at Cape Mudge supported populations dominated by laminarians in summers of 1975 and 1976, but these species were replaced by a nearly monotypic stand of I. cordata in 1977 (Figure 38). Mean sample biomass on ropes immersed for three years at Cape Mudge was 0.41 ±

Table IX. Abundance of *I. cordata* colonizing polypropylene ropes immersed for various time periods.

Date Ropes Immersed	Date Biomass Measured	Mean *I. cordata* Biomass±S.E./0.5m^2	N	Length (m) Measured	Notes
A. Kye Bay					
Aug. 28, 1973	July 29, 1974	0.05 ± 0.017	3	15	*M. fuscum* dominant
Aug. 28, 1973	July 22, 1975	0.42 ± 0.07	7	7	*G. exasperata* and *Halymenia* sp. present in small quantities
Aug. 28, 1973	July 29, 1976	0.41 ± 0.06	15	7.5	Other species include *G. exasperata*, and *B. farlowianum* in small quantities.
July 19, 1974	May 24, 1975	no *I. cordata* >1 cm long			covered by diatom film
July 19, 1974	July 9, 1975	no *I. cordata* >1 cm long			covered by diatom film
July 19, 1974	July 29, 1976	0.21 ± 0.03	10	5	Some gaps with no colonizing species. A few *G. exasperata* present.
B. Cape Mudge					
July 29, 1974	July 10, 1975	*I. cordata* very rare			*M. fuscum* dominant with abundant *A. tenuifolia*, *N. luetkeana*, *S. muticum* and *O. lyallii*.
July 29, 1974	July 23, 1976	*I. cordata* very rare			*A. tenuifolia* and *N. luetkeana* dominant with *O. lyallii* and *R. californicum*.
July 29, 1974	July 31, 1977	0.41 ± 0.06	11	5.5	Other species rare but include *E. linza* *G. exasperata*, *O. lyallii*, *Halymenia* sp., *L. saccharina* and *R. californicum*.
C. Willow Point					
July 29, 1974	July 7, 1975	*I. cordata* >10 cm rare, but 300 sporelings <5 cm long were counted along 3 m length.			
July 11, 1974	July 28, 1976	*I. cordata* sporelings only with scattered *L. saccharina*, *R. californicum* and *O. lyallii*.			

Figure 38. Dense population of I. cordata naturally recruited on rope substrate immersed for three years at Cape Mudge, July, 1977.

0.06 kg/0.5 m (maximum 0.68 kg) measured on July 31, 1977. Mean density of fronds greater than 15 cm long was 17.7 ± 5.6/0.5 m. All of these samples of biomass from rope substrates were taken shortly after the time of peak standing crop in natural populations and therefore may not be the maximum attained.

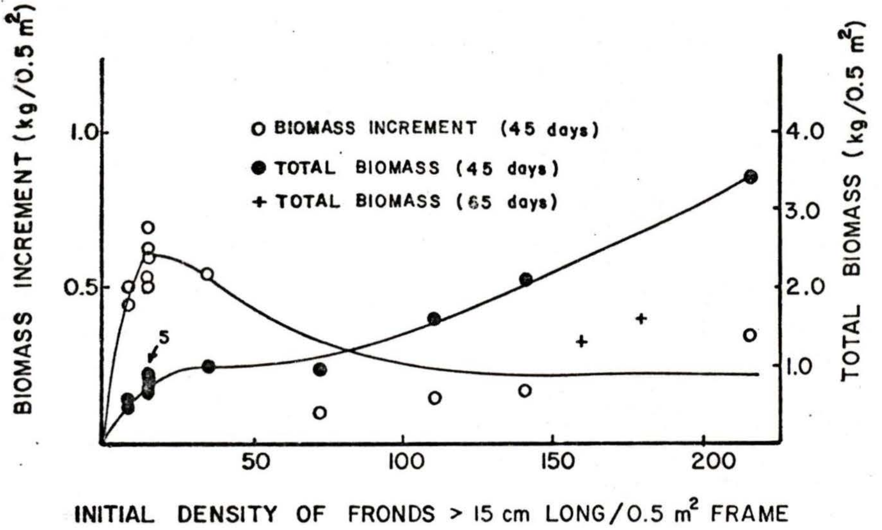
Growth Rate as a Function of Density in Artificial Populations

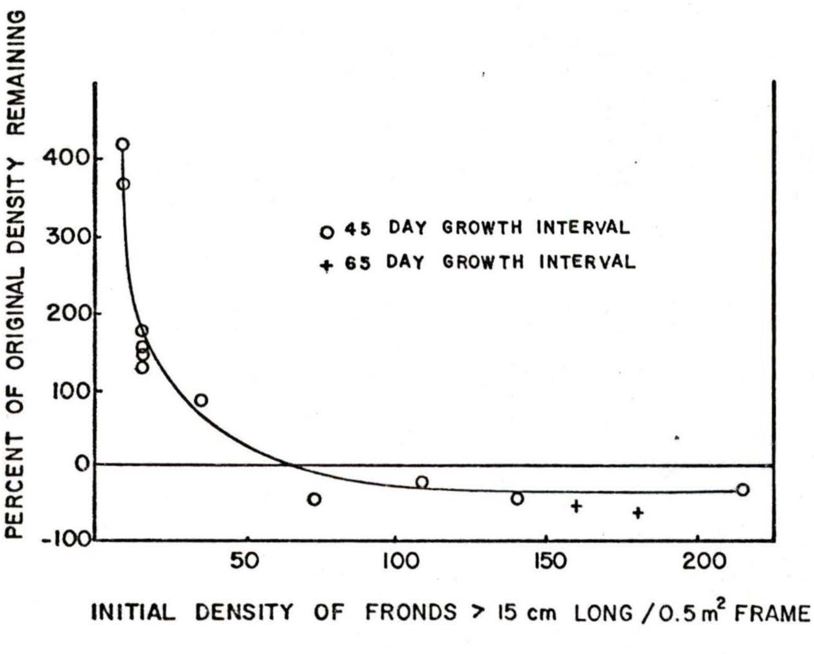
(a) natural substrate

In the artificial populations constructed on natural cobble substrate in 0.5 m^2 frames, the biomass of I. cordata after 45 days showed a positive relation with initial frond density (Figure 39). At the lowest initial density of 8 (15-25 cm long) fronds per 0.5 m^2, the final biomass was 0.50 kg, and at the highest initial density of 217 fronds per 0.5 m^2, the final biomass was 3.40 kg. This latter biomass was considerably higher than the maximum quadrat sample biomass (n = 5) collected from the adjacent natural population in mid-August (1.02 kg/0.5 m^2). However, I. cordata fronds in 65 day old dense artificial populations (160 and 180 fronds/0.5 m^2) were mature and commencing exfoliation. Biomass in these 65-day old artificial populations (1.3 - 1.6 kg/0.5 m^2) was less than the 45 day old populations of similar density, indicating that growth in the artificial populations was followed by biomass loss within 45-65 days. The high biomass of some 45 day old populations was likely an artifact of their artificially high initial density of large fronds.

Figure 39. Relation of density of young _I. cordata_ fronds to growth rate and final biomass in 0.5 m^2 frames after 45 and 65 days (lines placed by eye).

Figure 40. Relation of initial _I. cordata_ frond density to frond loss or gain in 0.5 m^2 frames after 45 and 65 days (lines placed by eye).


BIOMASS INCREMENT (kg/0.5 m^2)
TOTAL BIOMASS (kg/0.5 m^2)
O BIOMASS INCREMENT (45 days)
● TOTAL BIOMASS (45 days)
+ TOTAL BIOMASS (65 days)
1.0
0.5
4.0
3.0
2.0
1.0
5
50
100
150
200
INITIAL DENSITY OF FRONDS > 15 cm LONG/0.5 m^2 FRAME

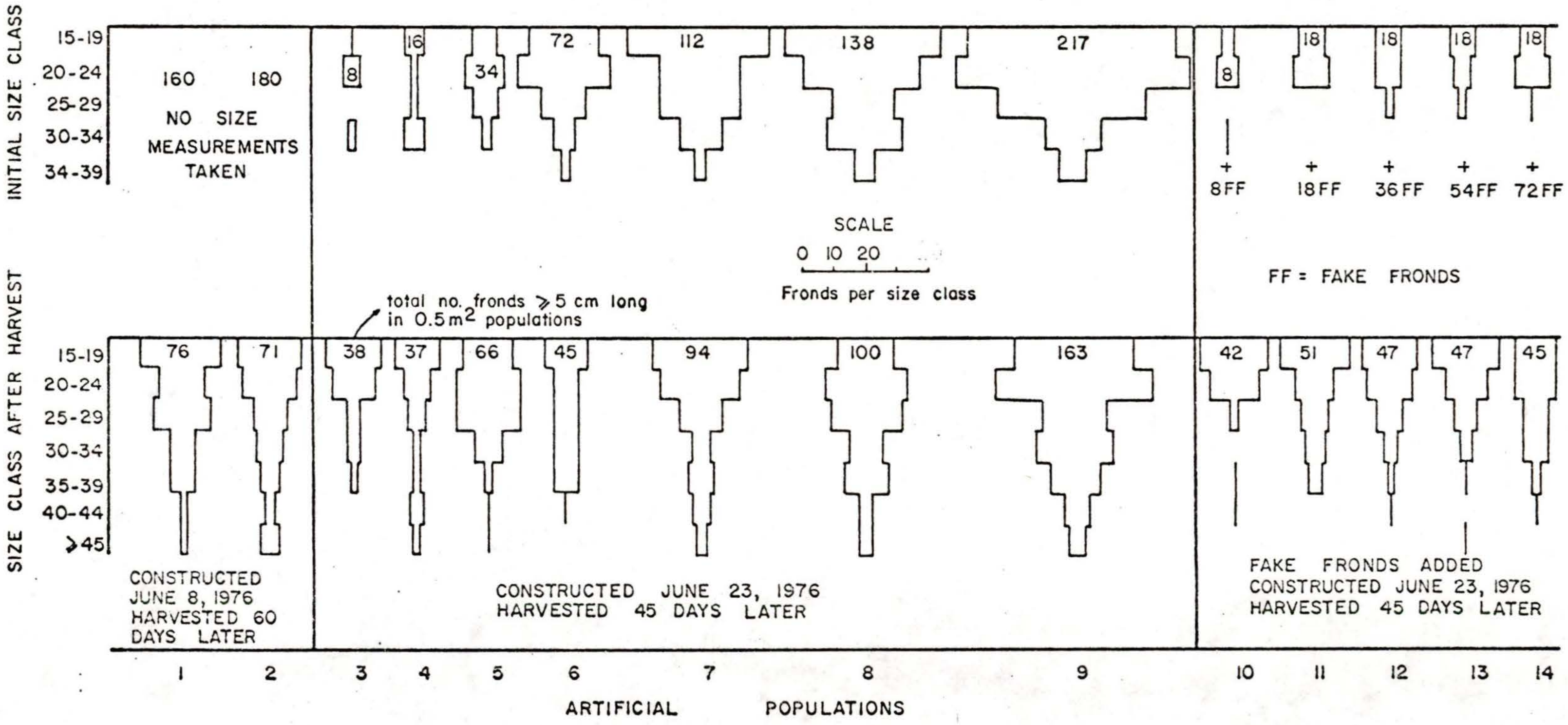

PERCENT OF ORIGINAL DENSITY REMAINING
400
300
200
100
0
-100
O 45 DAY GROWTH INTERVAL
+ 65 DAY GROWTH INTERVAL
50
100
150
200
INITIAL DENSITY OF FRONDS > 15 cm LONG / 0.5 m^2 FRAME

The biomass increment (growth rate) over 45 and 65 days in the artificial populations was not positively related to initial density (Figure 39). The highest growth increment was 0.72 kg/0.5 m^2 in 45 days (16 gm/day) from an initial density of 16 fronds/0.5 m^2. Frond surface area of this population ranged from 0.05 at the beginning to 0.5 m^2 at the end of 45 days. The mean growth increment of five populations constructed at this density was 0.58 ± 0.11 kg/0.5 m^2 (13 gm/day). In the population with highest initial density (217 fronds/0.5 m^2) the growth increment was 0.38 kg in 45 days (8 gm/day).

The smaller growth increment at high densities was partially explained by the exfoliation of a large number of fronds (Figure 40). High density populations observed after 65 days showed a greater loss (50-60 percent) than those observed after 45 days (20-40 percent). Low density plots showed a large increase in frond density (up to 400 percent) resulting from the growth of frond initials from holdfasts. Changes in size class structure of _I. cordata_ fronds in these artificial populations are illustrated in Figure 41. At low densities, all sizes of fronds increased in number over 45 days. At high densities, there was an increase in the number of large fronds, but a decrease in the number of small fronds over 45 days.

All of the populations with "fake fronds" had biomass increments similar to the populations with real fronds alone (Figure 41). At the end of 45 days, most of the "fake fronds" were observed to be lying flat and many were weighted down by sand or twisted around one another. Apparently they did not simulate real fronds by shading or retarding growth of adjacent fronds. Probably a thicker more rigid

Figure 41. Frequency of _I_. _cordata_ fronds per size class (length in cm) in artificial populations on cobbles, immediately after construction and after 45-60 days.


