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Population Biology of Iridaea cordata (Rhodophyta: Gigartinaceae)

Author

Hansen, Judith E.

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(RHODOPHYTA: GIGARTINACEAE).

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UNIVERSITY OF CALIFORNIA
SANTA CRUZ

Population Biology of *Iridaea cordata* (Rhodophyta: Gigartinaceae)

A Dissertation submitted in partial satisfaction
of the requirements for the degree of
DOCTOR OF PHILOSOPHY
in
BIOLOGY
by
Judith Evelyn Hansen

September 1976

The dissertation of Judith Evelyn Hansen is approved:

Isabella A. Abbott

John A. West

William Doyle
(Committee Chairman)

Dean of the Graduate Division

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I dedicate this dissertation to my husband, John, who helped me in every way and in all phases of this study, who endured many, many cold, wet and sometimes perilous hours with Iridaea cordata and me, and who showed incredible patience with me throughout; and to my parents, Norton A. and Katherine O. Forsyth who, somehow long ago instilled in me the desire and fortitude to achieve, who have encouraged me all along, and provided the loving care for Jenny that enabled me to complete the preparation of this dissertation.

Thank you.

Judith E. Hansen

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INTRODUCTION

Iridaea cordata, including varieties *cordata* (Turner) Bory and *splendens* (Setchell and Gardner) Abbott, has a geographic distribution that rims the north Pacific basin from Honshu, Japan to northern Mexico with its major populations from central California to southern Oregon (Abbott, 1972). Morphological and cytological descriptions of the life history stages have been reported (Setchell and Gardner, 1903; Kylin, 1928; Smith, 1938; Norris and Kim, 1972; Fralick and Cole, 1973; Kim, 1976) and the taxonomy of the genus has been reviewed (Abbott, 1971; Kim, 1976). The life history described (Kylin, 1928), involves the alternation of morphologically similar haploid and diploid generations. *I. cordata* is a source of the polysaccharide carrageenan and sporadic commercial harvesting of natural populations of this plant has occurred in northern California (Tseng, 1947) and Washington (Silverthorne and Sorensen, 1971). Some quantitative work on the population biology of *Iridaea* spp. (Hasegawa and Fukuhara, 1952; 1955; Fralick, 1971; Austin and Adams, 1974; Waaland, 1973; 1976; Hansen, in press) and other closely related genera, *Gigartina* spp. (Marshall et al., 1949; Burns and Mathieson, 1972) and *Chondrus* (Marshall et al., 1949; Taylor, 1970;

Prince and Kingsbury, 1973; Mathieson and Prince, 1973; Mathieson and Burns, 1975) has been done.

This is the first detailed study designed to explore the relationships between the population biology and physiological ecology of a red alga: *Iridaea cordata*.

CHAPTER ONE - THE ENVIRONMENT

Study Sites

Iridaea cordata populations from four sites in central California, U.S.A. (Fig. 1) were studied between 1972 and 1975. Site selection was based on the following criteria: 1) access availability, 2) expansive rocky intertidal platform, and 3) relative homogeneity of the substratum at any one particular site.

Scott Creek - 37° 26' N/ 122° 14' W

The Scott Creek site is in Santa Cruz county, 19.1 km north of Santa Cruz, 77.0 km south of San Francisco, and 0.3 km north of the California Highway 1 bridge over Scott Creek. The expansive platform is occasionally subject to strong surf action typical of the unprotected California open coast. The Tertiary substratum, Santa Cruz mudstone, is a slightly siliceous organic rock containing both silt and clay particles. Bedding is irregular and nowhere does this block-weathering mudstone possess sufficient fissility(1) to be properly designated a shale. Silt to very fine angular grains of quartz, feldspar, and biotite mica are scattered throughout the mudstone. Siliceous diatoms, sponge spicules, and phosphatic fish fragments (mainly scales) occur throughout the formation. Opaline (silica) cement is common and rounded dolomite concretions occur in a few areas (Clarke, J. C., 1966).

(1) Fissility is the tendency to break along a distinct planar structure in the rock, parallel to bedding.

FIGURE 1

Iridaea cordata study sites.

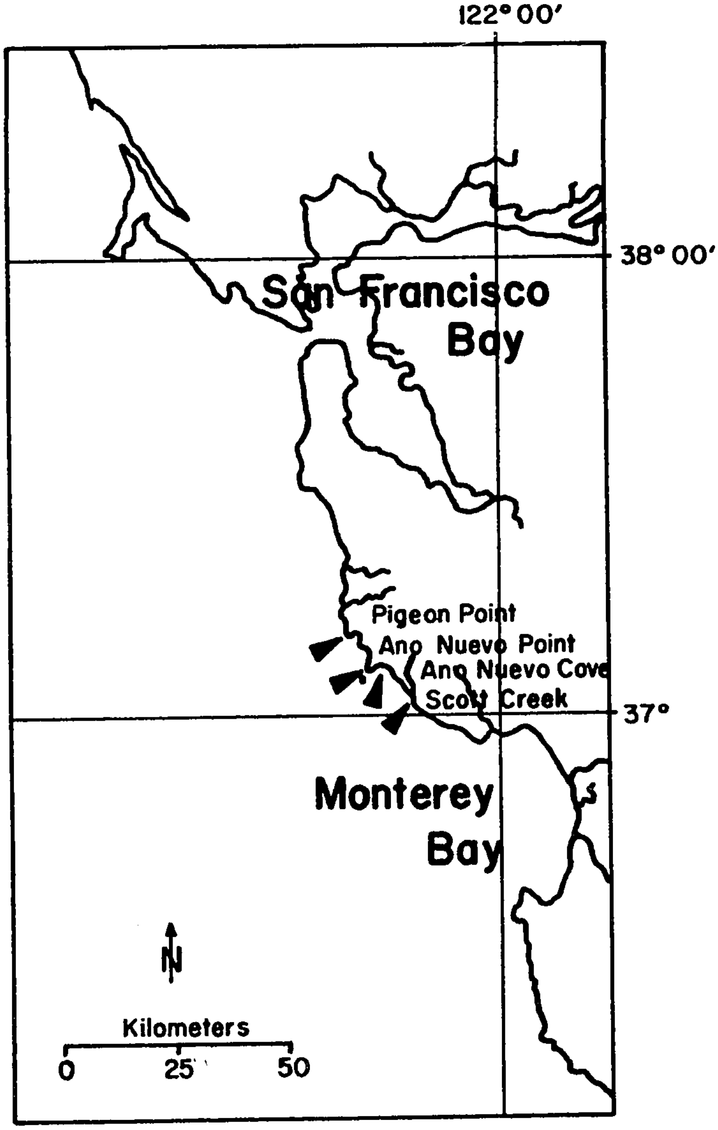

122° 00′
38° 00′
San Francisco Bay
Pigeon Point
Ano Nuevo Point
Ano Nuevo Cove
Scott Creek
37°
Monterey Bay
N
Kilometers
0
25
50

FIGURE 1

Año Nuevo Cove - 37° 6.8' N/ 122° 19.5' W

The Año Nuevo Cove site lies in the most southern reaches of San Mateo county, 30.7 km north of Santa Cruz, 64.1 km south of San Francisco, and 3 km north of the New Year's Creek Bridge. This rocky outcropping is more narrow than the other sites studied and lies in a shallow depression in the open coast topography, Año Nuevo Bay. Surf action is slightly less than that typical of the unprotected outer coast.

The littoral extension of both Año Nuevo Cove and Año Nuevo Point has a substratum of miocene cherty shale, characteristic of the Monterey Formation (Brabb, 1970). It consists primarily of hard, silica-cemented and soft diatomaceous rocks. The rock is composed of pods and lenses of chert and is easily recognized as the cherts and cherty shales crop out in conspicious ledges. Both of these rock types are thinly bedded or laminated and include dark and light layers. In many areas the bedding and laminae are contorted and minor folding is quite common.

A cherty shale generally consists of a matrix of clay to silt-sized clastic particles ($< {}^{1}/256$ mm) cemented together by cryptocrystalline silica (SiO_2-chert). Chemical analyses indicate that SiO_2 may compose 75-97% of the rock. The fine-grained clastic particles may consist of clay or other minerals or even chert. The silica cement has largely formed from the solution of included microfossils with silica tests. The cherty shale is nearly a cherty claystone an Año Nuevo for the rock does not display good fissility but breaks rather in small block-shaped chips (Bramlette, 1946).

Año Nuevo Point - 37° 07' N/ 122° 20' W

Año Nuevo Point is 64 km south of San Francisco and 0.5 km northeast of Año Nuevo Island. During tides below -1.0 ft (MLLW) a large area of the point is exposed. This area is over 0.25 km wide and extends over one-half the distance to Año Nuevo Island. The expansive rocky intertidal platform at the western tip of the point and nearest to Año Nuevo Island, was used for the study area. Wave shock in the study area is diminished as compared to the more exposed open coast due to the protection provided by Año Nuevo Island.

Pigeon Point - 37° 11' N/ 122° 23.3' W

The Pigeon Point site lies 6.5 km north of Año Nuevo Point and 0.3 km south of the Pigeon Point lighthouse. This open coast area is slightly protected from direct wave action by the point itself and by a massive offshore rock between the point and the study site.

The substratum is of late cretaceous derivation and has a wide textural variety. The rock composition includes erosion-prone mudstone, pebbly mudstone, sandstones, and conglomerates. The conglomerate is composed of rocks ranging in size from pebbles to boulders, cemented together with medium-course silica or silty mudstone (Tyler, 1972).

Solar Radiation and Daylength

Solar radiation, both direct and diffuse, was measured using a Weather Measure Corporation Pyrheliograph R 401. This model is a field instrument with a borosilicate glass dome and transmission coefficient of 90% for wavelengths from 0.36 to 2.0 μM. It is accurate to ± 5% with a sensitivity of 0.1 gm cal/cm^2/min.

The instrument was located near the center of Año Nuevo Island in a clear area unobstructed by shadows. Solar radiation (gm cal/cm^2/min or langleys) was measured from 13 February 1974 to 31 March 1975. Weekly means in langleys (ly/day) were calculated using a Keuffel and Esser Compensating Polar Planimeter on weekly chart recordings (Fig. 2, App. 1). For comparative purposes, Kimball's values (42° N 124° W)(App. 2)(Kimball, 1928) for potential solar radiation received on a horizontal surface in the absence of clouds are also given (ly/day). Daylength (hrs) is given for the twenty-first of each month (Fig. 3) (NOAA, 1974-1975).

Lowest solar radiation levels (300 ly/day) occur from October to February. High levels vary from 400 to 630 ly/day between March and August. Peak levels in 1974 were greater than those in 1975 indicating annual variability.

Notable aspects of the solar radiation data are the seasonal changes in levels. Most important in relation to plant production, are the major, sharp increases in early spring: $\bar{X} = 127.3$ to $\bar{X} = 501.6$ ly/day in 1974, $\bar{X} = 147.7$ to $\bar{X} = 445.6$ ly/day in 1975.

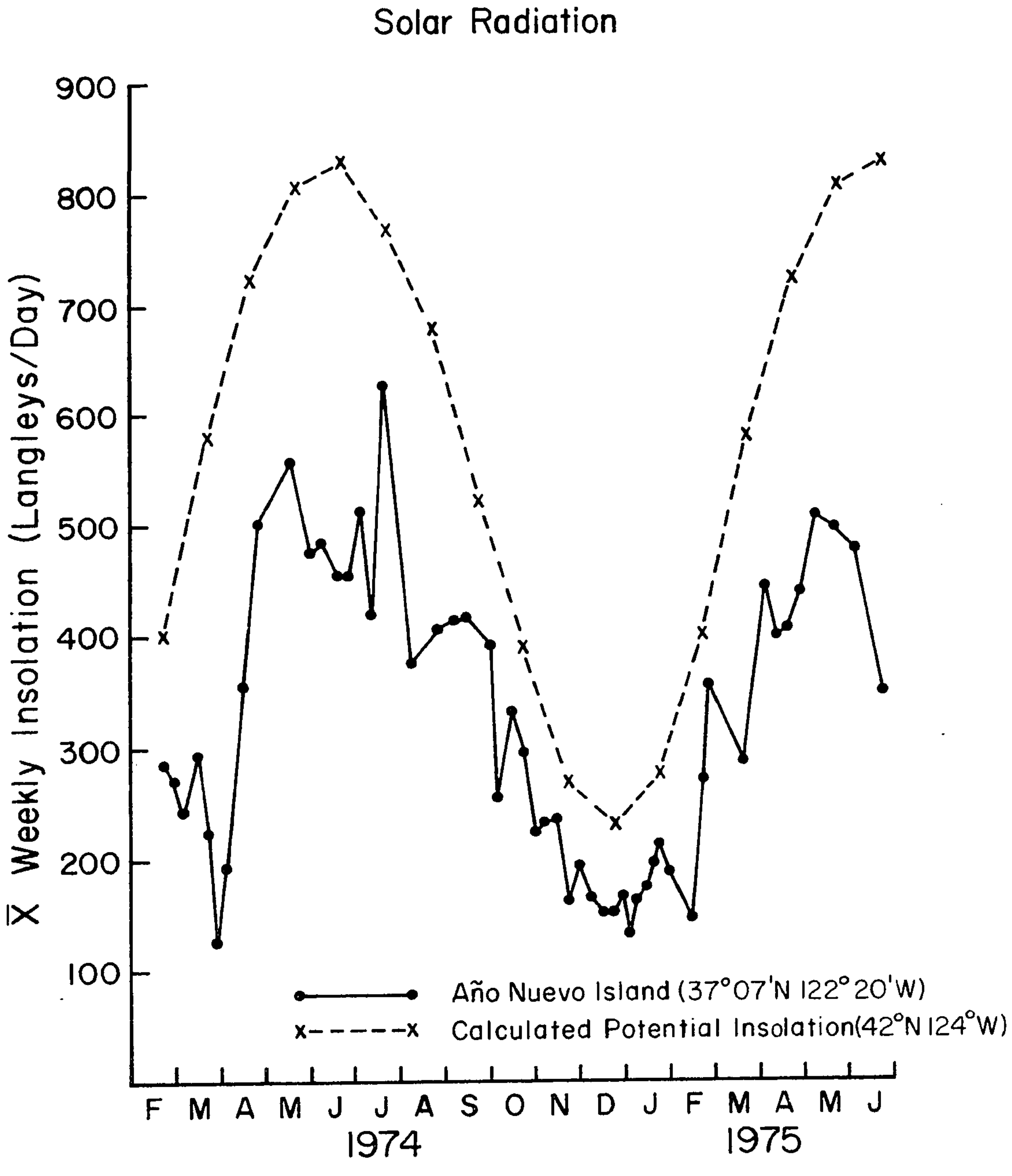

Solar Radiation
X̄ Weekly Insolation (Langleys/Day)
900
800
700
600
500
400
300
200
100
Año Nuevo Island (37°07'N 122°20'W)
Calculated Potential Insolation(42°N 124°W)
F M A M J J A S O N D J F M A M J
1974
1975

FIGURE 2

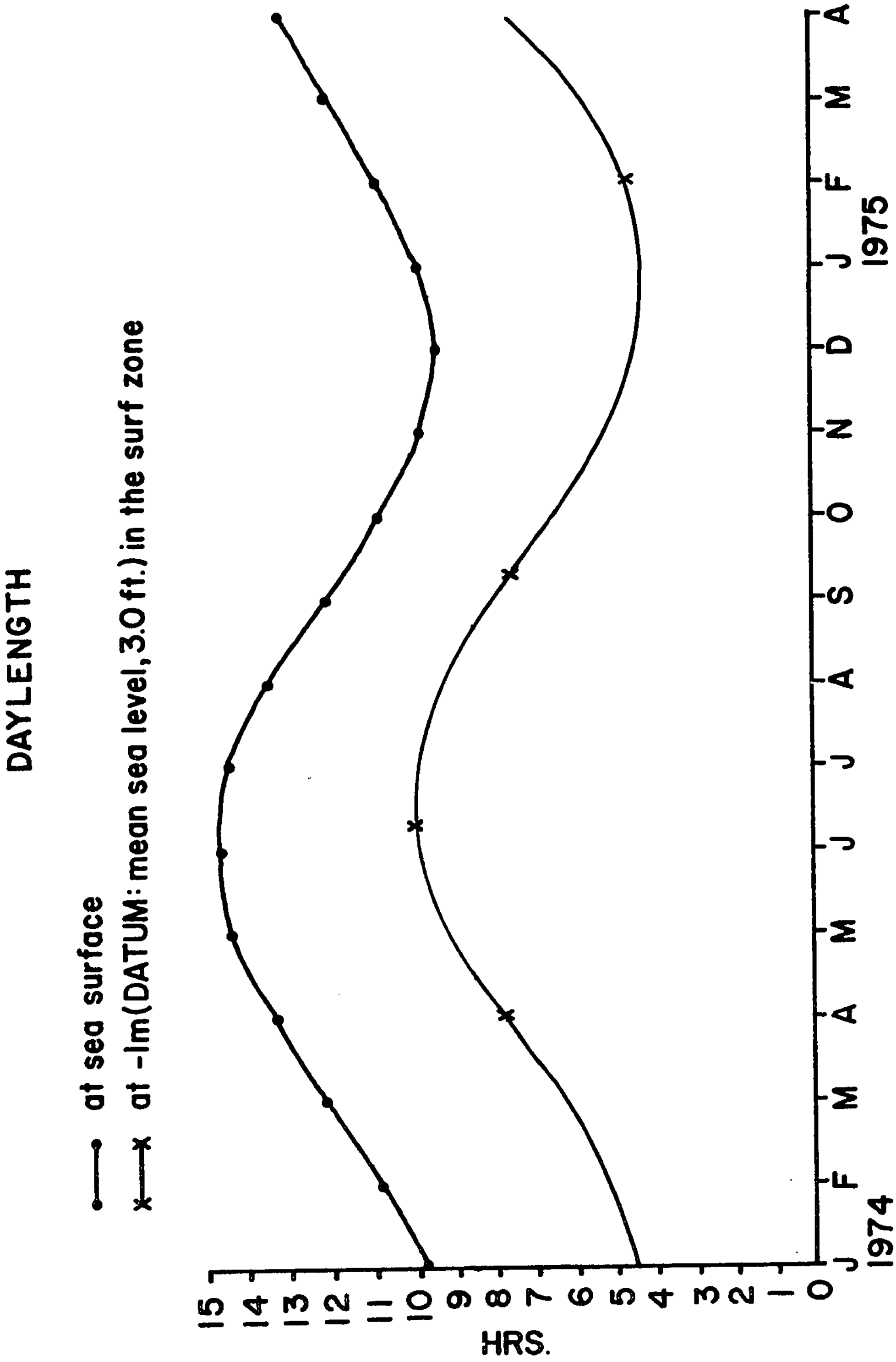

DAYLENGTH
at sea surface
at -1m(DATUM: mean sea level, 3.0 ft.) in the surf zone
HRS.
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1974
1975

FIGURE 3

The autumn to winter decline is variable and considerably more gradual.

Kimball's calculated monthly values for solar radiation under cloudless conditions give an indication of the general reduction in overall radiation due to cloud cover and due to the locally prominent factor during summer months, fog.

Daylength increases from a low in December (9.5 hrs) to a peak of 14.7 hrs in June.

Seawater Temperature

Seawater surface temperature was measured on a variable basis from 5 February 1974 to 23 April 1975 (Fig. 4 , App. 3). Measurements at Año Nuevo Point were made at low tide using several standard laboratory thermometers (as breakage rate was high). The thermometer was swirled under water to constant temperature and kept in a water-filled bottle for reading, as wind conditions cause extensive variations if read in air. Measurements at Año Nuevo Island were made using a bucket thermometer or a Yellow Springs Telethermometer with a probe mounted within an *I. cordata* population. The telethermometer recordings were terminated almost immediately after installation of the probe, as it and the fifty foot lead were removed by an elephant seal.

The temperature varied between 9.7°C in January and 15.6°C in October, comparable to data from other monitoring programs in temperate coastal and nearshore localities (e.g., NOAA, 1974-1975).

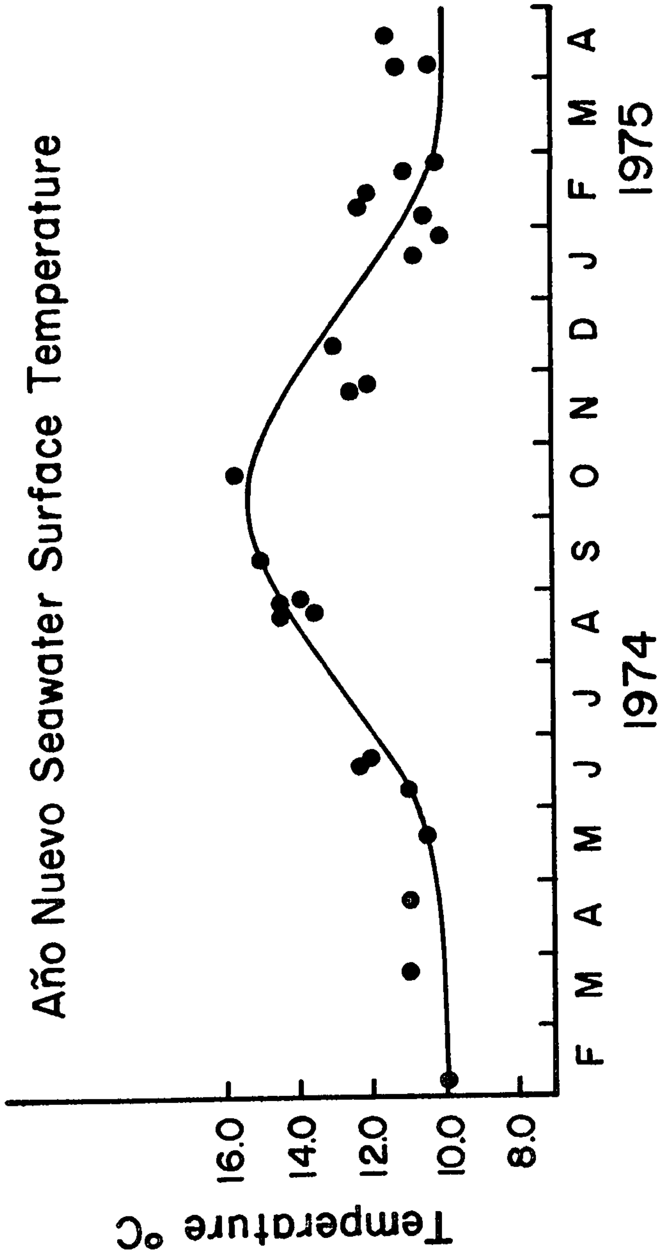

Año Nuevo Seawater Surface Temperature
Temperature °C
16.0
14.0
12.0
10.0
8.0
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1974
1975

FIGURE 4

The variability over short time periods is large within this range, but the seasonal changes are gradual unlike comparable latitudes on the Atlantic coast (Prince and Kingsbury, 1973; Mathieson and Burns, 1975).

Carrageenan

Iridaea cordata carrageenan was monitored to determine whether the life history stages differed in certain biochemical characteristics. Cystocarpic, male, tetrasporangial, and immature thalli were collected at Año Nuevo Point, California on the following dates: 5-6 February, 1974; 20 May 1974; 11 September 1974; and 31 October 1974. The thalli were rinsed in ambient seawater, freed of debris, invertebrates, and epiphytes and dried at 50°C. Carrageenan and infra-red spectrophotometric analyses were carried out in the laboratory of Dr. M. S. Doty (University of Hawaii).

The results (Table 1) indicate that the percentage of carrageenan by dry weight does not vary appreciably among life history stages or with data sampled. Similar seasonal stability in carrageenan content has also been demonstrated for *Chondrus crispus* in Nova Scotia (McCandless & Craigie, 1974). The viscosity, gel strength, and IR spectroscopy results suggest basic differences between the gametangial (male and cystocarpic) and the tetrasporangial and immature stages. Viscosity is quite variable with sampling date, but is consistently higher for tetrasporangial and juvenile

TABLE 1

Iridaea cordata - Carrageenan

C% = Percentage carrageenan in sample by dry weight

viscosity (cps) = Centipoise, as determined with a Brookfield viscometer

Gel strength (gs) = Grams required to force the small plunger to break a 2% gel at 20°C.

Infra Red Spectroscopy - Critical Wavelengths:

935 cm^{-1} (3,6AG) = 3,6 Anhydrogalactose

845cm^{-1} (f-sulfate)

805cm^{-1} (2-sulfate)

+(S) = strong absorption

+(W) = weak absorption

\- = no absorption

\+ = detectable absorption, but broad

TABLE 1

Iridaea cordata - Carrageenan*

Date of Collection	C% Dry	Viscosity (cps)	Gel Strength (gs)	935cm^{-1} (3,6AG)	845cm^{-1} (f-sulfate)	805cm^{-1} (2-sulfate)
5-6 February 1974						
Cystocarpic	59.50	67	40			
Tetrasporangial	58.25	472	no gel			
20 May 1974						
Cystocarpic	49.75	78	40			
Male	56.25	44	64			
Tetrasporangial	57.00	3100	no gel			
Juvenile	58.25	950	no gel			
11 Sept. 1974						
Cystocarpic	58.40	152	88	+(S)	+(S)	+(W)
Male	56.25	156	156	+(S)	+(S)	+(W)
Tetrasporangial	50.43	681	40	-	broad absorption 845-800 cm^{-1}	
Juvenile	55.75	9200	no gel	+	broad absorption	
31 Oct. 1974						
Cystocarpic	57.65	32	130	+(S)	+(S)	+(W)
Male	41.80	167	240	+(S)	+(S)	+(W)
Tetrasporangial	65.75	844	no gel	broad absorp. 850-800 cm^{-1}		
Juvenile	64.45	862	no gel	broad absorp. 850-800 cm^{-1}		

* Analyses done in the laboratory of M. S. Doty, University of Hawaii

stages. Further, IR spectra are similar for male and cystocarpic stages, but different from tetrasporangial and immature stages (Fig. 4.5).

These results suggest basic biochemical differences between the haploid gametangial stages and the diploid tetrasporangial stage. Based on the biochemical similarities between the tetrasporangial and immature stages, it is suggested that the immature thalli in the population sampled (on four separate occasions) were predominately tetrasporangial in nature. These results support the findings the KCl solubilities differ in the gametangial and tetrasporangial stages in I. cordata from Washington (Waaland, 1975). In addition, these results provided the basis for a definitive study that characterized the different carrageenans synthesized by I. cordata life history stages from California (McCandless, et al., 1975). They demonstrated that gametangial stages synthesize predominately kappa carrageenan (with gelling properties) while the tetrasporangial stage synthesizes lambda carrageenan, having viscous and non-gelling properties. Observations or characterization of this biochemical differentiation have been reported for related genera in the Order Gigartinales (Pickmere et al., 1973; Chen et al., 1973; McCandless et al., 1973; McCandless et al., 1975).

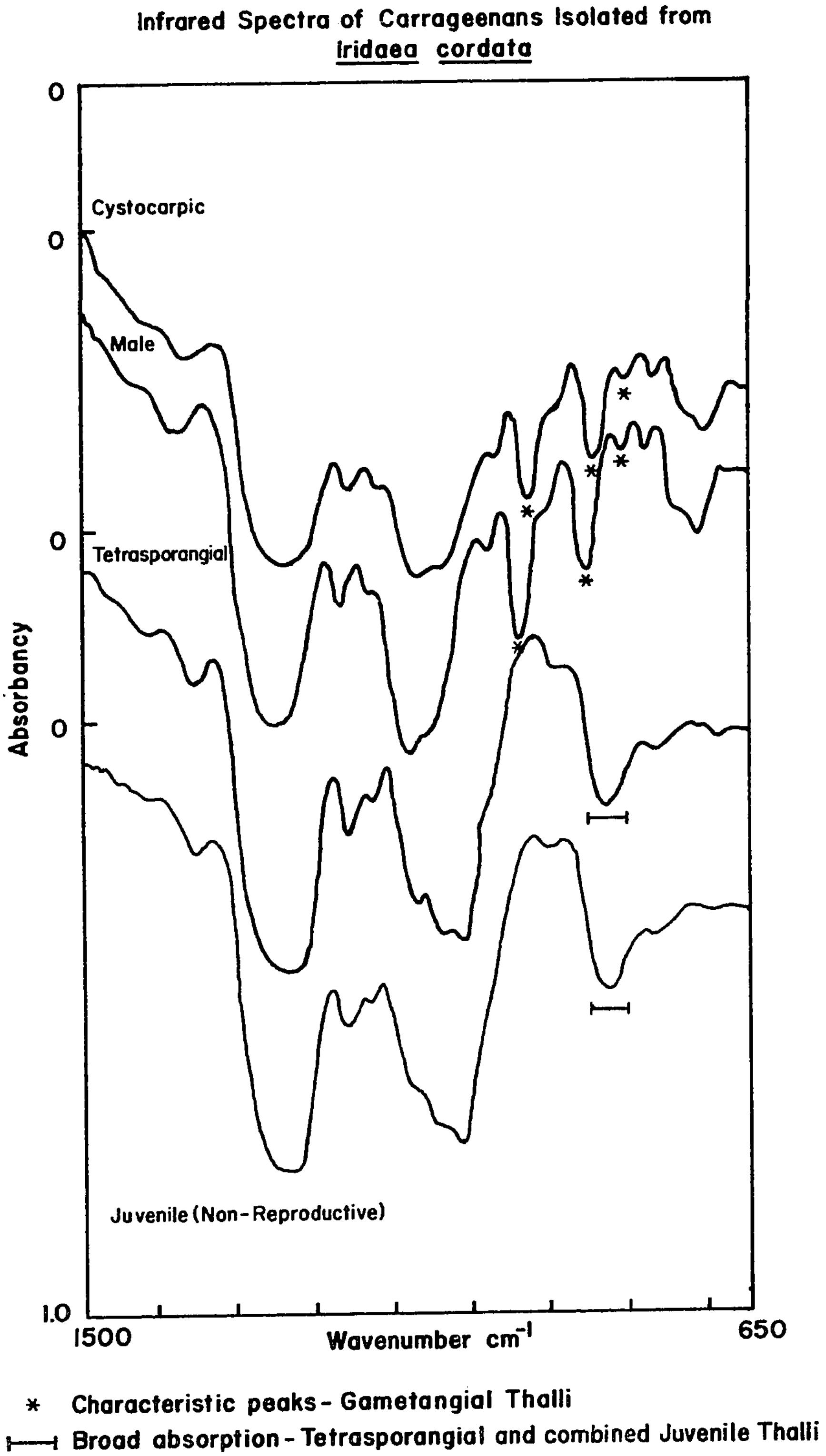

Infrared Spectra of Carrageenans Isolated from
Iridaea cordata
Absorbancy
0
0
0
0
1.0
Cystocarpic
Male
Tetrasporangial
Juvenile (Non-Reproductive)
1500
Wavenumber cm^{-1}
650
* Characteristic peaks - Gametangial Thalli
⊢⊣ Broad absorption - Tetrasporangial and combined Juvenile Thalli

FIGURE 4.5

Nutrients

The essential plant nutrients, nitrogen and phosphorus were sampled monthly in a preliminary study at Año Nuevo Point (23 February 1970 - 28 March 1971) to determine the surface nutrient regime and to determine whether correlations existed between this regime and the annual pinniped population on Año Nuevo Island. The results demonstrated that NH_4-N (ammonia-nitrogen) is a good indicator of pinniped excreta in surface waters and suggested that it might be an important source of nitrogen enrichment for algae. The NO_3-N (nitrate-nitrogen), NO_2-N (nitrite-nitrogen), and PO_4-P (phosphate-phosphorus) regimes were correlated with wind velocities and were derived principally from local upwelling processes (Hansen, J.C., 1972).

Measurements of surface seawater NH_4-N, NO_3-N, NO_2-N, and PO_4-P were continued at the Año Nuevo Point study site from 1 February 1973 to 24 January 1975 (Fig. 5, Apps. 4 , 5). Single, duplicate, or triplicate seawater samples were taken at low tide in 200 ml polyethylene bottles that were rinsed twice in ambient seawater then three-fourths filled and frozen within two hours of sampling. All samples were analyzed with a Technicon II Autoanalyzer using methods previously described (Technicon, 1972).

The regenerated nutrient NH_4-N is derived primarily from metabolic wastes. It remains at fairly low levels (< 1.0 μM/l) typical of open coastal waters, throughout

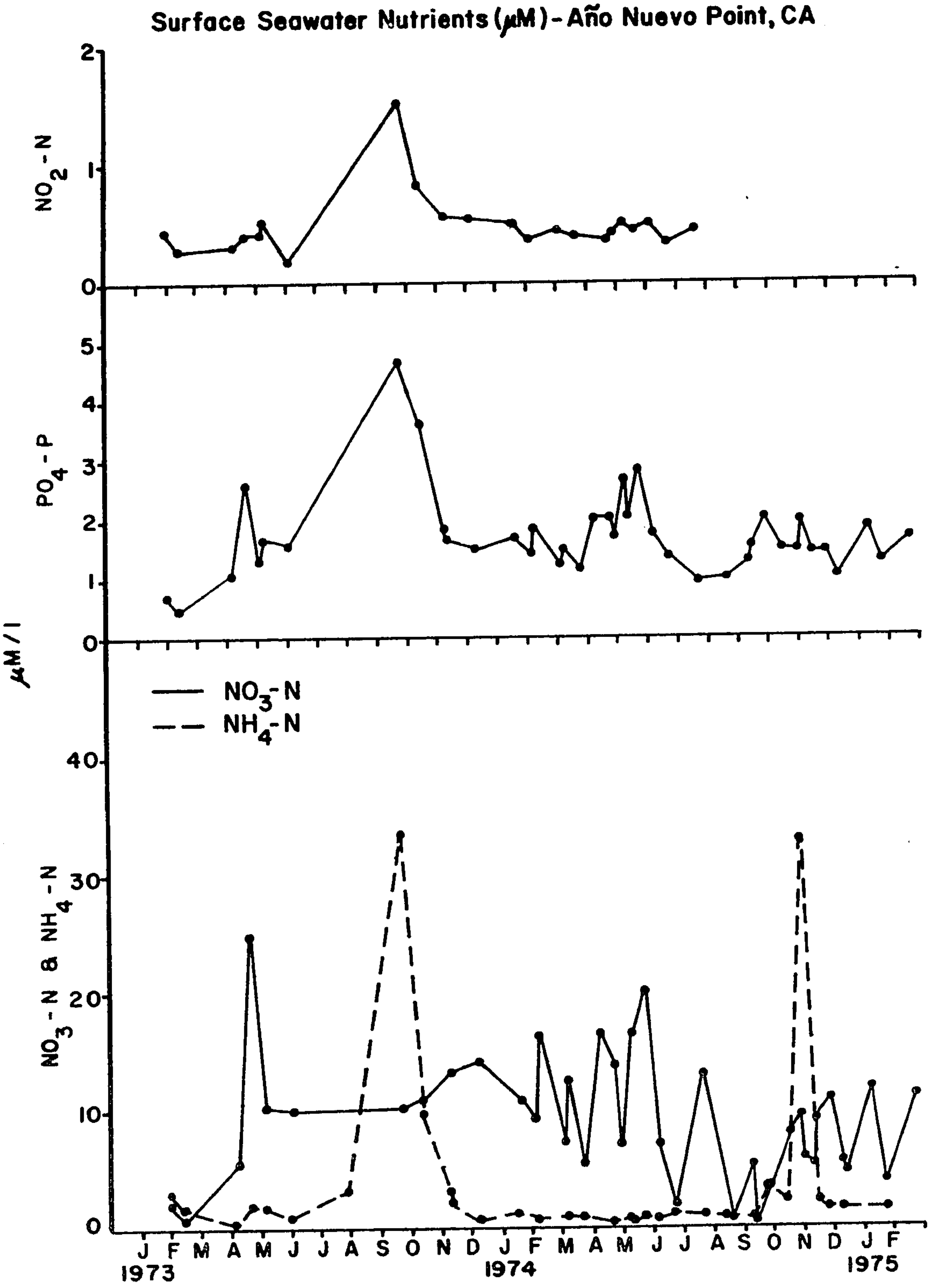

Surface Seawater Nutrients (μM) - Año Nuevo Point, CA
NO_2-N
0
1
2
PO_4-P
0
1
2
3
4
5
μM/l
NO_3-N
NH_4-N
NO_3-N & NH_4-N
0
10
20
30
40
J F M A M J J A S O N D J F M A M J J A S O N D J F
1973
1974
1975

FIGURE 5

most of the year. During autumn or early winter it exhibits sharp peaks of extremely high concentrations (20-30 μM/l). These high concentrations were coincident with either the peak pinniped population on Año Nuevo Island; August-September, 1970 (Hansen, J. C., 1972), September, 1973, or with heavy precipitation (App. 6) that washed accumulated deposits from the island in December, 1970 (Hansen, J. C., 1971) and November, 1974. Similar reports of temporally high concentrations of NH_4-N and or urea in marine surface waters have been correlated with: ducks in Great Bay, New York (Ryther, 1954), a shark migration in California (McCarthy and Kamykowski, 1972), anchovies off Peru (Whitledge and Packard, 1971), sewage outfalls off southern California (Thomas et al., 1974; Eppley et al., 1973), and following heavy precipitation and runoff off Bermuda (Beers and Kelly, 1965). NH_4-N is directly available to primary producers. Temporally, high concentrations could act as stimulatory agents to plant processes and could enhance algal growth if nitrogen were a limiting factor.

NO_3-N, NO_2-N, and PO_4-P are principally derived from upwelled waters. Upwelling, caused by high velocity northwest winds, can occur along the California open coast throughout the year, but is most prevalent during spring. Deep, nutrient-rich water comes to the surface. Consequently, high, erratic nutrient concentrations occur in surface waters, its presence dependent on wind patterns.

NO_2-N and PO_4-P showed anomalous peaks during September-October, 1973 coincident with the 1973 NH_4-N and pinniped peak in Año Nuevo Island. PO_4-P has been associated with the input of excreta from extensive bird rookeries, into marine waters off the Barents Sea (Golovkin and Gurevich, 1973). Similarly, the PO_4-P peak off Año Nuevo Island could reflect the large input of seal excreta. However, the PO_4-P did not re-occur in 1974. High precipitation levels (App. 6) and a relatively low pinniped population in 1974 were coincident with the 1974 NH_4-N peak.