INITIAL SIZE CLASS
15-19
20-24
25-29
30-34
34-39
160
180
NO SIZE MEASUREMENTS TAKEN
8
16
34
72
112
138
217
18
18
18
18
8
+ 8FF
+ 18FF
+ 36FF
+ 54FF
+ 72FF
SCALE
0 10 20
Fronds per size class
FF = FAKE FRONDS
total no. fronds ≥ 5 cm long in 0.5 m² populations
SIZE CLASS AFTER HARVEST
15-19
20-24
25-29
30-34
35-39
40-44
>45
76
71
38
37
66
45
94
100
163
42
51
47
47
45
CONSTRUCTED JUNE 8, 1976 HARVESTED 60 DAYS LATER
CONSTRUCTED JUNE 23, 1976 HARVESTED 45 DAYS LATER
FAKE FRONDS ADDED CONSTRUCTED JUNE 23, 1976 HARVESTED 45 DAYS LATER
1
2
3
4
5
6
7
8
9
10
11
12
13
14
ARTIFICIAL POPULATIONS

material was required (e.g. 3-6 mil plastic sheet).

(b) rope substrate

The mean biomass of I. cordata per linear 0.5 m in artificially constructed populations on rope substrate is graphed in Figure 42 for monthly sample intervals. Ropes immersed on April 3, 1976 with a density of 50/0.5 m and an initial mean biomass of 0.15 kg/0.5 m (n = 2, range = 0.013 kg)[1] increased rapidly to 0.42 kg/0.5 m (range = 0.012) by May 8 (7.7 g/day), then increased very slowly to 0.49 kg/0.5 m (range = 0.010) by July 3 (1.2 gm/day) and declined to 0.36 kg/0.5 m (range = 0.037) by July 29. Ropes at five densities immersed on June 3 and 4 all increased rapidly in weight to July 1. Biomass of the most dense populations (63/0.5 m) then declined, while the other populations increased to July 29 when all were harvested. After 26 days, the biomass of ropes suspended off the bottom on July 3, 1976, was not significantly different to biomass of ropes lying on the bottom (Figure 42).

Biomass after 50 days was compared with initial density on the five rope populations constructed on June 3 and 4 (Figure 43). The highest biomass observed was 0.78 kg/0.5 m (n = 2, range = 0.07) on the highest density ropes which was only a little higher than the maximum attained on naturally colonized ropes (0.68 kg/0.5 m and a density of 24 fronds > 15 cm long). However, the highest mean growth increment of 0.29 kg/0.5 m (range = 0.037) or 5.8 g/day was not

---

[1] range was calculated as difference between two sample values.

Figure 42. Mean biomass of I. cordata per 0.5 linear meter (± standard error; n=2) in artificial populations constructed at various densities on rope substrate.

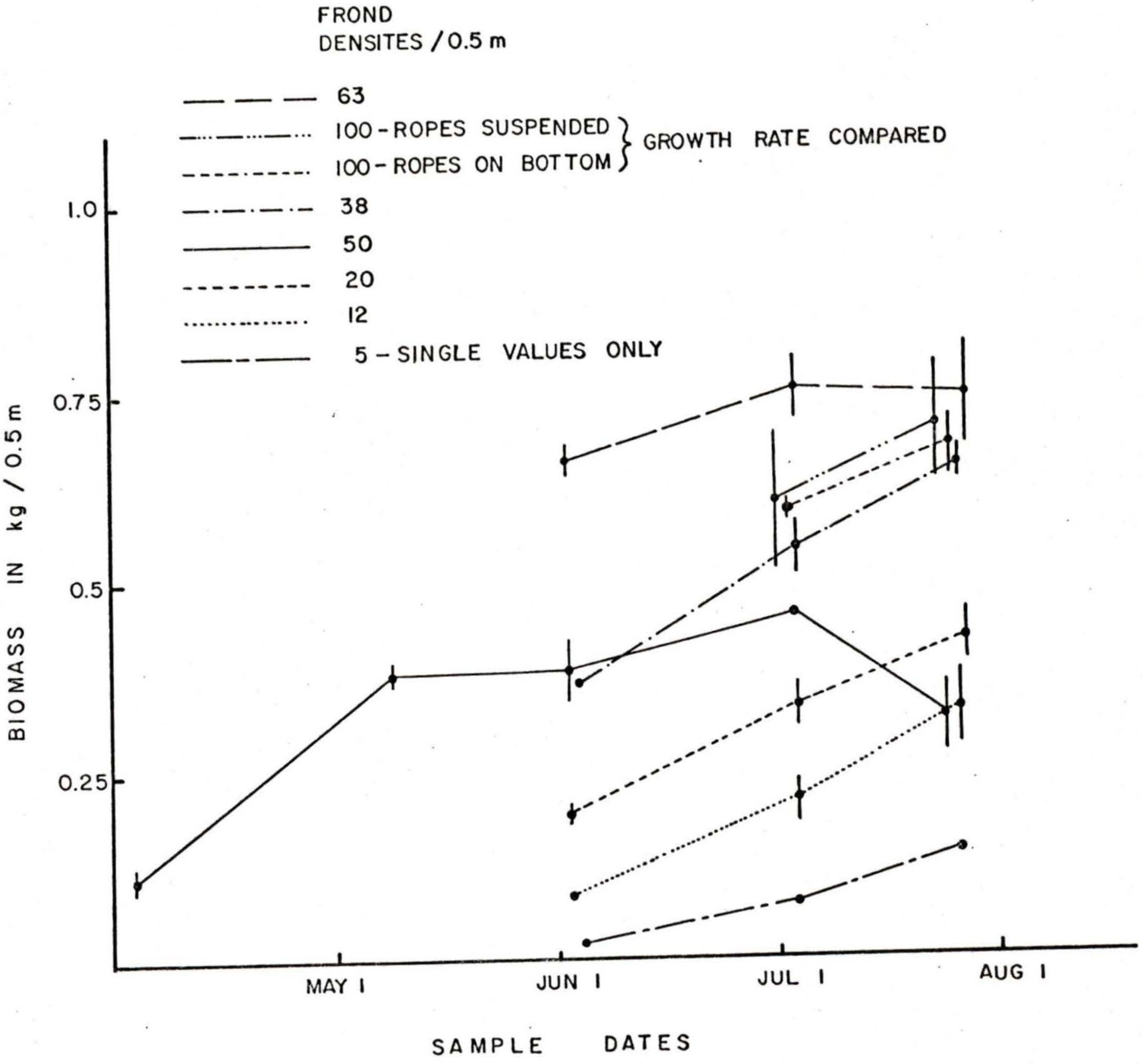
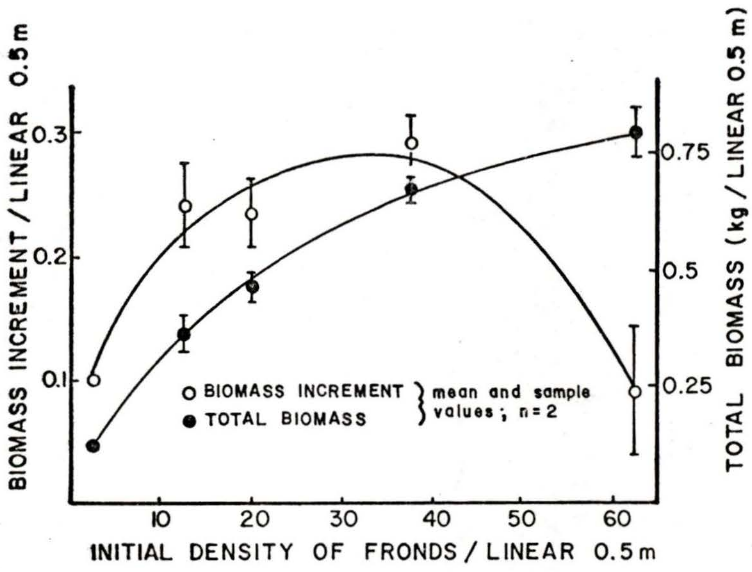
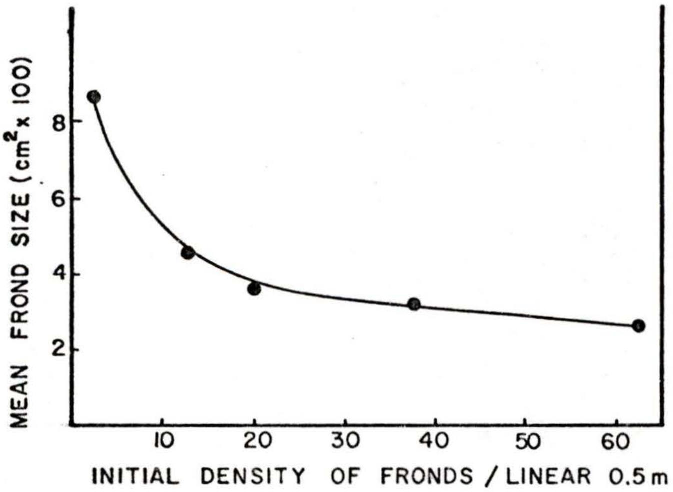

FROND
DENSITES / 0.5 m
63
100 - ROPES SUSPENDED
100 - ROPES ON BOTTOM
GROWTH RATE COMPARED
38
50
20
12
5 - SINGLE VALUES ONLY
1.0
0.75
0.5
0.25
BIOMASS IN kg / 0.5 m
MAY 1
JUN 1
JUL 1
AUG 1
SAMPLE DATES

Figure 43. Relation of initial *I. cordata* frond density to growth rate and final biomass in artificial populations on ropes after 50 days (lines placed by eye).

Figure 44. Relation of initial *I. cordata* frond density to the mean size of fronds in artificial populations after 50 days (line placed by eye).


BIOMASS INCREMENT / LINEAR 0.5 m
0.1
0.2
0.3
TOTAL BIOMASS (kg / LINEAR 0.5 m)
0.25
0.5
0.75
○ BIOMASS INCREMENT
● TOTAL BIOMASS
mean and sample values ; n = 2
10
20
30
40
50
60
INITIAL DENSITY OF FRONDS / LINEAR 0.5 m


MEAN FROND SIZE (cm² x 100)
2
4
6
8
10
20
30
40
50
60
INITIAL DENSITY OF FRONDS / LINEAR 0.5 m

observed at the highest density (Figure 43). Growth increments were similar for densities of 12, 20 and 38 fronds/0.5 m, but reduced at lower (2.5/0.5 m) and higher (63/0.5 m) densities.

A marked reduction in growth rate of individual fronds was observed at high densities. After 50 days, fronds at a density of 2.5/0.5 m averaged 450 cm^2, while fronds at a density of 63/0.5 m averaged 225 cm^2 in surface area (Figure 44). This explains the similarity of population growth rates within a range of densities. At very high densities there was a reduction in growth rate due to frond exfoliation.

At the highest growth rate measured on the rope populations (7.7 g/0.5 m/day), observed between April 3 and May 8, the frond surface area (FA) ranged between 0.4 and 1.4 m^2 per linear 0.5 m rope.

DISCUSSION

These studies indicate the importance of intraspecific competition to the growth and yields of crowded populations of this small frondose red alga, Iridaea cordata. During spring growth in I. cordata populations, frond size was reduced and sample biomass did not increase with density at the highest densities. Thus the maximum standing crop of I. cordata sampled in natural populations (just before mid-summer frond exfoliation) appears to be a good indication of the maximum that could be obtained from cultivation on similar bottoms in northern Georgia Strait with oceanographic conditions that prevailed during this study.

Even in the uniformly vegetated sample plots observed in this study however, the density of I. cordata varied considerably and biomass was reduced at low densities. Thus if cultivation provided a uniformly high density the mean population standing crop of I. cordata could be enhanced.

It appears that increasing the density of juveniles above the maximum which occurred naturally would not increase the maximum standing crop. On artificial frames set out in winter in Puget Sound with laboratory grown artificially dense I. cordata juveniles on rope netting, the mean biomass in June was approximately 1.6 kg fresh wt/0.5 m^2 (Waaland, in press). This biomass was somewhat less than the mean 0.5 m^2 quadrat biomass at Cape Mudge in 1975 (2.0 ± 0.23 kg).

Intraspecific growth inhibition also has been observed in populations of several other algal species. Yoshida (1972) found that cultivated Porphyra also was governed by a "law of constant final yield", such that maximum standing crop was independent of the density of individuals. Population density and leaf area index of Laminaria species near Helgoland were observed to decrease with increasing depth, as light was reduced (Luning, 1969). Kain (1976) indicated that the growth rate of individuals of Laminaria hyperborea in dense populations is remarkably similar at different depths because self shading (density) is reduced as light is reduced in deeper water. If populations were thinned, however, growth rate increased considerably.

In artificial populations of I. cordata on cobble and rope substrates, growth rate is maximum at an optimum range of frond area and does not increase with frond area. The optimum frond area is less than that found in dense natural populations during mid-summer. In theory, at optimum frond area, all incident sunlight is intercepted by the algal fronds and growth rate is a function of photosynthetic efficiency which for I. cordata varied with respect to location of the study area (current and/or nutrient differences). Above a critical FAI, frond losses occur which reduce the net growth rate, until, in theory, losses equal growth, and instantaneous ceiling standing crop is achieved. However, rapid frond losses which occurred in I. cordata populations at high FAI suggest that such a ceiling standing crop, if attained, is shortlived. When population growth is slow, frond senescence and exfoliation probably occur before the optimum FAI is exceeded, and when growth is rapid, FAI exceeds the optimum but continued growth may result in severe shading of stipes and small fronds causing possible weakening and defoliation of many fronds irrespective of their maturity or life phase. Such frond loss was evidenced in natural I. cordata populations at Kye Bay and Cape Mudge during mid July, 1975.

Maximum seasonal biomass production in I. cordata populations theoretically would be obtained by harvesting large fronds at frequent intervals to maintain the population at a young age and optimum FAI. Maximum growth rate observed on cobble substrate at an optimum FAI of 0.05 to 0.5 during 45 days in mid-summer was 16 g/0.5 m^2/day. This value was recorded during the summer of 1976 which was not as favourable for I. cordata growth as 1975 and at Kye Bay which attained a lower standing crop than Cape Mudge. Given this growth rate between April and September (120 days), the maximum summer production on cobble substrate would be 1.9 kg/0.5 m^2, plus the biomass of frond initials (in April), which equals roughly 2.0 kg/0.5 m^2. This value is 100 percent more than the maximum standing crop in the location where the growth rate was obtained and is a little more than the total of three I. cordata harvests which were taken from the same location at two to three month intervals in one year (1.65 kg/0.5 m^2 reported by Austin and Adams, 1975).

Observations of I. cordata growth in northern Washington on netting, confirmed that a high growth rate can be maintained through the summer by repeated harvesting (Mumford, in press). Maximum net yield with one harvest in 1977 was 2.6 kg fresh wt./0.25 m^2 and with three harvests was 3.9 kg fresh wt./0.25 m^2. As in the present study, yields were reduced considerably in 1976. Direct comparison of yields on netting in northern Washington with cobbles in northern Georgia Strait is not possible in view of the different sample sizes and because samples of growth on nets included fronds at edges which may grow larger in the absence of shading from neighbouring fronds. However, the data suggest considerably higher standing crops were obtained on nets in northern Washington than on cobbles in this study.

The maximum biomass production which could be obtained from rope substrates in northern Georgia Strait in one 120 day season also was calculated. The maximum growth rate over a 35 day period at a FA between 0.5 - 1.2 m^2 per linear meter was 7.7 g/0.5 m/day. The maximum biomass production during one 120 day growth season would be 0.92 kg/0.5 m which is 1.6 times the maximum standing crop recorded on naturally colonized rope. By comparison, experimental field cultivation of the red alga Gracilaria edulis (Gmel.) Silva on rope substrates off the coast of India yielded about 1.75 kg fresh/0.5 linear meter with a year round growth season (Raju and Thomas, 1971). This biomass was obtained from three harvests over a period of 350 days (11.5 months).

For I. cordata cultivated on natural cobble or rope substrates in northern Georgia Strait, practical harvest yields would lie between maximum standing crop obtained with one harvest per season, and potential seasonal biomass production obtained with frequent harvesting. Harvest of algal fronds from rope substrate may prove to be more simple mechanically than from natural substrate or netting.

CONCLUSIONS AND SUMMARY

1. Maximum summer standing crop, frond area and density of _I. cordata_ on natural substrate were examined at two locations in northern Georgia Strait. In samples with high frond densities taken near to the time of peak standing crop, intraspecific competition reduced the size of individual _I. cordata_ fronds and above a certain density, biomass did not increase with density per unit area. Maximum sample _I. cordata_ biomass of 1.34 and 2.53 kg/0.5 m^2 in respective areas were considered to be close to the maximum that could be achieved with oceanographic conditions of that year (1975). Differences in magnitude of standing crop between locations was attributed to variation in current velocity and summer nutrient concentrations. Reduced standing crop at low densities indicated the possibility of enhancing natural standing crop through cultivation to reduce density variability. This variability in density occurred even in the very uniform sample plots of this study and would be much more in the highly non-uniform populations characteristic of most of the coastline.

2. Maximum standing crop, frond area and density of _I. cordata_ naturally colonizing rope substrate fastened to the bottom were examined at three locations in northern Georgia Strait. The time required to develop dense _I. cordata_ populations varied from two to three years at Kye Bay and Cape Mudge and none developed in three years at Willow Point. Maximum sample biomass ranged from 0.58 to 0.68 kg/0.5 linear m on ropes with near monotypic _I. cordata_

populations. Ropes would have to be spaced 0.25 - 0.5 m apart to produce the magnitude of standing crop per unit area of bottom as natural substrate.

3. Observation of artificially constructed populations at varying densities on natural and rope substrate indicated that summer growth rate was maximum at an optimum frond area and that frond losses increased as frond area exceeded the optimum. At low frond areas, new fronds grew rapidly from frond initials. Maximum population growth rate could only be maintained by repeated harvesting.

4. Calculation of biomass production in one summer using growth rates obtained at optimum frond area yielded estimates of 2.0 kg/0.5 m^2 on natural substrate and 0.9 kg/0.5 linear meter on rope substrate. These values are approximately 1.6 - 2.0 times the maximum standing crop attained in natural populations adjacent to the artificial populations where growth rates were estimated. Thus seasonal production at optimum frond area could be considerably higher than maximum summer standing crop. Maximum harvest yields would lie between the peak seasonal standing crop and maximum seasonal production.

LITERATURE CITED

Abbott, I.A. 1972. Field studies which evaluate criteria used in separating species of *Iridaea* (Rhodophyta). *In*: Contributions to the Systematics of Benthic Marine Algae of the North Pacific, Abbott, J. and M. Kurogi (ed.), Japanese Phycological Soc., Kobe, Japan. pp. 253-65.

Anderson, E.K. and W.J. North. 1966. *In situ* studies of spore production and dispersal in the giant kelp *Macrocystis*. *In*: Proc. 5th Int. Seaweed Symp. pp. 73-86.

Anon. 1957. Observations of seawater temperature and salinity on the Pacific coast of Canada. Fish. Res. Bd. Canada. Pacific Oceanogr. Group 16: 1956. 84 p.

Anon. 1958. Observations of seawater temperature and salinity on the Pacific coast of Canada. Fish. Res. Bd. Canada. Pacific Oceanogr. Group 17: 1957. 100 p.

Austin, A.P. 1960. Life history and reproduction of *Furcellaria fastigiata* (L.) Lam. Ann. Bot., Lond., Vol. 24, No. 94.

Austin, A.P. and R.W. Adams. 1970. Observations on the carrogeenophytes *Iridaea cordata* (Turner) Bory, and *Gigartina exasperata* Harvey and Bailey in the vicinity of Victoria, British Columbia. M.S. report from The University of Victoria, Victoria, B.C. to the Department of Recreation and Conservation of The Province of British Columbia. 32 p.

__________________________ 1971. Observations on the Carrageenophyte *Iridaea cordata* (Turner) Bory in the vicinity of Victoria, B.C. during 1971. A report from The University of Victoria, Victoria, B.C. submitted to the Brisish Columbia Department of Recreation and Conservation, Commercial Fisheries Branch, Victoria, B.C. 86 p.

__________________________ 1973. Development of a method for surveying red algal resources in Canadian Pacific waters. A report from The University of Victoria, Victoria, B.C. submitted to The Federal Ministry of Fisheries and The Provincial Minister of Recreation and Conservation. 173 p.

__________________________ 1974. Red algal resource studies in Canadian Pacific waters. A report from The University of Victoria, Victoria, B.C. submitted to The Federal Minister of Fisheries and The Provincial Minister of Recreation and Conservation. 256 p.

____________________ 1975. Red algal resource studies in Canadian Pacific waters. Carrageenophyte inventory and Experimental/Cultivation Phase 1974/75. A report from The University of Victoria, Victoria, B.C. submitted to The Federal Minister of Fisheries and The Provincial Minister of Recreation and Conservation. 215 p.

Baardseth, E. 1955. A statistical study of the structure of the _Ascophyllum_ zone. Norwegian Inst. of Seaweed Res., Rept. No. _11_, pp. 1-34.

Barilotti, D.C. (unpublished). An ecological study of populations of a benthic alga: Genetic differences that affect life history strategies in diverse habitats. Manuscript.

Boney, A.D. 1966. A biology of marine algae. Hutchinson Educ. Ltd. London. 216 pp.

Black, J.N. 1962. The interrelationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover (_Trifolium_ _subterraneum_ L.). Aust. J. Agric. Res. _14_: 20-38.

Burns, R.L. and A.C. Mathieson. 1972. Ecological studies of economic red algae. III. Growth and reproduction of natural and harvested populations of _Gigartina_ _stellata_ (Stackhouse) Batters in New Hampshire. J. Exp. Mar. Biol. Ecol. _9_: 77-95.

Castenholtz, R.W. 1967. Stability and stresses in intertidal populations. _In_: Pollution and Marine ecology, T.A. Olson and F.J. Burgess (ed.), Interscience, New York. pp. 15-25.

Chapman, A.R.O. and E.M. Burrows. 1970. Experimental investigations into the controlling effects of light conditions in the development and growth of _Desmarestia_ _aculeata_ (L.) Lamour. Phycologia _9_: 103-8.

Charters, A.C., Neushul, M. and D. Coon. 1973. The effect of water motion on algal spore adhesion. Limnol. Oceanogr. _18_: 884-896.

Conover, J.T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. Publs. Inst. Mar. Sci. Univ. Tex. _5_: 97-147.

__________ 1964. The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. Botanica Mar. _7_: 4-41.

Dawes, C.J., A.C. Mathieson, and D.P. Cheney. 1974. Ecological studies of Florida _Eucheuma_ (Rhodophyta, Gigartinales). I. Seasonal growth and reproduction. Bull. Mar. Sci., _24_: 235-272.

Dayton, P.F. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389.

——— 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45: 137-158.

Demopulos, P.A. 1975. Diet, activity and feeding in *Tonicella lineata* (Wood, 1815). The Veliger 18 (Supplement): 42-45.

Donald, C.M. 1961. Competition for light in crops and pastures. *In*: Mechanisms in Biological Competition. 15th Symp. Soc. Exptl. Biol. Cambridge: At the University Press. pp. 282.

Doty, M.S. 1971. Antecedent event influence on benthic marine algal standing crops in Hawaii. J. Exp. Mar. Biol. Ecol. 6: 161-166.

——— 1973. Farming the red seaweed *Eucheuma* for carrageenans. Micronesica 9: 59-73.

Doty, M.S. and V.B. Alvarez. 1975. Status, problems, advances and economics of *Eucheuma* farms. MTS Journal 9: 30-35.

Druehl, L.D. 1967. Distribution of two species of *Laminaria* as related to some environmental factors. J. Phycol. 3: 103-108.

Edwards, P. and D.F. Kapraun. 1973. Benthic marine algal ecology in the Port Aransas, Texas area. Contr. Mar. Sci. 17: 15-52.

Fager, E.W. 1971. Pattern in the development of a marine community, Limnol. Oceanogr. 16: 241-253.

Foster, M.S. 1975a. Regulation of algal community development in a *Macrocystis pyrifera* forest. Mar. Biol. 32: 531-542.

——— 1975b. Algal succession in a *Macrocystis pyrifera* forest. Mar. Biol. 32: 313-329.

Fralick, J.E. 1971. The effect of harvesting *Iridaea* on a sublittoral marine plant community in northern Washington. M.A. Thesis, Western Washington State College, Bellingham. 60 p.

Fralick, R.A. and H.C. Mathieson. 1973. Ecological studies of *Codium fragile* in New England, U.S.A. Marine Biology 19: 127-132.

Fukuhara, E. 1958. Ecological studies on *Iridophycus cornucopiae*. 7. On the germination of spores. Bull. Hokkaido. Reg. Fish. Res. Lab. 17: 137-145.

Fulton, F.T. 1975. The diet of the chiton *Mopalia lignosa* (Gould, 1846). The Veliger *18* (Supplement); 38-41.

Hansen, J.E. 1976. Population biology of *Iridaea cordata* (Rhodophyta: Gigartinaceae). Ph.D. Thesis, University of California, Santa Cruz. 341 p.

__________ (in press a). Studies on the population dynamics of *Iridaea cordata* (Gigartinaceae, Rhodophyta). *In*: Proc. 8th Int. Seaweed Symp. (in press).

__________ (in press b). Productivity of *Iridaea cordata* (Rhodophyta: Gigartinaceae). *In*: Proc. 9th Int. Seaweed Symp. (in press).

Hansen, J.E. and W.T. Doyle. 1976. Ecology and natural history of *Iridaea cordata* (Rhodophyta; Gigartinaceae): Population Structure. J. Phycol. *12*: 273-278.

Harvey, M.J. and J.M. McLachlan (eds.). 1973. *Chondrus crispus*. Nova Scotian Institute of Science. Halifax, Nova Scotia. 155 p.

Hasegawa, Y. and E. Fukuhara. 1952. Ecological studies on *Iridophycus cornucopiae* (P. *et* R.) Setchell *et* Gardner. 1. On the seasonal change in the number of gametophytes and sporophytes. Bull. Hokkaido Reg. Fish. Res. Lab. *3*: 20-30.

__________ 1955a. Ecological studies on *Iridophycus cornucopiae* (P. *et* R.) Setchell *et* Gardner. 3. On the seasonal change of the number of female gametophytes and tetrasporophytes. Bull. Hokkaido Reg. Fish. Res. Lab. *12*: 16-22.