APPENDIX 1

Año Nuevo Island, California

Mean Weekly Totals of Solar Radiation (langleys /day)

1974-1975

Dates	Days	$\bar{X}$ Weekly Solar Radiation (ly/day)
1974		
13 Feb-20 Feb	7.0	283.9
20 Feb-1 March	8.25	268.3
1 Mar-8 Mar	7.75	238.5
8 Mar-15 Mar	6.3	282.3
15 Mar-21 Mar	7.0	220.5
23 Mar-26 Mar	4.0	125.8
29 Mar-2 Apr	5.0	191.1
12 Apr-19 Apr	8.0	353.7
19 Apr-27 Apr	7.5	487.9
13 May-19 May	5.6	552.4
26 May-1 June	6.7	471.1
1 June-10 June	9.3	481.4
10 June-17 June	7.0	449.2
17 June-25 June	7.0	449.2
26 June-5 July	9.1	509.9
5 July-15 July	9.6	415.2
15 July-18 July	3.5	621.6
30 July-4 August	4.7	371.9
4 Aug-20 Aug	12.0	403.0
21 Aug-26 Aug	4.0	408.5
26 Aug-4 Sept	10.0	411.8
16 Sept-26 Sept	9.0	386.9
1 Oct-7 Oct	7.0	256.0
8 Oct-14 Oct	7.0	333.8
15 Oct-21 Oct	7.0	296.1
22 Oct-28 Oct	7.0	222.7
29 Oct-4 Nov	7.0	234.8
5 Nov-11 Nov	7.0	237.4
12 Nov-18 Nov	7.0	162.9
19 Nov-25 Nov	7.0	197.2
26 Nov-2 Dec	7.0	167.1
3 Dec-9 Dec	7.0	153.9
10 Dec-16 Dec	7.0	152.0
17 Dec-23 Dec	7.0	168.2
24 Dec-30 Dec	7.0	134.3

Appendix 1 (continued)

Dates	Days	$\bar{X}$ Weekly Solar Radiation (ly/day)
1975		
31 Dec-6 Jan	7.0	164.3
7 Jan-13 Jan	7.0	175.7
14 Jan-20 Jan	7.0	198.3
21 Jan-27 Jan	7.0	214.1
29 Jan-6 Feb	7.0	186.8
6 Feb-10 Feb	5.0	145.9
14 Feb-21 Feb	7.0	269.5
21 Feb-28 Feb	7.0	353.9
17 Mar-22 Mar	5.0	284.2
31 Mar-6 Apr	6.0	440.1
7 Apr-16 Apr	9.0	395.6
16 Apr-23 Apr	7.0	402.6
23 Apr-1 May	7.9	436.3
1 May-7 May	6.0	503.2
9 May-17 May	7.0	487.9
17 May-13 June	14.0	472.6
13 June-20 June	6.5	344.5

APPENDIX 2

Kimball's Values*

Daily totals of solar radiation (direct & diffuse) received on a horizontal surface in the absence of clouds. Gram calories per cm^2 (langleys/day) 42°N 124°W

Date	langleys/day
21 January	278
21 February	404
21 March	582
21 April	723
21 May	807
21 June	830
22 July	770
22 August	674
22 September	522
20 October	391
21 November	270
21 December	233

* From Kimball, H. H. 1928.

APPENDIX 3

Año Nuevo Point, California

Seawater Surface Temperature (°C) 1974-1975

Date	Temperature
5 February 1974	10.0
28 March	11.0
25 April	11.0
24 May	10.5
6 June	11.0
20 June	12.3
21 June	12.0
23 August	14.4
24 August	13.5
25 August	14.5
26 August	13.8
13 September	15.0
16 October	15.6
28 November	12.5
29 November	12.0
11 December	13.0
19 January 1975	10.8
27 January	9.7
2 February	10.5
8 February	12.5

Appendix 3 (continued)

Date	Temperature
9 February	12.3
20 February	11.0
26 February	10.1
4 April	11.3
5 April	10.3
23 April	11.5

APPENDICES 4 and 5

Surface Seawater

Nutrients - Año Nuevo Point, California

$\mu M/l$ = Micromoles per liter

NH_4-N = Ammonia-Nitrogen

NO_2-N = Nitrite-Nitrogen

NO_3-N = Nitrate-Nitrogen

PO_4-P = Phosphate-Phosphorus

± = Sampling + Analytical Error if replicate samples were taken

APPENDIX 4

Año Nuevo Point, California

Seawater Surface Ammonia-Nitrogen (µM/1) 1970-1975

Date	NH_4-N µM/1	Date	NH_4-N µM/1
1970		6 February	0.70
23 February	2.34	6 February	0.93
4 April	4.63	5 March	0.73
9 May	6.98	5 March	0.73
8 June	6.44	6 March	0.75
14 July	8.84	6 March	0.73
4 August	17.00	22 March	0.65
18 September	30.23	22 March	0.74
11 November	4.57	25 April	0.10
17 December	26.96	25 April	0.10
1971		25 April	0.20
11 January	2.20	26 April	0.30
8 February	3.68	26 April	0.30
28 March	4.52	7 May	0.50
16 November	1.22	7 May	0.70
1972		7 May	0.90
11 February	2.40	8 May	0.20
25 February	1.09	8 May	0.20
23 October	8.10	8 May	0.20
1973		23 May	0.68
1 February	3.15	23 May	0.77
15 February	1.80	24 May	0.86
8 April	0.46	24 May	0.80
21 April	1.52	6 June	0.61
21 April	2.17	6 June	0.63
6 May	1.87	22 June	1.10
9 May	1.75	23 June	0.75
3 June	1.00	19 July	0.83
30 July	3.31	19 July	0.85
23 September	33.10	20 July	0.94
23 September	33.75	20 July	1.05
13 October	9.86	17 August	0.65
10 November	3.21	17 August	0.72
11 November	2.27	11 September	0.68
8 December	0.67	11 September	0.72
1974		13 September	0.64
19 January	1.17	26 September	3.35
4 February	0.83	15 October	2.34
4 February	0.72	15 October	2.34

Appendix 4 (continued)

Date	NH_4-N µM/1
16 October	1.95
16 October	1.92
1 November	32.00
1 November	30.50
1 November	36.00
13 November	1.63
13 November	1.55
14 November	2.35
14 November	2.33
28 November	1.42
28 November	1.40
11 December	1.55
11 December	1.55
1975	
24 January	1.57
24 January	1.04

APPENDIX 5

Surface Seawater Nutrients (µM/1)

Año Nuevo Point, California

Date	NO_2-N µM/1	NO_3-N µM/1	PO_4-P µM/1
1971			
16 November	.25	2.18	1.12
1972			
11 February	.23	1.92	1.24
25 February	.07	0.18	0.65
23 February	.68	3.49	1.80
1973			
1 February	.45	2.20	0.70
15 February	.28	0.95	0.50
8 April	.31	5.86	1.07
21 April	.40 ± .10	25.00 ±5.09	2.60 ±.14
5 May	.42	10.25	1.35
6 May	.52	10.55	1.69
3 June	.18	10.24	1.60
23 September	1.52	10.38	4.67
13 October	.83	11.22	3.67
10 November	.60	14.10	1.83
11 November	.57	13.00	1.68
8 December	.55	14.33	1.51
1974			
19 January	.50	10.75	1.70
4 February	.39 ± .02	9.37 ± .07	1.45 ± .10
6 February	.32 ± .01	16.51 ± .08	1.88 ± .07
5 March	.43	7.30 ± .10	1.28
6 March	.48	12.55 ± .10	1.52 ± .03
22 March	.40 ± .02	5.67 ± .12	1.20 ± .05
10 April		16.50 ±1.08	2.03 ± .07
25 April	.38 ± .01	13.95	2.03 ± .05
26 April	.43 ± .06	7.16 ± .06	1.70 ± .03
7 May	.51 ± .01	>17.00	2.63 ± .05
8 May	.47	15.93 ± .01	2.02 ± .02
23 May	.41 ± .03	20.25 ±3.01	2.78 ± .55
24 May	.51 ± .02	19.29 ± .72	2.90 ± .03
6 June	.50 ± .02	7.42 ± .26	1.72 ± .04
22 June	.34	3.00	1.51
23 June	.34	1.58	1.38
19 July	.57 ± .01	17.83	1.09
20 July	.36 ± .18	9.86	0.77
17 August		0.80	1.03 ± .23
11 September		5.60	1.36 ± .95
13 September		0.40	1.63

Appendix 5 (continued)

Date	NO_2-N µM/1	NO_3-N µM/1	PO_4-P µM/1
1974			
26 September		3.9	2.05
15 October		8.3	1.53 ± .09
16 October		8.1	1.57 ± .06
31 October		9.7	1.54
1 November		6.1	2.03
13 November		5.6	1.42 ± .03
14 November		9.5	1.61 ± .06
28 November		11.1	1.66 ± .06
29 November		11.7	1.53 ± .07
11 December		5.7	1.19 ± .05
12 December		4.9	1.05 ± .11
1975			
9 January		12.2	1.90
24 January		4.2	1.32
23 February		11.4	1.72

APPENDIX 6

Precipitation 1970-1975

* trace

Date	Amount (cm.)
Feb 28 1970	4.39
Mar 1	2.64
" 2	*
" 4	3.61
" 5	.08
" 8	.41
" 9	.15
" 10	.43
" 11	*
" 12	*
Apr 13	.03
" 19	.20
" 21	*
" 26	.20
" 27	.05
May 12	*
" 13	.15
June 5	.03
" 9	1.73
" 13	.05
July 9	*
" 10	*
" 11	*
" 24	*
" 25	*
" 26	*
" 27	*
Aug 21	*
Sep 12	.03
Oct 16	*
" 17	*
" 18	*
" 20	1.63
" 21	*
" 22	1.19
" 23	.51
" 24	.03
" 30	*
Nov 3	.20
" 4	3.48
" 5	.66
" 6	2.13
Nov 7 1970	.41
" 8	*
" 9	*
" 11	.36
" 12	.15
" 25	3.63
" 26	1.27
" 27	.25
" 28	4.14
" 29	6.53
" 30	1.12
Dec 1	1.63
" 2	1.57
" 3	.05
" 4	2.03
" 5	*
" 6	*
" 7	*
" 8	1.80
" 9	*
" 13	.18
" 14	*
" 15	*
" 16	1.35
" 17	1.02
" 18	2.06
" 19	.23
" 20	1.55
" 21	3.07
" 22	.05
" 28	2.67
" 29	.64
Jan 4 1971	*
" 10	.36
" 11	1.83
" 12	1.04
" 13	.33
" 14	.38
" 15	*
" 16	*
Feb 7	*
" 8	*

Appendix 6 (continued)

Date	* trace Amount (cm.)
Feb 15	.10
" 16	.18
" 17	.56
" 18	*
" 19	1.09
" 20	*
" 21	*
" 22	*
" 27	.41
" 28	.03
Mar 12	2.16
" 13	.43
" 14	.69
" 15	.43
" 16	*
" 23	.20
" 25	.89
" 26	2.21
Feb 2 1973	*
" 3	.43
" 4	.48
" 5	.46
" 6	1.42
" 7	.05
" 9	*
" 10	1.37
" 11	2.46
" 12	.61
" 13	.48
" 14	1.22
" 16	*
" 24	.23
" 26	1.65
" 27	1.14
" 28	.84
Mar 3	.79
" 4	1.40
" 5	.08
" 6	.79
" 7	.03
" 8	1.14
" 10	.05
" 11	.94
" 17	.08
" 19	.38
" 20	2.41
" 21	.56
" 22	.13
Mar 26 1973	.03
" 31	.13
Apr 1	.08
" 13	.15
" 14	*
" 17	.03
May 4	*
" 25	.03
" 31	.03
June 16	*
July 4	*
" 10	*
" 18	*
" 31	*
Aug 3	*
" 6	.01
Sep 13	*
" 15	*
" 23	.05
Oct 5	*
" 7	2.39
" 8	.80
" 9	.19
" 11	*
" 15	*
" 16	*
" 21	*
" 22	.56
" 23	.96
" 25	*
Nov 6	.68
" 7	.15
" 9	*
" 10	.05
" 11	.44
" 12	2.03
" 13	*
" 14	.13
" 16	.66
" 17	1.57
" 18	.13
" 20	.08
" 21	.10
" 22	1.01
" 24	.08
" 25	.05
" 26	.23
" 31	*

Appendix 6 (continued)

* trace

Date			Amount (cm.)
Dec	1	1973	2.92
"	11		.05
"	13		.10
"	17		.22
"	21		.89
"	22		.79
"	25		*
"	26		.46
"	27		3.03
"	28		.41
"	29		.43
"	31		*
Jan	1	1974	.56
"	3		1.68
"	4		2.72
"	5		.56
"	6		.41
"	7		2.92
"	8		.09
"	11		.13
"	12		.11
"	14		*
"	16		.56
"	17		.25
"	18		.50
"	20		1.02
Feb	1		.19
"	12		.74
"	16		.20
"	18		*
"	19		.71
"	21		.02
"	26		*
"	28		.11
Mar	1		.59
"	2		3.42
"	3		1.32
"	7		1.39
"	11		.07
"	18		*
"	25		.53
"	27		.15
"	28		3.29
"	30		.41
Apr	1		2.82
"	2		.61
"	5		.02
Apr	9	1974	.88
"	18		.35
"	23		1.67
"	24		.91
"	25		*
"	26		.05
June	17		*
"	18		.61
"	19		*
July	9		.89
"	10		.02
Oct	28		1.20
"	29		.23
"	31		.58
Nov	16		*
"	21		.56
"	25		*
Dec	2		.78
"	3		2.33
"	4		1.02
"	21		*
"	27		.43
"	28		.86
"	30		.18
Jan	6	1975	.71
"	7		.10
"	8		.51
"	9		.25
"	10		.05

CHAPTER TWO - POPULATION STRUCTURE

INTRODUCTION

Detailed studies of population structure are rarely reported since life histories as determined in culture are commonly assumed to characterize natural populations. Invaluable advances and contributions in this field have been made through experimentation with cultures. It cannot be assumed, however, that the life history that is determined in culture, represents the total expression of the life history of the organism (Dixon, 1970). Environmental variables are necessarily controlled or eliminated from cultures. "The life histories of organisms, like all other phenotypic attributes, represent a series of selective compromises to a series of environmental variables. Components of any life history constitute life history 'strategies', implying a set of adaptive responses accumulated over evolutionary time" (Wilbur, et al., 1974). Therefore, in addition to the life history framework, as established in culture, it is essential to consider aspects of life histories in the field in order to more realistically describe the ecology, distribution, or life history expressions of an alga.

Preliminary studies consistently revealed a significant disproportional representation of one phase of morphologically similar life history stages in natural populations.

This has prompted the hypothesis that Iridaea cordata populations exhibit an adaptive response of tetrasporangial, or diploid dominance. To investigate this hypothesis, a detailed quantitative study was conducted of population structure including seasonal variations in the biomass, density, and size-class distributions of the life history stages in some California populations.

These data were also used to establish baseline information concerning the biomass levels of this species in central California for comparative purposes.

MATERIALS AND METHODS

Open coast Iridaea cordata populations at Scott Creek, Año Nuevo Cove, Año Nuevo Point, and Pigeon Point South, California were studied from 1972 to 1973. Nine to sixteen samples were taken seasonally (Autumn: 19-21 November, Winter: 17-18 January, Spring: 5-6 May, Summer: 30 July) from each population depending on the homogeneity of the respective rocky intertidal platform. A controlled random quadrat (625 cm^2) technique was used and the populations were sampled between the -.17 m and -.0.5 m tide levels (datum: mean lower low water). The sampling method was controlled in that the quadrat was randomly tossed without definite aim or direction only within the delineated I. cordata populations and tide pools were excluded. All thalli larger than 3 cm in length were removed from the sample areas. A 5 cm^2 quadrat was then tossed randomly three times into the cleared sample area and the thalli less than 3 cm

← in length (juveniles) were enumerated. Because one must be very close to the substratum to see the juveniles and surf zone conditions are limiting, the density values for juveniles are estimates. The thalli greater than 3 cm in length were rinsed in freshwater and invertebrates, debris, and epiphytes were removed. The thalli were sorted by life history stage: reproductively mature female, reproductively mature tetrasporangial, and combined immature and male thalli. In a subsequent study, the males were distinguished from immature thalli and occurred in approximately a 1:1 ratio of reproductively mature male to female thalli (App. 7). For each sorted sample, the number of individuals was summed to determine population density. The individual thalli from all or a representative portion of the samples were blotted and the fresh biomass (gm) determined for size-class frequency analysis. The sorted samples were dried at 60°C for 24-48 hrs depending on sample size, and the dry biomass determined. The total dry biomass value for each sample is the sum of the biomass of all sorted life history stages.

For statistical analyses of biomass and population density data, the Friedman 2-Way analysis of variance test was used (Sokal & Rohlf, 1969). The Kolmogorov-Smirnov two-sample test for differences between populations was employed for size-class frequency analysis (Tate & Clelland, 1959). Statistical significance was set at the 95% confidence level.

RESULTS

Population Density

The density (individuals/625 cm^2) structure (Fig. 6 , App. 8) shows that throughout the year the populations were dominated by juveniles, followed by the combined immature and male, then tetrasporangial thalli. The cystocarpic thalli contributed the smallest component. The estimated densities of juvenile thalli ranged from 196 to 263 thalli/ 625 cm^2 in autumn, spring and summer, and averaged 424 thalli/ 625 cm^2 in the winter.

The densities of the combined immature and male thalli were similar for three of the four populations studied and showed no significant seasonal fluctuations (22.3-40.1 thalli/ 625 cm^2). The densities of this stage in the most southern population were significantly higher in the spring and summer ($\overline{X} = 116.4 \pm 12.8$ and 70.0 ± 8.6 thalli/ 625 cm^2) than densities in the three northern populations. Because all four populations are subject to similar open coast conditions, the cause for this anomaly is unknown.

The densities of the tetrasporangial as well as the cystocarpic thalli were not significantly different among the populations studied. In addition, neither stage showed significant seasonal fluctuations (Fig. 6). The annual densities of the tetrasporangial and cystocarpic thalli ranged from 9.9 - 16.9/625 cm^2 and 1.4 - 3.6/625 cm^2, respectively. Since male and cystocarpic thalli occur in approximately

FIGURE 6

The mean density (individuals/625 cm^2) of *Iridaea cordata* life history stages. ---- represents the calculated density of combined male and cystocarpic thalli using a 1:1 ratio. Combined immature and male densities for Scott Creek (spring and summer) are not included.

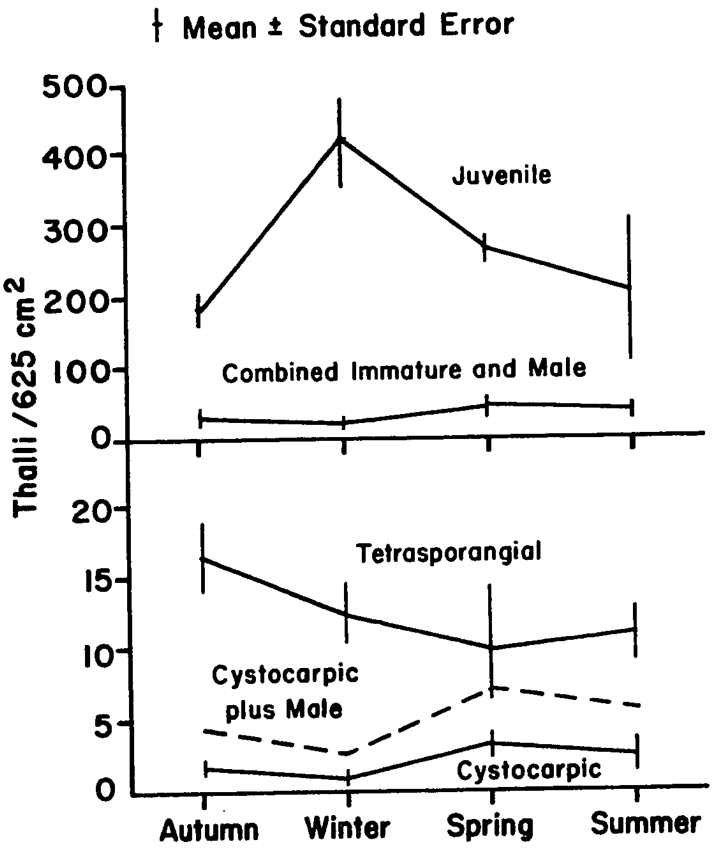

Mean ± Standard Error
Thalli /625 cm^2
500
400
300
200
100
0
20
15
10
5
0
Juvenile
Combined Immature and Male
Tetrasporangial
Cystocarpic plus Male
Cystocarpic
Autumn
Winter
Spring
Summer

FIGURE 6

equal numbers, a combined density of these stages can be calculated (2.8 - 7.2/625 cm^2). There were significantly more tetrasporangial than gametangial thalli during most of the year except spring.

Population Biomass

The total dry biomass for the four open coastal populations studied was similar ($.20 > p > .50$) and exhibited a definite structure (App. 8).

Biomass of the tetrasporangial stage dominated throughout most of the year over other life history stages.

The combined immature and male biomass was next and became dominant in the spring. The cystocarpic stage represented a small fraction of the total. The 1:1 gametangial ratio could not be employed to calculate the combined male and cystocarpic biomass because the two differ in size, the cystocarpic thalli being heavier.

The seasonal trend in total biomass for the four populations studied was the same, with lows during winter ($\overline{X} = 14.3 \pm 2.4$ gm/625 cm^2) and the peak occurring in summer ($\overline{X} = 84.8 \pm 17.7$ gm/625 cm^2) (Fig. 7).

The seasonal variations in biomass of the life history stages was similar for three of the four populations studied (Fig. 8). For the three similar populations, the biomass of tetrasporangial thalli peaked in the summer ($\overline{X} = 43 \pm 9.6$ gm/625 cm^2), followed in biomass by the autumn ($\overline{X} = 22 \pm 3.1$ gm/625 cm^2), spring ($\overline{X} = 11 \pm 4.8$ gm/625 cm^2), and

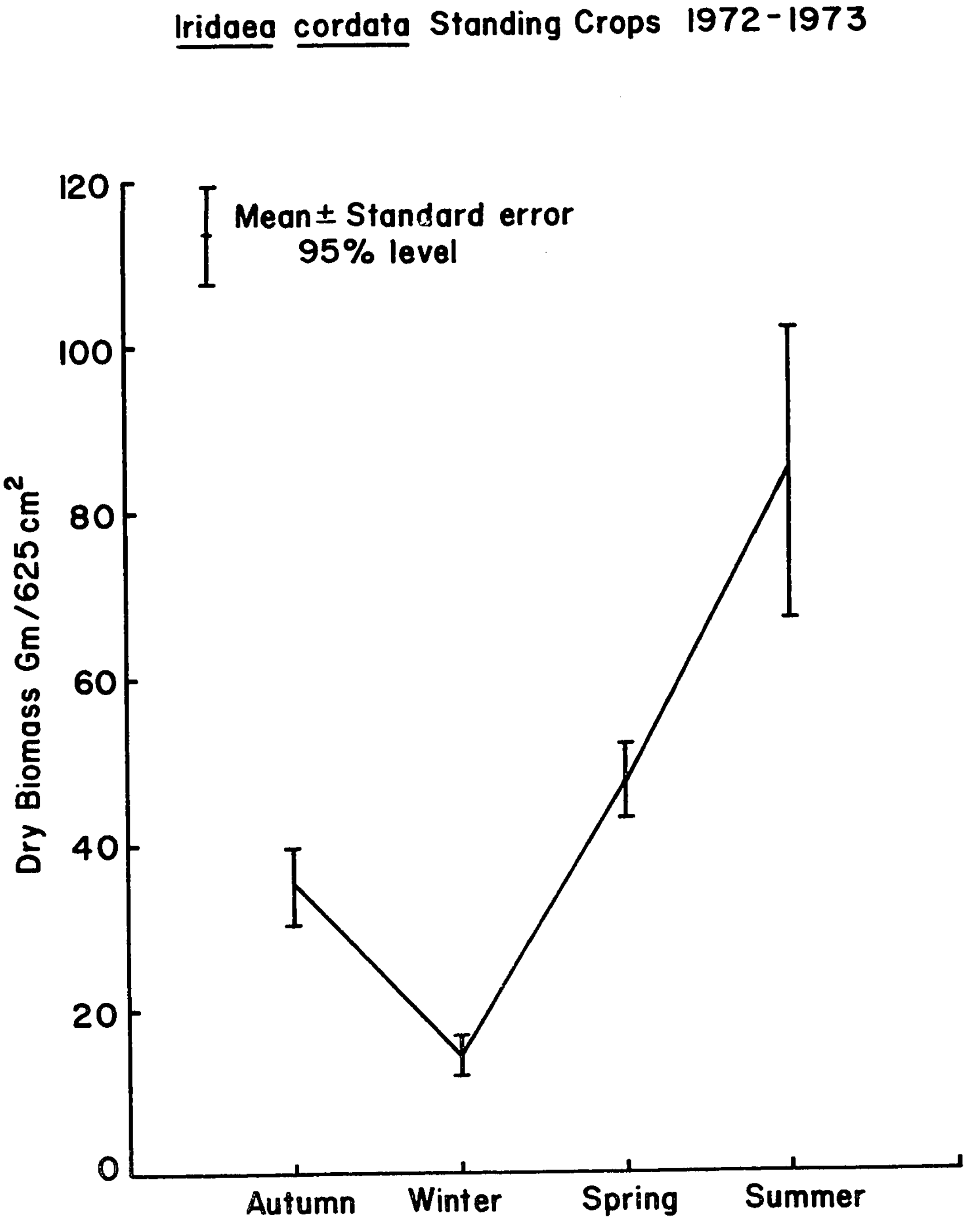

Iridaea cordata Standing Crops 1972-1973
Mean ± Standard error
95% level
Dry Biomass Gm/625 cm^2
120
100
80
60
40
20
0
Autumn
Winter
Spring
Summer

FIGURE 7

FIGURE 8

Mean standing crop of *Iridaea cordata* life history stages. The autumn tetrasporangial crop from Año Nuevo Point (ANP) was significantly greater (additional biomass in bracket) than crops from the other populations studied.

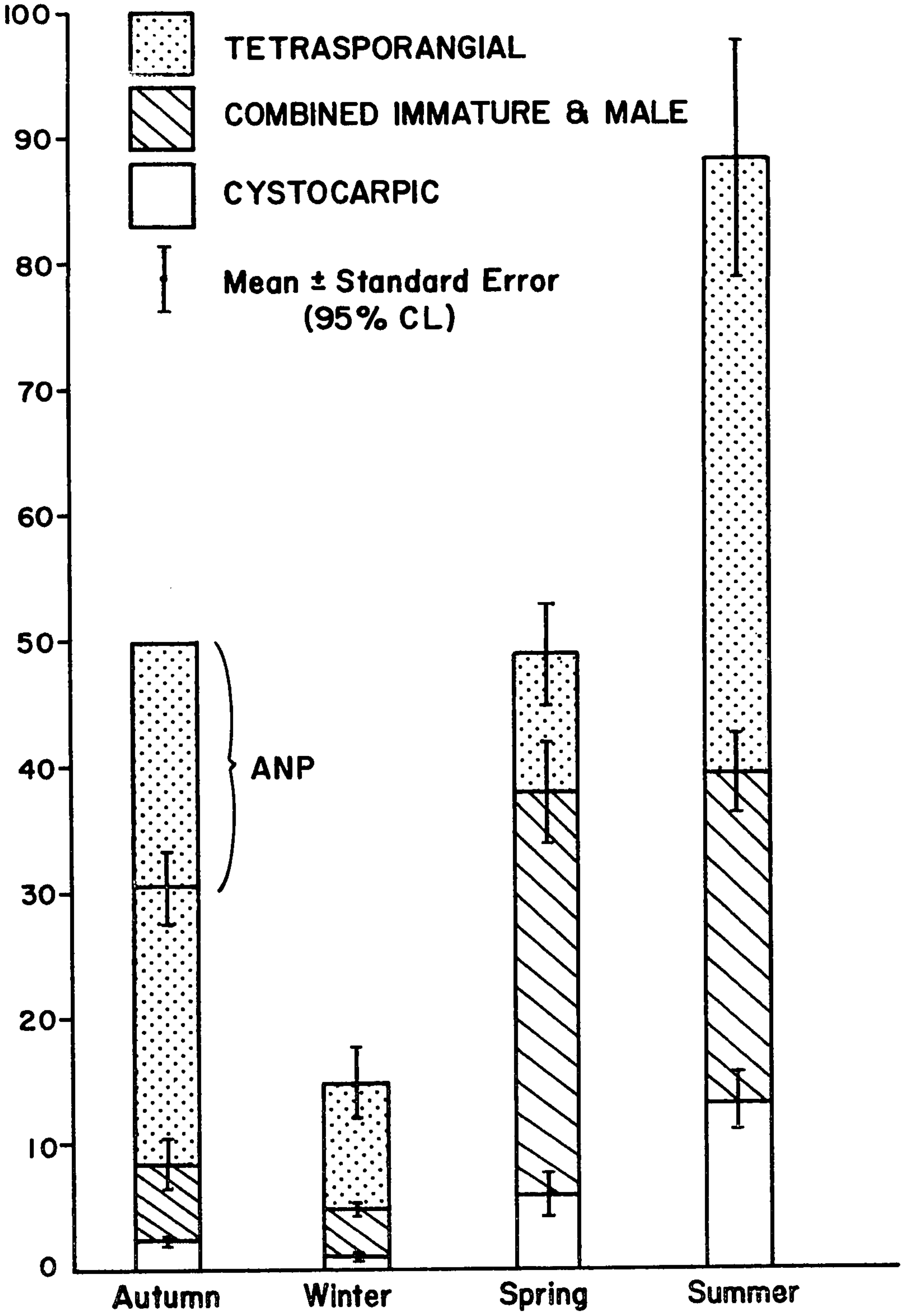

100
90
80
70
60
50
40
30
20
10
0
TETRASPORANGIAL
COMBINED IMMATURE & MALE
CYSTOCARPIC
Mean ± Standard Error
(95% CL)
ANP
Autumn
Winter
Spring
Summer

FIGURE 8

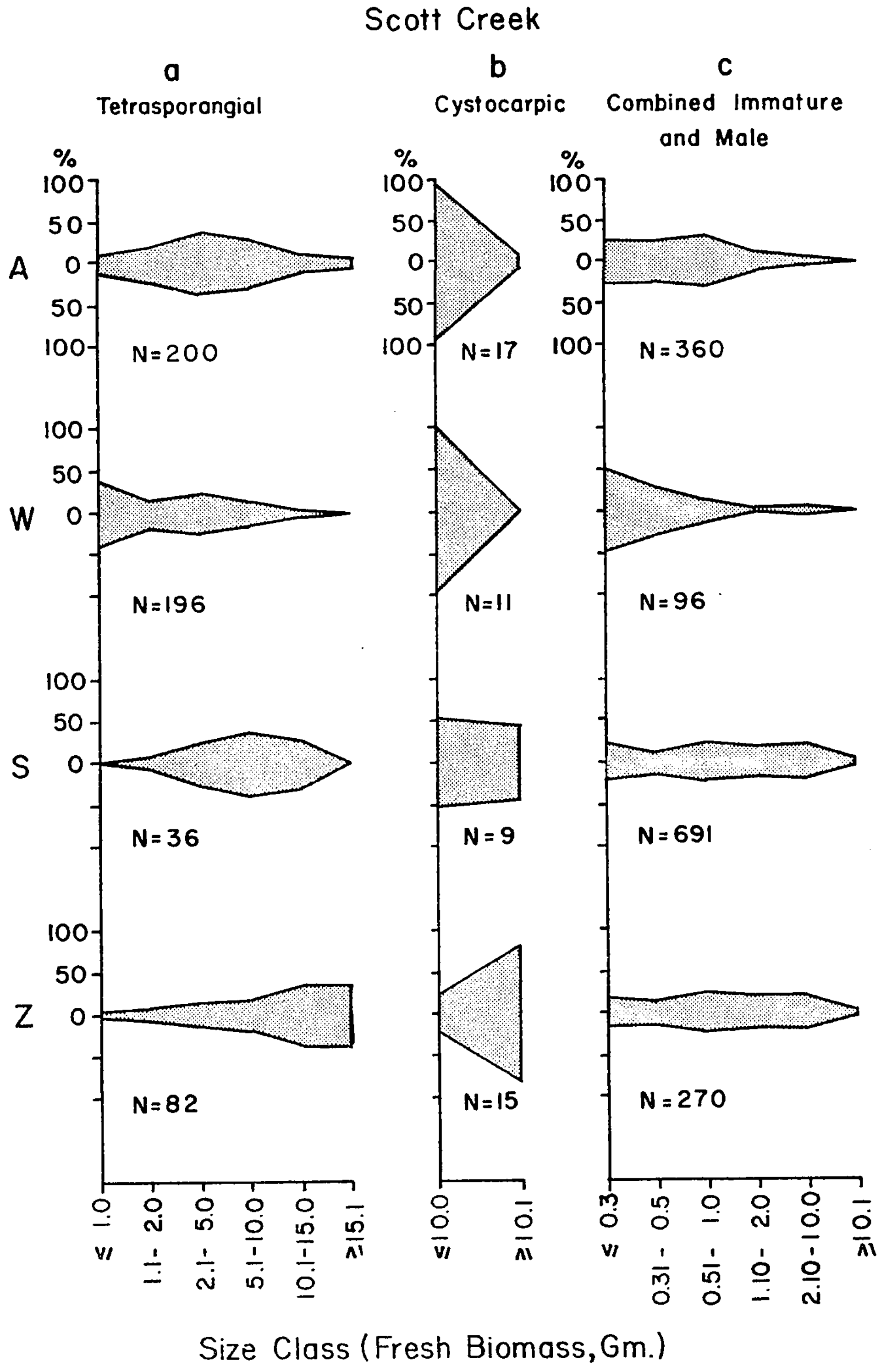
winter ($\bar{X}$ = 10 ± 3.6 gm/625 cm^2) levels. The biomass of the combined immature and male thalli was largest in the spring ($\bar{X}$ = 30 ± 4.1 gm/625 cm^2) with a slight decrease in the summer ($\bar{X}$ = 26 ± 3.4 gm/625 cm^2) and lows in the autumn ($\bar{X}$ = 9.5 ± 2.0 gm /625 cm^2) and winter ($\bar{X}$ = 2 ± 0.6 gm/625 cm^2). The seasonal trend of the cystocarpic crop was not significant, however the larger crops tended to be in the summer ($\bar{X}$ = 13.5 ± 2.3 gm/625 cm^2).

The biomass of tetrasporangial thalli ($\bar{X}$ = 45.3 ± 6.1 gm/625 cm^2) from the Año Nuevo Point population was significantly larger than those from the other populations studied during autumn (Fig 8 , in bracket).

Size-Class Distribution

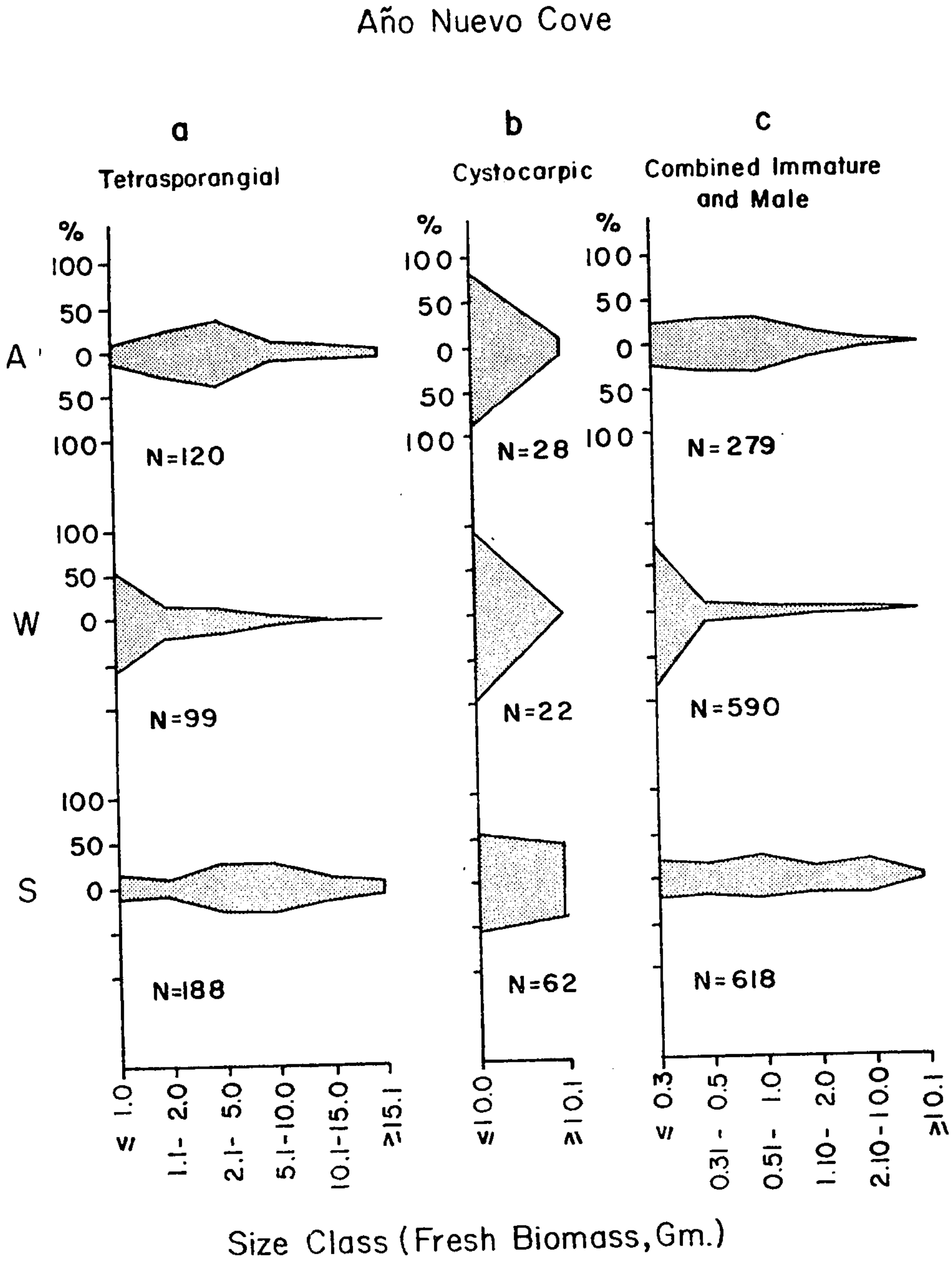
The fresh biomass distributions exhibited similar trends for all populations studied, however, they differed somewhat in percentage distribution (Figs. 9-12 , App. 9).