__________ 1955b. Ecological studies on *Iridophycus cornucopiae* (P. *et* R.) Setchell *et* Gardner. 4. On the liberation of carpospores and tetraspores. Bull. Hokkaido Reg. Fish. Res. Lab. *12*: 23-28.

Herlinveaux, R.H. and Giovando, L.F. 1969. Some oceanographic features of the inside passage between Vancouver Island and the Mainland of British Columbia. Fis. Res. Bd. Canada, Tech. Rept. No. 142. 47 p.

Hruby, T. 1974. A study of several factors influencing the growth and distribution of *Iridaea cordata* (Turner) Bory in coastal waters of Washington State. M.S. Thesis, University of Washington, Seattle. 68 p.

__________ 1975. Seasonal changes in two algal populations from the coastal waters of Washington State. J. Ecol. *63*: 881-889.

__________ 1976. Observations of algal zonation resulting from competition. Esturine and Coastal Marine Science. 4: 231-233.

Hutchinson, G.E. 1953. The concept of pattern in ecology. Proc. Acad. Natur. Sci., Phila. 105: 1-2.

Ikusima, I. 1966. Ecological studies on the productivity of aquatic plant communities II. Seasonal changes in standing crop and productivity of a natural submerged community of Vallisneria denseserrulata. Bot. Nag. Tokyo 79: 7-19.

John, D.M. 1971. The distribution and net productivity of sublittoral populations of attached macrophytic algae in an estuary on the Atlantic coast of Spain. Mar. Biol. 11: 90-97.

Kain, J.M. 1966. The role of light in the ecology of Laminaria hyperborea. In: Light as an ecological factor, R. Bainbridge, G.C. Evans and O. Rackham (eds.), Oxford: Blackwell. pp. 319-334.

__________ 1971. Continuous recording of underwater light in relation to Laminaria distribution. In: Proceedings of the IVth European Marine Biology Symposium, D.J. Crisp (ed.), Cambridge: University Press. pp. 335-346.

__________ 1976. Light and the ecology of Laminaria hyperborea II. In: Light as an Ecological Factor II, G.C. Evans, R. Bainbridge and O. Rackham (eds.) Oxford: Blackwell, pp. 63-92.

Kapraun, D.F. 1974. Seasonal periodicity and spacial distribution of benthic marine algae in Louisiana. Contr. Mar. Sci. 18: 139-167.

Katada, M. and M. Satomi. 1975. Ecology of Marine Algae. In: Advance of Phycology in Japan, J. Tokida and H. Hirose (eds.). The Hague: Dr. W. Junk, pp. 211-239.

Kemp, C.I. and T.F. Mumford. 1976. The mariculture of Iridaea cordata (Turner) Bory (Rhodophyta, Gigartinales) on nets. I. Seeding techniques, substrate preferences and projected yields. Paper presented at 27th Annual AIBS Meeting in New Orleans.

Kim, D.H. 1975. A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae. Ph.D. Thesis. University of Washington, Seattle. 157 p.

Kjeldsen, C.K. and H.K. Phinney. 1972. Effect of salinity and temperature on macro-algae. In: Proc. 8th Int. Seaweed Symp. pp. 301-309.

Krishnamurthy, V. 1965. Marine algal cultivation-necessity, principles and problems. In: Proc. Sem. Sea, Salt and Plants, Krishnamurthy, V. (ed.), Bhaunager, India. pp. 327-333.

Kylin, H. 1928. Entwicklungsgeschichtliche Florideenstudien Lunds Univ. Arsskr., N.F. 24: 127.

Lee, R.K.S. 1965. Development of marine benthic algal communities on Vancouver Island, British Columbia. In: The evolution of Canada's flora, R.L. Taylor and R.A. Ludwig (eds.). Univ. Toronto Press. pp. 100-120.

Luning, K. 1969. Standing crop and leaf area index of the sublittoral *Laminaria* species near Helgoland. Mar. Biol. 3: 282-286.

Marshall, S.M., L. Newton, and A.P. Orr. 1949. A study of certain British seaweeds and their utilization in the preparation of agar. H.M.S.O. London. 184 p.

Mathieson, A.C. and R.L. Burns. 1975. Ecological studies of economic red algae. V. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. J. exp. mar. Biol. Ecol. 17: 137-156.

McCandless, E.L., Craigie, J.S. and J.E. Hansen. 1975. Carrageenans of gametangial and tetrasporangial stages of *Iridaea cordata* (Gigartinaceae). Can. J. Bot. 53: 2315-2318.

Mumford, T.F., Jr. 1978. Growth of Pacific Northwest marine algae on artificial substrates: Potential and practice. In: The Marine plant biomass of The Pacific Northwest Coast: A potential economic resource, R. Kraus (ed.) Oregon State University Press, Corvallis.

_________________ (in press). Field and laboratory experiments with *Iridaea cordata* (Florideophyceae, Gigartinales) grown on nylon netting. Seeding techniques, growth rates, yields, and harvesting strategies. In: Proc. 9th Int. Seaweed Symp. (in press).

Neushul, M. 1967. Studies of subtidal marine vegetation in western Washington. Ecology 48: 83-94.

Neushul, M., Foster, M.S. Coon, D.A., Woessner, J.W., and B.W.W. Harger. 1976. An *in situ* study of recruitment, growth, and survival of subtidal marine algae: Techniques and preliminary results. J. Phycol. 12: 397-408.

Niell, F.X. 1975. Primary production in rocky intertide of the N.W. Spain. C.M. - I.C.E.S. K7.

Norris, R.E. and D.H. Kim. 1972. Development of thalli in some Gigartinaceae In: Contributions to the Systematics of Benthic Marine Algae of the North Pacific, Abbott, I.A. and Kurogi, M. (eds.). Japanese Society of Phycology, Kobe. pp. 265-280.

North, W.J. 1971. Mass-cultured Macrocystis as a means of increasing kelp stands in nature. In: Proc. 7th Int. Seaweed Symp. pp. 394-399.

Northcraft, R.D. 1948. Marine algal colonization of the Monterey peninsula, California. Am. J. Bot. 35: 396-404.

Norton, T.A. and E.M. Burrows. 1969. Studies on marine algae of The British Isles 7. Sacchoriza polyschides (Lightf.) Batt. In: Proc. 6th Int. Seaweed Symp. pp. 287-296.

Parker, H.S. 1974. The culture of the red algal genus Eucheuma in the Philippines. Aquaculture 3: 425-439.

Parsons, T.R. 1965. A general description of some factors governing primary production in The Strait of Georgia, Hecate Strait and Queen Charlotte Sound and The N.E. Pacific Ocean. Fish. Res. Bd. Can. Tech. Rept. No. 193. 52 p.

Pickard, G.L. and D.C. McLeod. 1953. Seasonal variation of temperature and salinity of surface waters of The British Columbia coast. J. Fish. Res. Bd. Canada, 10: 125-145.

Powell, J. 1964. The life-history of a red alga Constantinea. Ph.D. Thesis. University of Washington, Seattle. 154 p.

Prince, J. 1971. An ecological study of the marine red alga Chondrus crispus in the waters off Plymouth, Massachusetts. Ph.D. Thesis. Cornell University. 191 p.

Prince, J.S. and J.M. Kingsbury. 1973. The ecology of Chondrus crispus at Plymouth, Massachusetts. II Field studies. Am. J. Bot. 60: 964-975.

Raju, P.V. and P.C. Thomas. 1971. Experimental field cultivation of Gracilaria edulis (Gmel.) Silva. Bot. Mar. 14: 71-75.

Reynolds, N.B. and A.C. Mathieson. 1975. Seasonal occurrence and ecology of marine algae in a New Hampshire Tidal Rapid. Rhodara 77: 512-533.

Round, F.E. 1968. Light and temperature. Some aspects of their influence on algae. In: Algae and environment, Jackson, D.F. (ed.), Syracuse Univ. Press, Syracuse, New York. pp. 73-102.

Saeki, T. 1963. Light relations in plant communities. In: Environmental control of plant growth, L.T. Evans (ed.). Proceedings of a conference held at Canberra, Australia, 1962. Academic Press, New York. pp. 79-94.

Schneider, C.W. 1976. Spacial and temporal distributions of benthic marine algae on the continental shelf of the Carolinas. Bull. Mar. Sci. 26: 133-151.

Sears, J.R. and R.T. Wilce. 1975. Sublittoral, benthic marine algae of southern Cape Cod and adjacent islands: seasonal periodicity, associations, diversity and floristic composition. Ecol. Mon. 45: 337-365.

Smith, G.M. 1951. Sexuality in algae. In: Manual of Phycology, Smith, E.M. (ed.). Chronica Botanica Co., Waltha, Massachusetts. pp. 229-241.

Stephens, K., Fulton, J.D. and O.D. Kennedy. 1969. Summary of biological and oceanographic observations in the Strait of Georgia, 1965-1968. Fish. Res. Bd. Canada, Tech. Rept. No. 110. 11 p.

Sundene, O. 1962. The implications of transplant and culture experiments on the growth and distribution of Alaria esculenta NYTT Mag. Bot. 9: 155-180.

Suto, S. 1950. Studies on shedding, swimming and fixing of the spores of seaweeds. Bull. Jap. Soc. Sci. Fish. 16: 1-9.

Svedelius, N. 1927. The seasonal alteration of generations of Ceramium corticatulum in the Baltic; Nova Acta Regiae Soc. Sci. Ups. Volumen Extra Ordinen Editum. 28 p.

Taylor, J.E. 1970. The ecology and seasonal periodicity of benthic marine algae from Barnegat Bay, New Jersey. Ph.D. Thesis. Rutgers University, New Jersey. 194 p.

Tully, J.P. and A.J. Dodimead. 1957. Properties of the water in the Strait of Georgia, British Columbia, and influencing factors. J. Fish. Res. Bd. Canada 14: 241-319.

Vadas, R.L. 1968. The ecology of Agarum and the kelp bed. Ph.D. Thesis. Univ. of Washington, Seattle. 282 p.

__________ 1972. Ecological implications of culture studies on Nereocystis luetkeana. J. Phycol. 8: 196-203.

Waaland, J.R. 1973. Experimental studies on the marine algae Iridaea and Gigartina. J. Exp. Mar. Biol. Ecol. 11: 71-80.

_____________ 1975. Differences in carrageenan in gametophytes and tetrasporophytes of red algae. Phytochemistry 14: 1359-1362.

_____________ 1976. Growth of the red alga Iridaea cordata (Turner) Bory in semi-closed culture. J. Exp. Mar. Biol. Ecol. 23: 45-53.

_____________ 1978. Growth of Pacific Northwest marine algae in semi-closed culture. In: The marine plant biomass of the Pacific Northwest Coast, R. Krauss (ed.) Oregon State University Press. pp. 117-137.

_____________ (in press) Colonization and growth of populations of Iridaea and Gigartina on artificial substrates. In; Proc. 8th Int. Seaweed Symp. (in press).

Waldichuk, M.L. 1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Bd. Canada. 14: 321-486.

Watt, K.E. 1968. Ecology and resource management. McGraw-Hill Book Co. New York. 450 p.

Westoby, M. 1977. Self-thinning driven by leaf area not by weight. Nature 265: 330-331.

Yoshida, T. 1972. Relations between the density of individuals and the final yield in the cultivated Porphyra. Bull. Tohoku Reg. Fish. Res. Lab. 32: 89-94.

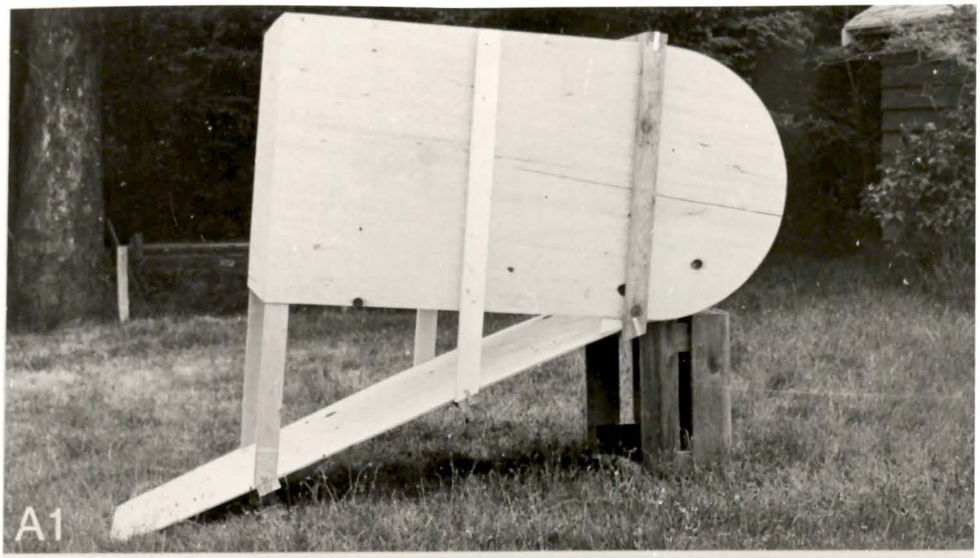
APPENDIX I

Photographs of growth chambers used without success to examine the growth of unattached *I. cordata* in areas subject to current and wave action.

Figure A-1. Floating growth chamber was positioned with scoop shaped end toward current to initiate circulation against rounded end. Wire mesh screen around bottom and covering top is not in place. Volume was approximately 2 m^2.

Figure A-2. Submerged growth chamber was weighted to bottom in -1.5 m depth at Kye Bay. Volume was approximately 1.75 m^2.

Figure A-3. Submerged growth chamber was weighted to bottom in -1.5 m depth at Kye Bay. Volume was approximately 0.7 m^2.


A1


A2


A3

APPENDIX II

Complete list of species, or closest taxonomic identity, and scientific authority, of macroalgae collected in sample quadrats, colonizing concrete blocks and settling plates and in immediate vicinity of *I. cordata* sample plots at Kye Bay, Cape Mudge and Willow Point.

Appendix II continued

CHLOROPHYTA

Enteromorpha linza (L.) J. Agardh
E. intestinalis (Linnaeus) Link
Ulva lactuca Linnaeus
Spongomorpha sp. Kutzing

PHAEOPHYTA

Ralfsia fungiformis Setchell and Gardner
Desmarestia aculeata (L.) Lamour.
D. ligulata var. *ligulata* (Lightfoot) Lam.
D. viridis (O.F. Muell) Lamour.
Petalonia fascia (O.F. Muell.) Kuntze
Laminaria saccharina (L.) Lamour.
L. groenlandica Rosenvinge
Cymathere triplicata (Postels and Ruprecht) J. Agardh
Costaria costata (Turner) Saunders
Nereocystis luetkeana (Mertens) Postels and Ruprecht
Alaria tenuifolia Setchell *in* Collins, Holden and Setchell
Sargassum muticum (Yendo) Gensholt

RHODOPHYTA

Porphyra sp. C.A. Agardh
Gelidium sinicola Gardner
Cryptosiphonia woodii J. Agardh
Farlowia mollis (Harvey and Bailey) Farlow and Setchell
Constantinea subulifera Setchell
Hildenbrandia sp. Nardo
Lithothamnion sp. Philippi
Bossiella chiloensis (Decaisne) Johansen
B. plumosa (Manza) Silva
Corallina officinalis var. *chillensis* (Harvey) Kuetzing
C. vancouveriensis Yendo
Calliarthron regenerans Manza
Grateloupia pinnata (Postels and Ruprecht) Setchell
    in Collins, Holden and Setchell
Halymenia sp. C. A. Agardh
Prionitis lanceolata Harvey
Callophyllis violacea J. Agardh
Schizymenia pacifica Kylin
Neoagardhiella baileyi
Plocamium coccineum var. *pacificum* (Kylin) Dawson
Gracilaria verrucosa (Hudson) Papenfuss
Ahnfeltia gigartinoides J. Agardh
    A. plicata (Hudson) Fries
Gymnogongrus leptophyllis J. G. Agardh
Gigartina exasperata Harvey and Bailey

Appendix II continued

G. stellata (Stackhouse) Batters
Rhodoglossum californicum (J. Agardh) Abbott
R. roseum (Kylin) G.M. Smith
Iridaea cordata (Turner) Bory var. cordata Abbott
Rhodymenia pacifica Kylin
Rhodymenia palmata var. *palmata* (Linnaeus) Greville
R. pertusa (Postels and Ruprecht) J. Agardh
Gastroclonium coulteri (Harvey) Kylin
Callithamnion pikeanum
Hollenbergia subulata (Harvey) Wollaston
Ceramium pacificum (Collins) Kylin
Microcladia borealis Ruprecht
M. coulteri Harvey
Delesseria decipiens J. Agardh
Polyneura latissima (Harvey) Kylin
Botryoglossum farlowianum (J.G. Agardh) G. Denfoni
Polysiphonia hendryi Gardner
P. pacifica Hollenberg
Pterosiphonia bipinnata F. *bipinnata* (Postels and Ruprecht) Falkenberg
P. dendroidea (Montagne) Falkenberg
Herposiphonia plumula (J. Ag.) Hollenberg)
Laurencia spectabilis Postels and Ruprecht
Rhodomela larix (Turner) C. Agardh
Odonthalia floccosa (Esper) Falkenberg
O. lyallii (Harvey) J. Agardh

APPENDIX III

Calculation of change in light radiation reaching an _I. cordata_ community at -1.0 m depth from a day with a spring low tide at noon to a day with a neap high tide at noon.

1. The mean daily surface radiation measured at Nanaimo, B.C. for May, 1975 was 507 langleys and varied per hour as graphed in Figure A-4, below.
2. The hourly tide height for May 19, 1975 with a neap high tide at noon and for May 26, 1975 with a spring low tide at noon can be interpolated from the tidal curves graphed in Figure A-5.
3. Surface radiation penetrating to a depth of -1.0 m was calculated for each hour of daylight for May 19 and May 26 using the formula $I_z = I_o \exp(-kz)$ where I_o is the radiation intensity through the surface, I_z is the remaining intensity at a depth of z meters below the surface and k is the absorption coefficient of the water (Pickard, 1970). k is calculated as 1.7/D where D is the secchi-disc depth determined to be approximately 10m in May, 1975 in northern Georgia Strait.
4. The sum of calculated hourly radiation values at -1.0 m depth was 252 langleys for May 19 and 306 langleys for May 26. Thus the bottom light radiation was 20 percent higher on a day with a spring low tide than a neap tide at noon, for days with average radiation in May.

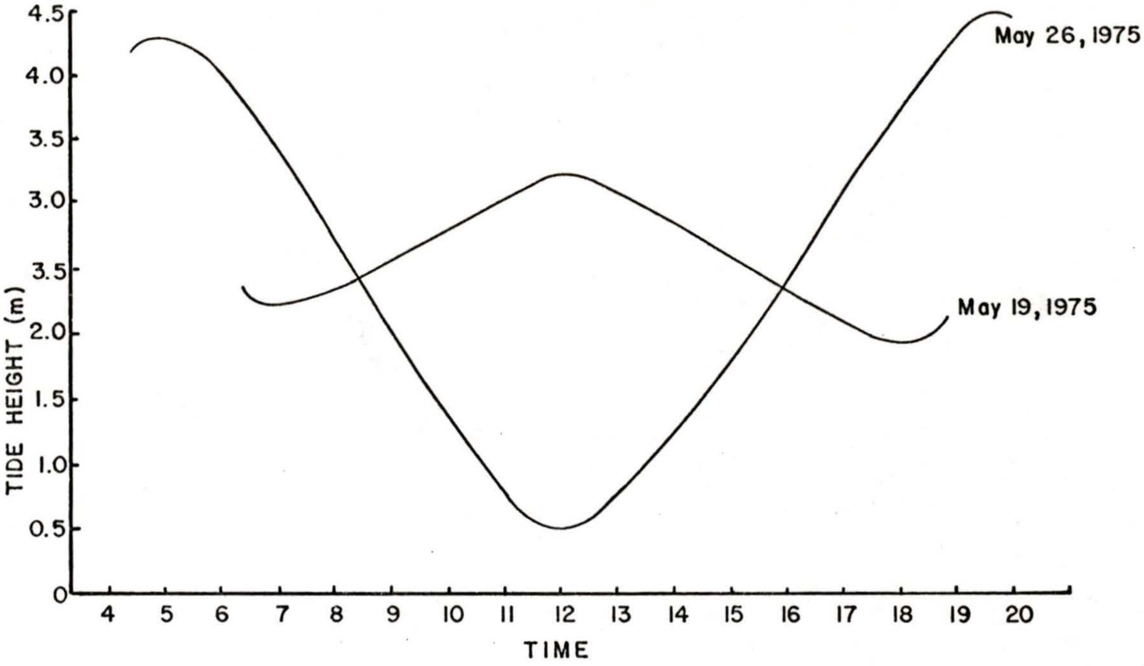


Figure 4A

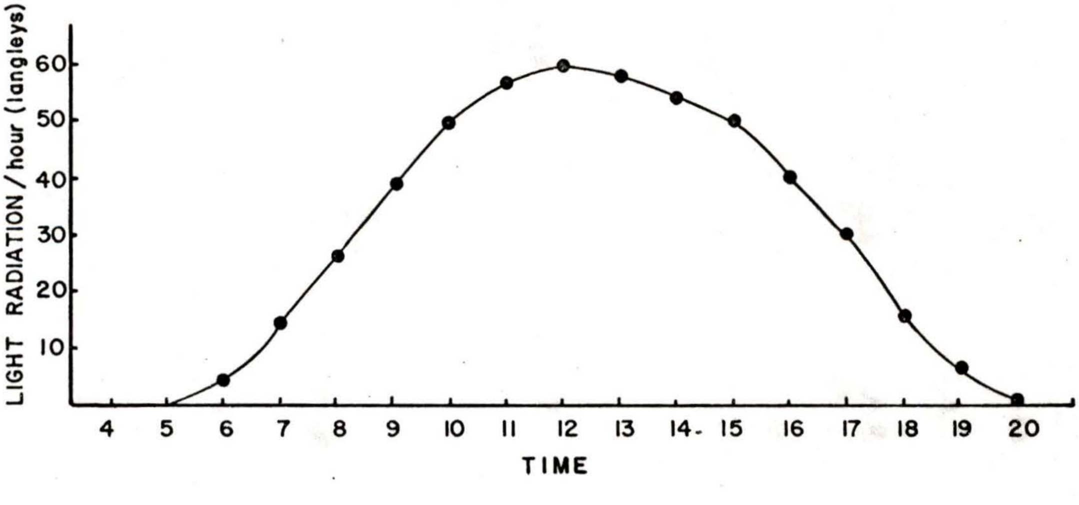


Figure 5A

APPENDIX IV

Mean fresh biomass ± S.E. of I. cordata life phases and biomass of associated macroalgae which attained mean values larger than 0.01 kg/0.5 m^2 harvested from 5, 0.5 m^2 quadrats per sample date. Values listed in kg/0.5 m^2 for Kye Bay (K), Cape Mudge (C) and Willow Point (W).

Notes: 1. Species present but not attaining a mean biomass greater than 0.01 kg/0.5 m^2 on any one sample date are designated with '+'.

2. Full species names are listed in Appendix II.

Appendix IV continued

		May 24-25/75			June 16-17/75			July 9-10/75		
		K	C	W	K	C	W	K	C	W
I. cordata	veg.	0.27 ± 0.04	0.54±0.08	0.48±0.07	0.27±0.05	0.30±0.05	0.24±0.08	0.17±0.02	0.12±0.03	0.10±0.03
	male	0.23 ± 0.03	0.52±0.22	0.41±0.09	0.20±0.07	0.50±0.10	0.21±0.06	0.15±0.06	0.62±0.22	0.09±0.04
	cyst.	0.16 ± 0.03	0.18±0.06	0.25±0.03	0.35±0.10	0.53±0.08	0.46±0.17	0.40±0.03	0.59±0.11	0.41±0.13
	tetra.	0.01 ± 0.01	0.04±0.03	0.06±0.03	0.06±0.02	0.30±0.05	0.28±0.07	0.32±0.08	0.58±0.19	0.33±0.14
	total	0.68 ± 0.05	1.22±0.15	1.19±0.19	0.92±0.09	1.63±0.06	1.19±0.36	1.06±0.08	1.97±0.25	0.92±0.32
M. fuscum		+	0.01 0.01		+	0.02 0.01		+	0.02 0.01	+
D. viridis		+	+	+		+	+	+		+
L. saccharina					0.01 0.01					
C. triplicata										
N. luetkeana										
A. tenuifolia										
C. subulifera		0.10 ± 0.02	0.03±0.02	0.09±0.06	0.29±0.09	0.07±0.03	0.04±0.04	0.19±0.07	0.05±0.02	0.01±0.01
C. regenerans			+			0.03±0.02			0.01±0.01	
P. lanceolata		0.04 ± 0.01	0.15±0.05	0.13±0.06	0.04±0.01	0.15±0.02	0.35±0.15	0.05±0.01	0.13±0.02	0.30±0.11
C. violacea		0.01 ± 0.00	0.09±0.03		+	0.08±0.02	+	+	0.02±0.01	
P. coccineum		0.39 ± 0.06		0.33±0.08	0.19±0.04		0.53±0.11	0.23±0.07		0.64±0.15
G. exasperata		0.04 ± 0.02			0.09±0.04	0.02±0.02		0.01±0.01		
R. roseum		0.01 ± 0.01	0.04±0.01	0.04±0.01	0.01±0.01	0.05±0.02	0.03±0.02	0.02±0.01	0.01±0.00	0.01±0.01
R. petusa		0.06 ± 0.02	0.09±0.02		0.04±0.01	0.05±0.02		0.03±0.02	0.02±0.01	
D. decipiens										
P. latissima		0.05 ± 0.01	0.01±0.01	+	0.02±0.00		+	0.01±0.00		
B. farlowianum		0.17 ± 0.04	0.01±0.01	0.03±0.02	0.09±0.05		0.08±0.03	0.08±0.03		0.08±0.02
O. floccosa							0.01±0.01		+	+