In autumn, size-class distributions of the tetrasporangial stage (Figs.9-12a) indicated that most of the large heavy thalli (15.1 gm>) had been lost from the populations. Further attrition was shown by the winter distribution, while a concurrent increase occurred in the small size-class (0.1-1.0 gm). This small size-class was composed mostly of reproductively mature thalli reduced to 'stubs' by the mechanical shearing of storm action. Morphologically, these 'stubs' include the apophysis and a small fraction of the



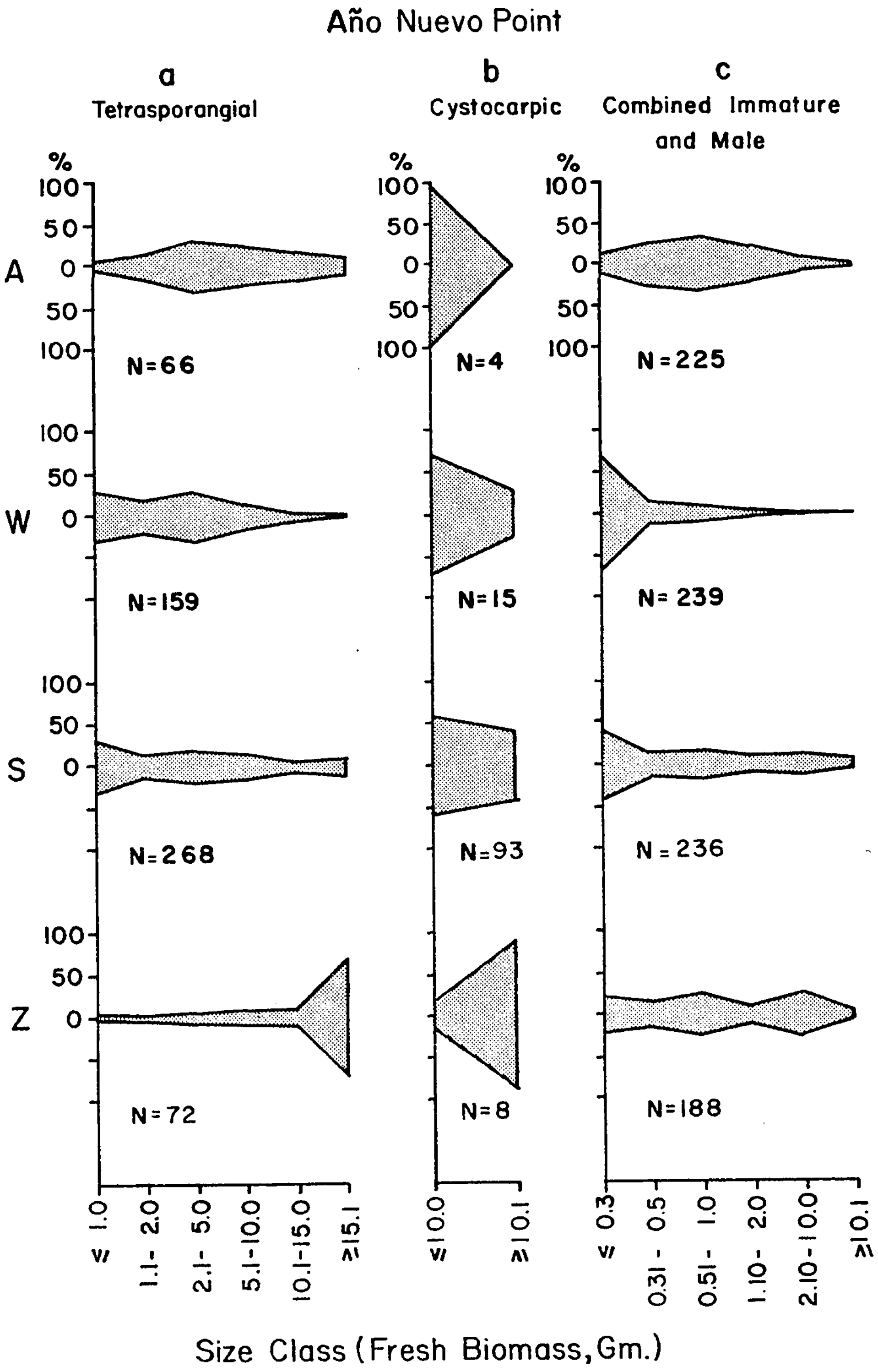
Z = Summer

FIGURE 9



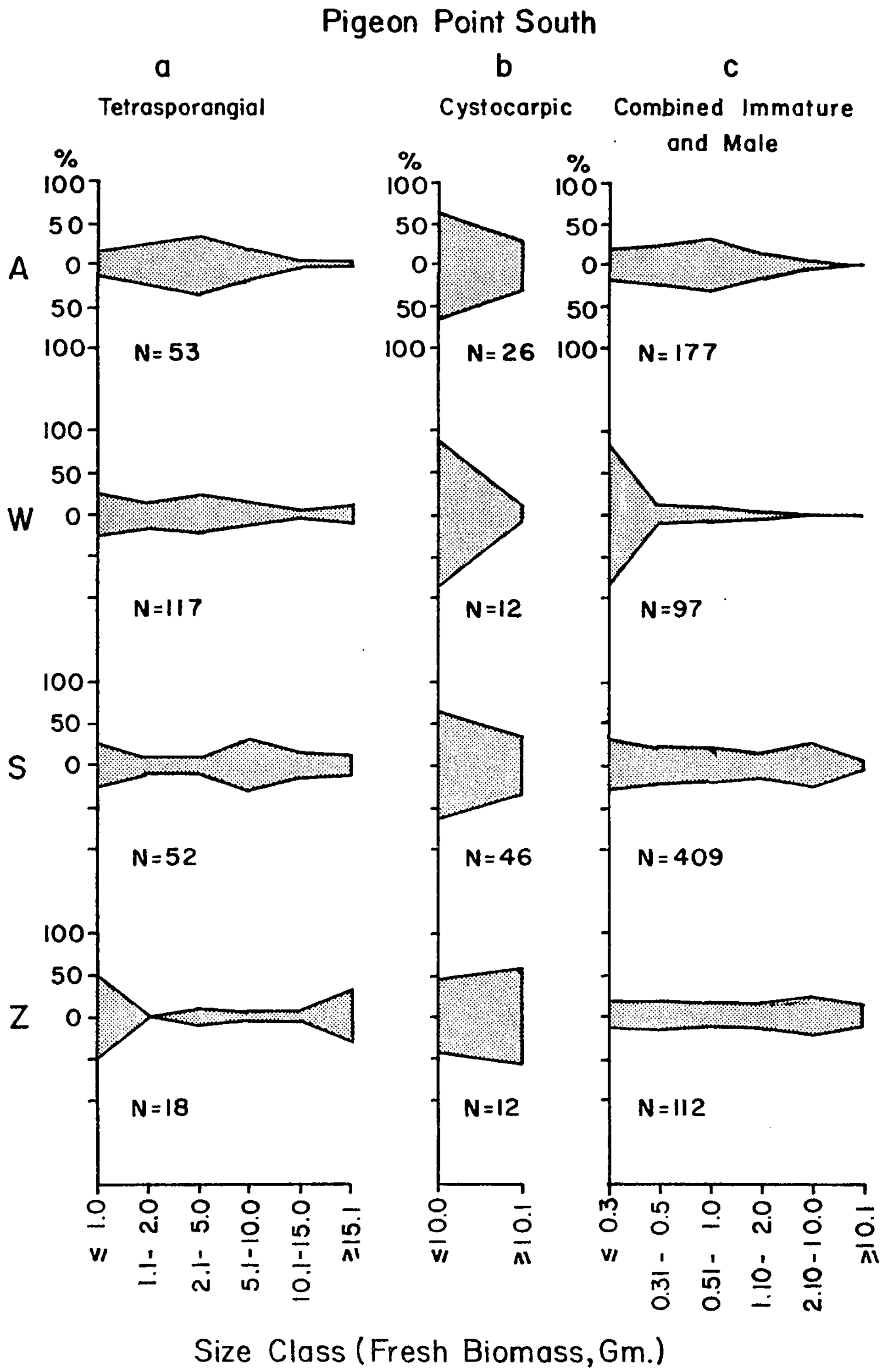
Z = Summer

FIGURE 10



Z = Summer

FIGURE 11



Z = Summer

FIGURE 12

thallus which includes sori. Growth was indicated in the spring by an increase in the frequency of thalli in the larger size-classes, culminating in the summer with the majority of thalli in the 15.1gm> class. The thalli in the Año Nuevo Point population were significantly heavier in the summer and autumn than those in the other populations studied. An anomalously large percentage of small thalli at Pigeon Point during summer is most likely due to the very small sample size.

The autumn and winter distributions of the cystocarpic stage (Figs. 9-12b) were characterized by small thalli. The majority of these were mature thalli reduced to 'stubs' by storm action. The spring distribution showed a notable increase in the larger size-class (10.0 gm>), which became predominant in the summer.

The autumn distribution of the combined immature and male thalli (Figs. 9-12c) indicated that most of the large thalli had matured, thus removing them from this combined category. The winter distribution was clearly dominated by small thalli. Growth was evident in the spring and summer with size-classes (0.1 gm through 10.0gm) nearly equally represented. Thalli greater than 10.0 gm rarely occurred and most likely represented the mature male thalli which did become greater than 10 gm in biomass and were not differentiated from immature thalli in this study.

DISCUSSION

The baseline biomass data for Iridaea cordata in central California puts this species into an ecological perspective both geographically and comparatively with other closely related genera.

The four California I. cordata populations studied (1972 -1973) produced similar biomass levels with lows in winter ($X = 14.2 \pm 2.4$ gm/625 cm^2) and peaked during summer ($X = 84.8 \pm 17.7$ gm/625 cm^2) and exhibited the same seasonal trends. Overall, these data indicate that open coastal habitats in central California support annually similar levels. Moreover, I. cordata biomass data for 1970-1971 for the Año Nuevo Point population (Hansen, J.E., 1972) was similar to that for the four populations studied during 1972-1973 indicating that biomass levels are relatively stable in central California. Comparatively, the California I. cordata biomass levels are greater throughout the year than those reported for Washington (Fralick, 1971) and Vancouver, B.C. (Austin & Adams, 1974), but exhibit the same annual fluctuations. This suggests that the environmental regime in California is more conducive than that of the north Pacific coast to growth of this species.

Further afield, California I. cordata biomass is similar in amount and seasonality to its east coast relative Chondrus crispus Stackhouse in Massachusetts (0.9 kgm dry weight/m^2 to 1.3 kgm dry weight/m^2)(Prince & Kingsbury, 1973).

While similar peak levels of C. crispus are reported in New Hampshire (0.6 gm fresh weight/cm^2) (Mathieson & Burns, 1975), they occur slightly later (early autumn). Peak C. crispus crops off Nova Scotia are half as large, but appear to be very stable, ranging from 0.4 to 0.43 kgm dry weight/m^2 (Taylor, 1970). Comparatively, Mann (1972) reports slightly larger C. crispus crops off Nova Scotia, whereas, peak Gigartina stellata (Stackh.) Batters crops from a dense population (approximately 37 gm fresh weight/100 cm^2 in August) in Britain were similar to C. crispus crops off Nova Scotia (Marshall et al., 1949). Natural I. cordata crops studied are much greater than Hypnea musciformis crops in India (Rao, 1970) and Eucheuma spp. in Florida which additionally exhibit an erratic seasonal pattern (Dawes et al., 1974).

The basic population information for I. cordata in California provides data for modeling of food web energy budgets and for rational assessment and planning for this marine natural resource. In addition, it forms a comparative background on which important ecological questions can be raised.

Field observations and populations studies have demonstrated that while conforming to the general Polysiphonia-type life history (Yamanouchi, 1906), Iridaea cordata populations exhibit a disproportionate life history stage representation in natural populations. Field observations of other red algal species suggest a wide occurrence of tetrasporangial dominance (Svedelius, 1927; Sjöstedt, 1928; Johnstone & Feeney, 1944; Marshall et al., 1947; Drew, 1955; Dixon, 1965; Knaggs, 1969; Rao, 1970; Barilotti & Silverthorne, 1971; Fralick, 1971; Dawes et al., 1974). The quantitative results in this study demonstrate that the tetrasporangial stage dominates over the gametangial stage in *I. cordata* populations, and suggestions are given as to the probable origin of this dichotomy.

Significant seasonal fluctuations in *I. cordata* population density occurred only in the juvenile stage. The juvenile density doubled in winter, thus establishing the new year's crop, a critical event in the *in situ* life history of an alga. This winter increase was produced primarily from the basal perennial crusts, indicating the importance of perennation and subsequent thallus production. Comparatively, reports by others have indicated that the season for thallus initiation can be quite variable. A relative increase in juvenile *Gigartina stellata* (Stackhouse) Batters thalli occurs during winter in New Hampshire (Burns & Mathieson, 1972) whereas initiation in Britain occurred in spring (Marshall et al., 1949). Growth of *C. crispus* is initiated in March and April in New Hampshire (Mathieson & Burns, 1975). The appearance of juvenile *Eucheuma nudum* and *Eucheuma* (Bahia Honda form) in Florida was evident by March (Dawes et al., 1974). In Japan, *Iridaea cornucopiae* Postels et Ruprecht thallus initiation occurred during October-November

(Hasegawa & Fukuhara, 1955), while immature Gelidium cartilagineum (L.) Gaill. (= G. robustum (Gardner) Hollenberg and Abbott) thalli showed no seasonality in southern California (Johnstone & Feeney, 1944; Barilotti & Silverthorne, 1971).

Speculation on the cause of dominance of one life history stage over another began with observations based on Ceramium; that annual algae exhibit a seasonal alternation of generations (Svedelius, 1927). Svedelius (op. cit.) stresses, however, " that the generations of perennial red algae are intermingled and develop synchronically, and therefore a seasonal alternation of generations is not apparent." Both the gametangial and tetrasporangial phases of I. cordata were present throughout the year and seasonal fluctuations in densities were minimal. Therefore, a seasonal alternation of generations was not apparent, as Svedelius (1927) had predicted for a perennial red alga, and does not account for the dominance of one stage over another in this species. Both phases of C. crispus in Massachusetts (Prince & Kingsbury, 1975) and in New Hampshire (Mathieson & Burns, 1975) and I. cornucopiae in Japan (Hasegawa & Fukuhara, 1952) also occur throughout the year and do appear to exhibit seasonal density fluctuations and reproductive capacity. However, comparisons to these studies are inappropriate since sampling error was not considered by these authors. Mathieson and Burns (1975) reported a dominance in the number of cystocarpic C. crispus thalli during most of the year in three intertidal populations in New Hampshire. In addition, they found that the number of tetrasporangial thalli increased with depth to -9 m. Again, however, sampling error was not reported.

The density of tetrasporangial I. cordata was significantly greater than that of the combined male and carposporic thalli (based on a 1:1 sex ratio) during all seasons but spring. The two morphological stages were approximately equal in spring when the new year's crop was just beginning to develop and mature. Between spring and summer the condition of tetrasporangial dominance was again re-established indicating that differential selection of life history stages had occurred by the time the plants had fully matured. Similarly, Johnstone and Feeney (1944) and Dawes, et al., (1974) reported significant tetrasporangial dominance throughout most of the year for Gelidium cartilagineum = (G. robustum) both intertidally and subtidally, and Eucheuma isiforme and Eucheuma (Bahia Honda form) respectively, using random sampling precedures.

The absence of significant I. cordata density fluctuations except in the juvenile stage indicates that observable differences in the natural populations are a result of size or biomass changes. Based on these results and qualitative natural history observations, the seasonal in situ development of this species can be characterized.

The majority of the thalli are initiated from the perennial crusts during winter while the biomass levels of all stages are at the annual low, due to senescence and mechanical shearing by storm action. This is shown by the high percentage of thalli in the smaller size-classes. However, juvenile density is lower during the remainder of the year suggesting that vegetative thallus initiation is lower, but continual. In spring, increases in daylength, solar radiation, and upwelled nutrients are accompanied by increases in the size and biomass of plants of all stages (Hansen, in press). Consequently, a high percentage of thalli occupy the larger size classes. It is only during this time, when the new year's crop is increasing, that the combined immature and male crop assumes the dominant position. The summer population structure, characterized by thallus maturation, culminates as biomass and dominance of tetrasporangial thalli reach a peak. This is shown by the reproductively mature thalli occupying primarily the larger size classes. The reproductive thalli can reach well over 100 gm (fresh biomass), whereas, the immature thalli rarely exceed a biomass of 10 gm. This suggests that maturation begins to occur before the thalli approach 10 gm in size and are consequently sorted into one of the reproductively mature categories. Curiously, the processes of senescence, characteristic of autumn populations, and severe storm action do not insure the removal of a thallus, but instead often reduce it to a 'stub'. Most of them overwinter in this condition. The occurrence of morphologically distinguishable 'stubs', and the fact that they overwinter, accounts for the constant population density throughout the year.

The normal autumnal senescence of the large tetrasporangial crops is consistently delayed at Año Nuevo Point. This phenomenon is highly correlated with the annual seal population peak at nearby Año Nuevo Island and precipitation levels that wash deposits from the island; and the resulting high NH_4-N concentrations in the surrounding waters (Hansen & Hansen, unpublished). This brief delay, however, is followed by rapid senescence and die-back to winter levels typical of the other populations.

The results from these studies imply that in the center of the geographic range of _I_. _cordata_, dominance of the tetrasporangial stage occurs early in thallus development. A winter (December, 1974) sampling on Vancouver Island, B. C. (Hansen, unpublished) showed that the described population structure also exists intertidally in a northern portion of the species range. These results raise the question: at what stage in the life history does this disproportionality arise, and is it evident in the large pool of isomorphic immature thalli? Results of Doty and Hansen (Table 1) show that carrageenan extracted from randomly collected batches of morphologically similar immature thalli is consistently (throughout four consecutive seasons) highly viscous and non-gelling. Moreover, the IR spectrum results indicate that the carrageenan from these immature thalli is mostly lambda, characteristic of tetrasporangial *I. cordata* thalli from the California populations studied (McCandless et al., 1975). This indirect evidence for the tetrasporangial nature of these plants strongly suggests that the selection for dominance of the tetrasporangial stage had occurred prior to thallus development.

Dominance has been attributable to 1) high mortality of tetraspores which would prevent sexual stages from becoming established (Johnstone & Feeney, 1944), 2) extension of a species into habitats at the northern limits of its range resulting in a loss of normal sexual life histories (Dixon, 1965), 3) adverse environmental conditions (Knaggs, 1969), and 4) habitation of the sublittoral (Knaggs, 1969; Mathieson & Burns, 1975). However, none except possibly the first of these suggestions appears to be applicable to the *I. cordata* populations under study, and further studies are to be carried out concerning the germination of tetraspores. Should factors influence high mortality of tetraspores, thus reducing the number of germinating plants, a suggestion could then be advanced that the carposporangia or carpospores are more "successful" since many more tetrasporangial plants are produced. Alternatively, the development of mature tetrasporangial thalli from tetraspores, probably through apomeiotic processes, has been demonstrated for this species in culture (Kim, 1976). If temporal apomeiosis does occur in natural populations, this could account for tetrasporangial dominance in this species. Such interpretation is complicated by the major contribution and possible replacement of alternation of gametangial and tetrasporangial stages by thallus perennation and vegetative production; a reproductive adaptation of benthic algae that has been underestimated or rarely considered in the past (Knight & Parke, 1931; Dixon, 1965).

Why tetrasporangial dominance occurs may involve the genetic advantage of diploidy versus haploidy. It remains to be determined how dominance occurs, during which specific developmental process it occurs, and what the mechanisms are that control or 'cue' its initiation.

APPENDIX 7

Iridaea cordata Gametangial Ratio

Number of males and cystocarpic blades/625 cm^2 from random samples taken at Año Nuevo Point during 1974.

Sample #	# Males	# Cystocarpic
1	1	0
2	0	0
3	2	1
4	3	1
5	0	1
6	0	0
7	1	1
8	0	0
9	1	2
10	2	0
11	2	5
12	1	0
13	4	1
N=14	1	3
Total =	18	16
$\overline{X}$ =	1.29	1.14
SE =	0.32	0.38

Null HO: The number of male and cystocarpic *I. cordata* blades in the populations studied is the same.

T-Test = 0.31

N = 14

probability > 0.10

* Null hypothesis accepted, there is no difference between the number of males and cystocarpic thalli in the population studied.

APPENDIX 8

Iridaea cordata:

Dry Biomass (Gm/625 cm^2)

Density (# of Blades/625 cm^2)

Symbols Legend:

A = Autumn, 1972
W = Winter, 1973
S = Spring, 1973
Z = Summer, 1973
TDW = Total Dry Weight
NR = Non-Reproductive Dry Weight
T = Tetrasporangial Dry Weight
C = Cystocarpic Dry Weight
T# = Total Number of Individuals
#J = Number of Juvenile Thalli
#NR = Number of Non-Reproductive Thalli
#T = Number of Tetrasporangial Thalli
#C = Number of Cystocarpic Thalli
$\overline{X}$ = Mean
SD = Standard Deviation
SE = Standard Error (95% CL)
V = Variance
N = Number of Samples

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass (gm/625cm^2)

Año Nuevo Cove

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	TDW	TDW	TDW	TDW	NR	NR	NR	NR	T	T	T	T
1	62.1	-	81.4	-	13.4	-	36.4	-	46.0	0.6	34.2	-
2	18.9	9.2	46.8	-	2.6	8.6	28.9	-	13.7	0	17.9	-
3	39.2	6.8	-	-	6.0	6.3	-	-	31.3	0	29.5	-
4	19.4	2.5	28.2	-	10.6	2.1	18.5	-	6.6	0	8.1	-
5	32.6	5.2	59.5	-	10.7	1.9	54.8	-	27.6	3.3	4.4	-
6	19.3	1.3	55.9	-	10.4	1.3	37.0	-	6.5	0	18.9	-
7	13.0	5.1	33.8	-	3.8	4.1	30.4	-	8.6	1.0	3.4	-
8	34.9	12.8	45.4	-	9.3	4.4	20.4	-	25.8	4.8	25.0	-
9	16.3	12.9	26.8	-	3.7	5.7	12.4	-	4.0	5.5	6.7	-
10	27.6	16.6	-	-	4.4	1.8	38.4	-	19.4	11.1	-	-
11	16.5	11.1	102.9	-	6.8	3.1	41.0	-	9.8	7.9	34.9	-
12	36.6	1.8	80.6	-	11.2	1.8	29.5	-	23.8	0	36.7	-
13	18.1	-	70.5	-	9.3	-	38.2	-	5.8	-	26.0	-
14	26.2	-	98.6	-	7.6	-	48.6	-	17.2	-	15.9	-
15	22.3	-	-	-	14.1	-	-	-	4.0	-	-	-
16	46.6	-	-	-	14.1	-	-	-	32.5	-	-	-
$\bar{X}$	28.1	7.75	60.87		8.63	3.74	33.42		17.66	2.85	20.12	
SD	13.26	5.13	26.14		3.78	2.34	11.88		12.48	3.74	11.95	
SE	3.31	1.55	7.55		0.95	0.70	3.29		3.12	1.08	3.31	
V	175.83	26.32	683.3		14.29	5.48	141.13		155.75	13.99	142.8	
N	16	11	12	0	16	11	13	0	16	12	13	0

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass/Density

Año Nuevo Cove

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	C	C	C	C	T#	T#	T#	T#	#J	#J	#J	#J
1	2.9	0.9	10.6	-	241	454	720	-	126	350	558	-
2	2.6	0.6	0	-	139	564	1031	-	88	411	875	-
3	1.9	0	23.7	-	131	614	554	-	86	466	533	-
4	2.2	0.4	1.6	-	506	863	1467	-	451	825	1363	-
5	-	0	0.3	-	186	258	506	-	135	225	338	-
6	2.3	0	0	-	240	51	974	-	159	28	963	-
7	0.5	0	0	-	124	503	620	-	96	416	613	-
8	-	3.6	0	-	129	712	1243	-	69	566	1175	-
9	8.8	1.7	7.7	-	938	1208	142	-	860	1075	88	-
10	3.8	3.7	0	-	347	470	-	-	282	391	608	-
11	-	0.1	27.0	-	170	438	618	-	146	385	588	-
12	1.6	0	14.4	-	465	636	1090	-	357	566	1038	-
13	1.5	-	6.3	-	287	-	743	-	225	-	725	-
14	1.4	-	34.1	-	120	-	538	-	79	-	508	-
15	4.3	-	-	-	242	-	-	-	167	-	-	-
16	0	-	-	-	293	-	-	-	238	-	-	-
$\overline{X}$	2.6	0.92	8.98		284.88	564.25	788.15		222.75	475.33	712.36	
SD	2.21	1.37	11.59		210.22	290.93	357.16		201.21	269.65	339.32	
SE	0.61	0.40	3.10		52.56	83.99	99.06		50.3	77.84	90.69	
V	4.88	1.88	134.33		44192.45	84640.26	127563.27		40485.46	72711.12	115138.06	
N	13	12	14	0	16	12	13	0	16	12	14	0

Appendix 8, continued

Iridaea cordata - 1972-73

Density

Año Nuevo Cove

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	#NR	#NR	#NR	#NR	#T	#T	#T	#T	#C	#C	#C	#C
1	72	101	135	-	39	1	20	-	4	2	7	-
2	25	151	137	-	22	0	19	-	4	2	0	-
3	23	146	-	-	18	2	14	-	4	0	7	-
4	36	37	94	-	16	0	11	-	3	1	1	-
5	32	30	163	-	16	3	4	-	5	0	1	-
6	62	23	-	-	16	0	11	-	3	0	0	-
7	22	79	-	-	5	8	7	-	1	0	0	-
8	43	114	64	-	12	26	4	-	5	6	0	-
9	64	105	37	-	9	26	14	-	5	2	3	-
10	36	50	-	-	23	21	-	-	6	8	0	-
11	19	42	-	-	4	12	16	-	1	1	14	-
12	79	70	-	-	26	0	41	-	3	0	11	-
13	52	-	-	-	8	-	15	-	2	-	3	-
14	30	-	-	-	9	-	11	-	2	-	19	-
15	68	-	-	-	4	-	-	-	3	-	-	-
16	39	-	-	-	16	-	-	-	0	-	-	-
$\overline{X}$	43.88	79.10	105.0		15.19	8.25	14.38		3.19	1.83	4.71	
SD	19.63	44.36	48.4		9.29	10.44	9.44		1.68	2.59	6.11	
SE	4.91	12.81	19.76		2.32	3.01	2.62		0.42	0.75	1.63	
V	385.34	1967.81	2342.56		86.3	108.99	89.11		2.82	6.71	37.33	
N	16	12	6	0	16	12	13	0	16	12	14	0

Appendix 8, continued

Iridata cordata - 1972-73

Dry Biomass (gm/625 cm^2)

Año Nuevo Point

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	TDW	TDW	TDW	TDW	NR	NR	NR	NR	T	T	T	T
1	40.5	5.0	83.3	120.4	-	4.6	5.9	65.7	-	0.4	40.5	54.7
2	45.2	7.0	13.7	185.9	9.9	1.8	1.4	57.2	-	5.2	2.2	127.5
3	39.3	5.0	6.5	85.8	10.8	4.9	6.5	21.5	30.5	0.0	0	64.3
4	40.5	43.7	38.3	58.6	8.7	0.5	1.9	18.8	-	43.2	24.8	29.0
5	46.2	14.8	88.7	69.0	15.2	1.2	6.0	24.8	-	12.0	70.0	44.2
6	88.7	-	18.7	-	32.1	0.1	12.0	43.8	61.1	-	5.0	60.2
7	74.7	6.6	23.5	-	19.4	0.3	2.1	21.6	59.1	3.7	13.2	-
8	17.1	13.3	68.7	-	-	1.3	39.2	12.4	18.0	6.8	17.2	1.1
9	42.6	27.9	19.0	142.4	12.4	0.1	0.1	20.8	-	27.8	18.9	77.2
10	63.9	25.5	63.9	87.1	-	1.6	26.3	2.5	63.9	17.2	22.7	59.2
11	67.4	14.2	56.8	87.8	-	0.8	29.5	25.3	-	8.7	25.5	54.5
12	49.9	37.9	17.6	28.2	-	0.9	15.4	29.2	-	36.7	2.0	4.0
13	27.0	-	71.5	50.1	-	-	35.1	13.5	-	-	24.9	30.3
14	50.9	-	65.3	48.6	14.6	-	63.9	40.8	38.9	-	0	0
15	31.9	-	-	55.4	-	-	-	5.9	33.5	-	-	3.4
16	54.6	-	-	-	-	-	-	-	52.4	-	-	-
$\overline{X}$	48.76	18.26	45.39	84.94	15.39	1.51	17.52	26.59	45.3	14.7	19.06	43.54
SD	18.13	13.59	28.6	45.07	7.57	1.61	18.85	17.93	17.23	14.87	19.04	35.78
SE	4.53	4.10	7.64	13.01	2.68	0.47	5.04	4.63	6.09	4.48	5.09	9.56
V	328.7	184.69	817.96	2031.3	57.3	2.59	355.32	321.48	296.87	221.12	362.52	1280.21
N	16	11	14	12	8	12	14	15	8	11	14	14

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass (gm/625 cm^2)/Density

Año Nuevo Point

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	C	C	C	C	T#	T#	T#	T#	#J	#J	#J	#J
1	-	0	36.9	0	292	494	290	-	221	441	233	-
2	1.2	0	10.1	1.2	120	346	347	-	87	308	306	-
3	-	0.1	0	0	215	525	164	-	167	443	106	-
4	-	0	11.6	10.8	219	247	899	130	137	208	856	75
5	-	1.6	12.7	0	469	562	316	336	410	491	225	260
6	-	0.4	1.7	-	188	572	-	440	100	566	-	360
7	-	2.6	8.2	0	272	169	211	317	100	150	145	255
8	-	5.2	12.3	-	167	403	337	-	147	366	213	-
9	-	0	0	44.4	355	127	56	106	258	100	45	50
10	-	6.7	14.9	25.4	238	487	939	36	175	441	806	20
11	-	4.7	1.7	8.0	254	218	292	146	202	183	225	85
12	-	0.3	0.2	0	281	381	208	55	232	316	186	20
13	1.4	-	11.6	6.3	293	-	190	108	242	-	156	90
14	-	-	1.3	7.8	228	-	37	-	166	-	-	-
15	-	-	-	46.1	180	-	-	-	135	-	-	-
16	-	-	-	-	112	-	-	-	82	-	-	-
$\overline{X}$	1.3	1.8	8.8	11.34	242.69	377.58	329.69	186.0	178.81	334.42	291.83	135.0
S	0.14	2.43	9.84	16.57	88.54	156.54	279.19	141.89	83.3	148.5	260.79	123.72
SE	0.10	0.70	2.63	4.59	22.14	45.19	77.43	47.3	20.82	42.87	75.28	41.24
V	.02	5.9	96.83	274.56	7839.33	24504.72	77947.06	20132.77	6938.89	22052.25	68011.42	15306.64
N	2	12	14	13	16	12	13	9	16	12	12	9

Appendix 8, continued

Iridaea cordata - 1972-73

Density

Año Nuevo Point

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	#NR	#NR	#NR	#NR	#T	#T	#T	#T	#C	#C	#C	#C
1	50	52	20	65	21	1	25	9	0	0	12	0
2	27	35	27	139	14	3	6	15	2	0	8	1
3	29	91	58	37	19	0	0	10	0	1	0	0
4	35	8	12	43	45	31	24	11	2	0	7	1
5	36	31	33	68	22	33	51	8	1	7	7	0
6	70	1	5	71	18	4	4	9	0	1	3	-
7	133	4	32	51	39	13	28	11	0	2	6	0
8	8	15	47	11	12	17	59	1	0	5	18	-
9	69	2	2	43	26	25	9	12	2	0	0	1
10	43	19	89	6	20	23	35	9	0	4	9	1
11	39	13	56	45	13	20	9	13	0	2	2	3
12	25	16	19	34	24	48	2	1	0	1	1	0
13	31	-	18	12	18	-	9	5	2	-	7	1
14	40	-	36	24	22	-	0	0	0	-	1	1
15	35	-	-	19	10	-	-	1	0	-	-	3
16	11	-	-	-	19	-	-	-	0	-	-	-
$\bar{X}$	41.94	23.92	32.43	44.53	21.38	18.17	18.64	7.67	0.56	1.92	5.79	0.92
SD	29.81	25.94	23.7	33.33	9.22	14.87	19.07	4.88	0.89	2.27	5.13	1.04
SE	7.45	7.49	6.33	8.61	2.31	4.29	5.10	1.26	0.22	0.66	1.37	0.29
V	888.64	672.88	561.69	1110.89	85.01	221.12	363.66	23.81	0.79	5.15	26.32	1.08
N	16	12	14	15	16	12	14	15	16	12	14	13

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass (Gm/625 cm^2)

Scott Creek

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	TDW	TDW	TDW	TDW	NR	NR	NR	NR	T	T	T	T
1	31.9	16.3	49.6	116.9	4.5	0.2	38.3	30.2	27.7	16.1	11.3	83.0
2	30.6	8.9	45.0	59.2	4.9	1.3	45.0	59.2	27.7	7.6	0	0
3	34.6	18.3	25.7	132.8	5.3	0.6	18.3	53.1	28.5	17.7	7.4	79.7
4	33.8	6.0	41.8	94.0	7.8	1.5	16.5	23.6	19.9	4.5	7.0	70.4
5	35.5	-	24.5	163.1	12.2	-	24.5	41.4	29.8	8.2	0	53.4
6	37.2	-	29.4	67.5	10.8	-	25.2	25.1	20.6	17.3	4.2	26.0
7	17.6	24.9	19.7	201.9	1.4	2.3	11.3	37.7	13.9	22.3	8.4	54.2
8	64.9	7.7	49.9	-	11.4	4.8	41.7	15.1	54.0	2.4	2.7	-
9	33.3	8.0	48.3	-	-	1.9	45.9	17.4	-	6.1	2.4	28.4
10	43.9	1.0	29.5	-	-	0.2	29.5	-	-	0.5	0	50.0
11	37.9	4.8	54.0	-	-	4.8	44.4	46.2	-	-	9.6	36.4
12	25.0	20.5	36.9	-	-	0.8	36.9	10.2	-	19.5	0	-
13	39.3	27.9	91.8	87.6	-	0.4	82.7	29.7	-	27.5	9.1	45.6
14	34.8	16.5	33.6	-	-	1.0	30.3	-	-	14.9	3.3	87.4
15	31.6	-	-	-	-	-	-	-	-	-	-	-
16	30.3	-	-	-	-	-	-	-	-	-	-	-
$\bar{X}$	35.14	13.4	41.41	115.38	7.92	1.65	35.04	32.41	27.76	12.66	4.67	51.21
SD	9.92	8.52	18.12	48.91	3.89	1.61	17.72	15.39	11.94	8.33	4.05	26.19
SE	2.48	2.46	4.84	17.29	1.37	0.46	4.74	4.44	4.22	2.31	1.08	7.56
V	98.41	72.59	328.33	2392.19	15.13	2.59	314.0	236.85	142.56	69.39	16.4	685.92
N	16	12	14	8	8	12	14	12	8	13	14	12

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass/Density

Scott Creek Cont'd.

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	C	C	C	C	T#	T#	T#	T#	#J	#J	#J	#J
1	0	0	0	3.7	189	125	135	-	146	100	17	-
2	0	0	0	0	408	482	476	277	356	437	325	225
3	0	0	0	0	444	482	89	321	380	267	55	225
4	6.6	0	18.3	0	349	531	363	641	283	487	315	519
5	2.8	1.0	0	68.3	249	-	173	-	168	40	31	-
6	4.3	1.7	0	16.4	372	-	147	-	247	443	41	-
7	5.9	0.3	0	10.0	305	465	147	503	259	425	93	350
8	0	0.5	5.5	-	285	-	353	-	175	838	188	-
9	-	0	0	-	269	-	774	-	162	533	605	-
10	-	0.3	0	-	168	-	609	-	104	288	480	-
11	-	0	0	-	489	346	282	-	400	175	161	425
12	-	0.2	0	28.7	244	351	849	-	206	313	661	137
13	-	0	0	12.3	290	160	316	548	221	113	175	475
14	-	0.6	0	42.5	152	157	576	803	107	125	438	706
15	-	-	-	-	550	-	-	-	491	-	-	-
16	-	-	-	-	399	-	-	-	318	-	-	-
$\overline{X}$	2.45	0.33	1.7	18.19	322.63	323.44	377.79	515.5	251.44	327.43	256.07	382.75
SD	2.85	0.50	5.0	22.41	115.04	151.74	245.9	197.15	112.53	217.19	218.12	186.92
SE	1.01	0.13	1.34	7.09	28.76	50.58	65.72	80.48	28.13	58.05	58.3	66.09
V	8.12	0.25	25.0	502.21	13234.2	23025.03	60466.81	38868.12	12663.0	47171.5	47576.33	34939.09
N	8	14	14	10	16	9	14	6	16	14	14	8

Appendix 8, continued

Iridaea cordata - 1972-73

Density

Scott Creek, cont.