Appendix IV continued

		July 29-31/75			August 18-21/75			Sept. 5-6/75		
		K	C	W	K	C	W	K	C	W
I. cordata	veg.	0.04±0.01	0.05±0.02	0.12±0.04	0.05±0.01	0.05±0.01	0.05±0.02	0.03±0.01	0.02±0.00	0.02±0.01
	male	0.14±0.03	0.17±0.03	0.09±0.02	0.06±0.02	0.06±0.02	0.02±0.01	0.05±0.01	0.05±0.02	0.01±0.00
	cyst.	0.21±0.05	0.31±0.06	0.38±0.11	0.08±0.02	0.25±0.03	0.12±0.05	0.15±0.02	0.19±0.04	0.08±0.05
	tetra.	0.05±0.02	0.23±0.05	0.45±0.18	0.40±0.05	0.50±0.09	0.28±0.09	0.34±0.13	0.44±0.06	0.33±0.07
	total	0.47±0.07	0.77±0.10	1.24±0.23	0.63±0.04	0.92±0.10	0.48±0.16	0.59±0.12	0.73±0.12	0.43±0.12
M. fuscum		+	0.02±0.01		0.01±0.01	0.01±0.01	+	+	0.01±0.01	
D. viridis		+			+		+	+	+	
L. saccharina										
C. triplicata										
N. luetkeana										
A. tenuifolia										
C. subulifera		0.38±0.10	0.07±0.03	0.02±0.02	0.15±0.03	0.08±0.03	0.01±0.01	0.22±0.05	0.13±0.08	0.01±0.01
C. regenerans			0.01±0.01			+			0.01±0.01	
P. lanceolata		0.02±0.01	0.35±0.13	0.42±0.11	0.03±0.02	0.21±0.05	0.34±0.08	0.03±0.00	0.18±0.00	0.40±0.05
C. violacea		0.01±0.01	0.02±0.01		0.01±0.01	0.04±0.01	+	0.05±0.02	0.01±0.00	
P. coccineum		0.18±0.04		0.36±0.11	0.07±0.02		0.18±0.05	0.07±0.03		0.12±0.04
G. exasperata		0.03±0.01			0.08±0.05	+		0.06±0.02	+	
R. roseum		0.01±0.01	+	0.03±0.01	0.04±0.01	0.03±0.02	0.02±0.01	0.01±0.01	0.02±0.01	0.03±0.02
R. pertusa		0.02±0.01	+		+		+		+	
D. decipiens										
P. latissima		0.02±0.01	+		+			+		
B. farlowianum		0.03±0.01	0.02±0.01	0.07±0.01	0.04±0.01	0.01±0.00	0.05±0.03	0.02±0.00		0.03±0.01
O. floccosa			+	+		+	+	+	+	+

Appendix IV continued

		Sept. 26-27/75		Dec. 10-11/75		Jan. 31-Feb. 1/76		Mar. 6-7/76	
		K	C	K	C	K	C	K	C
I. cordata	veg.	0.02±0.01	0.01±0.00	+	+	+	+	0.02±0.01	+
	male	+	0.01±0.01						
	cyst	0.08±0.02	0.18±0.07	+	+	+	+		
	tetra.	0.31±0.11	0.34±0.05	0.02±0.01	0.01±0.00	0.02±0.01	+		
	total	0.45±0.09	0.61±0.06	0.03±0.01	0.02±0.00	0.03±0.01	0.01±0.00	0.02±0.01	+
M. fuscum		0.01±0.00	0.01±0.01	+	+	+	+	+	+
D. viridis									
L. saccharina									
C. triplicata									
N. luetkeana									
A. tenuifolia									+
C. subulifera		0.15±0.05	+	0.04±0.02	0.01±0.00	0.03±0.01	0.01±0.00	0.02±0.01	0.04±0.01
C. regenerans			+	+	0.05±0.02		+		0.02±0.01
P. lanceolata		0.03±0.02	0.23±0.07	0.07±0.02	0.10±0.01	0.03±0.02	0.02±0.01	0.03±0.01	0.03±0.01
C. violacea		0.02±0.01	0.01±0.01	+		+	+	+	0.02±0.01
P. coccineum		0.06±0.02		0.03±0.02		0.16±0.01		0.23±0.09	
G. exasperata		0.03±0.02	+	0.01±0.00		0.05±0.03	+	0.07±0.02	
R. rosuem		0.03±0.03	0.02±0.01	0.01±0.01	+	+	+	+	+
R. pertusa		+		+	+	+	0.02±0.01	+	0.02±0.01
D. decipiens			+		+			+	0.08±0.02
P. latissima		+		+		+	+	0.01±0.00	
B. farlowianum		0.01±0.00	+	0.01±0.01		0.04±0.01		0.09±0.05	+
O. floccosa		+		+					

Appendix IV continued

		April 3-4/76		May 9-11/76			June 2-3/76		
		K	C	K	C	W	K	C	W
I. cordata	veg.	0.15±0.03	0.06±0.02	0.14±0.03	0.15±0.01	0.41±0.04	0.22±0.04	0.06±0.01	0.15±0.07
	male	+		0.12±0.04	0.03±0.01	0.16±0.02	0.15±0.04	0.04±0.02	0.15±0.06
	cyst.	+	+	0.09±0.02	+	0.17±0.03	0.19±0.02	0.03±0.01	0.23±0.10
	tetra.	+		+	0.01±0.01	0.02±0.01	0.03±0.01	0.01±0.01	0.09±0.05
	total	0.16±0.03	0.06±0.02	0.35±0.09	0.20±0.02	0.76±0.07	0.63±0.03	0.15±0.05	0.63±0.25
M. fuscum		+	+	0.01±0.01	+		+	+	
D. viridis		+	0.01±0.01		0.01±0.01		+	0.01±0.00	
L. saccharina			+		0.01±0.01			0.01±0.01	
C. triplicata					0.02±0.01			0.05±0.02	
N. luetkeana			+		0.16±0.09			0.29±0.29	
A. tenuifolia			0.13±0.04		1.09±0.29			1.44±0.38	
C. subulifera		0.21±0.06	0.05±0.3	0.15±0.03	0.01±0.01	0.03±0.03	0.19±0.03	0.04±0.02	0.03±0.03
C. regenerans			+		+			0.01+0.01	
P. lanceolata		0.03±0.01	0.03±0.01	0.11±0.04	0.04±0.01	0.09±0.02	0.03±0.01	0.03±0.01	0.14±0.07
C. violacea		0.01±0.01	0.01±0.01	0.01±0.01	0.02±0.01	0.01±0.01	0.02±0.01	0.01±0.01	
P. coccinum		0.24±0.07		0.46±0.11		0.29±0.12	0.25±0.05		0.49±0.17
G. exasperata		0.04±0.02	+	0.21±0.06	0.02±0.02		0.01±0.01		
R. roseum		+	+	0.01±0.01	0.01±0.01	0.02±0.01	0.01±0.01	0.01±0.01	0.03±0.01
R. pertusa		+	0.07±0.03	0.06±0.03	0.04±0.01		0.03±0.03	0.02±0.01	
D. decipiens			0.01±0.00						
P. latissima		0.03±0.01	0.01±0.01	0.01 0.01	0.01±0.01	0.01±0.01	0.02±0.01	0.01±0.01	+
B. farlowianum		0.11±0.03	+	0.07 0.02		0.06±0.03	0.15±0.05	0.01±0.01	0.07±0.04
O. floccosa			+	+	0.01±0.01	0.04±0.03	+	0.01±0.01	+

Appendix IV continued

		June 29-30/76			July 24-28/76			Aug. 26-Sept. 1/76		
		K	C	W	K	C	W	K	C	W
I. cordata	veg.	0.12±0.02	0.13±0.04	0.22±0.05	0.12±0.03	0.10±0.02	0.06±0.02	0.08±0.01	0.08±0.01	0.02±0.01
	male	0.11±0.02	0.06±0.02	0.14±0.03	0.09±0.02	0.03±0.01	0.04±0.01	0.06±0.02	0.04±0.01	0.01±0.01
	cyst	0.33±0.10	0.11±0.02	0.73±0.09	0.23±0.04	0.06±0.03	0.48±0.07	0.07±0.02	0.09±0.03	0.05±0.01
	tetra.	0.05±0.02	0.10±0.05	0.36±0.08	0.16±0.08	0.03±0.02	0.57±0.19	0.46±0.05	0.19±0.07	0.17±0.05
	total	0.59±0.09	0.41±0.09	1.44±0.18	0.66±0.12	0.24±0.05	1.10±0.20	0.69±0.05	0.41±0.08	0.18±0.05
M. fuscum		+	+		+	+		0.01±0.01	+	+
D. viridis		+								
L. saccharina			0.02±0.01			+			0.03±0.01	
C. triplicata										
N. luetkeana			0.25±0.16			1.33±0.72			1.57±0.58	
A. tenuifolia			0.45±0.11			0.71±0.07			0.19±0.06	
C. subulifera		0.24±0.07	0.07±0.02	0.21±0.08	0.10±0.02	0.01±0.01	0.10±0.07	0.25±0.12	0.07±0.02	0.02±0.02
C. regenerans			0.01±0.01			+			0.01±0.01	
P. lanceolata		0.03±0.03	0.04±0.01	0.28±0.08	0.06±0.02	0.05±0.01	0.23±0.05	0.03±0.01	0.08±0.02	0.41±0.10
C. violacea		0.01±0.00	0.04±0.02		0.01±0.01	0.01±0.01		0.02±0.01	0.09±0.04	
P. coccineum		0.33±0.04		0.32±0.07	0.15±0.06		0.18±0.06	0.07±0.02		0.06±0.02
G. exasperata		0.20±0.10	+		0.25±0.12			0.04±0.03		
R. roseum		0.01±0.00	+	0.03±0.01	0.02±0.01	+	0.02±0.02	0.01±0.00	0.01±0.01	0.02±0.01
R. pertusa		0.05±0.02	0.02±0.01		0.02±0.01	0.01±0.01		+	+	
D. decipiens										
P. latissima		0.03±0.01	0.01 0.01		0.02±0.01	+		+	0.02±0.01	
B. farlowianum		0.13±0.04	0.03 0.02	0.09±0.04	0.13±0.04	+	0.06±0.02	0.06±0.02	0.01±0.01	0.15±0.07
O. floccosa			+	+		+	+		+	0.03±0.03

APPENDIX V

Occurrence in sample quadrats of macroalgal species which did not attain a mean fresh biomass greater than 0.01 kg/0.5 m^2 in five 0.5 m^2 samples per date at Kye Bay (K), Cape Mudge (C) and Willow Point (W).

Notes:
1. The number of quadrats in which the species occurred per date is indicated (1-5).
2. Full species names are listed in Appendix II.

Appendix V. continued

	1975 May 24-25			1975 Jun. 16-17			1975 Jul. 9-10			1975 Jul. 29-31			1975 Aug. 18-21			1975 Sept. 5-6		
	K	C	W	K	C	W	K	C	W	K	C	W	K	C	W	K	C	W
E. linza											1							
Spongomorpha sp.																		
D. aculeata														2	1	1		
P. fascia																		
C. costata																		
C. woodii							1											
F. mollis													1					1
B. chiloensis																		
B. plumosa																		
C. officinalis																		
G. doryphora	1	1																
Halymenia sp.		1			3	1		1	1	1	1		1			2		
N. baileyi	3						1			4			1			5		
G. verricosa																		
A. gigartinoides	1			1						1						1		
A. plicata																	1	
G. leptophyllus					1			4						3		1		
S. interrupta																1		
G. setllata					1									1			1	
R. californicum	1			1														
R. pacifica																	1	
R. palmata																		
G. coulteri																		
H. subulata																		
C. pikeanum																		
C. pacificum	1	5	1	1	2		1							4			4	
M. borealis																		
M. coulteri	5	3	1	2	2		3	1			2			3		2	3	
P. hendryi		1																
P. bipinnata	1			1	2		1	1					1	1				
P. dendroidea													1					
H. plumula					1													
L. spectablis																		
R. larix										1								
S. grevillei																		

Appendix V continued

	1975		1975		1976		1976		1976	
	Sept.		Dec.		Jan. 31-		March		April	
	26 - 27		9 - 10		Feb. 1		6 - 7		3 - 4	
	K	C	K	C	K	C	K	C	K	C
E. linza		2								
U. fenestrata										
Ulva spp.										
Spongomorpha sp.										
D. aculeata										
P. fascia										1
C. costata										
C. woodii										
F. mollis	2									
B. chiloensis										
B. plumosa										
C. officinalis										
G. doryphora	2		1							5
Halymenia sp.		1	1					1		1
N. baileyi			1						1	
G. verrucosa	1									
A. gigartinoides			1						1	
A. plicata		1								
G. leptophyllis		2				3		1		2
S. interrupta										
G. stellata	1							1		
R. californicum		2							2	
R. pacifica										
R. palmata			1							1
G. coulteri										
H. subulata										
C. pikeanum										
C. pacificum										2
M. borealis					2				1	
M. coulteri	5	2	2				2		1	2
P. hendryi										
P. bipinnata										1
P. dendroidea										
H. plumula										
L. spectablis										
R. larix										
S. grevillei	1									

Appendix V continued

	1976 May 9-11			1976 June 2-3			1976 June 29-30			1976 July 24-28			1976 Aug. 26-Sept. 1		
	K	C	W	K	C	W	K	C	W	K	C	W	K	C	W
E. linza										2			1	1	
U. fenestrata															
Ulva spp.															
Spongomorpha sp.					1										
D. aculeata	2														
P. fascia															
C. costata		1			1										
C. woodii	1			1											
E. mollis													1		
B. chiloensis					4						1				
B. plumosa								1							
C. officinalis					3										
G. doryphora							1								
Haolmenia sp.		2		3	1	1	2				1			1	
N. baileyi				1											
G. verrucosa				1											
A. gigartinoides	1									1			1		
A. plicata															
G. leptophyllis														2	
S. interrupta															
G. stellata					1										
R. californicum	4	4			4	4		1							
R. pacifica					4										
R. palmata															
G. coulteri													1		
H. subulata				1											
C. pikeanum															
C. pacificum	1	1													
M. borealis				3			1			3			1		
M. coulteri	5			1	2		4			1					
P. hendryi															
P. bipinnata				3	4										
P. dendroidea				3	3										
H. plumula															
L. spectoblis										1					
R. larix															
S. grevillei	2			1											

APPENDIX VI

ANOVA tables and information on analysis of I. cordata frond weight increments with depth, time and life phase.

Analysis of frond weight increments was complicated due to unequal sample sizes. A computer program for multivariate analysis was selected which facilitated changing the order of main effects to observe how the order affected the source of variance. The ANOVA tables for one order is given below in which there is a high probability that all three main effects are significant sources of variation.

Special Order of Effects S, D, T, SD, ST, DT, SDT.

Source of Variation	SS	DF	MS	F	P less than
Within Cells	2392.192	41	58.346		
S	578.877	1	578.877	9.921	0.003
D	2821.612	3	940.537	16.120	0.001
T	4927.398	1	4927.398	84.451	0.001
SD	109.342	3	36.447	0.625	0.603
ST	9.143	1	9.143	0.157	0.694
DT	384.416	3	128.139	2.196	0.103
SDT	342.293	3	114.098	1.956	0.136

Mean ± S.E. growth rates for main effects

	Mean	S.E.	n
S: cystocarpic	23.7	2.77	26
tetrasporangial	15.2	2.38	32
D: -0.5 m depth	29.9	4.18	16
-2.0 m depth	19.0	4.42	11
-4.0 m depth	17.0	2.51	16
-6.0 m depth	9.6	1.87	15
T: mid summer	26.8	2.54	32
late summer	9.5	1.47	26

APPENDIX VII

Colonization of settling plates attached to platform in *I. cordata* community at Kye Bay, May 30, 1975 to August 29, 1976.

Note: Full species names are listed in Appendix II.

Appendix VII. continued

Date of Observation	No. *I. cordata* spore discs/cm^2	Max. size disc (μm)	No. uprights/plate	Max. length (cm)	Diatom cover (%)	Total algal cover (%)	Other algal species noted
Plates immersed May 30, 1975							
Jan 16, 1975	90	60	0	0	50	60	
Jan 16, 1975	670	65	0	0	20	30	
July 8, 1975	75	192	0	0	40	45	*E. linza*
July 8, 1975	50	150	0	0	20	30	
July 29, 1975	640	210	3	0.5	50	60	*M. fuscum*
July 29, 1975	30	200	0	0	15	25	
Aug 15, 1975	4	540	3	0.5	50	60	
Sept 13, 1975	4	1000	3	0.4	35	40	
Sept 13, 1975	0	0	0	0	10	60	*M. fuscum*, *N. baileyi*, brown crust, *A. plicata*
Sept 26, 1975	0	0	0	0	30	40	*N. baileyi*, brown crust
Dec 10, 1975	1	60	3	0.6	35	40	*M. fuscum*, *E. linza*, brown crust
Jan 31, 1976	0	0	0	0	50	60	*N. baileyi*, brown crust
Jan 31, 1976	0	0	1	0.5	20	25	*A. plicata*
Mar 5, 1976	0	0	0	0	40	45	*M. fuscum*, *N. baileyi*, brown crust
Apr 3, 1976	0	0	0	0	30	40	*N. baileyi*, brown crust
May 11, 1976	0	0	1	0.25	30	60	*E. linza*
June 3, 1976	4	60	0	0	20	25	*M. fuscum*, brown crust
June 30, 1976	410	175	0	0	5	20	*M. fuscum*, brown crust
Aug 29, 1976	0	0	0	0	10	30	*M. fuscum*
Aug 29, 1976	0	0	0	0	5	5	*M. fuscum*, *E. linza*, brown crust, *Lithothamnion* sp.
Aug 29, 1976	2	36	0	0	10	20	brown crust
Plates immersed June 16, 1975							
July 8, 1975	80	132	0	0	50	50	
July 8, 1975	60	150	0	0	20	25	
Plates immersed July 8, 1975							
July 29, 1975	0	0	0	0	80	90	
July 29, 1975[a]	0	0	0	0	20	80	
July 29, 1975[a]	0	0	0	0	15	30	
Aug 18, 1975	1	120	0	0	180	90	
Plates immersed July 29, 1975							
Aug 18, 1975	0	0	0	0	90	95	
Sept 13, 1975	0	0	0	0	10	60	
Sept 26, 1975	0	0	0	0	5	10	
Sept 26, 1975	1	48	0	0	10	80	*N. baileyi*
Dec 10, 1975	0	0	1	1	30	80	*N. baileyi*
Jan 31, 1976	0	0	0	0	20	20	*E. linza*
Mar 5, 1976	0	0	0	0	80	90	*C. pacificum*
Apr 3, 1976	0	0	0	0	30	75	*N. baileyi*, *C. pacificum*
May 11, 1976	0	0	1	0.5	20	70	*E. linza*, brown crust
June 30, 1976	70	175	0	0	10	30	*M. fuscum*
Aug 29, 1976	0	0	0	0	0	10	*L. groenlandica*
Aug 29, 1976	0	0	0	0	5	10	

---

[a] Dense spore set on plates before immersion

Appendix VII. continued

Date of Observation	No. I. cordata spore discs/cm^2	Max. size disc (µm)	No. uprights/plate	Max. length (cm)	Diatom cover (%)	Total algal cover (%)	Other algal species noted
Plates immersed August 18, 1975							
Sept 13, 1975	0	0	0	0	90	95	
Plates immersed September 13, 1975							
Sept 26, 1975	0	0	0	0	50	55	
Dec 10, 1975	0	0	0	0	25	5	
Mar 5, 1976	0	0	0	0	75	80	
April 3, 1976	0	0	0	0	70	90	M. fuscum
April 3, 1976	0	0	7	1	95	100	E. linza, brown crust
May 11, 1976	0	0	1	0.5	30	40	M. fuscum
June 3, 1976	8	85	0	0	60	80	M. fuscum
June 3, 1976	10	100	8	2	25	45	M. fuscum
June 30, 1976	30	150	1	1	10	20	
Aug 29, 1976	0	0	1	0.8	5	60	P. bipinnata
Aug 29, 1976	4	50	2	1	5	50	E. linza, M. fuscum
Aug 29, 1976	0	0	3	0.3	5	15	M. fuscum, R. californicum
Plates immersed September 26, 1975							
Dec 10, 1975	0	0	0	0	30	70	
Dec 10, 1975			1	0.1	65	70	M. fuscum
Plates immersed December 10, 1975							
Jan 31, 1976	0	0	0	0	30	35	
June 30, 1976	650	100	0	0	25	40	
Aug 29, 1976	0	0	2	3	5	50	
Aug 29, 1976	0	0	8	1	5	30	P. bipinnata
Plates immersed January 31, 1976							
Mar 5, 1976	0	0	0	0	80	80	
Plates immersed March 5, 1976							
April 3, 1976	0	0	0	0	80	85	
Plates immersed April 3, 1976							
May 11, 1976	10	75	0	0	60	60	
Plates immersed May 11, 1976							
June 3, 1976	10	30	0	0	50	70	
Aug 29, 1976	0	0	0	0	5	50	M. fuscum
Aug 29, 1976	0	0	0	0	5	15	N. baileyi
Plates immersed June 3, 1976							
June 30, 1976	30	30	0	0	10	35	
Plates immersed June 30, 1976							
July 28, 1976	10	100	0	0	80	90	

APPENDIX VIII

Colonization of settling plates attached to platform in *I. cordata* community at Cape Mudge, May 29, 1975 to September 2, 1976.

Note: Full species names are listed in Appendix II.

Appendix VIII. continued

Date of Observation	No. *I. cordata* spore discs/cm^2	Max. size disc (µm)	No. uprights/plate	Max. length (cm)	Diatom cover (%)	Total algal cover (%)	Other algal species noted
Plates immersed May 29, 1975							
June 18, 1975	0	0	0	0	100	100	
June 18, 1975	0	0	0	0	90	95	
July 10, 1975	0	0	0	0	100	100	*E. linza*
July 31, 1975	0	0	0	0	80	85	*E. linza*
July 31, 1975	0	0	0	0	20	25	*E. linza*
Aug 21, 1975	2	28	0	0	90	95	*E. linza*, *M. fuscum*
Sept 12, 1975	0	0	0	0	75	95	*E. linza*, *M. fuscum*
Sept 27, 1975	0	0	0	0	5	80	*M. fuscum*, *E. linza*
Dec 11, 1975	0	0	0	0	90	100	
Feb 1, 1976	0	0	0	0	60	80	*A. tenuifolia*, *Spongomorpha* sp., *M. fuscum*
Mar 6, 1976	0	0	0	0	90	95	
Apr 4, 1976	0	0	0	0	75	80	*C. triplicata*, *M. fuscum*
Apr 4, 1976	0	0	1	0.3	15	20	*A. tenuifolia*, *M. fuscum*
May 9, 1976	0	0	1	5	50	60	*A. tenuifolia*, *Polysiphoria* sp.
June 2, 1976	0	0	0	0	5	10	*A. tenuifolia*
June 29, 1976	0	0	0	0	5	10	*M. fuscum*
July 28, 1976	0	0	3	1	5	10	*Lithothamnian* sp.
Sept. 2, 1976	0	0	2	0.6	5	30	*M. fuscum*, *C. subulifera*, brown crost
Sept. 2, 1976	4	72	1	0.5	10	25	*R. roseum*, *Lithothamnian* sp.
Sept. 2, 1976	0	0	4	10	5	10	*Lithothamnian* sp.
Sept. 2, 1976	0	0	2	5	5	60	*Lithothamnian* sp.
Sept. 2, 1976	0	0	2	0.5	5	20	*Lithothamnian* sp. brown crust
Sept. 2, 1976	0	0	3	0.4	16	20	*Lithothamnian* sp.
Sept. 2, 1976	0	0	0	0	5	5	*Lithothamnian* sp. brown crust
Sept. 2, 1976	0	0	1	0.8	5	10	*Lithothamnian* sp. brown crust
Plates immersed June 18, 1976							
July 10, 1975	0	0	0	0	50	50	*E. intestinalis*
July 10, 1975	0	0	0	0	20	20	*E. intestinalis*
July 10, 1975	0	0	0	0	90	90	*E. linza*
Plates immersed July 10, 1975							
July 31, 1975	0	0	0	0	50	55	
Sept 12, 1975	0	0	0	0	25	30	*E. linza*
Sept 12, 1976	0	0	2	0.1	5	5	*Lithothamnion* sp.
Plates immersed July 31, 1975							
Aug 21, 1975	2	25	0	0	50	60	
Sept 12, 1975	0	1	120	0	30	40	
Sept 27, 1975	0	0	0	0	35	60	
Dec 11, 1975	0	0	0	0	90	100	
Feb 1, 1976	0	0	0	0	100	100	

Appendix VIII. continued

Date of Cbservation	No. *I. cordata* spore discs/cm^2	Max. size disc (μm)	No. uprights/plate	Max. length (cm)	Diatom cover (%)	Total algal cover (%)	Other algal species noted
							Plates immersed July 31, 1975 - continued
Mar 6, 1976	0	0	0	0	90	95	*E. linza*
May 9, 1976	0	0	0	0	10	20	
June 2, 1976					80	90	*Polysiphonia* sp.
June 29, 1976	0	0	3	0.3	5	10	*M. fuscum*
July 28, 1976	0	0	1	0.9	80	85	
Sept 2, 1976	4	150	2	0.8	50	55	
Sept 2, 1976	0	0	0	0	40	50	*Lithothamnion* sp.
Sept 2, 1976	0	0	0	0	5	10	*Lithothamnion* sp.
Sept 2, 1976	0	0	1	0.1	5	10	*Lithothamnion* sp. brown crust
Sept 2, 1976	0	0	8	1.5	5	10	*Lithothamnion* sp. brown crust
							Plates immersed August 21, 1975
Sept 12, 1975	0	0	0	0	40	50	
							Plates immersed September 12, 1975
Sept 27, 1975	0	0	0	0	5	90	
Sept 27, 1975	0	0	0	0	80	85	
Dec 11, 1975	0	0	0	0	100	100	
Feb 1, 1976	0	0	0	0	80	90	*A. tenuifolia*
Mar 6, 1976	0	0	5	0.2	80	90	*E. linza*, brown crust
May 9, 1976	0	0	0	0	10	30	*A. tenuifolia*, *M. fuscum*
June 2, 1976	3	75	0	0	10	20	*M. fuscum*, *Polysiphonia* sp.
June 29, 1976	1	200	0	0	40	50	
July 28, 1976	0	0	1	1	5	20	brown crust
Sept 2, 1976	0	0	0	0	5	20	brown crust
Sept 2, 1976	0	0	2	1.5	5	10	*Lithothamnion* sp., brown crust
Sept 2, 1976	3	75	0	0	5	30	*Lithothamnion* sp.
Sept 2, 1976	0	0	0	0	10	20	*Lithothamnion* sp., brown crust
Sept 2, 1976	0	0	5	0.3	15	20	*Lithothamnion* sp.
							Plates immersed September 27, 1975
Dec 11, 1975	0	0	0	0	90	90	
							Plates immersed December 11, 1975
Feb 1, 1976	0	0	0	0	100	100	
Mar 6, 1976	0	0	0	0	25	40	
Mar 6, 1976	0	0	0	0	25	30	*E. linza*, *C. triplicata*
May 9, 1976	0	0	0	0	10	20	
June 2, 1976	0	0	0	0	40	50	
June 29, 1976	2	30	0	0	10	15	*Pterosiphonia* sp.
Sept 2, 1976	3	210	0	0	10	15	*Lithothamnion* sp.
Sept 2, 1976	0	0	1	0.6	5	10	*Lithothamnion* sp.