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	#NR	#NR	#NR	#NR	#T	#T	#T	#T	#C	#C	#C	#C
1	21	4	111	78	23	21	5	22	0	0	0	1
2	33	14	151	52	19	31	0	0	0	0	0	0
3	33	4	31	83	31	23	3	13	0	0	0	0
4	40	20	40	104	21	24	4	18	5	0	5	0
5	53	-	142	110	26	-	0	16	2	2	0	8
6	99	-	99	72	22	-	7	26	4	3	0	6
7	15	21	51	135	25	18	5	16	6	1	0	2
8	77	-	158	33	33	-	2	27	0	1	5	-
9	84	-	166	40	20	-	3	13	3	0	0	-
10	42	-	129	56	22	-	0	25	0	1	0	-
11	80	171	93	77	9	0	6	9	0	0	0	-
12	11	12	184	13	27	1	0	-	0	1	0	3
13	52	16	138	58	12	0	3	12	5	0	0	3
14	28	7	136	79	16	2	2	11	1	2	0	7
15	35	-	-	-	21	-	-	-	3	-	-	-
16	67	-	-	-	14	-	-	-	0	-	-	-
$\bar{X}$	48.13	29.89	116.36	70.71	21.31	13.33	2.86	16.0	1.81	0.79	0.64	3.0
SD	26.42	53.29	47.97	32.25	6.48	12.43	2.35	7.67	2.2	0.97	1.65	3.02
SE	6.6	17.76	12.82	8.62	1.62	4.14	0.63	2.13	0.55	0.26	0.44	0.95
V	698.02	2839.82	2301.12	1040.06	41.99	154.5	5.52	58.33	4.84	0.94	2.72	9.12
N	16	9	14	14	16	9	14	13	16	14	14	10

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass (gm/625 cm^2)

Pigeon Point South

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	TDW	TDW	TDW	TDW	NR	NR	NR	NR	T	T	T	T
1	-	34.4	38.5	19.5	14.1	1.7	18.4	8.2	22.6	32.7	14.9	11.2
2	36.2	24.5	62.0	11.1	6.8	0	41.4	3.4	21.5	24.5	8.5	5.8
3	31.0	52.3	55.6	86.0	8.2	0.9	32.7	35.6	17.2	50.4	17.7	18.3
4	-	-	54.6	140.4	-	0	44.6	72.6	-	0.3	0	60.6
5	39.7	10.1	75.8	21.3	6.6	2.3	60.9	10.0	20.8	4.4	10.1	1.6
6	52.0	1.5	41.6	40.5	5.5	1.5	40.0	17.5	44.0	0	0	14.4
7	-	19.3	25.2	45.1	-	1.0	22.6	23.8	-	17.5	2.6	21.3
8	28.3	41.8	18.4	68.7	0.4	0	14.8	5.5	4.6	41.8	3.6	51.9
9	26.4	1.4	8.6	101.5	9.5	0	8.6	22.1	34.7	1.4	0	45.8
10	40.5	1.9	34.9	59.7	17.8	0.1	33.3	27.8	51.6	1.0	0.5	18.9
11	13.5	3.5	18.6	7.4	3.2	3.5	18.6	0.7	9.0	0	0	6.7
12	7.0	1.2	37.3	70.4	0.8	0.7	36.8	22.3	5.1	0	0.1	24.2
13	36.2	-	82.2	30.6	6.0	-	65.3	5.7	4.2	-	10.2	24.9
14	34.4	-	64.8	-	3.3	-	12.5	26.3	29.0	-	29.2	60.3
15	-	-	-	-	-	-	-	-	9.4	-	-	-
16	10.8	-	-	-	6.6	-	-	-	0	-	-	-
$\overline{X}$	29.67	17.45	44.15	54.01	6.83	0.98	32.18	20.11	19.55	14.5	6.96	26.14
SE	3.86	5.57	6.0	10.85	1.36	0.32	4.66	4.94	4.21	5.34	2.35	5.4
V	179.06	341.47	503.49	1529.0	24.01	1.23	304.43	341.82	248.36	341.97	77.6	407.94
N	12	11	14	13	13	12	14	14	14	12	14	14

Appendix 8, continued

Iridaea cordata - 1972-73

Dry Biomass (gm/625 cm^2)

Pigeon Point South

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	C	C	C	C	T#	T#	T#	T#	#J	#J	#J	#J
1	-	0	5.2	0	-	1195	184	38	87	1158	125	17
2	1.9	0	12.1	1.9	141	331	425	57	95	318	325	42
3	5.6	1.0	5.2	32.1	101	483	444	226	39	441	375	167
4	-	0	10.0	7.2	-	557	-	210	-	558	156	58
5	12.3	3.4	4.8	9.7	240	601	-	111	190	558	181	75
6	2.5	0	1.6	8.6	108	779	-	122	71	725	175	75
7	-	0.8	0	0	-	227	44	174	-	200	0	142
8	0	0	0	11.3	100	321	25	321	90	308	6	258
9	7.0	0	0	33.6	155	395	121	-	130	381	94	-
10	2.8	0.9	1.1	13.0	-	421	-	-	227	418	175	-
11	0.6	0	0	0	127	1347	216	-	103	1308	156	-
12	1.1	0.6	0.4	23.9	31	363	622	-	21	350	456	-
13	2.6	-	6.7	0	364	-	-	-	315	-	562	-
14	2.1	-	23.1	-	78	-	-	-	58	-	581	-
15	2.0	-	-	-	-	-	-	-	-	-	-	-
16	4.2	-	-	-	319	-	-	-	281	-	-	-
$\overline{X}$	3.44	0.56	5.02	10.87	160.36	5.85	260.13	157.38	131.31	560.25	240.5	104.25
SD	3.29	0.98	6.53	11.95	103.88	353.74	214.16	94.31	93.2	344.63	189.13	79.59
SE	0.91	0.28	1.74	3.32	31.32	102.12	75.72	33.34	25.85	99.49	50.55	28.14
V	10.82	0.96	42.64	142.8	10791.05	12531.99	45864.51	8894.38	8686.24	118769.84	35770.16	6334.57
N	13	12	14	13	11	12	8	8	13	12	14	8

Appendix 8, continued

Iridaea cordata - 1972-73

Density

Pigeon Point South

	A72	W73	S73	Z73	A72	W73	S73	Z73	A72	W73	S73	Z73
Sample #	#NR	#NR	#NR	#NR	#T	#T	#T	#T	#C	#C	#C	#C
1	70	11	44	16	9	28	11	5	-	0	4	0
2	30	0	84	8	13	15	5	5	3	0	11	2
3	38	11	59	52	19	28	7	2	5	3	3	5
4	-	0	0	135	-	1	0	15	-	0	6	2
5	26	23	-	23	16	12	4	8	9	8	2	5
6	22	54	-	38	13	0	0	6	2	0	2	3
7	-	6	41	29	-	20	3	3	-	1	0	0
8	3	0	18	18	7	13	1	31	0	0	0	14
9	33	0	27	32	14	14	0	9	5	0	0	6
10	25	1	-	42	-	1	2	17	3	1	2	5
11	16	41	60	7	7	0	0	4	1	0	0	0
12	7	11	157	33	2	0	2	3	1	2	7	10
13	35	-	-	8	11	-	6	8	3	-	2	0
14	6	-	-	41	12	-	12	18	2	-	7	-
15	-	-	-	-	5	-	-	-	1	-	-	-
16	34	-	-	-	0	-	-	-	4	-	-	-
$\bar{X}$	26.54	13.17	61.25	34.43	9.85	11.0	3.79	9.57	3.0	1.25	3.29	4.0
SD	17.54	17.7	43.82	32.18	5.51	10.67	4.0	8.08	2.38	2.34	3.34	4.24
SE	4.87	5.11	15.49	8.6	1.53	3.08	1.07	2.16	0.66	0.68	0.89	1.18
V	307.65	313.29	1920.19	1035.55	30.36	113.85	16.0	65.29	5.66	5.48	11.16	17.98
N	13	12	8	14	13	12	14	14	13	12	14	13

APPENDIX 9

Iridaea cordata

Size Class Frequency Distributions:

Scott Creek

Año Nuevo Cove

Año Nuevo Point

Pigeon Point South

Symbols Legend:

NR = Non-Reproductive Thalli
T = Tetrasporangial Thalli
C = Cystocarpic Thalli

A = Autumn, 1972
W = Winter, 1973
S = Spring, 1973
Z = Summer, 1973

Appendix 9, continued

IRIDAEA CORDATA - SIZE CLASS FREQUENCY DISTRIBUTIONS

-Scott Creek-

	Size Class (gm fresh biomass)		# Thalli				%			
			A	W	S	Z	A	W	S	Z
NR	≤	0.3	97	49	154	52	26.9	51.0	22.3	19.3
	0.31	-0.5	87	28	95	40	24.2	29.2	13.7	14.8
	0.51	-1.0	117	15	159	62	32.5	15.6	23.0	23.0
	1.1	-2.0	41	1	126	52	11.4	1.0	18.2	19.3
	2.1	-10.0	18	3	145	54	5.0	3.1	21.0	20.0
	≥	10.0	0	0	12	10	0	0	1.7	3.7
total #			360	96	691	270				
T	≤	1.0	13	78	0	4	6.5	39.8	0	4.9
	1.1	-2.0	38	38	3	6	19.0	19.4	8.3	7.3
	2.1	-5.0	75	46	9	13	37.5	23.5	25.0	15.9
	5.1	-10.0	53	29	14	16	26.5	14.8	38.9	19.5
	10.0	-15.0	15	4	10	31	7.5	2.0	27.8	37.8
	≥	15.1	6	1	0	31	3.0	0.5	0	37.8
total #			200	196	36	82				
C	≤	10.0	16	11	5	3	94.1	100	55.6	20.0
	≥	10.1	1	0	4	12	5.9	0	44.4	80.0
total #			17	11	9	15				

Appendix 9, continued

Iridaea cordata Size Class Frequency Distribution

-Año Nuevo Cove-

	Size Class (gm fresh biomass)	# Thalli				%			
		A	W	S	Z	A	W	S	Z
NR	≤ 0.3	62	474	141		22.2	80.3	22.8	
	0.31 - 0.5	77	59	108		27.6	10.0	17.5	
	0.51 - 1.0	82	45	142		29.4	7.6	22.9	
	1.1 - 2.0	49	9	106		17.6	1.5	17.2	
	2.1 - 10.0	9	3	118		3.0	0.5	19.1	
	≥ 10.1	0	0	3		0	0	0.4	
total #		279	590	618					
T	≤ 1.0	14	58	29		11.7	58.6	15.4	
	1.1 - 2.0	29	22	21		24.2	18.3	11.2	
	2.1 - 5.0	46	14	48		38.3	14.1	25.5	
	5.1 - 10.0	16	5	48		13.3	5.1	25.5	
	10.1 - 15.0	11	0	31		9.2	0	16.5	
	≥ 15.1	4	0	11		3.3	0	5.9	
total #		120	99	188					
C	≤ 10.0	25	22	36		89.3	100	58.1	
	≥ 10.1	3	0	26		10.7	0	41.9	
total #		28	22	62					

Appendix 9, continued

Iridaea cordata Size Class Frequency Distributions

-Año Nuevo Point -

	Size Class (gm fresh biomass)	# Thalli				%			
		A	W	S	Z	A	W	S	Z
NR	≤ 0.3	28	173	100	39	12.4	72.4	42.4	20.7
	0.31 - 0.5	56	35	33	27	24.9	14.6	74.0	14.4
	0.51 - 1.0	76	23	40	42	33.8	9.6	16.9	22.3
	1.1 - 2.0	47	6	25	23	20.9	2.5	10.6	12.2
	2.1 - 10.0	15	2	31	49	6.7	0.8	13.1	26.1
	≥ 10.1	3	0	7	8	0.8	0	3.0	4.3
total #		225	239	236	188				
T	≤ 1.0	3	45	91	1	4.5	28.3	33.9	1.4
	1.1 - 2.0	9	33	34	1	13.6	20.8	12.7	1.4
	2.1 - 5.0	21	43	53	3	31.8	27.0	19.8	4.2
	5.1 - 10.0	15	24	43	6	22.7	15.1	16.0	8.3
	10.1 - 15.0	12	10	17	9	18.2	6.3	6.3	12.5
	≥ 15.1	6	2	30	52	9.1	1.3	11.2	72.2
total #		66	159	268	72				
C	≤ 10.0	4	11	55	1	100	73.0	59.1	12.5
	≥ 10.1	0	4	38	7	0	26.7	40.9	87.5
total #		4	15	93	8				

Appendix 9, continued

Iridaea cordata Size Class Frequency Distributions

-Pigeon Point South-

	Size Class (gm fresh biomass)	# Thalli				%			
		A	W	S	Z	A	W	S	Z
NR	≤ 0.3	35	84	131	19	19.8	86.6	32.0	17.0
	0.31 - 0.5	42	11	87	20	23.7	11.3	21.3	17.9
	0.51 - 1.0	59	8	83	17	33.3	8.2	20.3	15.2
	1.1 - 2.0	33	2	64	17	18.6	2.1	15.6	15.2
	2.1 -10.0	8	0	102	24	4.5	0	24.9	21.4
	≥ 10.1	0	0	25	15	0	0	6.1	13.4
total #		117	97	409	112				
T	≤ 1.0	8	28	12	9	15.1	23.9	23.1	50
	1.1 - 2.0	14	22	5	0	26.4	17.2	9.6	0
	2.1 - 5.0	19	29	4	2	35.8	22.7	8.0	11.1
	5.1 - 10.0	10	19	16	1	18.9	14.8	30.8	5.6
	10.1 - 15.0	1	6	8	1	1.9	4.7	15.4	5.6
	≥ 15.1	1	13	7	5	1.9	10.2	13.4	27.8
total #		53	117	52	18				
C	≤ 10.0	18	11	30	5	69.2	91.7	65.2	41.7
	≥ 10.1	8	1	16	7	30.8	8.3	34.8	58.3
total #		26	12	46	12				

CHAPTER THREE: ASPECTS OF IRIDAEA CORDATA ONTOGENY: GROWTH, MATURATION, AND SENESCENCE

INTRODUCTION

The chronological patterns of growth, maturation, and senescence (ontogenetic progression) are the cumulative and synergistic expressions of the entire genotype as it is influenced by the complex of environmental factors. Growth of natural algal populations or individuals transplanted from them has been measured for a few genera of benthic red algae: (Marshall, et al., 1949; Taylor, 1954, 1970; Foster, 1955; Jones, 1959; Seone-Camba, 1966; Cendrero & Ramos, 1967; Dixon, 1966; Raju & Thomas, 1971; Barilotti & Silverthorne, 1972; Burns & Mathieson, 1972; Prince & Kingsbury, 1973; Waaland, 1973; Dawes, et al., 1974; Mathieson & Burns, 1975). But, rarely has *in situ* annual ontogeny of a population of any red algal species been studied or quantified, with respect to its major contributing mode (perennation and vegetative reproduction), and its relationship to fluctuating environmental factors.

These field studies were designed to provide the data necessary to interpret the several components of ontogenetic patterns and were based on the following questions. 1) What are the roles and contributions of perennation and vegetative reproduction? 2) Is there a change in population structure following a physical disturbance?

3) Is growth synchronous? 4) Do maturation and senescence correlate with thallus size, age, or time of the year? 5) Does thallus growth terminate with maturation? 6) Is growth pattern correlated with or 'cued' by fluctuations in the environmental factors monitored?

To investigate these questions, _in situ_ growth rates, maturation and senescence times of tetrasporangial and gametangial thalli were measured.

MATERIALS AND METHODS

All _I. cordata_ growth experiments were carried out at Año Nuevo Point. To measure regrowth from the basal perennial crusts, sixteen 625 cm^2 areas with relatively uniform surfaces were selected within the _I. cordata_ population.

The sixteen experimental plots were identified by securing 3 cm (diameter) stainless discs to the rock substratum with cement nails. The exact position of the plots was measured from two stainless steel rods set 0.5 m into the substratum with marine epoxy.

The experimental plots were originally harvested at the end of autumn (10 November, 1973). An autumn harvest was selected to correspond with the normal autumnal senescence and winter die-back of natural _I. cordata_ populations. All _I. cordata_ thalli, but not associated species, were removed down to the basal, perennial crusts using scissors.

To determine cumulative vegetative growth from the basal crusts, four of the plots were randomly selected and reharvested at the end of each consecutive season: winter (5-6 February, 1974), spring (7 May, 1974), summer (19-20 July, 1974), and autumn (31 October, 1974). Cumulative seasonal growth rate (G_c) was calculated as follows:

$$G_c = \frac{(\Sigma i/N)_2 - (\Sigma i/N)_1}{t_2 - t_1}$$

Where: G_c = Growth Rate (mg dry weight/625 cm^2/day)

Σi = Sum of biomass values

N = Number of samples

$(\Sigma i/N)_2$ = Mean biomass

$(\Sigma i/N)_1$ = Mean biomass from previous season

$t_2 - t_1$ = Number of days between consecutive harvests

In addition, discrete seasonal growth rate (G_d) (approximately three month increments) was measured by reharvesting the four plots harvested each previous season and was calculated as follows:

$$G_d = \frac{\Sigma i/N}{t}$$

Where: G_d = Growth Rate (mg dry weight/625 cm^2/day)

Σi = Sum of biomass values

N = Number of samples

t = Discrete number of days between harvests

Samples from each plot were rinsed in seawater, freed of invertebrates, epiphytes, and debris and sorted to life history stage: non-reproductive (not including juveniles < 3 cm in length), reproductively mature male, reproductively mature female (cystocarpic), and reproductively mature tetrasporangial. Juveniles (< 3 cm in length) were not considered due to a variable loss of the very tiny thalli during thallus cutting procedures. The life-history-stage-samples were dried in aluminum pans at 60°C for 24-72 hrs depending on sample size, and dry weights determined.

The relative growth rate (Evans, 1972), or number of doublings in dry weight of I. cordata per day, total number of doublings, and doubling times were based on discrete seasonal regrowth and were determined using the following formulas.

$$R_E = \frac{\log_2 X_2 - \log_2 X_1}{t_2 - t_1}$$

$$R_E \cdot t = \text{Total \# of doublings}$$

$$t/R_E t = \text{Doubling time (days)}$$

Where: R_E = Relative growth rate (# doublings in dry weight/day)

X_1 = dry weight, beginning

X_2 = dry weight, end

t = time (days)

In order to quantify I. cordata maturation, an index based on 1) cumulative, and 2) discrete seasonal biomass was developed according to the following relationship.

$\frac{R}{T} : T$ Where: R = Total reproductive biomass(gm dry weight)

T = total biomass (gm dry weight)

The resulting index ranges from 0 to 1.0. As the value approaches 1.0, the component of reproductively mature biomass approaches 100%.

The following statistical tests were employed for data analysis at the population level, and confidence limits were set at 95%: F ratio, t-test, Mann-Whitney test (U-test) (Sokal & Rohlf, 1969).

Ontogenetic aspects (growth and development) of individual _I._ _cordata_ thalli were also measured. A stainless steel, rectangular punch (1.0 cm X 0.5 cm) was designed to tag the thalli in the apophysis area (the expanded portion of the blade just above the stipe). To identify different thalli, a code based on number and position of punches was utilized. The tagged thalli were located by coordinates off two stainless steel rods permanently set into the substratum.

182 individual _I._ _cordata_ thalli were tagged in groups throughout the year (6 February 1974, 5 March, 25-26 April, 24 May, 19 June, 12 July, 16 October, 30 November, 25-27 January 1975, 23-24 February, 29 March, 26 April, 26 May). When initially tagged, all thalli were non-reproductive and less than 6 cm in length. The number of thalli tagged on each date was variable depending on surf zone conditions prevailing.

Thallus growth was measured in surface area (cm^2), thickness ($cm \times 10^{-3}$), length (cm), and width (cm). During the low tide recording periods, each tagged thallus was photographed lying on a white grid (mesh = 5 cm^2) and thickness was measured using a vernier caliper. Initially, thickness was measured at the thallus tip, mid, and base. After three months, it was found that tip measurements were constant and base measurements were highly variable. These were discontinued and three replicate mid measurements made. For surface area, length, and width measurements, the photographs were developed and the negatives projected on a glass grid (mesh = 5 cm^2) mounted in a wooden frame. The grid in the photograph was aligned with the glass grid using a highly flexible Leitz slide projector; the thallus outline was then traced. The surface area of each thallus was measured from the tracings using a Keuffel and Esser Compensating Polar Planimeter. The greatest thallus length and width were also measured from the tracings. In addition, the photographs and tracings provide a permanent record of morphological development of thalli in a natural population. Growth rates (G_t) of individual thalli were calculated as follows.

$$G_t = \frac{A_b - A_a}{t_b - t_a}$$

Where: G_t = Growth rate of individual thalli (cm^2/day)

A(a,b) = Surface areas (cm)

t(a,b) = times (days)

Maturation and senescence times were recorded as the number of days from initial tagging of the non-reproductive thallus, to 1) the first date reproductive sori were observed on the thallus surface and 2) the first date marking the onset of continuous thallus loss (cm^2).

Statistical analyses employing linear regressions, Friedman two-way analysis of variance, Kendall's Tau, T-test, and F-ratio are described in Sokal and Rohlf (1969) and Tate and Clelland (1959).

RESULTS

Measurements of vegetative regrowth from perennating basal crusts and growth dynamics of individual, erect thalli indicate that the reproductive adaptation of perennation and vegetative growth may play the prime role in the distribution and maintenence of *Iridaea cordata* populations in the temperate regime studied.

Vegetative Population Growth

Experimental plots of *I. cordata*, denuded to the perennating crusts, produced biomass levels by summer (9 mo) and autumn (12 mo) that were not significantly different from those of control plots from the untreated natural population (Fig. 13, App. 10). Little biomass accumulated in experimental plots during the winter months

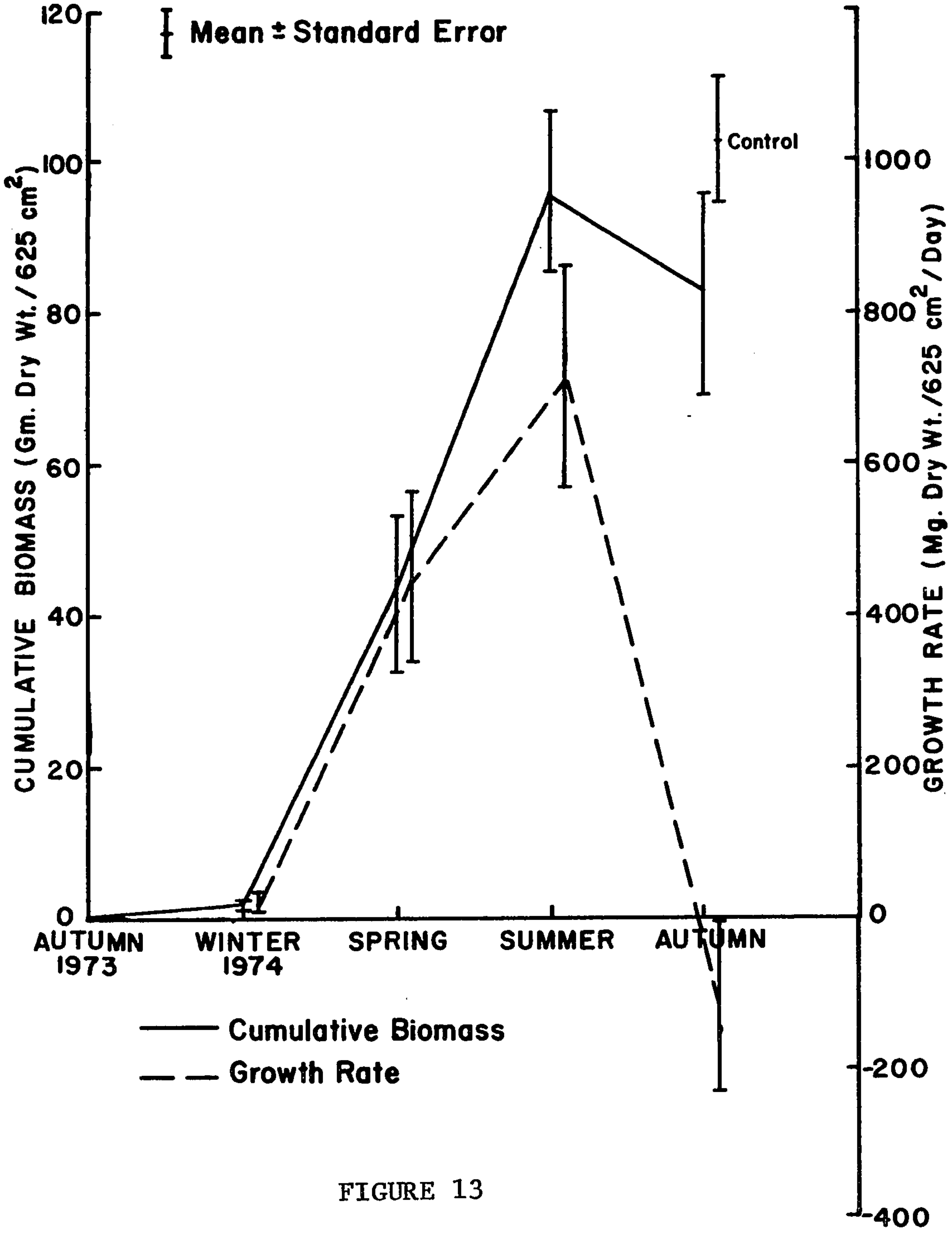

Mean ± Standard Error
Control
CUMULATIVE BIOMASS (Gm. Dry Wt./625 cm^2)
GROWTH RATE (Mg. Dry Wt./625 cm^2/Day)
120
100
80
60
40
20
0
1000
800
600
400
200
0
-200
-400
AUTUMN 1973
WINTER 1974
SPRING
SUMMER
AUTUMN
Cumulative Biomass
Growth Rate

FIGURE 13

($\overline{X}$ = 1.8±0.7 gm dry wt./625 cm^2). A major increase in biomass level followed in spring ($\overline{X}$ = 42.9±10.2 gm dry wt./625 cm^2) and reached a peak at the end of summer ($\overline{X}$ = 95.9 ±10.6 gm dry wt./625 cm^2). There was no significant change ($P = .10$) in biomass between summer and autumn, though overall biomass tended to decrease in autumn.

Correspondingly, the growth rates based on these data (Fig. 13, App. 10) indicate that a significant increase in growth occurred during spring ($\overline{X}$ = 452±112 mg dry wt./625 cm^2/day) from the low winter rates of $\overline{X}$ = 20±8 mg dry wt./625 cm^2/day. There was no significant difference ($p = .10$) between the spring and summer rates though overall summer rates tended to be higher. Biomass decreased between summer and autumn resulting in a highly variable negative rate, or more appropriately, a senescence rate of -116±115 mg dry wt./625 cm^2/day. Despite the high variability of this senescence rate, it was considerably lower than ($.01<p>.005$) the peak summer rate ($\overline{X}$ = 717±143 mg dry wt./625 cm^2/day).

Comparisons were made between discrete seasonal growth (3 mo increments) from perennating crusts (App. 11) and growth rates based on cumulative biomass (Fig. 14). The analyses indicate that there was no significant difference ($p>.10$) between cumulative and discrete *I. cordata* growth during spring. This suggests that nearly all growth of erect thalli from perennating crusts that obtained

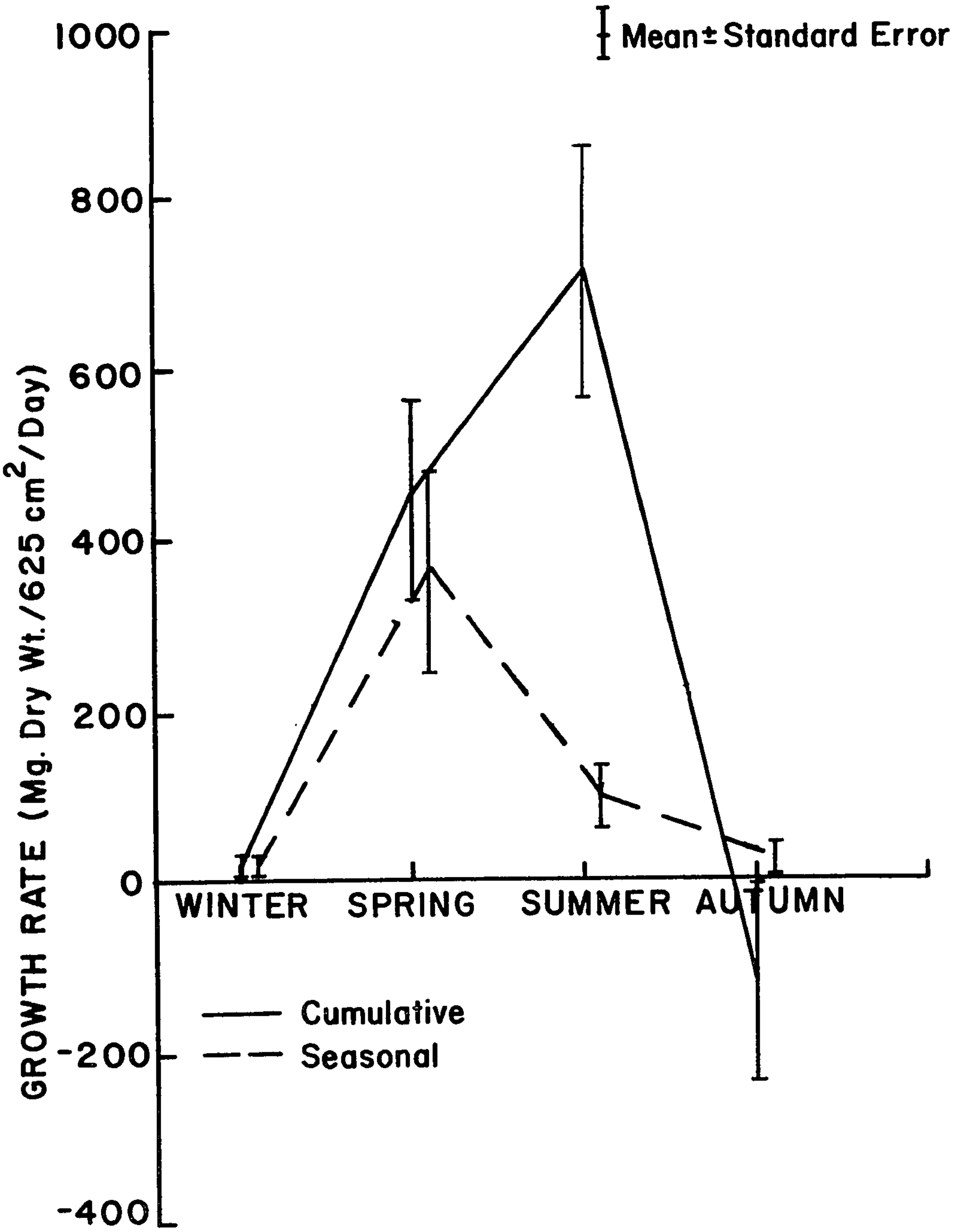

Mean ± Standard Error
GROWTH RATE (Mg. Dry Wt./625 cm^2/Day)
1000
800
600
400
200
0
-200
-400
WINTER
SPRING
SUMMER
AUTUMN
Cumulative
Seasonal

FIGURE 14

between autumn (November, 1973) and spring (May, 1974) occurred during the spring months. This was not the case in summer; discrete growth rate of significantly lower ($\overline{X}$ = 95±35 mg dry wt./625 cm^2/day) than the cumulative rate ($\overline{X}$ = 717±143 mg dry wt./625 cm^2/day). The two rates were similar in autumn. The cumulative rate for autumn is veritably a senescence rate therefore, the mean discrete growth rate of 21±19 mg dry wt./625 cm^2/day is a more appropriate estimate for this season.

To evaluate _I. cordata_ growth as the turnover of organic material, R_E (the doubling rate/day or relative growth rate) and t/R_{Et} (the doubling time in days) were calculated from discrete seasonal biomass values because all samples represent similar developmental stages. The data in Table 2 show that doubling rate increased between winter and spring and correspondingly, the doubling time decreased (23.8±2.7 days to 11.2±.51 days). Values were similar among spring, summer, and autumn.

TABLE 2

			(1)	(2)
Date	R_E/day (1)	t/R_{Et} (2)	Probability	
Winter 1974	.044±.005	23.8±2.7	$p<.001^*$	$p=.05^*$
Spring	.090±.004	11.2±0.5	$p>.10$	$p>.20$
Summer	.075±.012	14.9±3.3	$p>.05$	$p>.20$
Autumn	.027±.014	64.8±28.8		
Spring vs Autumn			$p<.001^*$	$p>.20$

* = A significant difference between seasons.

Values in autumn tended to be lower and doubling time longer, but variability was high. Seasonal R_E and t/R_{Et} were compared using a T-test. Significant differences are indicated in Table 2 by an asterisk. When spring values were compared to those of autumn, the difference in R_E was evident, but t/R_{Et} was so variable in autumn that differences were not significant.

Vegetative Growth and Population Structure

In addition to measuring the specific contributions of vegetative growth in a natural population, it was important to determine whether there was a change in population structure when experimental plots within the population were cleared, leaving only the associated species and *I. cordata* perennial crusts. The results (Fig. 15) demonstrate that the biomass values of the non-reproductive, tetrasporangial, and carposporic life history stages from the original harvest (autumn, 1973) (App. 12) were not significantly different ($P>.10$, $p>.10$, $p>.20$) from those measured in the experimental plots twelve months later (autumn, 1974) (App. 13).

Moreover, there were no significant differences between the biomass values of tetrasporangial, cystocarpic, and male life history stages from the autumn, 1974 harvest and the corresponding biomass values from the autumn, 1974 control samples ($p>.10$, $p>.10$, $p>.20$).

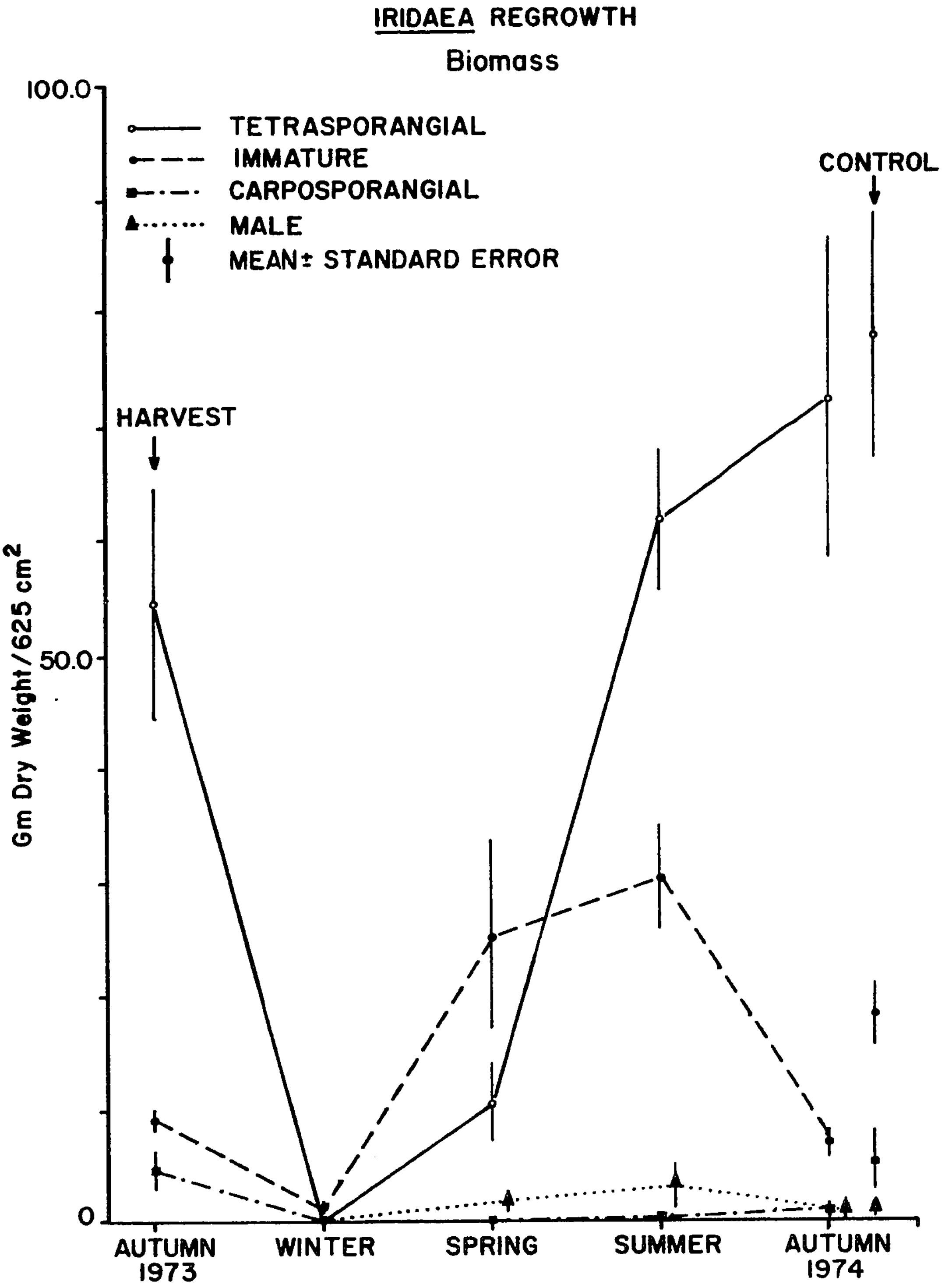

IRIDAEA REGROWTH
Biomass
100.0
50.0
0
Gm Dry Weight/625 cm²
TETRASPORANGIAL
IMMATURE
CARPOSPORANGIAL
MALE
MEAN± STANDARD ERROR
HARVEST
CONTROL
AUTUMN 1973
WINTER
SPRING
SUMMER
AUTUMN 1974

FIGURE 15

However, the cumulative 12 month biomass of the non-reproductive stage in the experimental plots ($\overline{X}$ = 7.3±1.3 gm dry wt./625 cm^2) was significantly less than that from the control samples ($\overline{X}$ = 18.4±3.1 gm dry wt./625 cm^2). This difference may be due to annual variation in the natural population, or the clearing treatment may have altered juvenile thallus initiation from the perennial crusts at some time during the year.

Growth of Individual Thalli

Thus far, results results report the contribution of *I. cordata* vegetative growth from perennating crusts in terms of the population as a whole (all developmental stages).

To take one important step further, into the genecological realm, the infraspecific variability in growth dynamics of individual *I. cordata* thalli was studied.

A contribution circumscribing the growth dynamics of individuals which make up a population is only as accurate and useful as the method employed. Therefore, great care and effort were taken in the design, execution, and comparison of various methods applicable for measuring thalli of *I. cordata* and other algal species of similar morphological stature.

The tagging method developed provided a permanent label for the positive identification of individual thalli, and was therefore the key to the success of all *in situ* measurements of individuals.

Four measurements were made on the 182 thalli tagged (App. 14). Table 3 rates these measurement methods in terms of nine criteria: 1) can be carried out *in situ*, 2) rapidity, 3) replicability, 4) provides a permanent record, 5) provides morphological data, 6) provides dimensional data, 7) provides a measure of the total thallus, 8) is linear, 9) amount of post-field operative time required.

Surface area (cm^2) provided the best quantitative assessment of thallus size and fulfills all criteria, but requires the greatest amount of post-operative time. This measurement is ideally suited to the morphology of the *I. cordata* thallus. However, experimental error is introduced in two ways: 1) ruffles, wrinkles and holes in the thallus, and 2) parallax in the photograph due to camera positioning. Care must be exercised to keep these error sources to a minimum. The use of a LICOR Area Meter is recommended for this measurement, though a permanent record is not provided. Since this method gives the most information about each individual thallus, surface area results were used in the subsequent comparative data analyses. The length X width (cm^2) calculation gives a good approximation of thallus size and is recommended for a less time-consuming measurement method (Fig. 16)

The regressions of length and width on surface area (Figs. 17-18) show that both relationships are slightly

TABLE 3

Measurement Methods

	in situ	Rapidity	Replica-bility	Permanent Record	Morpho-logical Data	Dimensional Data	Measure of Total Thallus	Linearity	Post-opera-tive Time Required
SURFACE AREA (cm^2)	X	G	G	X	E	E	E	E	High
LENGTH (cm)	X	G	G	-	-	F	F	G	None
WIDTH (cm)	X	G	G	-	-	F	P	P	None
THICKNESS ($cm \times 10^{-3}$)	X	F	F	-	-	P	P	F	Low
LENGTH x WIDTH (cm^2)	X	G	G	-	-	E	G	E	Fair

Symbols: X = satisfies the criterion
- = does not satisfy the criterion
E = Excellent
G = Good
F = Fair
P = Poor

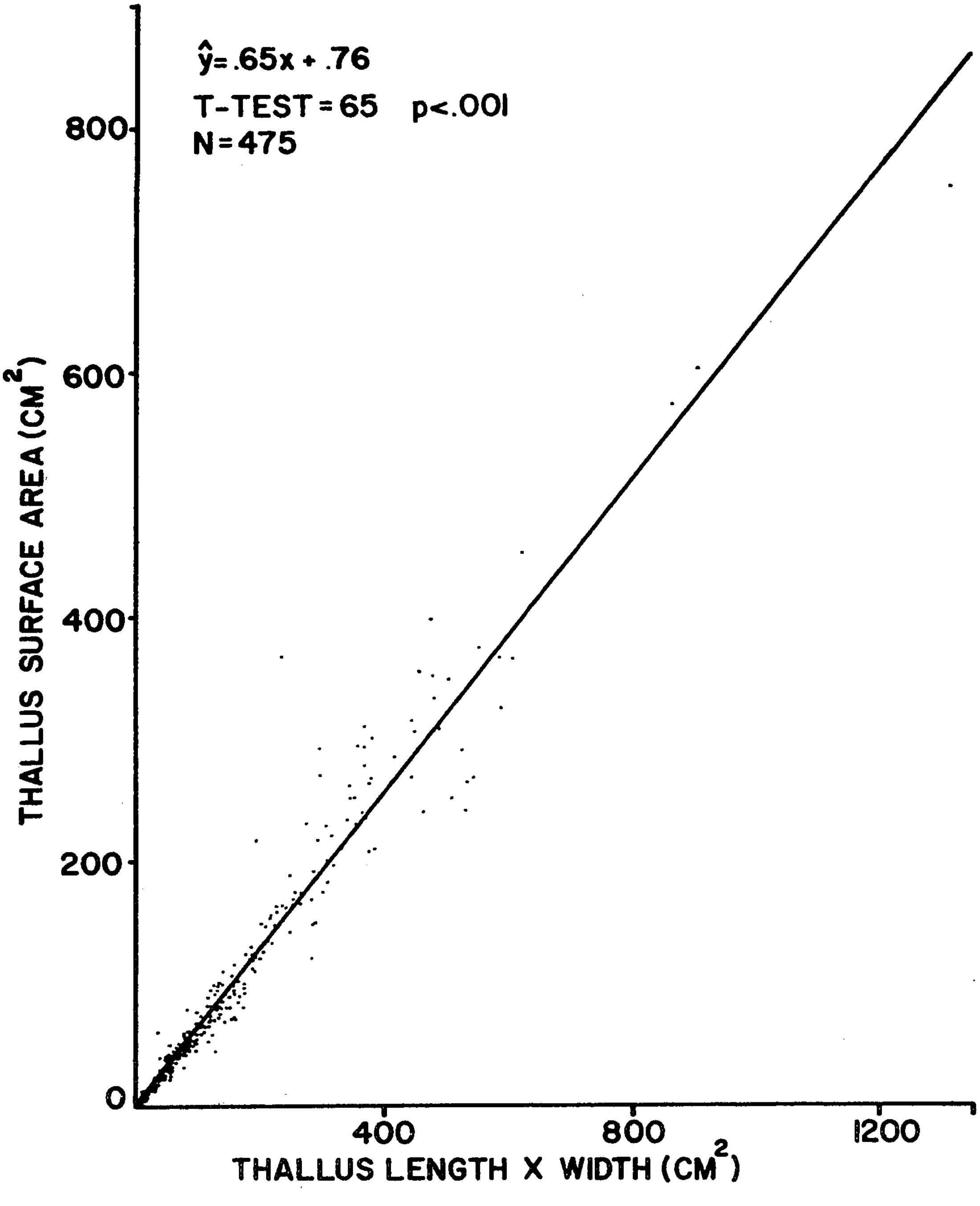

ŷ=.65x+.76
T-TEST=65 p<.001
N=475
THALLUS SURFACE AREA (CM²)
0
200
400
600
800
400
800
1200
THALLUS LENGTH X WIDTH (CM²)

FIGURE 16

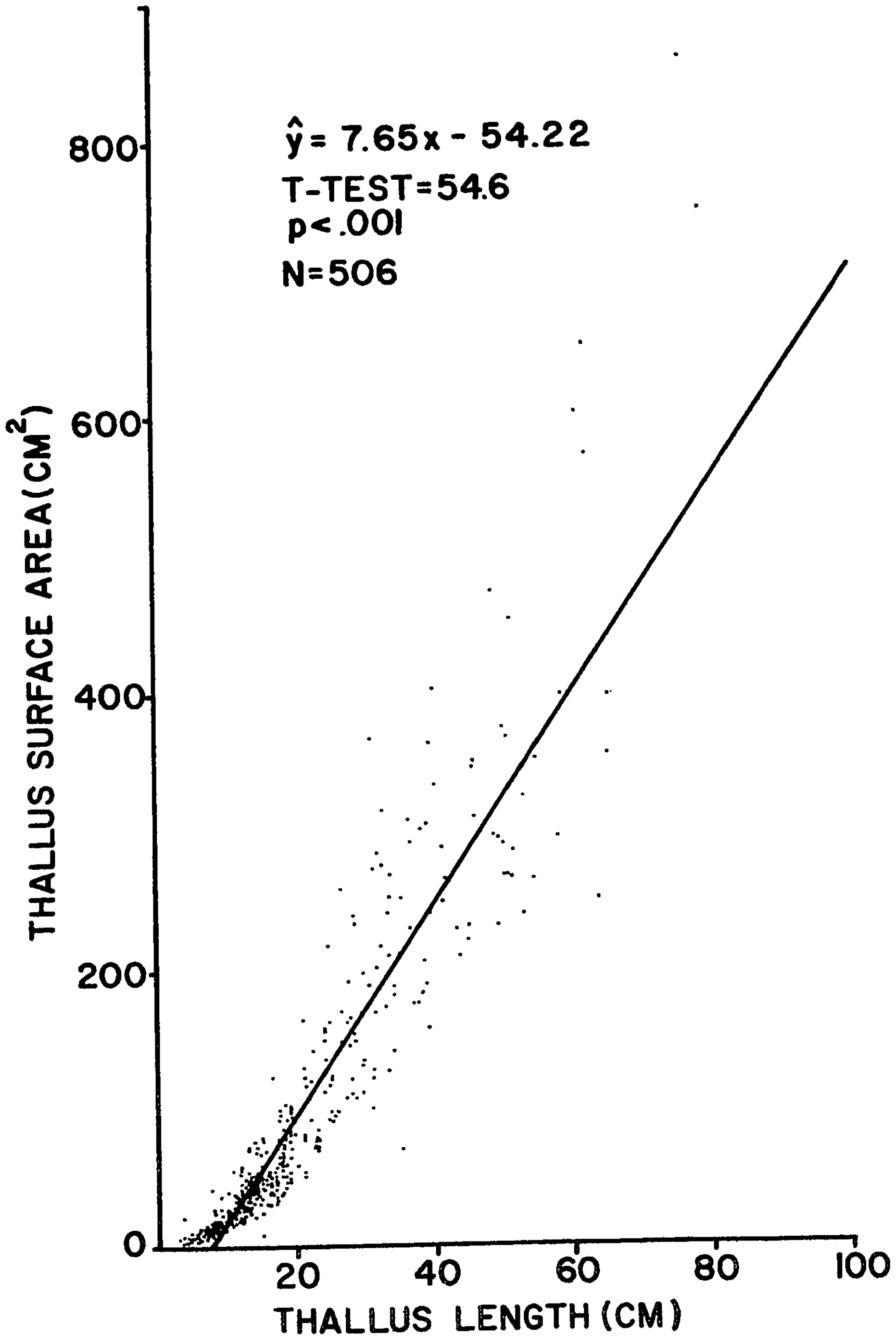

$\hat{y}$= 7.65x - 54.22
T-TEST=54.6
p<.001
N=506
THALLUS SURFACE AREA (CM^2)
0
200
400
600
800
20
40
60
80
100
THALLUS LENGTH (CM)

FIGURE 17

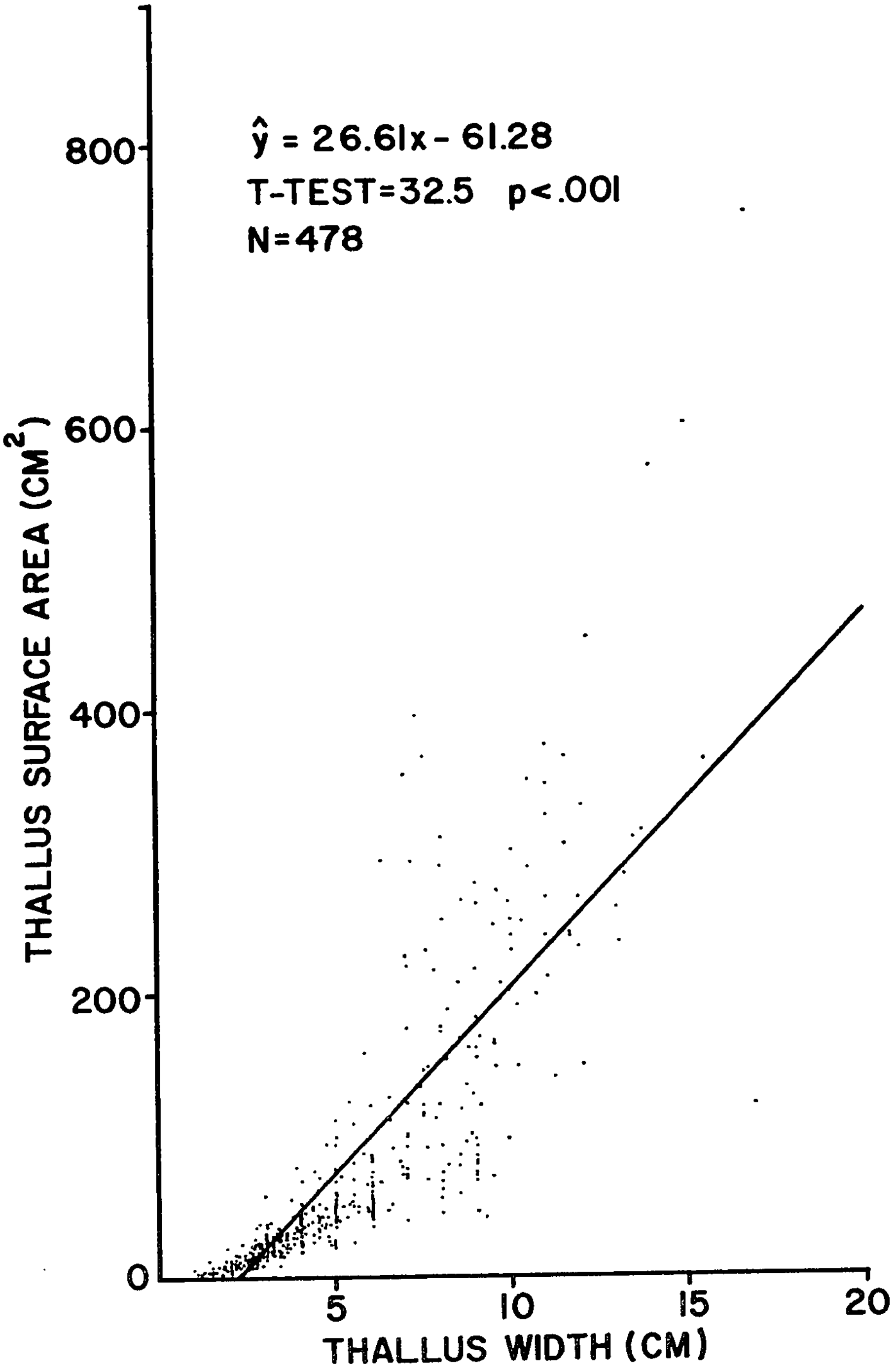

$\hat{y} = 26.61x - 61.28$
T-TEST=32.5 p<.001
N=478
THALLUS SURFACE AREA (CM^2)
800
600
400
200
0
5
10
15
20
THALLUS WIDTH (CM)

FIGURE 18

curvilinear and probably are more appropriately represented as a logarithmic function. The length measurements give a good approximation of size only for thalli 10 cm or longer and width measurements only for thalli 3 cm or broader. Thickness is related to surface area in a linear fashion (Fig. 19), but is complicated due to morphological changes in the thallus due to development and life history stage.

The infraspecific, cumulative increase in surface area (App. 14) and corresponding growth rates of individual thalli within any one tagging group were generally similar (App. 15). However, variability among successively tagged groups (Fig. 20) was high suggesting that thallus development exhibited modifications with time. Two basic possibilities for this variability were considered; age(2) and time of the year tagged.

When age (the number of days from tagging) was compared to corresponding mean growth rate of a group, there was no correlation (Fig. 21). Therefore, thalli ranging in age between 25 and 300 days from initial tagging, can have similar growth rates.

However, when mean growth rate of a group was compared to the corresponding time of the year that the individuals were tagged, there was a highly significant correlation ($.001>p>.01$) suggesting that growth rate is dependent upon time (Fig. 22).

(2) Age includes the assumption that all small thalli tagged were reasonably similar in age.

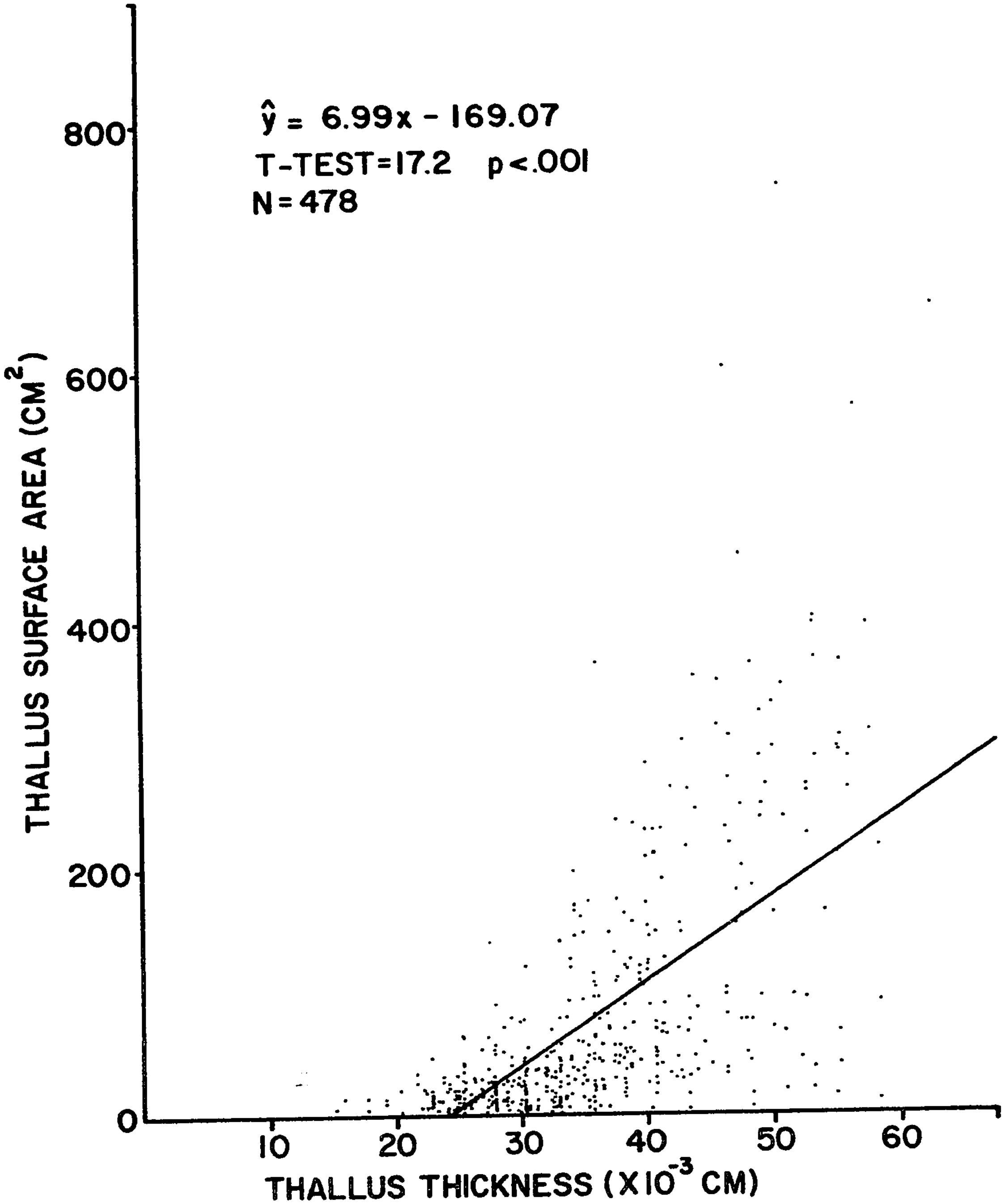

$\hat{y} = 6.99x - 169.07$
T-TEST=17.2 p<.001
N=478
THALLUS SURFACE AREA (CM^2)
0
200
400
600
800
10
20
30
40
50
60
THALLUS THICKNESS (X10^{-3} CM)

FIGURE 19

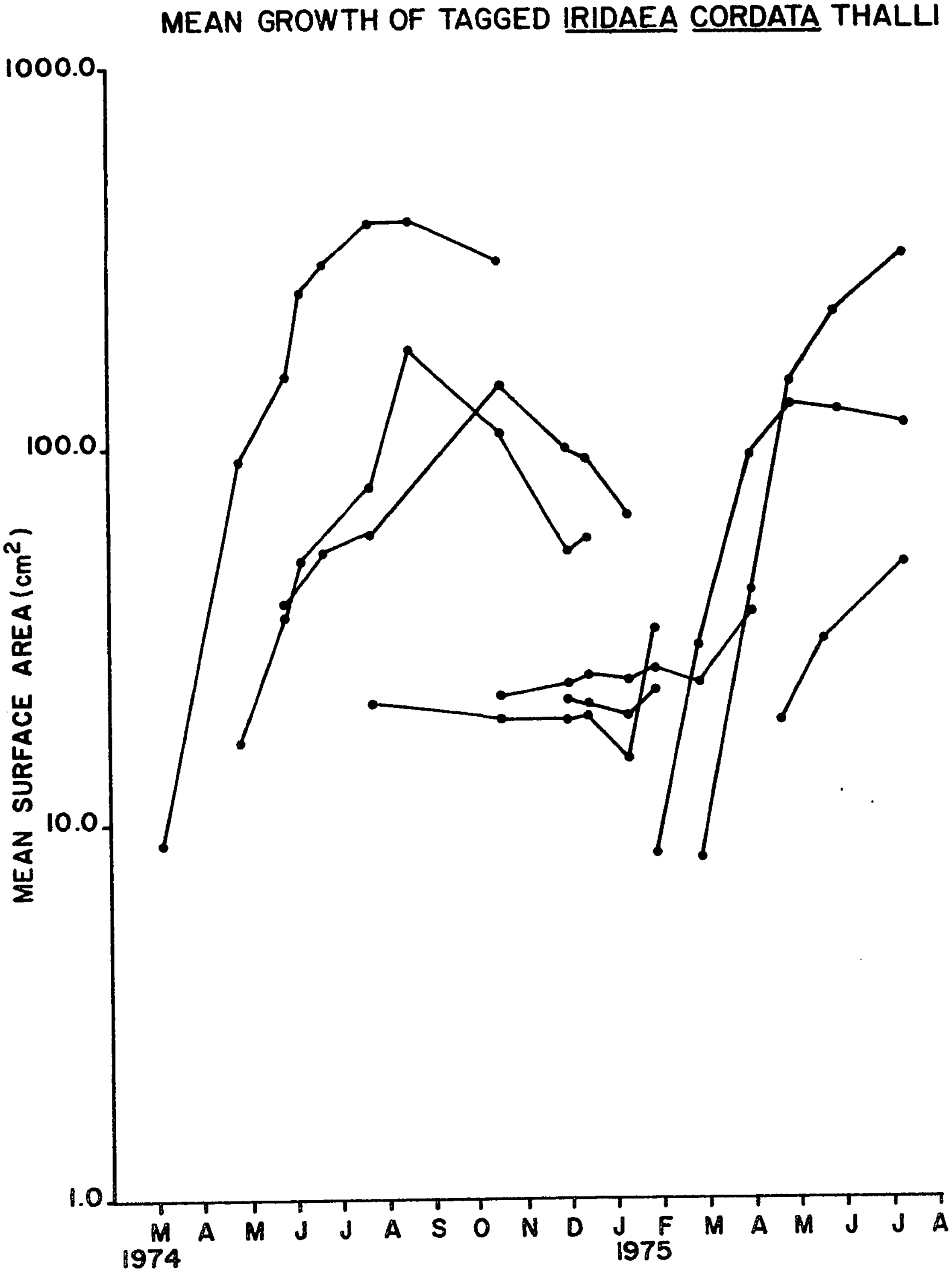

MEAN GROWTH OF TAGGED IRIDAEA CORDATA THALLI
1000.0
100.0
10.0
1.0
MEAN SURFACE AREA (cm2)
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1974
1975

FIGURE 20

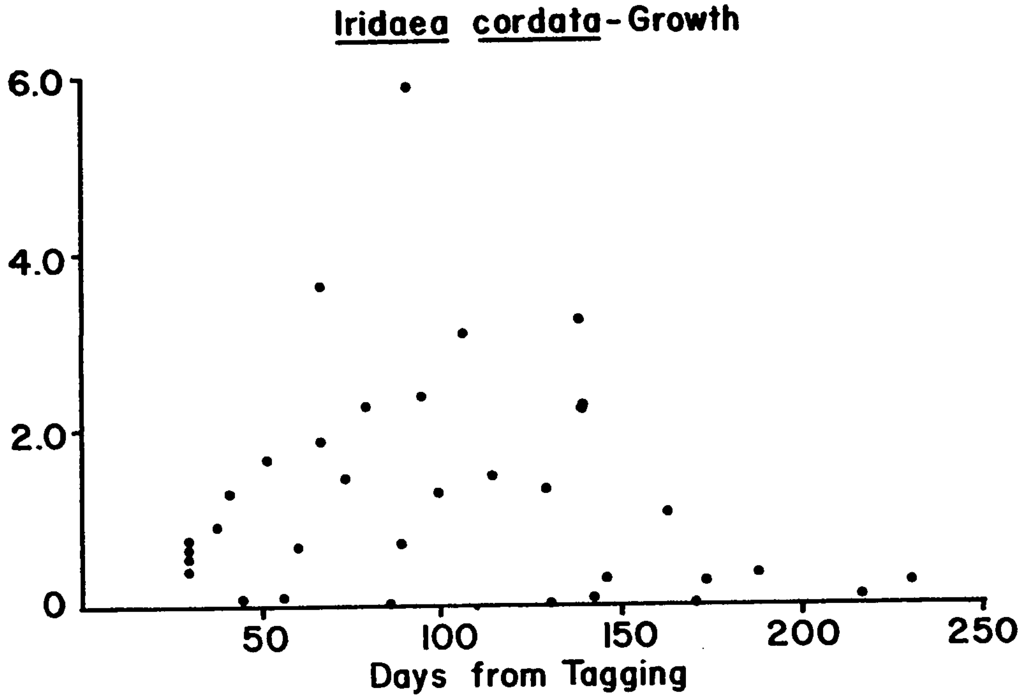


FIGURE 21

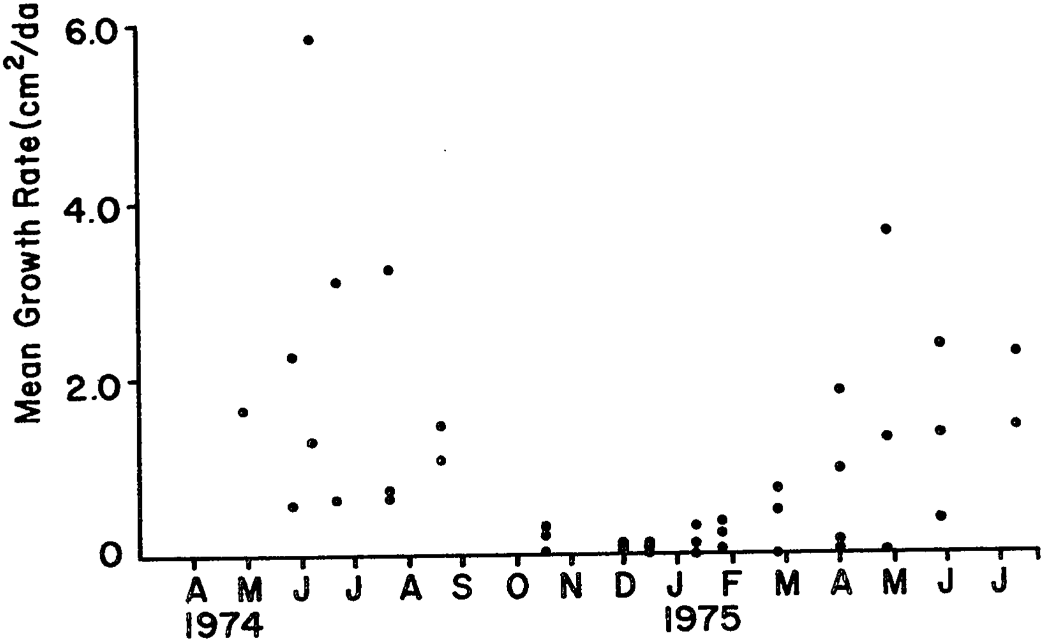


FIGURE 22

To determine what time(s) of the year the different growth potentials were exhibited, the first four consecutive mean growth rates of groups of thalli tagged in: March, April, May, July, October, 1974, and January and February, 1975 were compared using the Friedman two-way analysis of variance (Fig. 23, Table 4). The tagged groups were measured a variable number of times throughout the year depending on thallus longevity, but all were measured at least four times. Therefore, only the first four dates were used, fulfilling the equal sample size requirement of the statistical analysis employed. In addition, measurements past the first four consecutive ones were often senescence rates and were not pertinent to the question regarding growth. The differences among growth rates of the groups of tagged thalli on the above dates were highly significant (p>.001) and are ranked in the following order according to the time of descending growth potential:

MARCH > FEBRUARY > JANUARY > APRIL>> MAY > OCTOBER > JULY

Continuously underlined months were closely ranked and circumscribe thalli of similar potential. The results of this analysis suggests that juvenile thalli initiated from late winter to early spring will attain high growth potentials, while those initiated from summer to winter will have less or very low growth potentials.

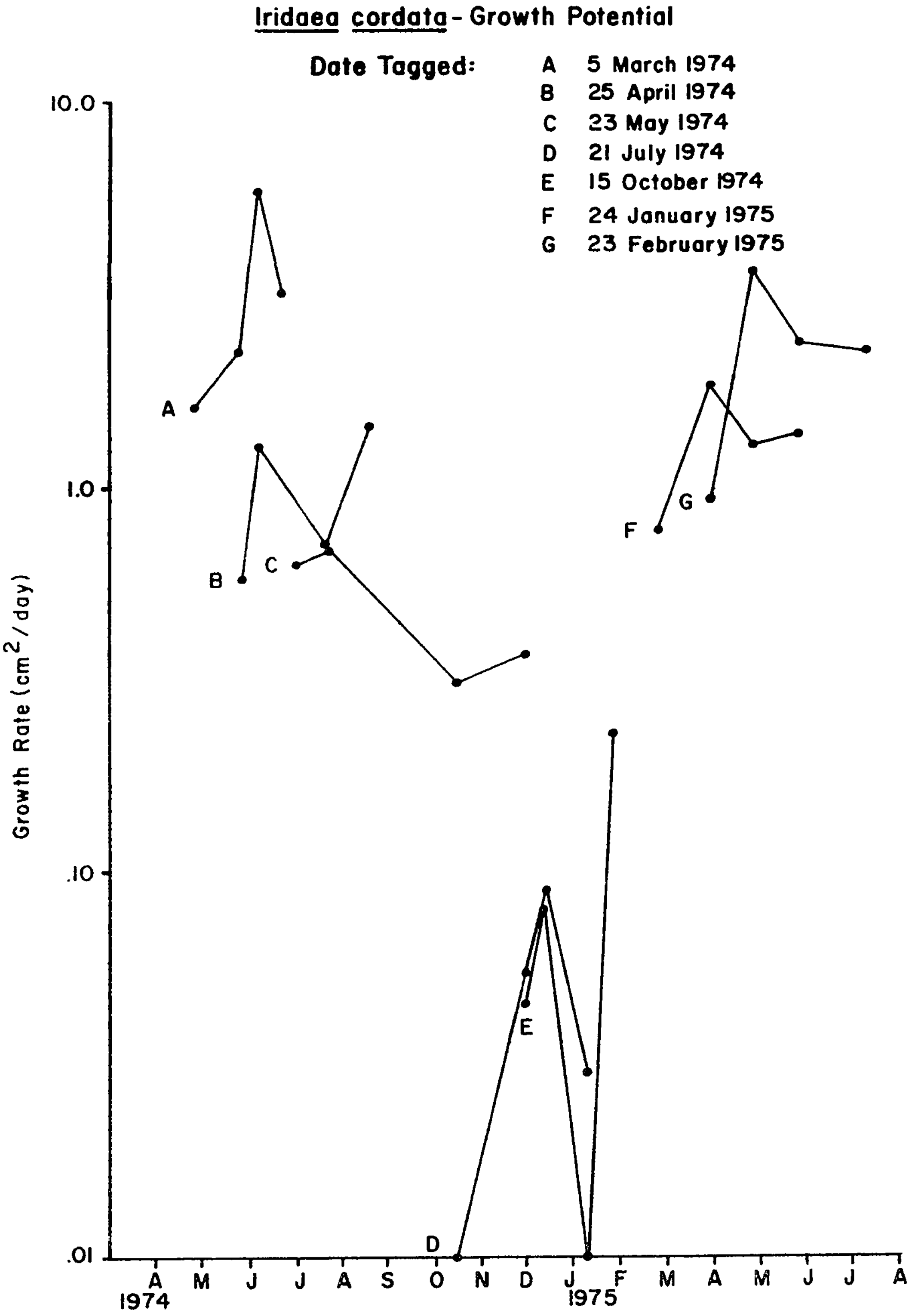

Iridaea cordata - Growth Potential
Date Tagged:
A 5 March 1974
B 25 April 1974
C 23 May 1974
D 21 July 1974
E 15 October 1974
F 24 January 1975
G 23 February 1975
10.0
1.0
.10
.01
Growth Rate (cm2 / day)
A
B
C
D
E
F
G
A M J J A S O N D J F M A M J J A
1974
1975

FIGURE 23

TABLE 4

Null hypothesis: There is no difference *in *Iridaea cordata* growth potential during the year.

Test: Friedman Two-way Analysis of Variance

	A	R	B	R	C	R	D	R	E	R	F		G		ΣR
Mean Growth Rate (cm^2/day)	1.64	7	.58	3	.63	4	.001	1	.046	2	.77	5	.93	6	28
	2.23	6	1.29	4	.69	3	.055	1	.08	2	1.85	5	3.61	7	28
	5.85	7	.71	4	.31	3	.09	2	-.02	1	1.28	5	2.37	6	28
	3.12	7	1.44	5	.37	1	.03	2	.23	3	1.36	4	2.24	6	28
ΣR		27		16		11		6		8		19		25	112

$\text{chi}^2_{4-1} = 80.91$ Probability < .001

*Null Hypothesis Not Accepted

A > G > F > B > C > E > D

Date Tagged:
A - 5 March 1974
B - 25, 26 April 1974
C - 24 May 1974
D - 21 July 1974
E - 16 October 1974
F - 25, 27 January 1975
G - 23, 24 February 1975

R = Rank

In addition, the mortality data provided by the sequential disappearance of tagged thalli throughout the year (Fig. 24, App. 16) indicate that the vigorous thalli tagged from late winter to early summer have life cycles that terminate in approximately 12 months. This suggests that the erect thalli of this species, in the population studied, are in general spring annuals. However, those thalli tagged during autumn and early winter exhibit sharp mortality curves and are quickly lost from the population.

Maturation

Reproductive maturation, the morphological preparation for sexual reproduction, is considered in terms of thallus ontogeny, longevity, and in light of perennation.

The dry biomass of reproductively mature *I. cordata* thalli produced from perennating crusts was compared to total dry biomass produced in experimental plots. These results give an indication of the percentage of the population that becomes mature throughout the year, how long it takes for this species to become mature, and what time of the year major maturation occurs. The simple maturation index $\frac{R}{T}$: T designed (Fig. 25, App. 17) shows that no thalli became reproductively mature during the first 3 months of growth (November to February-Winter). When plants were allowed to grow for six consecutive months (November to May-Winter to Spring), 31±5% of the total

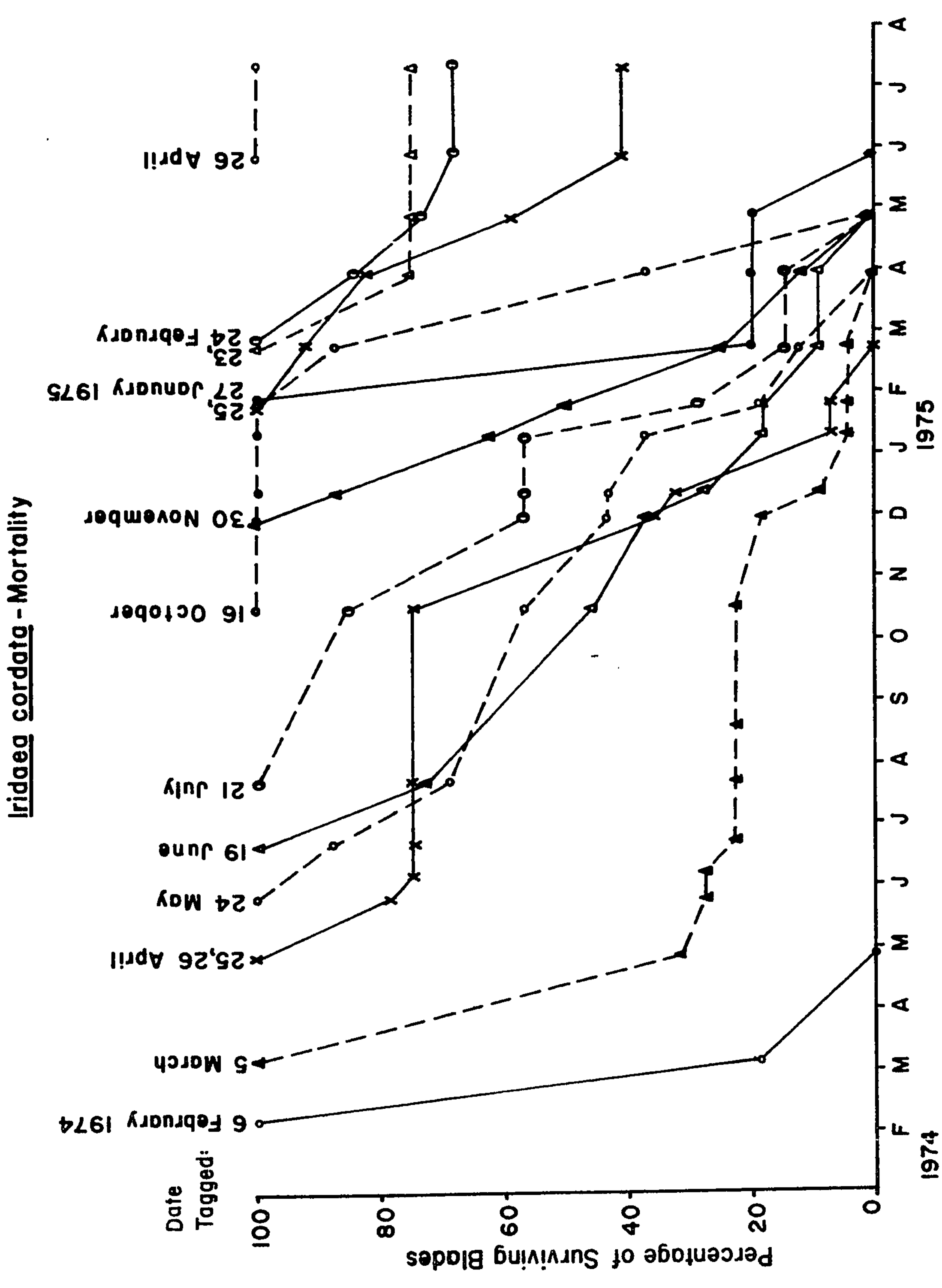

Iridaea cordata - Mortality
Date Tagged:
6 February 1974
5 March
25,26 April
24 May
19 June
21 July
16 October
30 November
25, 27 January 1975
23, 24 February
26 April
Percentage of Surviving Blades
100
80
60
40
20
0
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1974
1975

FIGURE 24

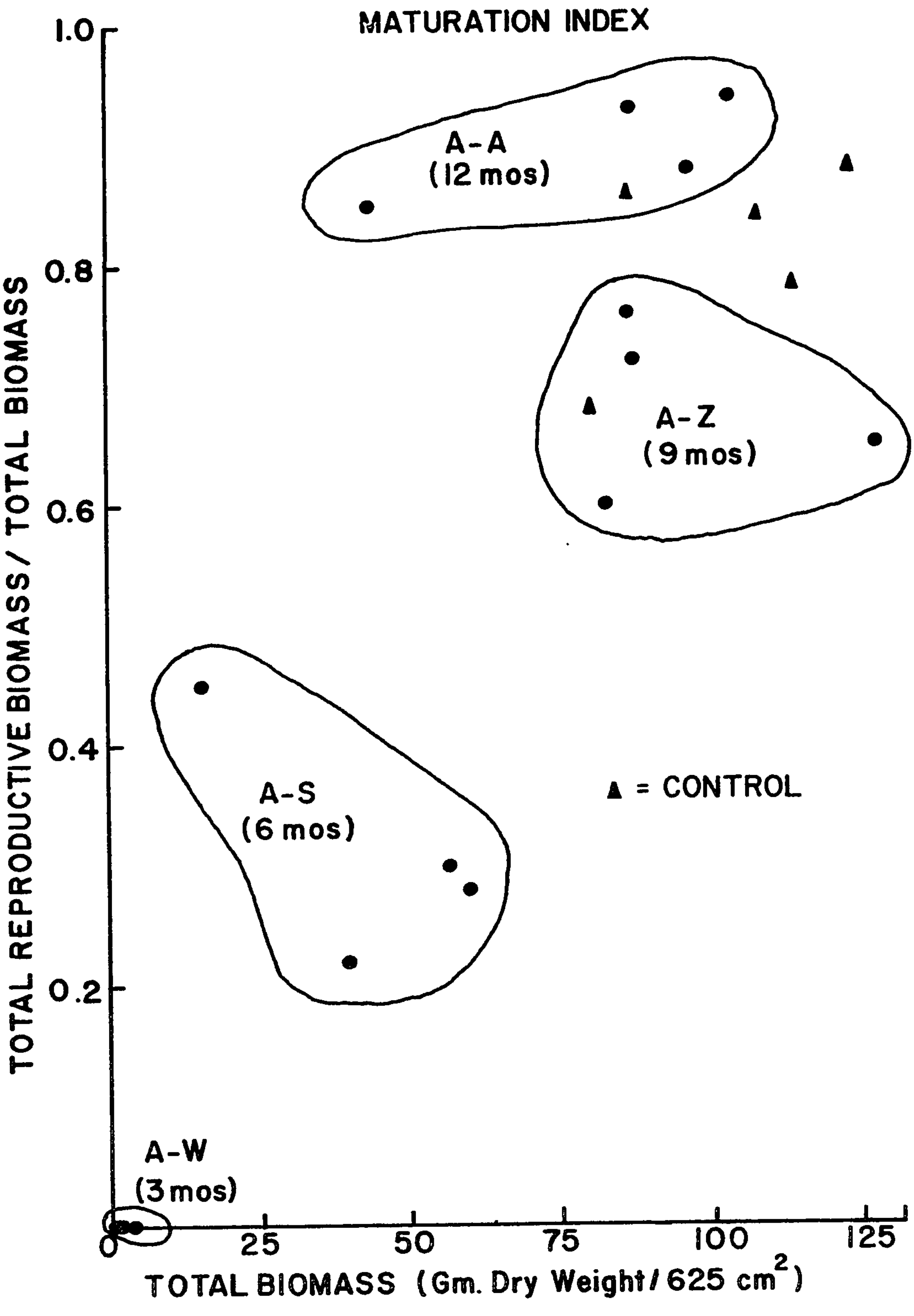

MATURATION INDEX
1.0
0.8
0.6
0.4
0.2
TOTAL REPRODUCTIVE BIOMASS / TOTAL BIOMASS
A-A
(12 mos)
A-Z
(9 mos)
A-S
(6 mos)
A-W
(3 mos)
▲ = CONTROL
0
25
50
75
100
125
TOTAL BIOMASS (Gm. Dry Weight / 625 cm²)

FIGURE 25

biomass was composed of reproductive thalli. Nine months from the onset of the experiment (November to July - Winter to Summer), the reproductive biomass was 68±4% and this level was just below levels of the twelve month natural population control ($.02<p<.05$) which is indicated in Fig. 25 by triangles. At twelve months, 90±2% of the population was reproductively mature and was similar to control levels in the natural population ($.05>p<.10$).