Appendix VIII. continued

Date of Observation	No. *I. cordata* spore discs/cm²	Max. size disc (µm)	No. uprights/plate	Max. length (cm)	Diatom cover (%)	Total algal cover (%)	Other algal species noted
Plates immersed February 1, 1976							
Mar 6, 1976	0	0	0	0	100	100	
July 28, 1976	0	0	0	0	5	50	*M. fuscum*
Plates immersed March 6, 1976							
April 4, 1976	0	0	0	0	30	60	
Plates immersed April 4, 1976							
May 9, 1976	0	0	0	0	70	80	
Plates immersed May 9, 1976							
June 2, 1976	0	0	0	0	100	100	
Sept 2, 1976	0	0	0	0	5	10	
Sept 2, 1976	0	0	1	0.2	10	15	
Plates immersed June 2, 1976							
June 29, 1976	0	0	0	0	10	15	
Plates immersed June 29, 1976							
July 28, 1976	0	0	0	0	70	80	

APPENDIX IX

Observations on macroalgae colonizing concrete blocks immersed in dense I. cordata communities at Kye Bay, Cape Mudge and Willow Point, June, 1975 to September, 1976.

Notes: 1. Visually estimated abundance of species is indicated with following scale: + = rare, < 1% cover; 1 = 1-5% cover; 2 = 5-25% cover; 3 = 25-50% cover; 4 = 50-75% cover; 5 = 75-100% cover.

2. Full species names are listed in Appendix II.

Appendix IX continued

A. Kye Bay

Dates of Immersion							
June 16 1975	July 9 1975	July 29 1975	Aug. 18 1975	Sept. 6 1975	Sept. 26 1975	Dec. 10 1975	Jan. 31 1975

1. Observation date: July 9, 1975

Species	Days block immersed 23
Diatoms (colonial)	+

2. Observation date: July 29, 1975

Species	Days block immersed 43	20
Diatoms (colonial)	+	+
E. linza	5	2

3. Observation date: August 18, 1975

Species	Days block immersed 63	40	20
Diatoms (colonial)			+
E. linza	3	3	
Spongomorpha sp.			+

4. Observation date September 6, 1975

Species	Days block immersed 92	69	49	29
Diatoms (colonial)			5	
E. linza	2	+		
M. fuscum	1	+		
U. lactuca	1	+		

5. Observation date September 26, 1975

Species	Days block immersed 112	89	69	49	20
E. linza	3	+		5	
M. fuscum	3				
green sporelings			+		+
C. pacificum		+			
N. baileyi		+	+		
I. cordata		+			

6. Observation date December 10, 1975

Species	Days block immersed 187	164	144	124	95	75
Diatoms (colonial)		+		3		5
M. fuscum	2				2	
U. lactuca	2		1			
N. baileyi		1	1			
I. cordata		+	1			

Appendix IX continued

A. Kye Bay

7. Observation date January 31, 1976

	Days block immersed						
Species	239	216	196	176	147	127	52
Diatoms (colonial)				4	3	3	3
green sporelings		+					
N. baileyi	+	+					
I. cordata	+	+					

8. Observation date March 5, 1976

	Days block immersed						
Species	273	250	230	210	181	161	86
Diatoms (colonial)	4	5	5	5	5	5	5
E. intestinalis		1					
D. viridis		1					
I. cordata	1						

9. Observation date April 3, 1976

	Days block immersed						
Species	302	279	259	239	210	190	63
Diatoms (colonial)	2	2	2	3	3	3	4
E. linza	+	+	2	3	3	3	
M. fuscum	2	+	1	1	1		3
Spongomarpha sp.							1
D. viridis	1	1					
D. ligulata	+	+			1	+	+
N. baileyi	+	+	+	+	+		
I. cordata	1	2	1	1	+	+	
G. exasperata	+	+	+	+	+		
P. latissina							
B. farlowianum	+						

10. Observation date June 3, 1976

	Days block immersed							
Species	363	340	320	300	271	251	176	124
M. fuscum		1		4	2		5	2
E. linza	4	2	5			2		
D. viridis	1	1	1	1				
D. ligulata			1	1	3			
M. baileyi	1	1						
I. cordata	2	3	3	3	1	1		
G. exasperata	2							
R. californuicum	+							
P. latissima	1							

Appendix IX continued

B. Cape Mudge

Dates of Immersion							
June 19 1975	July 10 1975	July 31 1975	Aug. 21 1975	Sept. 5 1975	Sept. 26 1975	Dec. 11 1975	Feb. 1 1975

1. Observation date July 10, 1975

Days block immersed

Species	21
Diatoms (colonial)	+
green sporelings	3

2. Observation date July 31, 1975

Days block immersed

Species	42	21
Diatoms (colonial)		4
E. linza	5	2

3. Observation date August 21, 1975

Days block immersed

Species	63	42	21
Diatoms (colonial)			5
E. linza			

4. Observation date September 5, 1975

Days block immersed

Species	78	57	36	15
Diatoms (colonial)			1	+
green sporelings			+	+
E. linza	3	3		
M. fuscum	1	1		

5. Observation date September 26, 1975

Days block immersed

Species	99	78	57	36	21
Diatoms (colonial)				2	2
E. linza	4	5	5	3	
M. fuscum	1				

6. Observation date December 11, 1975

Days block immersed

Species	175	154	133	122	97	75
Diatoms (colonial)	5	5	5	5	5	5
M. fuscum	1	1	1	+		
S. muticum	+					
I. cordata	+					
Prionitis sp.	+					
red sporelings		+	+			

Appendix IX continued

B. Cape Mudge continued

7. Observation date Feburary 1, 1976

Species	225	204	183	162	147	125	51
	Days block immersed						
Diatom (colonial)	5	5	5	+	5	5	5
green sporelings		+					
M. fuscum	1		1	+			
A. tenuifolia			+	+			+
I. cordata							

8. Observation date March 6, 1976

Species	259	238	217	196	181	159	85	34
	Days block immersed							
Diatoms (colonial)	5	5	5	5	5	5	4	4
green sporelings			+		+		+	
M. fuscum	2	1	1	2				
A. tenuifolia	+	+	1	+	1			
C. triplicata							5	
N. luetkeana	1	+	+					
D. viridis				+				
I. cordata		+	+	+				

9. Observation date April 4, 1976

Species	288	267	246	225	210	188	114	63
	Days block immersed							
Diatoms (colonial)	3	3	3	2	1	+	+	3
M. fuscum	1	1	1	1	1	1		
A. tenuifolia	+	1	+	1	1	1		
C. triplicata							5	
N. luetkeana	1	1	+	1	1	1		
D. ligulata	+							
I. cordata	+	+	+					
R. californicum	+	1	+					

10. Observation date May 9, 1976

Species	323	302	281	260	245	233	149	98
	Days block immersed							
Diatoms (colonial)								5
M. fuscum	1	1	1	+	2	+		2
A. tenuifolia	3	3	2	3	2	2		
C. triplicata							5	
N. luetkeana	1			+	2	+		
D. viridis		1	+					
D. ligulata		+	+		+			
I. cordata	+	1	1					
R. californicum	1	1	1					
Porphyra sp.								+

Appendix IX continued

C. Willow Point

Note: Only colonial diatoms, *M. fuscum*, *E. linza* and *Ceramium* species were observed to colonize the concrete blocks immersed at 3 week intervals between June 21 and September 26, 1975, up to the last observation date of February 1, 1976. After this date, most blocks were overturned by action and observations were discontinued.

VITA

Surname: ADAMS Given Names: ROBERT WILLIAM

Place of Birth: Vancouver, B.C. Date of Birth: December 18, 1949.

Educational Institutions Attended, with Dates of Entering and Leaving:

University of Victoria, B. C. 1967 to 1971

University of Victoria, B. C. 1973 to 1979

Degrees

B.Sc. 1971 University of Victoria, B. C.

Publications:

Adams, R. 1975. Species Analysis of Prince Rupert Intertidal Macro-Algal Collection; July 18-21, 1974. Report submitted to the Pollution Control Branch, Water Resources Service, Department of Lands, Forests and Water Resources of B. C. March 31, 1975. 78 pages.

Adams, R. W. and A. P. Austin. (in press) Potential yields of the red alga *Iridaea cordata* (Turner) Bory in natural and artificial populations in the north-east Pacific. *In*: Proc. 8th Int. Seaweed Symp. (in press).

Adams, R. W. and R. Foucher. 1976. Species Analysis of Prince Rupert Intertidal Macro-Algal Collection; July 9-11, 1975. Report submitted to the Water Investigations Branch, B.C. Water Resources Service. February 1976. 94 pages.

Austin, A. and R. Adams. 1971. Observations on the Carogeenophytes *Iridaea cordata* (Turner) Bory, and *Gigartina exasperata* Harvey and Bailey in the vicinity of Victoria, British Columbia. Submitted to the British Columbia Department of Recreation and Conservation, Commercial Fisheries Branch, March 31, 1971. 45 pages.

______________ 1971. Selected Bibliography on Seaweed Resource Utilization. Submitted to the British Columbia Department of Recreation and Conservation, Commercial Fisheries Branch. March 31, 1971. 71 pages.

PUBLICATIONS (continued)

____________________ 1972. Observations on the Carrogeenophyte *Iridaea cordata* (Turner) Bory in the vicinity of Victoria, B.C. during 1971. Submitted to the B.C. Department of Recreation and Conservation, Commercial Fisheries Branch, March 31, 1972. 86 pages.

____________________ 1972. Development of a Method for Surveying Red Algal Resources in Canadian Pacific Waters, First Interim Report. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation. June 30, 1972. 17 pages.

____________________ 1972. Second Interim Report on Development of a Method for Surveying Red Algal Resources in Canadian Pacific Waters. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation. November 7, 1972. 130 pages.

____________________ 1973. The Development and Implementation of Survey Techniques for Inventory of Some Commercially Useful Red Algae in Canadian Pacific Waters. Interim Report. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation. November 15, 1973. 28 pages.

____________________ 1973. Second Interim Report on the Development and Implementation of Survey Techniques for Inventory of some Commercially Useful Red Algae in Canadian Pacific Waters. Submitted to the Federal Minister of Fisheries and Provincial Minister of Recreation and Conservation. November 15, 1973. 28 pages.

____________________ 1974. Red Algal Resource Studies in Canadian Pacific Waters. Annual Report. 1973-1974. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation. June 1, 1974. 256 pages.

____________________ 1974. Quantitative Ecological Studies on *Iridaea cordata* in Georgia Strait, B.C. Prior to Possible Harvesting. Paper presented by R. W. Adams at the 55th Annual Meeting of the Western Society of Naturalists, University of British Columbia, Vancouver, B. C. Canada. December 27-30, 1974.

____________________ 1975. Methodology for Exploration of Cultivation and of Enhancement of Natural Populations in the Red Seaweed *Iridaea cordata*. Progress Report, May, 1975 to April, 1976. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation. May, 1976. 15 pages.

PUBLICATIONS (continued)

________________________ 1975. Red Algal Resource Studies in Canadian Pacific Waters. Carrageenophyte Inventory and Experimental/Cultivation Phase, 1974-1975. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation. November, 1975.

________________________ 1978. Aerial Color and Color Infrared Survey of Marine Plant Resources. Photogram. Eng. 44:469-480

Austin, A., R. W. Adams, K. Anders, and A. Jones. 1973. Development of a Method for Surveying Red Algal Resources in Canadian Pacific Waters, Annual Report 1972-1973. Submitted to the Federal Minister of Fisheries and the Provincial Minister of Recreation and Conservation, May 1, 1973. 172 pages.

PARTIAL COPYRIGHT LICENSE

I hereby grant the right to lend my thesis or dissertation (the title of which is shown below) to users of the University of Victoria Library, and to make single copies only for such users or in response to a request from the library of any other university, or similar institution, on its behalf or for one of its users. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by me or a member of the University designated by me. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Title of Thesis

A STUDY OF GROWTH, REPRODUCTION AND COMPETITION IN POPULATIONS OF IRIDAEA CORDATA (TURNER) BORY (RHODOPHYTA) IN GEORGIA STRAIT, B. C.

Author [redacted]
Signature

Robert W. Adams
Name

April 26, 1979.
Date