However, when plots were denuded at the beginning and end of each season (discrete seasonal biomass), a small component of the population became mature during all seasons but winter (Table 5; App. 17B).

TABLE 5

SEASON	$\frac{R}{T}:T$ (3)
Winter	0
Spring	.20
Summer	.08
Autumn	.10

As shown previously, the majority of the reproductively mature component of both the natural and treated populations was tetrasporangial. The gametangial stages contributed only a small component to the total reproductive biomass.

(3) R = dry biomass/ 625 cm^2 of reproductively mature thalli(tetrasporangial+cystocarpic+male). T = total dry biomass/625 cm^2. The index ranges from 0 to 1.0.

Similar data gathered from tagged thalli in the natural population give not only an indication of infra-specific variability, but allowed comparisons to be made among: time of thallus maturation, thallus size, and time of the year tagged (App. 18).

The data show that reproductive maturation occurs throughout the year. Further, the results indicate (Fig. 26) that if thalli matured during winter they tended to be small, while those maturing during other seasons were highly variable in size. The small winter thalli reflected the diminutive growth rates for that season. Fig. 27 indicates that if thalli were tagged in autumn-winter, they matured rapidly. Though it cannot be absolutely assumed that all small thalli were juveniles.

Further, the interactions between growth and maturation appear to be influenced more by the time of year than the onset of reproductive maturation itself (Fig. 28). Fifty-nine percent of all thalli that matured, continued to grow after maturation. Those maturing between April and August exhibited variable, but generally higher growth rates than those maturing between October and March.

Senescence

Senescence is defined as the onset of continuous loss in population biomass or thallus surface area.

Population biomass in experimental plots declined

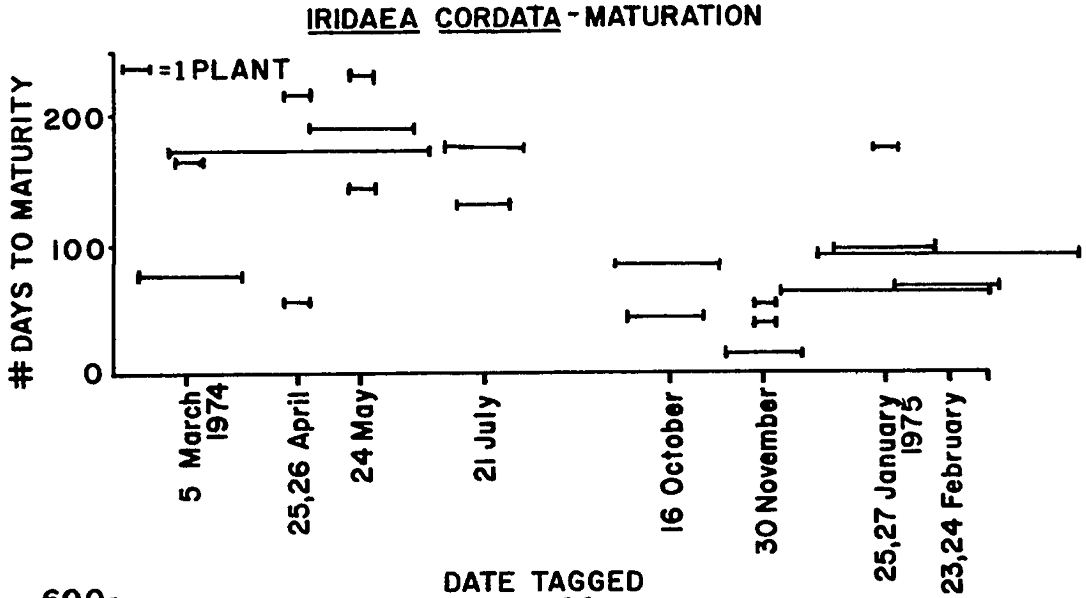


FIGURE 26

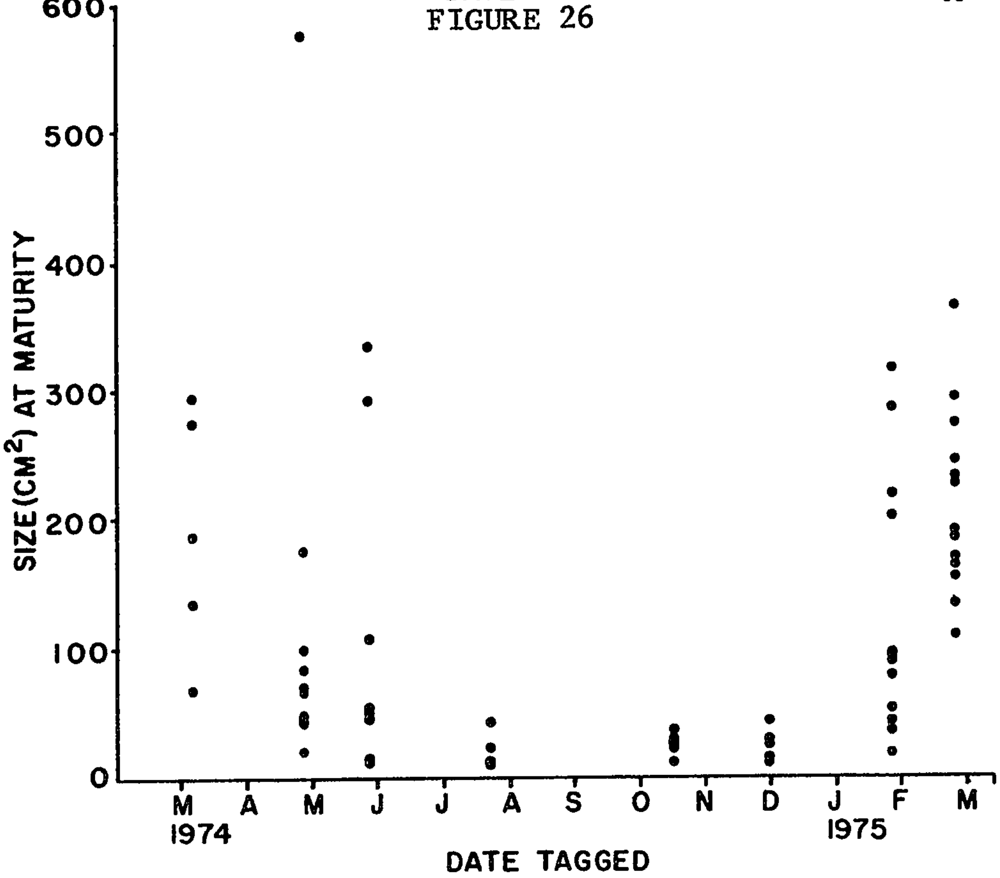


FIGURE 27

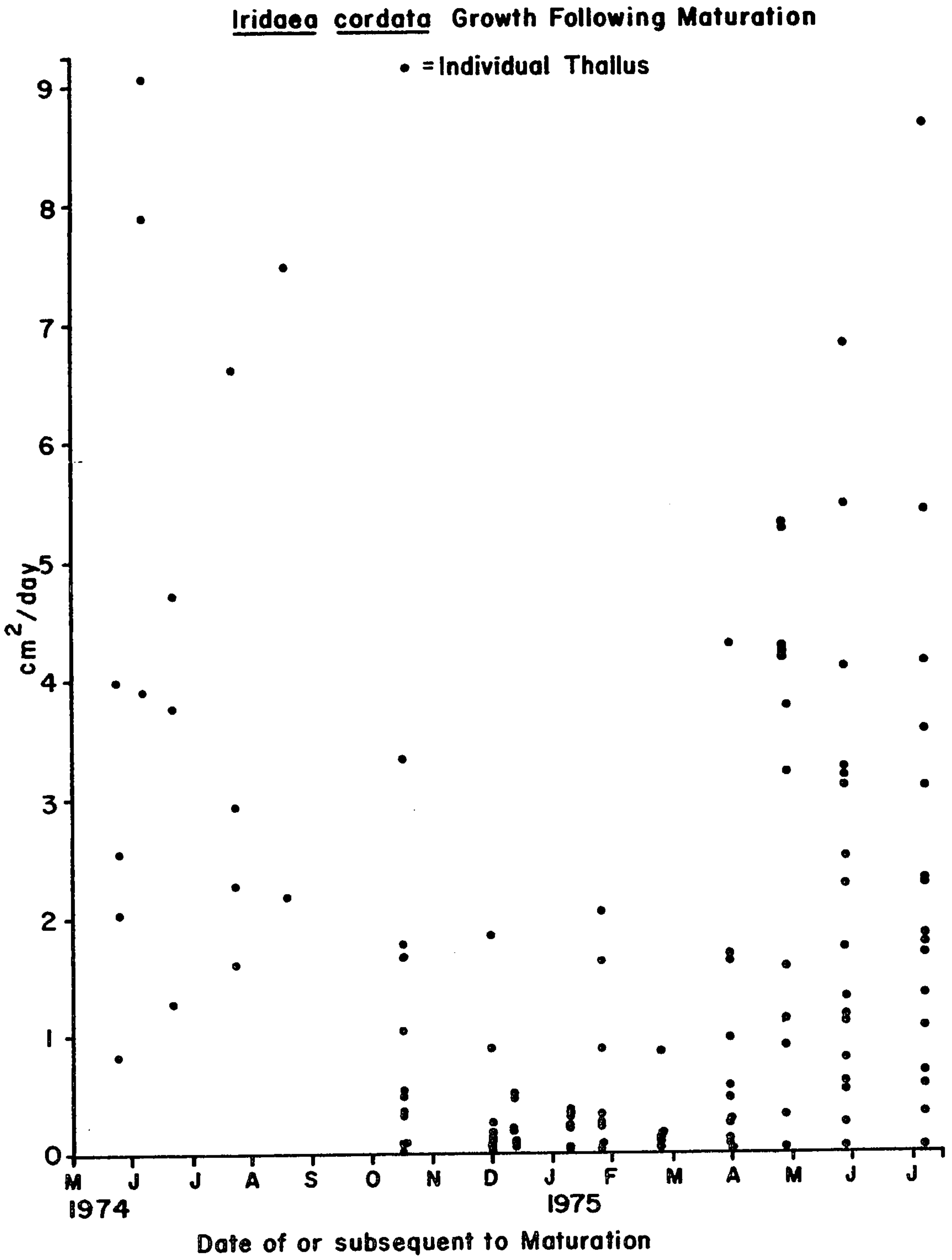

Iridaea cordata Growth Following Maturation
● = Individual Thallus
cm²/day
0
1
2
3
4
5
6
7
8
9
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1974
1975
Date of or subsequent to Maturation

FIGURE 28

after reaching a peak in July, 1974 at a highly variable senescence rate of -116±115 gm dry wt./625 cm^2/day (Fig. 13).

The data show that individual tagged thalli senesce throughout the year (App. 19). Those thalli that were tagged during spring, took a longer time to senesce than those tagged during other times of the year (Fig. 29). Additionally, thalli tagged during autumn-winter were small at senescence (<80 cm^2) suggesting that their whole life cycle was contained within a relatively short period of low growth potential conditions. Thalli tagged during spring ranged the total spectrum in size indicating that they had previously realized varying growth potentials (Fig. 30).

Iridaea Ontogeny and Environmental Factors

The ontogenetic patterns of this species are expressions of the genotypic constitution of the population and the complex of environmental factors. This study attempted to unravel this highly complex interaction by considering, separately, the influences of solar radiation, daylength, surface seawater temperature, and nutrients on aspects of *I. cordata* ontogeny (biomass and growth).

Solar radiation ($\overline{X}$ = ly/day), daylength (hrs), and temperature were compared to 1) cumulative biomass (gm dry wt./625 cm^2) and 2) discrete seasonal growth rates (mg dry wt./625 cm^2/day) derived from experimental plots

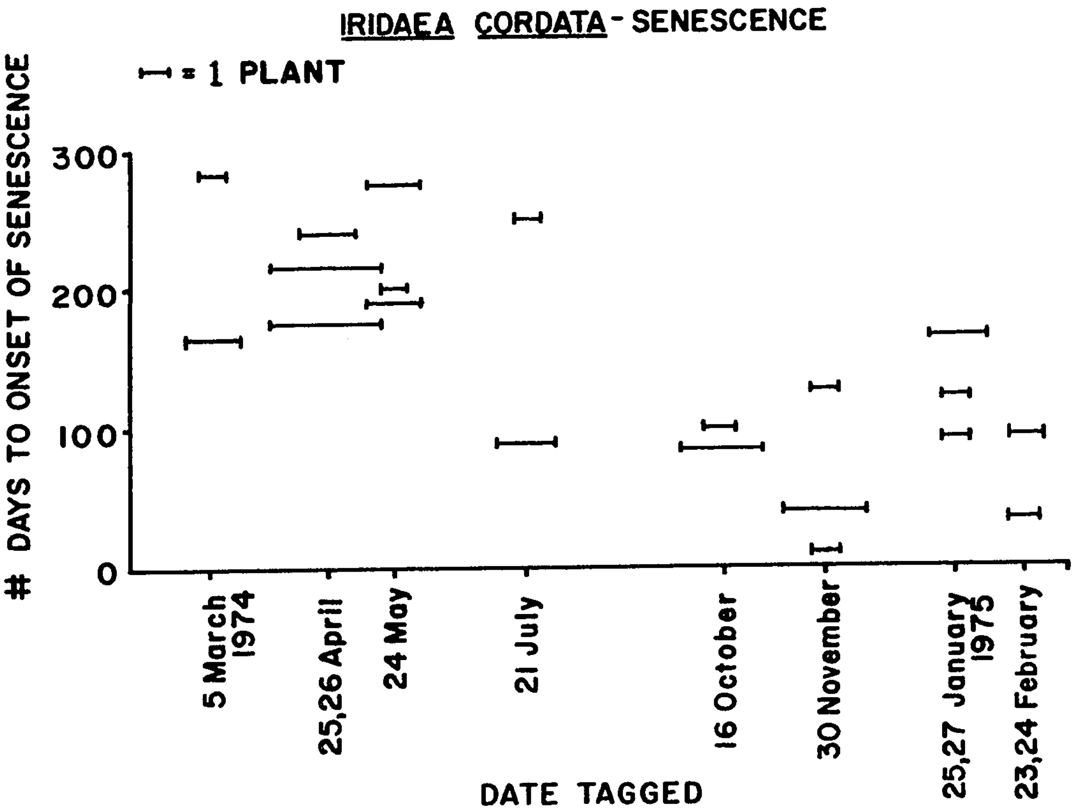


FIGURE 29

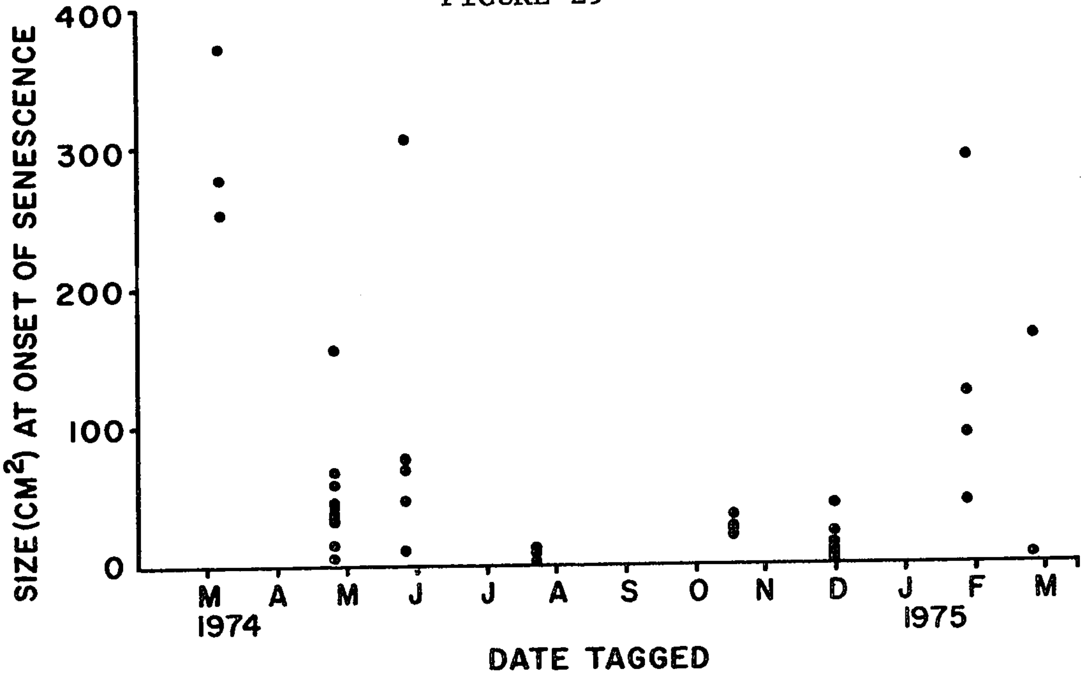


FIGURE 30

using Kendall's Tau test for correlation (Table 6). Cumulative biomass was positively correlated (p=.02) with solar radiation and daylength, but not with surface seawater temperature (p>.10).

Cumulative biomass and solar radiation exhibit an abrupt increase during spring and peak in summer when the population matures (see maturation index, Fig. 25) followed by a decrease between summer and autumn. Daylength exhibits a similar annual progression with a corresponding increase in photoperiod from winter to spring of 10.4 to 12.6 hrs. Discrete growth rate for each season was not correlated with any of the variables considered. However, it abruptly increased during spring as did solar radiation, but thereafter resumed a low rate as solar radiation and daylength continued to increase.

In contrast, surface seawater temperature reached a peak when both biomass and growth rate began to decline (summer-autumn).

Changes in the environmental variables monitored and the growth (cm^2) of tagged thalli were compared (Figs. 31-32). As was stated previously, thalli tagged between March -April, 1974 and late January-March, 1975 demonstrated greatest growth potentials. While thalli tagged at other times had lower potentials; the lowest coinciding with the winter months. Correspondingly, solar radiation displayed acute increases during the high growth potential periods

TABLE 6

Iridaea cordata and Environmental Factors

Variable	1973-1974 Winter	 Spring	 Summer	 Autumn
1) $\bar{X}$ Cumulative Biomass (gm dry weight/625 cm^2)	1.76	42.9	95.9	82.4
2) $\bar{X}$ Discrete Seasonal Growth Rate (mg dry weight/625 cm^2/day)	10.0	365.0	95.0	21.0
3) $\bar{X}$ Solar Radiation (lys/day)	218.8	275.4	499.2	346.1
4) $\bar{X}$ Daylength (hrs)	10.4	12.6	14.3	12.7
5) $\bar{X}$ Surface Seawater Temperature	10.0	10.5	11.4	14.5

Kendall's Tau Test for Correlation

Variables Tested	Probability
1 vs 3	$p = .02$*
1 vs 4	$p = .02$*
1 vs 5	$p > .10$ NS
2 vs 3	$p > .10$ NS
2 vs 4	$p > .10$ NS
2 vs 5	$p = .50$ NS

* Correlation significant
NS No significant correlation

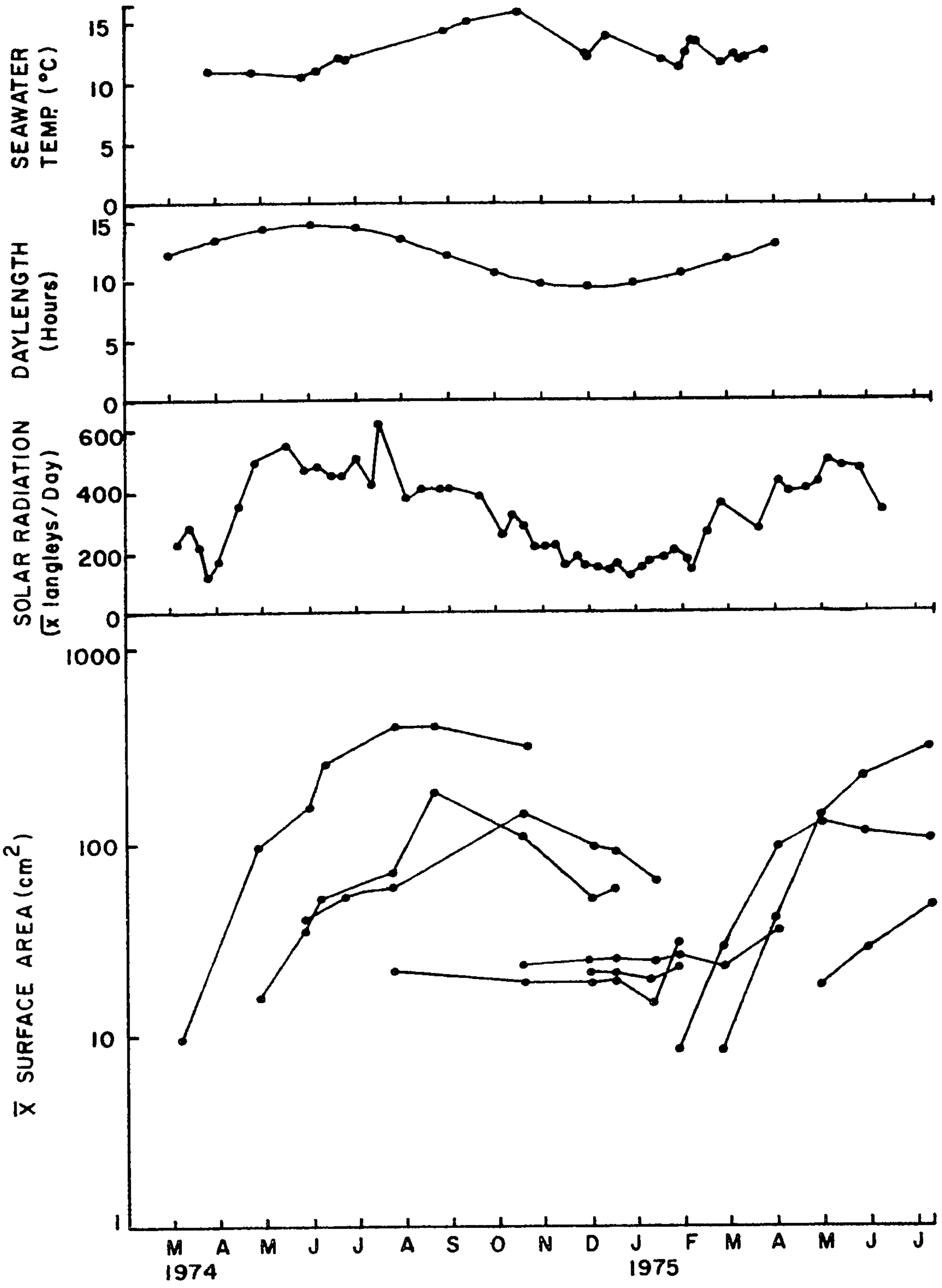

SEAWATER TEMP. (°C)
15
10
5
0
DAYLENGTH (Hours)
15
10
5
0
SOLAR RADIATION ($\bar{x}$ langleys/Day)
600
400
200
0
$\bar{x}$ SURFACE AREA (cm^2)
1000
100
10
1
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1974
1975

FIGURE 31

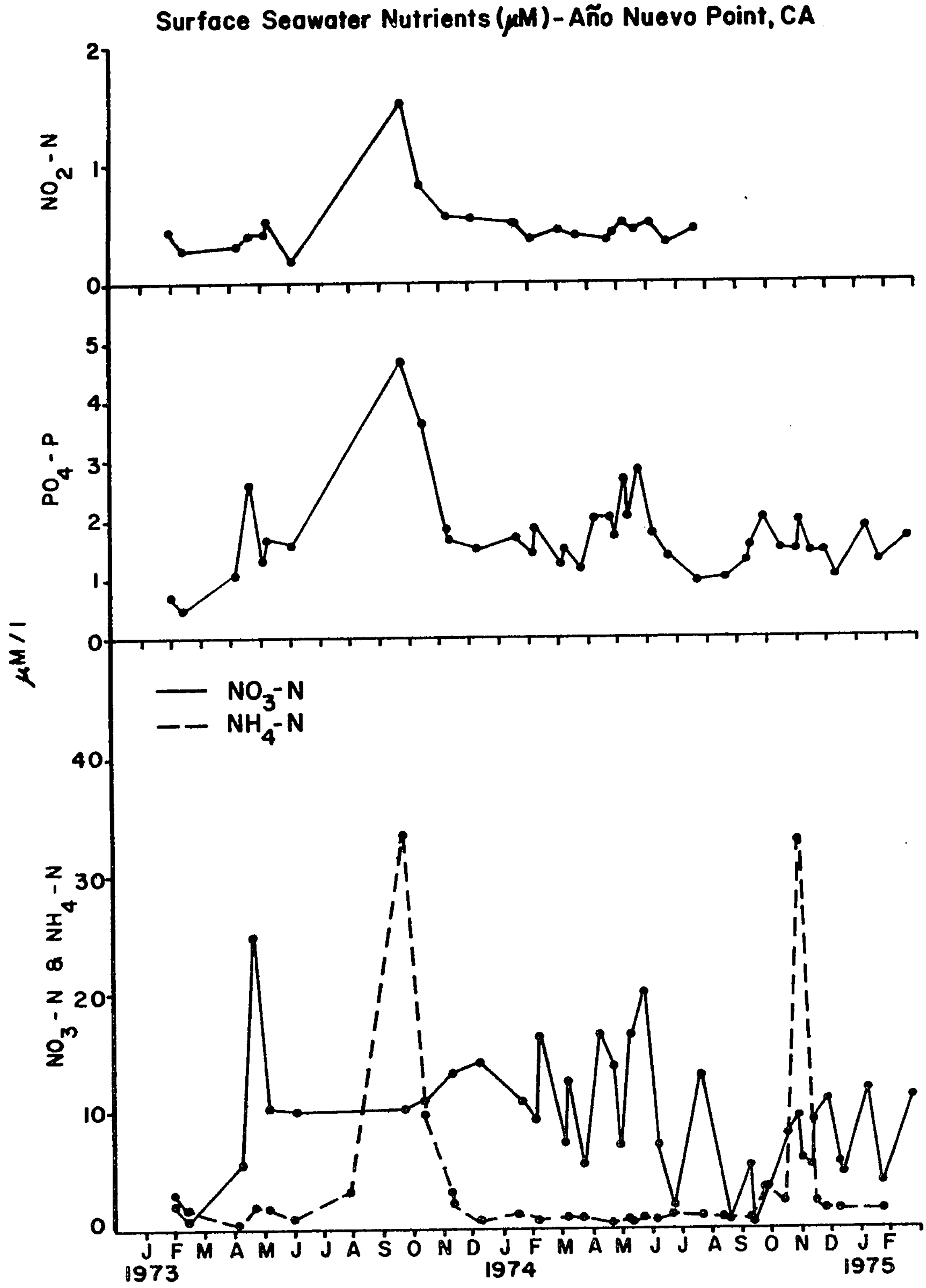

Surface Seawater Nutrients (µM) - Año Nuevo Point, CA
NO$_2$-N
0
1
2
PO$_4$-P
0
1
2
3
4
5
µM/l
NO$_3$-N
NH$_4$-N
NO$_3$-N & NH$_4$-N
0
10
20
30
40
J F M A M J J A S O N D J F M A M J J A S O N D J F
1973
1974
1975

FIGURE 32

in both 1974 and 1975. Further, these time periods coincided with the largest increases in annual daylength. Increases in thallus surface area diminished during seasons of low solar radiation and short daylength (autumn and winter).

Increases in surface seawater temperature did not coincide with increasing growth potential, but transpired with the onset of the slow-growth period.

Nutrients showed fairly erratic patterns during the experimental period (Fig. 32). During the slow growth period (winter), total nitrogen and phosphorus levels were high and remained high and erratic during the spring growth period. During summer the nutrient levels declined (except for a sharp NO_3-N peak in July), while cumulative *I. cordata* biomass reached a peak. However, discrete summer growth rate was very low. During autumn, total nutrients were at a low point, coinciding with die-back of the *I. cordata* population and the low growth potential period of individual tagged thalli. The NH_4-N peak occurred during November, 1975 concurrent with the lowest growth potential period, low light intensity, short daylength, and fairly high temperature conditions.

DISCUSSION

The ontogenetic progression of a natural Iridaea cordata population is primarily driven by perennation and vegetative reproduction. The results of denuding experimental plots down to the basal, perennating crusts in November showed that, through the mode of vegetative reproduction, biomass levels similar to the untreated natural population were produced in nine to twelve months. The crusts were perennating after denudation of the erect thalli; that is, they were active, viable, and functioned as efficient 'space-savers' when the erect thalli were mechanically removed or died-back. Therefore, the crust is an effective adaptation for successful space competition among associated organisms. Interestingly, a parallel adaptation of flowering plants, the successful lateral spread of tissue on and in the substratum, is a characteristic implicated with those species exhibiting the 'competitive strategy' for survival (Grime, 1974).

When experimental plots were denuded to the crusts in November, essentially no growth occurred for three months (winter). During this period the crusts remained viable without their erect system and actively initiated tiny new thalli. Any bare spots (which were rare) were not actively colonized by I. cordata sporelings during this period.

Similar observations were noted for Gigartina stellata in Wales, "there was no colonization of the bare patches by Gigartina, but the plants grew larger and produced more fronds" (Marshall, et al., 1949). This overwintering and thallus initiation demonstrates the integral role of the perennating crust and the importance of this morphological unit. As expected, the genotype of the crust was preserved in experimental plots and the resulting population structure and proportions of erect thalli (in terms of reproductive life history stages) were identical to the original.

These studies of perennation and vegetative reproduction in I. cordata support the contentions of Knight and Parke (1931) and Dixon (1965) that these processes can be instrumental in the in situ life history of perennial red algal species. Moreover, numerous studies, most designed to investigate the effects of harvesting, and natural history observations, suggest that these adaptations are prevalent throughout the orders Gigartinales and Gelidiales (Marshall, et al, 1949; MacFarlane, 1952; Foster, 1955; Conover, 1964; Seone-Camba, 1965; Taylor, 1970; Fralick, 1971; Barilotti & Silverthorne, 1972; Burns & Mathieson, 1972; Austin & Adams, 1974; Dawes, et al., 1974; Mathieson & Dawes, 1975; Thomas, et al., 1975; Hansen, in press).

Growth is primarily a matter of energy supply directed by the genetic capabilities of the plant. It should be expected then, that growth of even closely related species should vary with life form (annual, perennial) and time. Table 7 summarizes growth rate measurements of I. cordata and other red algal species. Initially, one is struck with the diversity of ways in which to express growth rate. These expressions can be divided into two groups. 1) Growth rates of the total population or a component thereof are given as organic matter (fresh weight, dry weight, carbon, ash, etc.)/ unit area/unit time. 2) Growth rates of individual thalli as organic matter, linear, square, or volume values/unit time. The first is used to express the rate at which the population is growing, changing, or accumulating as a whole and can be used to estimate and predict production. The second is used to express vegetative growth, ontogenetic change, and infraspecific variation within a population. Comparatively, I. cordata is a rapidly growing species by both types of measurements. This is most likely a reflection of the annual nature of the erect system, the portion that was measured.

According to Feldmann's (1951) nomenclature I. cordata would be classified a hemicryptophycean perennial because the basal crust can persist for more than one year, while Knight and Parke (1931) would consider it a pseudoperennial, because the majority of the thallus is not perennial. This term, pseudoperennial, is applied to Eucheuma nudum (Dawes et al., 1974) in Florida and Gigartina stellata (Marshall et al., 1949) in Britain, though Hehre and Mathieson (1970) consider the latter

TABLE 7

GROWTH RATES OF RED ALGAE

Species/Comments	Growth Rate	Author
Iridaea cordata[1]		
California		
Cumulative/Seasonal		
Winter 1973-74	20.0/23.0 mg DW/625 cm^2/day	Hansen, J. E.
Spring 1974	452/365 "	
Summer 1974	717/95 "	
Autumn 1974	-116/21 "	
Biomass (Dry Weight)[2] Doubling Time		
Winter, 1973-74	23.8 ± 2.7 Days	
Spring 1974	11.2 ± .51 Days	
Summer 1974	14.9 ± 3.3 Days	
Autumn 1974	64.6 ± 28.8 Days	
Net Carbon Production[3]	384 Gm C/M^2/yr	

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(1) Vegetative regrowth from basal crusts.
(2) Calculated from discrete seasonal regrowth
(3) Calculated from cumulative regrowth from crusts. Total Carbon = 25% of dry weight.

Table 7, continued

Species/Comments	Growth Rate					Author
$\overline{X}$ Thallus Growth (Surface Area)						Hansen, J. E.
April to June 1974[4]	1.64	2.23	5.85	3.25	cm^2/Day	
"	.2	.02	.03		cm^2/cm^2/Day	
May to August	.58	1.3	.71	1.44	cm^2/Day	
"	.04	.03	.01	.01	cm^2/cm^2/Day	
June to October	.63	.69	.31		cm^2/Day	
"	.009	.02	.006		cm^2/cm^2/Day	
October to January 1975	.01	.06	.09	.03	cm^2/Day	
November to January 1975	.05	.08	.02	.23	cm^2/Day	
"	.003	.003	.005		cm^2/cm^2/Day	
February 1975 to May	.77	1.85	1.28	1.36	cm^2/Day	
"	.10	.06	.03	.01	cm^2/cm^2/Day	
March to July	.93	3.61	2.37	2.24	cm^2/Day	
"	.12	.09	.02	.01	cm^2/cm^2/Day	

---

(4) Chronological rates between dates.

Table 7, cont.

Species/Comments	Growth Rate					Author
Iridaea cordata						
$\bar{X}$ growth in length						
March to June 1974	.27	.38	.62	.40	cm/Day	Hansen, J. E.
April to August	.17	.21	.07	.36	"	
May to November	.10	.05	.13	0	"	
July to January 1975	.0023	.0114	0	0	"	
October to January 1975	.02	0	0	.02	"	
November to January 1975	-	.018	-	-	"	
January 1975 to May	.15	.20	.12	-	"	
February to July	.23	.46	.24	.24	"	
April to July	.11	.08			"	
Iridaea cordata						
Washington*						
Individuals -3.0 ft (Mar-July)	$\bar{X}$ = 1.1 gm FW/Day					Waaland, 1973
" May-June (peak)	$\bar{X}$ = 1.6 gm FW/Day					
Gigartina exasperata						
Individuals (March-July)	1.25 gm GW/Day					Waaland, 1973

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* Recalculated from data, or estimated from graph.

Table 7, Cont.

Species/Comments	Growth Rate	Author
Iridaea cordata		
Washington Tank culture (March-July)	14 gm DW/m^2/Day	Waaland, 1974
G. stellata		
Great Britain* Regrowth from basal crust		
April-September	4.2 gm FW/.1 cm^2/Mo	Marshall et al., 1947
Gigartina stellata		
New Hampshire Regrowth from basal crust*		
August-November	5 gm/100 cm^2/Mo	Burns & Mathieson, 1972
June-August	8 gm/100 cm^2/Mo	"
January-April	2 gm/100 cm^2/Mo	"
Chondrus crispus Nova Scotia Individuals		
late spring & summer	.01 mm^2/mm^2/Day	Taylor, 1954
winter	.002 mm^2/mm^2/Day	"
young, erect fronds (summer)	.44 mm/Day	Taylor, 1970
branched individuals (summer)	.02 mm/day	"

Table 7, Cont.

Species/Comments	Growth Rate	Author
C. crispus Maine*		
Regrowth from basal crusts		
June-July	4.5 lbs/yd^2/Mo	Foster, 1955
July-August	3.8 lbs/yd^2/Mo	"
August-September	1.0 lbs/yd^2/Mo	"
C. crispus Massachusetts		
Young fronds (Aug-Sept)	$\overline{X}$ = .31 mm/Day	Prince & Kingsbury, 1973
" Max.	.37 mm/Day	"
Sporelings on glass slides	8-10 days doubling time	"
Gracilaria verrucosa[5]		
Wales		
transplanted individuals		
November-April	1% increase FW/day	Jones, 1959
May-June	2.6% increase FW/day	"

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(5) Measurements made with plants completely immersed.

Table 7, Cont.

Species/Comments	Growth Rate	Author
Gracilaria edulis India		
rope culture $\bar{X}$ annual	.30 gm FW/linear M/Day .02 gm DW/linear M/Day	Raju & Thomas, 1971
$\bar{X}$ individuals (length)	30 mm/Day	"
Euchemena isiforme Florida		
transplants on lines peak early spring-summer	7% increase FW/Day	Dawes et al., 1974
$\bar{X}$ rest of year	1-2% increase FW/Day	"
individuals *in situ* increase in length	approx. 1.4 cm/mo	"
Gelidium robustum		
California, individuals	9 cm/Yr	Barilotti & Silverthorne, 1972
G. crinale England		
individuals	6 cm/Yr	Dixon, 1966
G. sesquipedale		
Galicia, Spain	9.72 ± 2.41 cm/13 Mos	Seone-Camba, 1966

Table 7, Cont.

Species/Comments	Growth Rate	Author
G. sesquipedale		
Santander, Spain May-October	1.53-2.25 cm/Mo	Cendrero & Ramos, 1967
Gymnogongus linearis		
Individuals (April/May)	Max. .23 mm/Day	Markham & Newroth, 1971

species a perennial in New Hampshire. It was determined from the mortality curves (Fig. 24) of 182 tagged *I. cordata* thalli that: 1) those juvenile thalli tagged from late winter through spring persisted for approximately twelve months and are considered spring annuals, 2) those tagged at other times had shorter, more variable life spans. From this evidence, it is most descriptive to describe *I. cordata* as a perennial with an annually deciduous erect system, based on the integral role of the crust and the longevity of the erect thallus. The quantitative results of this study are based solely on the annual erect system.

The growth rates in Table 7 reflect such differences in life form. For example, the growth rates of erect, perennial *Chondrus crispus* thalli on the Atlantic coast are much lower than those of annual *I. cordata* thalli studied. This is congruent with reports for annual and perennial genera of the Order Rhodymeniales from Japan (Lee & Kurogi, 1971). Similarly, extensive comparative studies of relative growth rate ($\overline{R}_E$) of annual and perennial vascular plant species show corresponding results (Grime & Hunt, 1975). It is speculated (op. cit.) that genetic characteristics conducive to rapid growth in productive conditions are disadvantageous to species subject to environmental extremes. The results indicate that habitats subject to environmental stress, particularly nutrient and light deficiences, are colonized by species of low potential growth rate. It is further stated, that low growth rates may be adaptive to conditions of stress in the following ways: 1) slow-growing plants make modest demands and are therefore less likely to exhaust resources in the immediate environment, 2) they may have lower photosynthetic and nutrient uptake rates, and 3) under conditions of protracted and extreme stress, they may be better fitted to survive periods when little or no growth is possible. These ideas provide interesting substance for similar comparisons between the annual/perennial erect systems of *I. cordata* and *C. crispus*. *I. cordata* occupies the productive, open coastal waters of the temperate Pacific coast, while *C. crispus* is subject to the comparatively extreme conditions (ie. temperature and nutrients) of the Atlantic coasts. Following the logic based upon the numerous studies of vascular plant species (op.cit.), it is suggested that the slow-growing perennial life form, exemplified by *C. crispus*, may be better fitted to survive the habitats of environmental stress, whereas, the high growth rate of the *I. cordata* erect system insures the rapid completion of the life history, terminating or morphologically 'dying-back' with the onset of relatively stressful conditions (winter); apparently intolerable to this annual life form. Such tempting ideas stress the need for quantitative ecological and physiological investigation into the selective (dis)advantages of the annual versus perennial life form of benthic marine algae.

Results in Table 7 also demonstrate that growth rates for I. cordata and related genera vary notably with time. The results of experiments on 1) cumulative growth from perennial crusts, 2) discrete seasonal (3 mo) growth from crusts, and 3) growth rates of individual I. cordata thalli are highly correlated with the time of the year, or in the case of the tagged juvenile thalli, with the time of the year that they were tagged.

Growth rates calculated from the cumulative vegetative regrowth from crusts were lowest during winter. While the population demonstrated a spectacular twenty-two fold increase in growth rate between winter and spring, and the rate continued to increase slowly thereafter until the end of summer. Between summer and the end of autumn, the population began to die-back resulting in a negative rate, or more appropriately a senescence rate. Comparatively, Waaland (1973) observed maximum crop increases of this species in Washington between March and September.

In contrast, when experimental plots were denuded at the beginning and end of each season to determine discrete three month growth rates, a variant pattern emerged. The discrete spring growth rate was eighteen fold higher than in winter, similar to the cumulative pattern. But contrary to growth rate being greatest during the summer months, it was only five times the low winter rate and the autumn rate was the same as that during winter. This suggests that plants initiated before, and sustaining the spring burst of growth, have a selective advantage in terms of growth potential (capacity to attain the largest size at the highest growth rate), over those not undergoing the spring transition (the summer and autumn initiated plants). These results also indicate that growth is dependent upon the physiological state of the plant. Metabolic rates are certainly different for the developing juvenile than for the aging plant as has been reported for unicellular algae (Krauss, et al., 1959) and vascular plants (Hari & Leikola, 1974). The differences between cumulative annual growth rates (based on juveniles, reproductive, and ageing plants) and discrete seasonal rates (based on simultaneously initiated non-reproductive plants) are probably a combined reflection of the physiological state of the population, as well as time-of-year.

The variations in I. cordata growth rate are further demonstrated by the results of tagging experiments.(4) Groups of thalli tagged throughout the year exhibited varying growth potentials correlated with time of the year tagged.

(4) Groups of individual thalli tagged at the same time throughout the year, showed low infra-specific growth rate variation. Therefore, the mean growth rate of tagged individuals within a group will be referred to throughout the remainder of the discussion.

Those thalli tagged during March and February of two successive years showed the greatest growth potential during the exponential growth phase (the first 4-5 mo). Growth potential was slightly lower for those tagged during January and April, still lower for those tagged during May, and thalli tagged during July and October exhibited lowest rates (Fig. 23). Moreover, thalli sustaining the distinctive spring growth period, have characteristic mortality curves (Fig. 24) and tend to have life spans of approximately twelve months, while those not undergoing the spring period have shorter, more variable life spans. Such seasonal variations in survivorship have also been reported for the few annual higher plant populations that have been studied to this extent (Antonovics, 1972; Sarukhán & Harper, 1973).

This evidence from experiments carried out at both the population and genecological (individual) levels demonstrates that growth potential in _I_. _cordata_ is synchronous and is characterized by distinct annual oscillations. It is known from _I_. _cordata_ density results (Fig. 6) that the majority of juveniles are initiated by the end of winter (though lesser numbers are initiated throughout the year). This critical initiation timing of the new year's crop of erect thalli begins thallus development in synchrony; fine-tuned by the "spring-growth-oscillation".

Those thalli initiated and beginning development during other other times of the year realize lower growth potentials, shorter more variable life spans, and are asynchronous. It is interesting to note that tank-grown *C. crispus* plants had different growth potentials (Neish & Shacklock, 1971). If *C. crispus* has similar synchronous growth oscillations, using field-picked plants of varying ages could account for the reported variance in growth potential of this species. Synchronous oscillations, present in virtually all biological systems in which they have been studied, suggest the presence of an annual biological clock for growth in *I. cordata*. In many related red algal species in which growth of natural populations has been studied for at least one year, an increase in biomass (the end-product of growth), or growth itself, has similarly been noted to occur during the spring period (Knight & Parke, 1931; Marshall, et al., 1949; Hasagawa & Fukuhara, 1955; Jones, 1955; Conover, 1964; Dixon & Richardson, 1970; Rao, 1970; Fralick, 1971; Neish & Fox, 1971; Prince & Kingsbury, 1973; Mathieson & Burns, 1975). This suggests that the genera in the Order Gigartinales, within the temperate regime may be a fairly homogeneous group in terms of growth dynamics; a concept worthy of further investigation.

Reproductive maturation of *I. cordata* thalli is given here as: that point when sori are first evident on the thallus surface.

However, it cannot be assumed that spores were necessarily ripe nor viable. Therefore, maturation is only considered in terms of ontogeny, longevity, and perennation and does not unequivocally imply sexual reproduction.

Maturation times were calculated from 1) experimental plots denuded before and after each season (discrete seasonal), and 2) plots denuded in November, 1973 and randomly reharvested in three month increments (cumulative). The results from harvesting the discrete plots showed that a small component of the population became reproductively mature by three months during all seasons but winter; spring- 20%, summer- 8%, autumn- 10%. Small as the reproductive components were, these results demonstrate that some of the perennial, crustose genotypes within the population are adapted to initiate erect thalli that grow and become mature within a very short time period. And further, this occurs throughout the year except winter, the slow-growth period. In contrast, Mathieson and Burns (1975) report that reproductive structures were found on the perennial thalli of C. crispus only after thirteen or more months of regrowth from similarly denuded plots.

Results from the cumulatively harvested experimental plots demonstrated that I. cordata thalli reach reproductive maturity within six months (by the end of spring). By twelve months the plots had reached control levels of the natural population and 90±2% of the total biomass was mature.

Consequently, through the processes of perennation and vegetative reproduction, a near-totally reproductively mature subpopulation was produced within one year. Similarly denuded plots of C. crispus in New Hampshire, originally harvested in July or December, took over one year to reach control levels which were less than 20% of the total population (Mathieson & Burns, 1975). No reproductive papillae were observed on G. stellata thalli in New Hampshire after one year's regrowth from crusts denuded in December or August (Burns & Mathieson, 1972). Growth studies of Gracilaria edulis in India (Raju & Thomas, 1971) indicate that plants become mature in five to six months, while in subtidal populations of Gelidium robustum from Baja, California, tetrasporangial thalli were mature one year after harvesting (Barilotti & Silverthorne, 1972).

The results from thalli tagged throughout the year show that I. cordata thalli mature year round. This concurs with the fact that mature thalli of all life history stages were present in the four populations studied during all seasons. Even though maturation occurs throughout the year, its onset appears to be closely related to thallus growth potential. For example, thalli tagged during spring-early summer take a longer, more variable amount of time to mature and are correspondingly larger plants than those tagged during autumn-winter which mature rapidly and are diminutive in stature.

This may be a result of the level and partitioning of energy. Thalli with a high growth potential (spring-early summer) are probably channeling more available energy into growth than into reproductive maturation. While the small winter thalli could have been fairly old when tagged which might account for their rapid maturation, as it cannot be absolutely assumed that all the small thalli tagged during autumn-winter were juveniles. Or these small winter thalli proceed through a truncated life cycle, as the mortality curves indicate. If the latter is the case, this life history adaptation would insure the small winter thalli of becoming mature before senescing or dying due to winter storm conditions.

In addition, there is a highly significant correlation between growth rate of individual thalli and maturation date. The results show that 59% of all tagged thalli that matured, continued to grow following maturation. Those thalli tagged during spring-early summer exhibited variable, but generally high post-maturation growth rates, while those tagged during autumn-winter had diminutive rates. From these results, it is suggested that growth processes constitute the primary energy sink for spring-early summer plants and reproductive maturation requirements are secondary. It follows that maintenance growth is carried out in the late summer-winter thalli and requirements of maturation are the primary energy sink.

Blade senescence follows a somewhat similar pattern to to that of maturation. However, the results are based upon less data (33 tagged thalli were followed through complete senescence) and are therefore, less comprehensive. The onset of senescence is given as: that point in time when population biomass declines, or when continual thallus loss (cm^2) began. General population senescence occurs between summer and autumn and again, is probably a reflection of the majority of thalli synchronized by the "spring oscillation". On the genecological level, thalli have the capibility of senescing throughout the year, but a seasonal pattern was evident. Those thalli tagged during spring-early summer had much longer life spans and were larger at senescence than thalli tagged during autumn-winter. This pattern is also shown by the mortality curves. Therefore, senescence and maturation of large as well as small thalli are inherent within the population and influenced by the time of year. This is apparently not the case for Eucheuma spp. in Florida. Dawes, et al. (1974) suggest that a maturation sequence is required before production of reproductive organs, because they are usually found on larger (older?) thalli.

It has been demonstrated throughout this study that aspects of I. cordata ontogeny are correlated with time. Consequently, a number of time-related ontogenetic patterns have become evident.

These patterns result from the complex of fluctuating environmental factors and the genotypic responses inherent in any algal population.

An attempt was made to further the understanding of these I. cordata time-related patterns evident at the population level. Comparisons were made between ontogenetic patterns and environmental factors that either exhibited predictable oscillations themselves, or were known to be instrumental in primary production phenomona. Chemical and physical monitoring was thus not comprehensive. For example, factors known to be important to the growth of related genera, ie. salinity and water movement, were not considered due to the type of habitat in which I. cordata grows (open coast, surf zone).

The environmental variables included herein: solar radiation, daylength, surface seawater temperature, and nutrients (NH_4-N, NO_3-N, NO_2-N, PO_4-P) cannot be considered as causal or limiting factors in the classical terms of Liebig (1840) and Shelford (1913) because their influences cannot be separated and they may act synergistically on primary production processes. It is stressed that the interpretation of any ecological data is limited by these unknown synergistic influences as well as those of the multitude of variables that were not considered. Consequently, it is only in the most general terms that comparisons are made and correlations drawn among the ontogenetic patterns identified in I. cordata and the environmental factors measured. Moreover, the type of factors measured in this study vary geographically, seasonally, and dimensionally (primarily with depth). Therefore, it is not suprising that conclusions have been drawn and speculations advanced by others, that concern nearly every combination of biological and chemical or physical factor measured.

The most notable patterns in the ontogenetic progression of I. cordata vary with time: growth potential, the annual nature of the erect system, and the "spring oscillation". Maturation and senescence of tagged thalli occur throughout the year, although the population in general matures in summer and senesces during autumn.

Results of the selected variables measured during this study indicate that light (combined intensity and daylength)(5) has the greatest identifiable influence on I. cordata ontogeny. A relationship between solar radiation and growth is not suprising, as photosynthesis, its efficiency, and ultimately the amount of organic material accumulated is directly dependent upon the utilizable energy received by the plant. The interesting questions here are: does light intensity have a direct photosynthetic effect (i.e., an increase in light intensity results in an increase in algal growth), if so can the critical intensities be circumscribed? and does light act as a stimulatory agent in 'cueing' or controlling ontogenetic phases?

(5) Influences of light intensity and photoperiod cannot be separated under field conditions.

The positive correlations between light and cumulative *I. cordata* biomass and respective growth rate, suggest a photosynthetic effect. Growth of the tagged plants in March-April, 1974 and February-March, 1975, corresponding to the respective annual light intensity increases also supports this type of a relationship. Increases in *I. cordata* cumulative biomass, respective growth rate, and greatest growth potential of tagged thalli coincide with solar radiation increases of $\overline{X}$ = 227 to 559 ly/day in 1974 and 152 to 478 ly/day in 1975, suggesting that the critical light level for growth may be within these limits. However, it must be stressed that during this time period, daylength increases from 9.6 hrs to 14.4 hrs; an inseparable component of the light factor when studying natural systems. Reports of direct light intensity influences on red algal growth in Texas lagoons (Conover, 1964), *C. crispus* in New Hampshire (Mathieson & Burns, 1975), *Gracilaria verrucosa* in Wales (Jones, 1955) and *Pterocladia capillacea* in North Wales (Dixon, 1970) suggest a similar photosynthetic effect. Other reports aid in clarifying critical field light intensity limits for related species. Neish and Fox (1971) have demonstrated in tank culture, that *C. crispus* growth is better at one-third natural light intensity during long days. Dawes, et al., (1974) have noted noted that maximum growth of *Eucheuma* spp. in Florida coincides with reduced light intensities and further suggests that high intensities may inhibit sexual reproduction.

Contrary to cumulative _I. cordata_ growth, discrete seasonal biomass and growth rate were not correlated with the light variables measured, except with the prominent spring increase. Thereafter, growth rate was low while solar radiation and daylength increased. Further, growth potential of spring-tagged thalli was higher during any other time of the year, even though summer light intensity and photoperiod continued to increase. These relationships, alternatively suggest a light-stimulus influence occurring during spring. If this in fact is the case, a light-stimulus could be instrumental in synchronizing the "spring-growth-oscillation"; suggestive of an annual biological clock. Early observations by Knight and Parke (1931) of British red algae alluded to such a spring, light-stimulus influence. Moreover, Powell (1964) observed that thallus growth of _Constantinea simplex_ was induced by a critical 14 hr daylength and inhibited by longer daylengths or a 15 min light break; suggestive of a photoperiodic response. As stressed by Dixon (1970), further understanding of such correlations and comparisons between benthic algal ontogeny and field-light conditions requires critical experimentation needed to differentiate among biological clocks, true photoperiodism, as defined by Terbourgh and Thimann (1964) and photosynthetic effects.

Surface seawater temperature varied between 9.7°C (January) and 15.6°C (October), an annual recorded range of 5.9°. There were no positive correlations among temperature and cumulative or discrete _I_. _cordata_ vegetative growth from crusts, nor was temperature related to high growth potential among tagged thalli. However, peak annual temperatures did occur simultaneously with the onset of population die-back. If _I_. _cordata_ metabolism is sufficiently increased by the late summer-autumn temperature regime, die-back could ensue. It is unlikely, though, that a gradual six degree rise in temperature would have this effect, as Waaland (1973) has shown that best _I_. _cordata_ growth in the laboratory occurs between 10-14°C. This range nearly spans the annual recorded temperature range at this latitude.

Decreases in light intensity and photoperiod also occurred during late summer-autumn, re-emphasizing the possibility of synergistic influences, or at the very least, the camouflaging nature of simultaneously-measured environmental variables; a perplexing ecological problem (Fritsch, 1945).

Changes in seawater temperature (±5°C) primarily with latitude, have been shown to correspond with changes in the general algal flora (Setchell, 1940). Correspondingly, temperature has been considered a primary influencing factor and has been extensively compared to algal growth, especially in areas having large annual temperature ranges. Conover (1964) reports that in Cape Cod estuaries (41°N) the vegetative algal growth peak occurs during the thermal maximum, while in Texas lagoons (Conover, 1958) temperature may contribute towards producing high metabolic rates which in turn limit additive growth among benthic algal communities. Mathieson and Burns (1975) note that increase in C. crispus growth in New Hampshire occurs when seawater temperature increases from 6-9° (spring) to 15-19° (summer). Neish and Fox (1971) speculate that decreasing C. crispus growth in autumn is not correlated with temperature because autumn temperatures are higher than those in spring when growth increases. Alternatively, they note that decreasing solar radiation is more instrumental in the growth decline. On the other hand, Prince (1971) suggests that growth of C. crispus in Massachusetts is closely related to seawater temperature and that the autumn decrease in growth rate is primarily due to increasing temperatures. Burns and Mathieson (1972) advance a similar growth/temperature relationship for G. stellata in New Hampshire. Santelices (1975) postulates that most Gelidioid species in which a temperature maximum has been detected, reach their maximum growth at the time that the submaximum temperature occurs in the locality. The species that start growing and reproducing in early spring start dying and bleaching during and at the end of summer when maximum temperatures usually occur. Conversely, Barilotti and Silverthorne (1972) report that increased seasonal growth of G. robustum off southern California correlates with increased seawater temperature.

The variety of reported temperature influences on natural benthic red algal populations indicates that temperature range (maximum-minimum), and duration of the warmest temperatures are the important aspects to be assessed, a concept initially advanced by Setchell (1915; 1920). Considering the small range off the temperate Pacific coast studied, this factor may have only minor influences on I. cordata ontogeny at the population level within this general latitudinal regime. It is also probable that the temperature range experienced by this species during a single low tide sequence may be greater than the annual seawater range. The relationships among ontogeny, temperature and dessication warrant further investigation.

A tremendous amount of time and fruitful energy has been devoted to furthering the understanding and development of optimal nutrient regimes for maximum plant growth; e.g., the field of agriculture itself and specifically, laboratory culturing.

Comparatively little has been contributed towards understanding the ecological interactions of the seawater nutrient regime and the primary producers that utilize and influence it. Notable here are the numerous studies of the *in situ* phytoplankton-nutrient system. Rarely has similar work been done for the benthic algae even though they account for the majority of primary production in the near-shore euphotic zone. A small part of this study was designed to illustrate any apparent relationship between the selected nutrients measured and *I. cordata* growth.

Surface seawater nutrients (NO_3-N, NO_2-N, PO_4-P) at the Año Nuevo Point site were not positively correlated with cumulative and discrete *I. cordata* growth, nor with growth potential during the growth study period (November, 1973 to July, 1975). The concentrations of surface seawater nutrients were fairly high, but erratic from the onset of the growth studies.

NH_4-N displayed a variant pattern. During August-September, 1971 (Hansen, J. C., 1971) and 1973, a tremendous NH_4-N peak occurred corresponding with the peak pinniped population on Año Nuevo Island, *I. cordata* biomass levels and thallus size. The results from these previous comparative studies indicate that in 1971, *I. cordata* biomass at Año Nuevo Point was significantly greater than that at Pigeon Point South (Hansen, 1971) and in 1973, biomass of the tetrasporangial stage was significantly greater than that at Scott Creek, Año Nuevo Cove, and Pigeon Point South (see Fig. 8). In addition, the size-class distributions indicated that during 1973, the thalli were larger at Año Nuevo Point than in the other populations indicating that nitrogen may have been limiting in those populations. In populations at the latter three study sites mentioned, _I. cordata_ thallus senescence and overall population die-back occurred in autumn, while at Año Nuevo Point the biomass of the tetrasporangial stage did not significantly decrease. The tetrasporangial thalli remained robust with little external signs of senescence until after the NH_4-N peak had passed, after which the population rapidly senesced and died-back similar to other populations studied. This intriguing correlation tempts the suggestion that high levels of NH_4-N could be integral in influencing senescence. The high NH_4-N levels available could contribute the necessary nitrogen needed to replace amino groups and ultimately plant protein that is normally catabolized during senescence. The overall influence of temporally high NH_4-N levels during autumn would then be a delay in population senescence and die-back, as has been observed of the Año Nuevo Point population in 1971 and 1973.

The NH_4-N regime differed in 1974. The pinniped population on Año Nuevo Island was relatively low (Le Boeuf, personal communication) and an NH_4-N peak did not occur in late summer-early autumn. Instead, a sharp, brief peak occurred in November following the initial heavy precipitation for the season. This brief NH_4-N peak was likely due to the dissolution and washing of seal excreta deposits from the island; similar to the December peak in 1971 (Hansen, J. C., 1971). It may be, that because the NH_4-N peak was brief and occurred late in the _I_. _cordata_ growing season (November), that a corresponding increase in growth, or delay in senescence of tagged thalli was not observed. Additionally, the simultaneous influences of low solar radiation levels, short photoperiod, and high seawater temperatures also recorded for late autumn, again cannot be segregated.

These thought-provoking comparisons among NH_4-N, thallus growth and senescence show the need for critical experimentation on the effects of nutrients on benthic algal physiology.

Other studies comparing red algal growth and nutrient regimes on the Atlantic coasts report highly variable results. Prince and Kingsbury (1971) suggest that in Maine NH_4-N is the primary nitrogen source for _C_. _crispus_ during May when it is growing rapidly since other nitrogen sources are negligible. While initiation of _C_. _crispus_ in New Hampshire occurs during spring, coincident with maximum nutrient levels, and maximum growth occurred during summer-autumn when nutrient levels were low (Mathieson & Burns, 1975). Similarly, Neish and Fox (1971) showed in tank culture that the spring growth of C. crispus is initiated in March when nutrient levels are high. Further (op. cit), NO_2-N and NH_4-N stimulated C. crispus growth indicating that nitrogen was limiting in the tank system. On the other hand, rapid growth of G. stellata in New Hampshire coincided with low April nutrient levels (Burns & Mathieson, 1972). Congruently, Gracilaria verrucosa in Wales exhibited rapid spring growth associated with minimal nitrogen and phosphorus values (Jones, 1955).

Identification of the factors that control or "cue" natural, benthic algal ontogentic progressions can only be deduced through detailed and extensive population studies in conjunction with corresponding analyses of environmental variables. The quantitative results of such studies can provide evidence and documentation of dynamic ontogenetic patterns and clues to the important chemical and physical variables that influence them. In the natural environment, the influences of these variables cannot be separated. Consequently, in situ population studies, besides contributing towards understanding the mechanisms of the natural algal population itself, can only provide extensive insight, correlations, and clues which are synthesized to ask more detailed and directed questions.

Two of the major questions derived from these population studies were approached through controlled laboratory investigation of the physiological effects of light and nutrients on *I. cordata* production.

APPENDIX 10

Iridaea cordata - Cumulative Regrowth from Experimental Plots Autumn 1973 to Autumn 1974

$$G_C = \frac{(\Sigma_i/N)_2 - (\Sigma_i/N)_1}{t_2 - t_1}$$

G_C = Growth Rate-Mg Dry Weight/625 cm^2/Day

Σ_i = Sum of total biomass values - Gm Dry Weight/625 cm^2

$(\Sigma_i/N)_2$ = Mean biomass

$(\Sigma_i/N)_1$ = Mean biomass from previous season

N = Number of samples

t_2-t_1 = Number of Days between consecutive harvests

$\overline{X}$ = Mean

SE = Standard Error of the Mean - 95% Confidence level

Var = Variance

APPENDIX 10

Iridaea cordata - Cumulative Regrowth
from Experimental Plots

Regrowth (Dry Weight Gm/625 cm^2)

	Original Harvest Autumn 1973		Winter 1974 (3 mos)	Spring (6 mos)	Summer (9 mos)	Autumn (12 mos)	Autumn (control)
Total Biomass	28.7	87.7	1.5	59.9	127.5	43.2	123.0
	66.3	151.8	0.8	15.3	86.4	86.7	86.1
	43.3	9.9	1.0	39.6	82.3	103.4	80.4
	34.1	100.0	3.7	56.6	87.5	96.2	114.6
	48.4	60.7					108.6
	8.2	66.5					
	88.6	69.8					
	111.1	130.7					
$\overline{X}$	68.99		1.75	42.85	95.93	82.38	102.54
SE	10.26		0.67	10.2	10.58	13.5	8.25
Var.	1683.46		1.77	416.4	448.14	728.9	340.3

Growth Rates (Mg Dry Weight/625 cm^2/Day)

	Winter 1974 (3 mos)	Spring (6 mos)	Summer (9 mos)	Autumn (12 mos)
1	17	639	1144	-451
2	9	149	589	-79
3	11	461	533	64
4	-12	603	603	2
Days	88	91	74	117
$\overline{X}$	20	452	717	-116
SE	8	112	143	115
Var	230	50	82	53

APPENDIX 11

Iridaea cordata - Discrete Seasonal Regrowth from Experimental Plots

(Three Month Increments)

Autumn 1973 to Winter 1974

$$G_D = \frac{\Sigma_i/N}{t}$$

G_D = Growth Rate-Mg Dry Weight/625 cm^2/Day

Σ_i = Sum of total biomass-Dues- Gm/625 cm^2

N = Number of samples

t = Discrete number of days between harvests

$\overline{X}$ = Mean

SE = Standard error of the mean - 95% Confidence level

V = Variance

APPENDIX 11

Iridaea cordata - Discrete Seasonal

Regrowth From Experimental Plots

Regrowth-Gm Dry Weight/625 cm^2

		Winter 1973-1974	Spring 1974	Summer 1974	Autumn 1974	Winter 1974-1975
Total Biomass	1	1.5	24.6	12.0	0	0.8
	2	0.8	24.6	0.8	0.2	1.5
	3	1.0	18.4	10.3	9.0	1.0
	4	3.7	65.2	4.9	0.4	3.7
	$\overline{X}$	1.75	33.2	7.0	2.4	1.75
	SE	0.67	10.77	2.56	2.2	0.67
	V	1.77	463.6	26.23	19.37	1.33

Growth Rates (Mg Dry Weight/625 cm^2/Day)

	Winter 1973-1974	Spring 1974	Summer 1974	Autumn 1974	Winter 1974-1975
1	17.0	270	162.0	0	11.0
2	9.0	270	11.0	2.0	20.0
3	11.0	202	139	77.0	13.0
4	42.0	716	66.0	3.0	49.0
$\overline{X}$	20.0	365	95.0	21.0	23.0
SE	8.0	118	35.0	19.0	9.0
V	0.23	56.0	5.0	1.0	0.32
Days	88	91	74	117	75

APPENDIX 12

Iridaea cordata Original Harvest from Experimental Plots
Dry Biomass (gm/625 cm^2)-Autumn 1973

Non-Reproductive	12.6	2.9	5.2	5.1	5.6	4.8	10.6	14.8
	12.0	15.8	8.4	13.2	13.1	12.8	7.0	7.1
Mean	9.44							
Standard Error	1.03							
Variance	16.96							
Tetrasporangial	6.8	63.4	30.3	24.0	42.8	3.4	76.0	93.7
	43.7	129.2	1.5	74.2	47.3	51.4	62.8	123.6
Mean	54.63							
Standard Error	9.66							
Variance	1494.5							
Cystocarpic	9.3	0	7.8	5.0	0	0	0	2.6
	32.0	6.8	0	12.6	0.3	2.3	0	0
Mean	4.92							
Standard Error	2.07							
Variance	68.41							

APPENDIX 13

Iridaea cordata: Cumulative Regrowth, Discrete Seasonal Regrowth from Experimental Plots Life History Stages

NR = Non-Reproductive Biomass

T = Tetrasporangial Biomass

C = Cystocarpic Biomass

M = Male Biomass

Control = Untreated Control Biomass from Natural Population

$\bar{X}$ = Mean

SE = Standard Error of the Mean

95% Confidence Level

V = Variance

APPENDIX 13

Iridaea cordata Discrete Seasonal Regrowth from Experimental Plots - Life History Stages

1973-1974

Biomass (Gm Dry Weight/625 cm^2)

		Winter	Spring	Summer	Autumn
NR		1.5	21.4	12.0	0
		0.8	20.6	0.8	0.2
		1.0	11.8	10.3	5.4
		3.7	54.5	3.4	0.4
	$\bar{X}$	1.8	27.1	6.6	1.5
	SE	0.7	9.4	2.7	1.3
	V	1.8	353.1	29.0	6.8
T		0	0	0	0
		0	0	0	0
		0	5.0	0	0.2
		0	10.7	0	0
	$\bar{X}$		3.9		.05
	SE		2.6		.05
	V		25.9		.01
C		0	0	0	0
		0	0	0	0
		0	0	0	3.4
		0	0	0	0
	$\bar{X}$				0.85
	SE				0.85
	V				2.89
M		0	3.2	0	0
		0	4.0	0	0
		0	1.6	0	0
		0	0	1.5	0
	$\bar{X}$		2.2	0.38	
	SE		0.89	0.37	
	V		3.1	0.56	

APPENDIX 13

Iridaea cordata Cumulative Regrowth from Experimental Plots - Life History Stages 1973-1974

Biomass (Gm Dry Weight/625 cm^2)

		Winter (3 mo)	Spring (6 mo)	Summer (9 mo)	Autumn (12 mo)	Autumn (control)
NR		1.5	40.0	44.2	6.6	15.2
		0.8	8.4	19.9	5.4	9.0
		1.0	14.1	32.9	6.1	25.5
		3.7	39.1	24.6	11.2	25.2
						17.0
	$\bar{X}$	1.75	25.4	30.4	7.33	18.38
	SE	0.67	8.3	5.33	1.31	3.14
	V	1.77	272.6	113.47	6.92	49.29
T		0	17.0	74.2	33.3	100.0
		0	3.2	66.5	81.3	75.5
		0	4.8	46.2	94.8	37.9
		0	16.1	61.7	81.6	88.9
						86.5
	$\bar{X}$	0	10.3	62.15	72.75	77.76
	SE	0	3.6	5.91	13.52	10.7
	V	0	53.0	139.53	731.24	572.21
C		0	0	0	1.8	7.6
		0	0	0	0	0
		0	0	.45	0.9	15.8
		0	0	0	1.9	0
						2.4
	$\bar{X}$	0	0	0.11	1.15	5.16
	SE	0	0	0.11	0.44	3.0
	V	0	0	.05	0.79	45.02
M		0	0	9.1	1.5	0.2
		0	3.7	0	0	1.6
		0	3.8	2.5	1.6	1.2
		0	1.4	1.2	1.5	0.5
						2.7
	$\bar{X}$	0	2.2	3.2	1.15	1.24
	SE	0	0.9	2.03	0.38	0.44
	V		3.4	16.5	0.59	0.98

APPENDIX 14

Iridaea cordata Tagged Thalli

Measurements:

S. A. = Thallus Surface Area (cm^2)
L = Thallus Length (cm)
W = Thallus Width (cm)
L×W = Thallus Length × Width (cm^2)
T = Thallus thickness ($cm \times 10^{-3}$)
# = Thallus identification number
Date = Date that measurements were made

( ) = Measurement dates if different from that of page heading.
(1) = 26 April 1974
(2) = 24 May 1974
(3) = 21 July 1974
(4) = 16 October 1974
(5) = 12 December 1974
(6) = 25 January 1975

Appendix 14, continued

Iridaea cordata Tagged Thalli

#	6 February 1974					5 March				
	S.A.	L	W	L×W	T	S.A.	L	W	L×W	T
1					38.1					38.1
2	18.7	10.2	2.6	26.5	48.3	19.9	11.5	2.5	28.8	43.2
4		9.1	2.2	20.0	38.1		8.8	2.8	24.6	40.6
5	22.2	10.5	2.8	29.4	35.6	21.3	10.2	2.9	29.6	35.6
29						9.3	5.6	2.5	14.0	22.8
32						9.5	6.2	2.1	13.0	22.8
33						13.4	6.9	2.6	17.9	25.4
36						6.4	4.7	1.8	8.5	40.6
37						7.5	7.0	2.0	14.0	33.0
38						5.8	6.0	1.0	6.0	27.9
40										25.4
44										
45										
47										
48										
51										
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62										
63										
64										

Appendix 14, continued

#	25,26 April S.A.	L	W	LxW	T	23,24 May S.A.	L	W	LxW	T
1										
2										
4										
5										
29	165.3	23.0	11.1	255.3	38.1	276.4	32.6	13.0	423.8	48.3
32	58.2	17.8	4.7	83.7	27.9	107.5	28.7	5.8	166.5	33.0
33	115.9	24.8	6.6	163.68	35.6	187.4	38.7	7.2	278.6	43.2
36	75.3	19.0	5.8	110.2	40.6	132.3	29.8	6.2	184.8	48.3
37	45.1	15.0	4.0	60.0	48.3	68.2	23	5.0	115.0	50.8
38	92.5	22.0	7.0	154.0	40.6					
40					35.6					35.6
44	11.7	8.0	3.0	24.0	30.5	[2]35.6	13.0	5.0	65.0	25.4
45	14.1	9.0	3.0	27.0	30.5	65.1	18.0	6.0	108.0	25.4
47					30.5					
48					30.5					35.6
51	10.5	7.0	2.5	17.5	22.8	26.1	10.0	4.0	40.0	30.5
52	8.1	6.0	2.0	12.0	22.8	18.0	10.0	3.0	30.0	27.9
53	7.6	6.0	2.0	12.0	30.5	13.2	8.0	3.0	24.0	30.5
54	19.7	9.0	4.0	36.0	22.9	28.6	12.0	4.0	48.0	30.5
55	21.8	11	4.0	44.0	27.9	37.8	16.0	4.0	64.0	30.5
56	25.3	12.0	4.0	48.0	33.0	41.3	19.0	4.0	76.0	38.6
57	7.8	6.0	2.0	12.0	22.8	12.4	8.0	2.5	20.0	27.9
58	21.7	10.0	4.0	40.0	27.9	25.0	15.0	3.0	45.0	33.0
60					25.4	77.6	23.0	5.0	115.0	30.5
61	7.6	7.0	2.0	14.0	17.8	17.7	10.0	3.0	30.0	22.8
62	6.6	6.0	2.0	12.0	27.9	8.8	7.0	2.0	14.0	27.9
63	8.5	7.0	2.0	14.0	22.8	11.3	8.0	2.5	20.0	25.4
64	22.3	10.0	3.0	30.0	27.9					
65	16.5	10.0	3.0	30.0	22.8	46.0	16.0	5.0	80.0	30.5
67					22.8	54.2	19.0	5.0	95.0	27.9
68	57.5	12.0	3.0	36.0	33.0	95.8	19.0	9.0	171.0	43.2

Appendix 14, continued

	25,26 April					23,24 May				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
69	16.6	9.0	3.0	27.0	17.8	30.2	12.0	4.0	48.0	25.4
71	9.7	7.0	2.5	17.5	27.9	19.2	8.0	3.0	24.0	27.9
72	24.4	8.0	5.0	40.0	30.5	51.8	14.0	5.5	77.0	38.1
73	16.4	7.5	4.0	30.0	35.6	37.3	11.5	5.5	63.3	38.1
74						14.0	8.0	3.0	24.0	27.9
75						36.2	9.0	6.0	54.0	30.5
76										30.5
77						146.1	28.0	7.5	210.0	40.6
79						12.0	6.0	2.0	12.0	30.5
81						50.3	18.0	4.5	81.0	35.6
82						64.3	18.0	6.0	108.0	35.6
83						28.3	11.0	4.0	44.0	35.6
84						22.7	9.5	3.5	33.3	38.1
85						33.0	12.0	4.5	54.0	27.9
86						45.0	13.5	6.0	81.0	35.6
87						8.5	5.0	2.5	12.5	27.9
88						5.2	4.0	2.0	8.0	27.9

Appendix 14, continued

	6 June					21 June				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
1						21st				
2										
4										
5										
29	403.5	40.1	15.7	626.6	53.3	474.5	48.6	16.0	777.6	
32	142.4	33.9	7.0	237.3	33.0	183.2	37.6	7.2	270.7	
33	298.3	48.7	8.4	409.1	50.0	354.8	54.7	8.5	465.0	
36	187.1	34.4	6.5	223.6	48.3	206.2	38.6	6.8	262.5	
37					50.0					
38										
40					46.5					
44	43.1	14.0	5.0	70.0	25.4					
45	122.9	25.0	8.0	200.0	30.5					
47	34.1	12.0	4.0	48.0	43.2					
48					35.6					
51	45.3	13.0	6.0	78.0	30.5					
52	27.9	12.0	4.0	48.0	27.9					
53	19.2	10.0	3.0	30.0	30.5					
54	37.5	12.0	4.0	48.0	33.0					
55	48.9	17.0	4.0	68.0	33.0					
56	50.2	21.0	4.0	84.0	40.6					
57	16.0	8.0	3.0	24.0	25.4					
58	32.0	16.0	3.0	48.0	40.6					
60	121.0	31.0	6.0	186.0	38.1					
61										
62										
63										
64										
66										
67										

Appendix 14, continued

#	6 June					21 June				
	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
68										
69										
71										
72										
73										
74						10.3	7.0	2.0	14.0	30.5
75						25.8	9.0	5.0	45.0	34.8
76						22.0	12.0	4.0	48.0	32.3
77						249.3	41.0	9.5	389.5	43.7
79						6.5	5.6	1.5	8.4	27.9
81						44.0	17.0	4.0	68.0	30.5
82						81.3	21.0	6.0	126.0	33.0
83						39.0	14.0	4.0	56.0	38.6
84						27.4	12.0	4.0	48.0	33.0
85						81.5	21.0	5.5	115.0	29.2
86						83.1	19.0	6.0	114.0	35.6
87						10.4	6.0	2.5	15.0	25.4
88						4.6	4.6	1.4	6.4	20.3

Appendix 14, continued

#	20,21 July S.A.	L	W	L×W	T	17 August S.A.	L	W	L×W	T
1										
2										
4										
5										
29	653.3	61.8	16.8	1038.2	63.0	862.9	76.0	18.8	1428.8	
32	233.8	49.3	7.5	369.8	40.6	295.1	58.0	6.3	365.4	
33	397.4	58.2	9.2	535.4	57.4	278.1	41.0	9.0	369.0	
36	285.6	51.5	6.8	350.2	55.9	250.5	63.5	8.0	508.0	
37										
38										
40					50.8					
44	49.2	15.0	6.0	90.0	31.2					
45	300.5	38.0	10.0	380.0	42.7	375.9	50.0	11.0	550.0	
47	98.2	19.0	7.0	133.0	46.2					
48					38.1					
51	74.0	17.0	8.0	136.0	36.8	99.7	19.0	7.0	133.0	
52	45.0	16.0	5.0	80.0	36.3	65.0	19.0	6.0	114.0	
53	20.7	12.0	3.0	36.0	30.5					
54	39.3	13.0	4.0	52.0	34.3					
55										
56	67.2	35.0	4.0	140.0	43.2					
57	16.7	9.0	3.0	27.0	27.9					
58	35.3	17.0	3.0	51.0	41.9					
60	[3]221.4	45.0	7.0	315.0	46.5					
61	54.0	16.0	6.0	96.0	26.7					
62	12.3	8.0	2.5	20.0	25.9					
63	15.7	8.5	3.0	25.5	24.6					
64										
66										
67	127.5	31.0	6.5	201.5	33.8					

Appendix 14, continued

	20,21 July					17 August				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
68	148.9	24.0	12.0	288.0	34.8					
69	42.2	14.0	4.5	63.0	25.4					
71	26.3	11.5	4.0	46.0	38.1					
72	115.0	21.0	7.5	157.5	39.4					
73	58.7	12.0	8.5	102.0	44.5					
74	14.5	9.0	2.5	22.5	31.2					
75	40.0	10.0	7.0	70.0	33.0					
76	40.0	13.0	5.0	65.0	34.3					
77	240.8	53.0	10.0	530.0	50.8					
79	8.9	6.5	2.0	13.0	36.8					
81										
82	121.9	28.0	7.0	196.0	39.4					
83	60.4	18.0	4.5	81.0	34.8					
84	41.5	14.0	5.0	70.0	38.1					
86					40.6					
87	14.1	6.5	3.0	19.5	31.2					
88	8.0	5.0	2.0	10.0	24.6					

Appendix 14, continued

#	15,16 October S.A.	L	W	LxW	T	29 November S.A.	L	W	LxW	T
1										
2										
4										
5										
29										
32	356.6	65.0	7.0	455.0	43.9	397.6	65.5	7.3	478.3	53.3
33	265.0	41.0	9.0	373.5	55.9	218.5	32.5	9.0	292.5	58.4
36										
37										
38										
40										
44	71.0	17.0	7.0	119.0	32.3					
45	573.5	62.0	14.0	868.0	56.6					
47					4					
48					37.6					
51	45.3	12.0	8.0	96.0	39.4	27.1	13.0	3.0	39.0	38.1
52	84.1	23.0	6.0	138.0	36.8	53.3	14.0	6.0	84.0	38.6
53					33.8					
54	46.6	14.0	4.0	56.0	36.1	57.0	17.0	5.0	85.0	37.3
55										
56	98.6	31.0	5.0	155.0	49.0					
57	20.0	10.0	3.0	30.0	28.7					29.2
58	42.2	19.0	4.0	76.0	45.0					
60	368.4	31.0	7.5	232.5	55.4					
61	71.0	19.0	6.0	114.0	28.5	57.0	20.0	6.0	120.0	32.5
62	14.0	8.0	3.0	24.0	27.4	5.2	4.8	2.3	11.0	35.6
63	15.5	9.0	3.0	27.0	22.9					
64										
66										
67	175.2	37.0	7.0	259.0	35.6					

Appendix 14, continued

#	15,16 October S.A.	L	W	LxW	T	29 November S.A.	L	W	LxW	T
68	45.1	14.0	9.0	126.0	37.3					
69	32.9	17.0	4.5	76.5	23.6	6.8	5.5	2.5	13.8	30.5
71	32.4	12.0	4.5	54.0	32.3	34.5	12.0	4.5	54.0	34.8
72	156.3	24.0	9.0	216.0	42.4	163.8	25.0	9.0	225.0	47.5
73	72.6	13.0	9.0	117.0	40.6	69.6	14.0	9.0	126.0	41.4
74										
75						55.6	11.0	8.0	88.0	35.1
76						53.5	16.0	5.0	80.0	32.3
77	252.2	35.0	10.0	350.0	49.0	334.7	40.0	12.0	480.0	50.0
79	14.4	8.0	2.5	20.0	32.3	11.9	7.5	2.0	15.0	29.7
81										
82	174.7	33.0	8.0	264.0	39.9					
83	94.6	25.5	5.0	127.5	33.8	97.8	25.0	5.0	125.0	35.6
84	45.2	15.5	5.0	77.5	33.8	48.4	15.4	5.2	77.0	37.3
85										
86	292.2	50.0	10.5	525.0	49.0	78.1	17.5	8.5	148.8	48.3
87										
88										

Appendix 14, continued

#	11 December					9 January				
	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
1										
2										
4										
5										
29										
32	370.3	67.9	8.0	543.2	53.3	325.8	53.4	11.0	587.4	49.0
33										
36										
37										
38										
40										
44										
45										
47										
48										
51	19.3	12.0	3.0	36.0	40.6					
52	26.4	13.0	3.0	39.0	40.6					
53										
54	58.6	15.0	5.0	75.0	37.6					
55										
56										
57	25.4	11.0	4.0	44.0	40.0					
58										
60										
61					32.5					
62					35.6					
63										
64										
66										
67										

Appendix 14, continued

#	11 December S.A.	L	W	LxW	T	9 January S.A.	L	W	LxW	T
68										
69										
71	31.9	12.0	4.5	54.0	31.8					
72	156.1	24.0	9.0	216.0	47.0					43.2
73	78.9	15.0	9.0	135.0	43.2	71.9	14.0	9.5	133.0	42.4
74										
75	61.3	12.0	8.0	96.0	34.3	72.2	13.0	9.0	117.0	36.8
76	54.2	17.0	5.0	85.0	32.3	61.6	18.0	6.0	108.0	34.8
77	306.0	39.0	11.5	448.5	55.4					
79	12.0	7.5	2.0	15.0	33.0	12.8	7.5	2.0	15.0	30.5
81										
82										
83	98.2	26.0	5.0	130.0	36.1	107.1	27.5	5.5	151.3	35.6
84	50.7	17.0	5.5	93.5	38.1	57.6	18.0	5.5	99.0	36.3
85										
86	72.1	18.0	8.5	153.0	47.8	80.9	19.0	9.0	171.0	46.2
87										
88										

Appendix 14, continued

#	24 January					23 February				
	S.A.	L	W	L×W	T	S.A.	L	W	L×W	T
1										
2										
4										
5										
29										
32	21.2	11.0	5.0	55.0	51.3					40.6
33										
36										
37										
38										
40										
44										
45										
47										
48										
51										
52										
53										
54										
55										
56										
57										
58										
60										
61										
62										
63										
64										
66										
67										

Appendix 14, continued

	24 January					23 February				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
68										
69										
71										
72	211.2	35.0	11.0	385.0	55.1					
73	76.0	14.0	7.0	98.0	47.5					
74										
75										
76										
77										
79										
81										
82										
83	110.2	28.0	5.0	140.0	37.6	67.1	18.0	5.5	99.0	41.2
84					37.3	47.9	14.5	5.0	72.5	42.4
85										
86	84.9	18.0	9.0	162.0						
87										
88										

Appendix 14, continued

#	21 July S.A.	L	W	LxW	T	16 October S.A.	L	W	LxW	T
96	11.9	8.4	2.3	19.3	32.3					
97	20.8	11.2	2.7	30.2	31.8					
98	12.7	7.9	2.1	16.6	30.5					
99	15.8	10.7	2.1	22.5	33.0	16.4	11.2	2.2	24.6	32.5
100	24.2	13.4	2.9	38.9	31.8	30.8	15.3	3.3	50.5	42.7
102	25.1	9.4	4.4	41.4	29.2	11.7	7.5	2.7	20.3	24.9
103	30.7	12.5	3.6	45.0	25.4	16.7	10.0	2.7	27.0	33.5
104	30.0	13.1	3.2	41.9	26.2	30.8	14.7	3.8	55.9	42.4
105	9.6	7.6	1.8	13.7	36.1	7.0	5.2	1.9	9.9	35.1
111						7.0	6.1	1.8	11.0	28.7
112						18.2	9.4	2.9	27.3	26.7
113						21.5	10.8	2.9	31.3	30.5
114						18.1	10.6	2.9	30.7	24.9
115						14.3	8.9	2.3	20.5	33.0
116						28.0	12.4	3.8	47.1	35.1
117						34.4	11.0	4.7	51.7	30.5
118						33.0	12.6	4.0	50.4	33.5
119										
121										
122										
123										
124										
125										
126										
127										
128										
129										
130										
131										
132										

Appendix 14, continued

	30 November					11,12 December				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
96	12.6	8.7	2.2	19.1	27.9	13.0	8.5	2.3	19.6	32.3
97										
98	12.3	8.6	2.3	19.8	27.9	13.4	8.5	2.3	19.6	29.2
99	22.8	13.7	2.3	31.5	28.1					
100	42.9	18.4	3.8	69.9	40.6	48.8	18.6	4.3	80.0	43.7
102	7.8	7.8	2.1	16.4	27.9	4.8	4.8	1.5	7.2	40.1
103	15.0	9.9	2.6	25.7	33.0	15.2	9.2	2.6	23.9	34.8
104										
105										
111	9.4	7.5	2.0	15.0	31.2	9.7	7.2	2.0	14.4	31.2
112	23.0	9.1	3.1	28.2	22.8	23.8	11.3	3.1	35.0	24.1
113	26.1	12.2	3.0	36.6	30.0	27.3	12.2	3.2	39.0	30.0
114	22.6	12.0	2.7	32.4	25.4	22.3	11.9	2.6	30.9	26.7
115	11.9	7.8	2.3	17.9	28.7	12.2	7.4	2.3	17.0	29.7
116	28.2	12.6	3.8	47.9	34.3	29.2	12.7	4.0	50.8	36.3
117	35.0	12.3	4.7	57.8	31.8	37.2	12.1	4.7	56.9	33.0
118	33.8	15.1	3.9	58.9	30.5	35.7	13.9	4.1	57.0	32.3
119	15.8	9.5	2.4	22.8	26.2	^{5}16.5	10.1	2.4	24.2	27.2
121	11.9	8.8	2.1	18.5	27.9	10.9	8.1	1.9	15.4	29.7
122	19.2	10.8	2.6	28.1	28.7	19.0	10.8	2.5	27.0	30.5
123	23.0	10.2	3.8	38.8	36.3	23.0	10.5	3.7	38.9	36.3
124	27.3	10.9	3.4	37.1	27.2	25.3	10.4	3.3	34.3	29.2
125	30.8	11.8	4.4	51.9	23.6	30.9	12.0	4.4	52.8	26.7
126	22.5	9.6	3.2	30.7	20.3	20.7	9.0	3.2	28.8	22.8
127										
128										
129										
130										
131										

Appendix 14, continued

#	9 January 1975					24,25 January				
	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
96	14.0	8.7	2.3	20.0	27.4	14.4	9.4	2.4	22.6	28.5
97										
98	13.3	8.5	2.3	19.6	29.7	13.8	8.9	2.3	20.5	26.2
99										
100										
102					50.8	95.6	17.7	8.7	154.0	52.6
103	16.8	10.1	2.6	26.3	40.6	7.4	5.5	2.7	14.9	58.4
104										
105										
111	10.2	7.8	2.1	16.4	27.9	7.6	5.7	2.1	12.0	30.5
112	24.3	11.1	3.2	35.5	24.6	23.4	10.7	3.1	33.2	24.6
113	24.4	11.6	2.8	32.5	26.7	28.1	11.5	3.4	39.1	28.5
114	23.1	12.0	2.7	32.4	24.1	23.2	11.7	2.7	31.6	25.4
115	11.4	8.0	2.2	17.6	25.9	12.2	7.5	2.4	18.0	29.2
116	27.1	12.7	3.8	48.3	35.6	51.7	21.0	5.4	113.4	38.6
117	37.6	11.7	4.8	56.2	30.5	35.7	11.4	4.6	52.4	31.8
118	34.8	13.8	4.1	56.6	29.7					33.0
119	15.0	9.5	2.4	22.8	28.7					
121										
122	13.9	11.1	2.5	27.8	23.6	3.7	3.8	2.0	7.6	
123	18.9	10.2	2.5	25.5	32.5	19.0	11.9	2.8	33.3	33.8
124					27.9	25.7	10.5	3.4	35.7	29.7
125	29.6	11.6	4.5	52.2	28.7	42.8	13.8	5.1	70.4	37.6
126										
127						[6]11.9	8.0	2.5	20.0	25.4
128						22.5	10.5	3.6	37.8	22.1
129						23.9	10.6	4.0	42.4	31.8
130						4.7	5.6	1.5	8.4	32.3
131						8.2	5.6	2.1	11.8	24.9

Appendix 14, continued

	9 January					24,25 January				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
132						4.4	3.9	1.5	5.9	27.9
133						8.4	6.5	1.7	11.1	25.9
134						8.4	6.4	2.0	12.8	27.2
135						3.5	3.6	1.8	6.5	
136						5.2	4.1	1.7	7.0	
137										19.8
139						4.7	4.2	1.5	6.3	25.4
140						6.1	4.5	2.1	9.1	31.2
141						9.8	5.7	2.9	16.5	24.9
142						3.4	4.2	1.3	5.5	33.0
143						3.2	4.2	1.1	4.6	38.1
147						7.5	5.9	1.8	10.6	15.2
149										
150										
151										
152										
153										

Appendix 14, continued

	23 February					29 March				
#	S.A.	L	W	L×W	T	S.A.	L	W	L×W	T
96										
97										
98	16.3	10.0	2.3	23.0	24.6	6.8	4.9	2.6	12.7	43.2
99										
100										
102										
103	7.3	6.0	3.4	20.4						
104										
105										
111	5.1	4.8	1.7	8.2	27.9					
112	22.9	11.5	3.0	34.5	24.9					
113	28.7	12.7	3.2	40.6	29.7	31.7	13.4	3.4	45.6	32.5
114	23.5	12.3	2.8	34.4	25.4	28.4	12.7	3.0	38.1	29.2
115	13.4	7.9	3.4	26.9	35.1					
116	31.3	12.9	4.1	52.9	37.3					
117	39.9	12.4	5.0	62.0	34.8	49.5	13.5	5.9	79.7	40.6
118										
119										
121										
122										
123										
124	20.9	11.6	3.1	36.0	28.7					
125	69.3	15.4	7.6	117.0	55.1	70.7	22.7	7.0	158.9	50.0
126										
127	41.2	12.3	4.0	49.2	33.0	200.5	31.1	9.9	307.9	47.5
128	78.6	18.5	6.9	127.7	29.7					
129	73.9	14.6	6.9	100.7	41.2	261.2	26.2	13.0	340.6	52.8
130	17.9	9.1	3.4	30.9	25.9	47.3	13.2	6.5	85.8	38.1
131	17.3	10.0	3.1	31.0	30.5	35.3	14.0	2.7	37.8	42.4

Appendix 14, continued

#	23 February S.A.	L	W	LxW	T	29 March S.A.	L	W	LxW	T
132	14.5	7.7	2.8	21.6	27.4	44.1	12.6	5.3	66.8	35.1
133	18.2	9.4	3.0	28.2	27.4	41.8	13.3	6.0	79.8	41.2
134	28.3	11.1	3.8	42.2	27.4	89.0	19.7	5.8	114.3	43.7
135	16.9	7.8	3.0	23.4	15.8	52.9	13.1	6.6	86.5	28.5
136	28.8	9.3	4.5	41.9	21.6	91.3	18.6	7.6	141.4	27.9
137	11.2	6.7	2.7	18.1	19.1	46.0	12.6	5.6	70.6	30.5
139	28.9	9.7	4.8	46.6	24.9	147.0	23.1	9.6	221.8	36.8
140	26.4	8.3	4.8	39.8	33.5	68.7	14.6	8.0	116.8	
141	48.9	12.8	4.3	55.0	29.2	234.2	28.6	11.9	340.3	46.2
142	7.8	5.6	2.2	12.3	48.3	17.7	8.1	3.6	29.2	55.4
143	10.0	8.1	2.6	21.1	27.4	38.5	15.9	4.5	71.6	46.2
147	35.8	11.9	4.2	50.0	21.6					
149	9.0	6.8	2.0	13.6	22.1	37.5	16.0	3.0	48.0	31.0
150	14.9	6.9	3.5	24.2	19.1					
151	14.5	8.2	2.6	21.3	27.9	79.0	21.0	3.9	81.9	36.1
152	15.1	8.0	2.9	23.2	23.4	75.3	22.7	4.4	99.9	38.9
153	3.3	3.9	1.2	4.7	24.1	11.7	7.4	1.4	10.4	27.9

Appendix 14, continued

	26 April					26 May				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
96										
97										
98										
99										
100										
102										
103										
104										
105										
111										
112										
113										
114										
115										
116										
117										
118										
119										
121										
122										
123										
124										
125	42.9	8.3	9.3	77.2	55.1					
126										
127	46.4	18.4	4.0	73.6	52.1					
128										
129	286.6	31.7	13.2	418.4	39.9					
130	79.3	18.3	8.2	150.1	47.8	98.9	17.3	9.9	171.3	51.6
131	35.8	14.8	3.9	57.7	46.2	37.0	13.9	2.8	38.9	43.9

Appendix 14, continued

	26 April					26 May				
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
132	82.1	19.2	6.8	130.6	33.5	149.2	26.6	7.6	202.2	42.7
133										
134										
135	142.9	22.3	11.2	249.8	27.4	237.0	28.5	13.1	370.5	38.9
136	197.6	29.7	10.7	317.8	34.3					
137	92.0	17.3	8.0	138.4	41.4	100.5	18.5	8.9	164.7	46.2
139										
140										
141	27th									
142	27.4	9.7	3.6	34.9	66.0	24.1	9.2	4.9	45.1	53.3
143	123.5	16.7	16.9	282.2	38.6	218.1	24.5	7.8	191.1	43.2
147	316.0	32.2	13.7	441.1	45.7					
149	94.0	24.8	4.8	119.0	34.8	125.7	33.0	5.4	178.2	39.9
150										
151	231.7	36.2	7.6	275.1	41.2	351.5	45.7	10.5	479.2	45.7
152	229.5	43.1	7.0	301.7	52.8	295.5	49.5	7.2	356.4	55.1
153	26.1	11.2	3.9	43.7	31.2					

Appendix 14, continued

	9 July									
#	S.A.	L	W	L×W	T	S.A.	L	W	L×W	T
96										
97										
98										
99										
100										
102										
103										
104										
105										
111										
112										
113										
114										
115										
116										
117										
118										
119										
121										
122										
123										
124										
125										
126										
127										
128										
129										
130	93.1	19.1	9.0	171.9	58.4					
131	38.3	13.8	4.3	59.3	53.3					

Appendix 14, continued

	9 July									
#	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
132										
133										
134										
135	121.7	21.0	9.1	191.1	33.8					
136										
137										
139										
140										
141										
142	25.1	10.0	5.5	55.0	73.7					
143	293.1	36.6	8.0	292.8	53.3					
147										
149	159.2	39.0	5.8	226.2	38.7					
150										
151	453.5	51.1	12.2	623.4	47.5					
152	311.0	45.9	8.0	367.2	57.7					
153										

Appendix 14, continued

#	24 February					29 March				
	S.A.	L	W	LxW	T	S.A.	L	W	LxW	T
155	8.7	6.8	2.1	14.3	27.2	65.6	17.1	5.9	100.9	27.2
156	7.6	6.3	2.0	12.6	24.6	49.9	14.1	5.6	79.0	27.9
157	6.0	5.6	1.6	9.0	27.9	41.6	13.5	4.8	64.8	29.2
158	4.3	4.7	1.4	6.6	27.2	24.3	11.3	3.7	41.8	27.9
160	5.1	4.6	1.6	7.4	25.4	26.5	12.0	2.7	32.4	24.1
162	6.8	5.6	1.8	10.1	23.4	47.9	14.5	5.0	72.5	35.3
163	6.8	5.5	1.9	10.5	24.9	37.9	13.9	4.5	62.6	31.8
164	7.9	7.6	1.8	13.7	24.1	49.2	16.4	4.7	77.1	22.9
165	7.5	6.7	1.8	12.1	25.4	45.3	17.4	4.1	71.3	38.1
166	9.4	7.9	1.8	14.2	22.4	39.9	17.9	4.5	80.6	31.2
167	10.9	8.0	2.3	18.4	29.2	25.6	13.3	3.2	42.6	
168	4.7	5.4	1.6	8.6	29.2	28.3	10.6	4.0	42.4	31.8
169	4.7	5.1	1.3	8.2	25.4	27.3	12.0	4.0	48.0	
170	9.1	6.6	2.3	15.2	28.7	67.6	16.6	6.3	104.6	35.6
171	7.3	6.1	1.8	11.0	27.9	5.8	5.7	2.1	12.0	
172										
173										
174										
179										
180										
181										
182										

Appendix 14, continued

#	27 April S.A.	L	W	LxW	T	26 May S.A.	L	W	LxW	T
155	240.2	33.3	11.0	366.3	37.6	273.9	31.0	9.6	297.6	46.5
156	136.7	24.4	8.7	212.3	34.3	191.7	28.5	10.1	287.9	41.2
157	149.4	28.3	10.2	288.7	40.6	241.5	39.4	11.7	461.0	49.0
158	123.6	25.0	7.5	187.5	40.0					40.0
160	129.9	21.0	8.9	186.9	41.4	154.5	28.2	8.2	231.2	40.0
162						366.2	39.3	15.5	609.2	48.3
163						183.6	34.3	9.0	308.7	47.0
164	169.8	29.7	8.5	252.5	34.3	267.2	33.6	11.0	373.0	41.9
165	169.9	31.1	9.1	283.0	34.3	367.9	50.8	11.5	584.2	36.1
166	175.1	37.6	8.0	300.8	37.6					
167	71.8	22.9	4.5	103.1	36.8	110.3	29.3	6.5	190.5	39.4
168	119.8	22.0	8.6	189.2	40.0	134.9	29.8	7.4	220.5	37.3
169	112.8	24.1	7.8	188.0	35.6	163.2	27.4	8.8	241.1	34.8
170	189.0	30.2	8.2	247.6	51.3	165.0	26.4	9.5	250.8	50.0
171										
172	8.7	6.3	1.9	12.0	32.5	16.4	9.0	2.7	24.3	33.0
173	8.7	6.6	1.9	12.5	28.7	23.6	11.4	3.2	36.5	27.4
174	11.8	7.6	2.4	18.2	28.7	43.9	15.4	4.6	70.8	31.8
179	12.2	9.0	2.0	18.0	28.7	20.1	12.1	1.9	23.0	23.6
180	21.1	12.7	3.0	38.1	26.7	39.2	17.6	3.1	54.6	27.4
181	33.3	13.2	3.6	47.5	26.2	56.0	18.2	3.7	67.3	30.5
182	34.6	15.6	3.4	53.0	24.6	14.0	9.7	2.7	26.2	35.6

Appendix 14, continued

#	9 July S.A.	L	W	LxW	T
155					51.6
156	251.4	33.8	10.3	348.1	47.5
157	267.9	45.5	11.9	541.5	52.6
158	349.7	45.6	11.0	501.6	50.8
160	232.4	35.1	10.0	351.0	39.9
162	604.3	60.6	15.0	909.0	46.5
163	265.4	54.3	9.8	532.1	43.2
164	309.9	36.2	13.5	488.7	46.5
165	750.3	79.0	16.7	1319.3	50.8
166					
167	267.6	51.4	8.6	442.0	49.5
168	209.5	43.9	8.5	373.2	39.9
169	210.7	33.8	9.7	327.9	40.6
170	165.9	27.7	9.5	263.2	54.1
171					
172					
173					
174					
179	18.9	10.2	3.2	32.6	38.1
180	72.0	22.9	5.1	116.8	38.1
181	90.4	25.2	6.6	166.3	38.1
182	16.0	9.6	3.2	30.7	38.1

APPENDIX 15

Iridaea cordata Tagged Thalli
Growth Rate (G) in Surface Area (cm^2)

$$G = \frac{A_b - A_a}{t_b - t_a}$$

A(a,b) = Surface Area (cm^2) on specific dates listed at top of page.

t(a,b) = Number of days between measurement dates.

= Thallus idenfification number.

Asterisk(s) = Dates if different from those listed at top of page

* = 21 July 1974

** = 12 December 1974

*** = 27 April 1975

**** = 24 February 1975

$\bar{X}$ = Mean growth rate of a tagged group of thalli.

SE = Standard error of the mean (95% confindence level) for growth rate of a group of tagged thalli.

-G = A minus growth rate indicates a loss in thallus surface area between two successive dates.

Appendix 15, continued

Iridaea cordata Annual Growth Rate

#	Dates 6 Feb 1974	5 March	25 April	23,24 May	6 June	20 June	20,21 July	17 Aug	15 Oct	29 Nov	11 Dec	9 Jan 1975	24 Jan
1													
2		0.04											
4													
5		0.03											
$\overline{X}$		.035											
N		2											
SE		.005											
29			3.06	3.97	9.08	4.73	6.62	7.49					
32			0.95	1.76	2.49	2.72	1.87	2.19	1.04	0.91	-2.10	-1.53	-20.31
33			2.01	2.55	7.92	3.77	1.58	-4.26	-0.22	-1.03			
36			1.35	2.04	3.91	1.27	2.94	-1.25					
37			0.74	0.83									
38			1.70										
$\overline{X}$			1.64	2.23	5.85	3.12	3.25	1.03					
N			6	5	4	4	4	4					
SE			0.34	0.52	1.58	0.74	1.16	2.52					
44				24th 0.82	0.58		0.14		0.25				
45				1.76	4.45		4.04	2.69	3.35				
47							1.46						
51				0.56	1.48		0.65	0.92	-0.92	-0.4	-0.65		
52				0.35	0.76		0.39	0.71	0.32	-0.68	-2.24		
53				0.20	0.46		0.03						
54				0.32	0.68		0.04		0.08	-0.23	0.13		

Appendix 15, continued

Dates

#	6 Feb 1974	5 March	25 April	23,24 May	6 June	20 June	20,21 July	17 Aug	15 Oct	29 Nov	11 Dec	9 Jan 1975	24 Jan
55				0.57	0.85								
56				0.57	0.68		0.39		0.36				
57				0.16	0.28		0.02		0.02		0.09		
58				0.12	0.54		0.08		0.08				
60					3.4		2.26		1.67				
61				0.36			*0.63		0.20	-0.31			
62				0.08			0.06		0.02	-0.19			
63				0.10			0.08		-.002				
66				1.05									
67							1.26		0.55				
68				1.35			0.92		-1.19				
69				0.49			0.21		-0.11	-0.58			
71				0.34			0.12		0.07	0.05	-0.22		
72				0.98			1.09		0.48	0.17	-0.64		1.25
73				0.75			0.37		0.16	-0.07	0.78	-0.24	0.27
$\overline{X}$				0.58	1.29		0.71	1.44	0.30	-0.25	-0.39		
N				19	11		20	3	18	9	7		
SE				0.10	0.41		0.22	0.63	0.23	0.09	0.36		

Appendix 15, continued

#	Dates 21 June 1974	21 July	16 Oct	29 Nov	11,12 Dec	9 Jan 1975	24 Jan	23 Feb	29 March
74	-0.13	0.14							
75	-0.37	0.46		0.12	0.48	0.38			
76		0.58		0.10	0.06	0.25			
77	3.69	2.95	-1.02	1.87	-2.39				
79	-.196	0.07	0.06	0.06	0.008	0.03			
81	0.23								
82	0.61	1.31	0.61						
83	0.38	0.69	0.39	0.07	0.03	0.31	0.21	-1.44	
84	0.17	0.45	0.04	0.07	0.19	0.24		-0.22	
85	1.73								
86	1.36		1.77	-4.87	-0.50	0.3	0.27		
87	0.07	0.12							
88	-0.02	0.11							
$\bar{X}$	0.63	0.69	0.31	-0.37	-0.3	0.25			
N	12	10	6	7	7	6			
SE	0.33	0.28	0.37	0.79	0.36	0.05			
96				0.005	0.036	0.034	0.027		
98				0.003	0.1	-0.003	0.033	0.083	-0.26
99			0.007	0.14					
100			0.077	0.26	0.54				
102			-0.16	-0.09	-0.23		2.06		
103			-0.16	-0.04	0.02	0.06	-0.63	0.01	
104			0.01						
105			-0.03						
$\bar{X}$			.001	.055	.09	.03	0.37		
N			6	6	5	3	4		

Appendix 15, continued

#	Dates 21 June 1975	21 July	16 Oct	29 Nov	11,12 Dec	9 Jan 1975	24 Jan	23 Feb	29 March
SE			0.023	.064	.125	.018	0.58		
111				0.06	0.02	0.02	-0.19	-0.08	
112				0.11	0.06	0.02	-0.06	-0.02	
113				0.11	0.09	-0.01	0.25	0.02	0.08
114				0.10	-0.02	0.03	0.01	0.01	0.13
115				-0.05	0.03	-0.03	0.05	0.04	
116				.0044	0.09	-0.07	1.64	-0.68	
117				0.01	0.20	0.01	-0.13	0.14	0.26
118				0.02	0.17	-0.03			
$\overline{X}$				0.046	0.08	0.019	0.23	-.081	0.16
N				8	8	8	7	7	3
SE				0.021	0.026	0.017	0.24	0.103	0.05
119					0.06	-0.05			
121					-0.08				
122					**-0.02	-0.18	-0.68		
123					0	-0.15	0.01		
124					-0.17		0.01	0.16	

Appendix 15, continued

Dates

#	12 Dec	9 Jan 1975	24 Jan	23,24 Feb	29 March	26,27 April	26 May	9 July
125	0.01	-0.05	0.88	0.88	0.04	-0.99		
126	0.15							
$\overline{X}$	-.077	-.108	.055					
N	7	4	4					
SE	0.04	0.034	0.32					
127				1.01	4.31	-5.5		
128				1.93				
129				1.72	5.06	0.91		
130				0.46	0.79	1.14	0.65	-0.13
131				0.31	0.49	0.02	0.04	0.03
132				0.35	0.80	1.36	2.24	
133				0.34	0.64			
134				0.69	1.64			
135				0.46	0.97	3.21	3.14	-2.62
136				0.81	1.69	3.8		
137					0.94	1.64	0.28	
139				0.83	3.19			
140				0.70	1.14			
141				1.35	5.01			
142				0.15	0.27***	0.33	-0.11	0.02
143				0.23	0.77	2.93	3.26	1.70
147				0.98		4.25		
$\overline{X}$				0.77	1.85	1.28	1.36	-0.2
N				16	15	11	7	5

Appendix 15, continued

Dates

#	12 Dec	9 Jan 1975	24 Jan	23,24 Feb	29 March	26,27 April	26 May	9 July
SE				0.13	0.43	0.8	0.56	0.69
149					0.77	1.95	1.09	0.76
151					1.73	5.27	4.13	2.32
152					1.63	5.32	2.28	0.35
153				****	0.23	0.50		
155					1.58	6.02	1.16	
156					1.18	2.99	1.90	1.36
157					0.99	3.72	3.18	0.60
158					0.56	3.42		3.10
160					0.59	3.57	0.84	1.78
162					1.14		5.49	5.41
163					0.86		2.51	1.86
164					1.15	4.16	3.36	0.97
165					1.05	4.3	6.83	8.69
166					0.85	4.66		
167					0.41	1.59	1.33	3.58
168					0.66	3.16	0.52	1.70

Appendix 15, continued

Dates

#	29 March	27 Apr	26 May	9 July
169	0.63	2.95	1.74	1.08
170	1.63	4.19	-0.83	0.02
171	-0.04			
$\bar{X}$	0.93	3.61	2.37	2.24
N	19	16	15	15
SE	0.113	0.36	0.55	0.59
172			0.26	
173			0.50	
174			1.07	
179			0.27	-0.03
180			0.62	0.75
181			0.78	1.61
182			-0.71	3.31
$\bar{X}$			0.40	1.41
N			7	4
SE			0.21	0.72

APPENDIX 16

Iridaea cordata Mortality of Tagged Blades

Percentage of Individual Blades Surviving

Date Tagged	No. Tagged	5 Mar 1974	25 Apr	23,24 May	6 June	20,21 June	20,21 July	17 Aug	15,16 Oct	28-30 Nov	11,12 Dec	9 Jan 1975	24 Jan	23 Feb	29 Mar	26 Apr	26 May	9 July
1974																		
6 Feb	21	19																
5 Mar	22		31.8	27.3	27.3	22.7	22.7	22.7	22.7	18.2	9.1	4.5	4.5	4.5	0			
25,26 Apr	28			78.6	75	75	75	75	35.7	32.1	7.1	7.1	0					
24 May	16					87.5	68.8		56.3	43.8	43.8	37.5	18.8	12.5	0			
19 June	11						72.7		45.5	36.4	27.3	18.2	18.2	9.1	9.1	0		
21 July	7								85.7	57.1	57.1	57.1	28.6	14.3	14.3	0		
16 Oct	8									100	100	100	100	87.5	37.5	0		
30 Nov	8										87.5	62.5	50	25	12.5	0		
1975																		
25 Jan	17													94.1	82.4	58.8	41.2	41.2
27 Jan	5													20	20	20	0	
23 Feb	4														75	75	75	75
24 Feb	19														84.2	73.7	68.4	68.4
26 Apr	3																100	
27 Apr	8																100	100

APPENDIX 17

Maturation Index [R:T]

Symbols Legend:

$$R:T = \frac{\text{Total Reproductive Biomass}}{\text{Total Biomass}}$$

T = Tetrasporangial Biomass

C = Cystocarpic Biomass

M = Male Biomass

A = Autumn, 1973

W = Winter, 1974

S = Spring,1974

Z = Summer, 1974

$\overline{X}$ = Mean

S^2 = Variance

SE = Standard Error (95% CL)

Appendix 17, continued

MATURATION INDEX [R:T]

Biomass (gm/625 cm^2)

		Total	T	C	M	TR	R:T	S^2	SE
A_{73} to W_{74} (3 mos)	1	1.5	0	0	0	0	0		
	2	0.8	0	0	0	0	0		
	3	1.0	0	0	0	0	0		
	4	3.7	0	0	0	0	0		
A_{73} to S_{74} (6 mos)	1	59.9	17.0	0	0	17.0	.28		
	2	15.3	3.2	0	3.7	6.9	.45		
	3	39.6	4.8	0	3.8	8.6	.22		
	4	56.6	16.1	0	1.4	17.5	.30		
							$\bar{X}$ = .31	.01	.05
A_{73} to Z_{74} (9 mos)	1	127.5	74.2	0	9.1	83.3	.65		
	2	86.4	66.5	0	0	66.5	.76		
	3	82.3	46.2	.45	2.5	49.2	.60		
	4	87.5	61.7	0	1.2	62.9	.72		
							$\bar{X}$ = .68	.005	.04
A_{73} to A_{74} (12 mos)	1	43.2	33.3	1.8	1.5	36.6	.85		
	2	86.7	81.3	0	0	81.3	.93		
	3	103.4	94.8	.9	1.6	97.3	.94		
	4	96.2	81.6	1.9	1.5	85.0	.88		
							$\bar{X}$ = .9	.0017	.02
control A_{74}	1	123.0	100.0	7.6	0.2	107.8	.88		
	2	86.1	75.5	0	1.6	73.9	.86		
	3	80.4	37.9	15.8	1.2	54.9	.68		
	4	114.6	88.9	0	0.5	89.4	.78		
	5	108.6	86.5	2.4	2.7	91.6	.84		
							$\bar{X}$ = .81	.0065	.04

APPENDIX 17B

MATURATION INDEX [R:T]

Discrete Seasonal Biomass (gm/625 cm^2)

		Total	T	C	M	TR	R:T
A_{73} to W_{74}	1	1.5	0	0	0	0	0
	2	0.8	0	0	0	0	0
(3 mos)	3	1.0	0	0	0	0	0
	4	3.7	0	0	0	0	0
W_{74} to S_{74}	1	24.6	0	0	3.2	3.2	.13
	2	24.6	0	0	4.0	4.0	.16
(3 mos)	3	18.4	5.0	0	1.6	6.6	.36
	4	65.2	10.7	0	0	10.7	.16
							$\bar{X}$ = .20
S_{74} to Z_{74}	1	12.0	0	0	0	0	0
	2	0.8	0	0	0	0	0
(3 mos)	3	10.3	0	0	0	0	0
	4	4.9	0	0	1.5	1.5	.31
							$\bar{X}$ = .08
Z_{74} to A_{74}	1	0	0	0	0	0	0
	2	0.2	0	0	0	0	0
(3 mos)	3	9.0	0.2	3.4	0	3.6	.40
	4	0.4	0	0	0	0	0
							$\bar{X}$ = .10

APPENDIX 18

Iridaea cordata Tagged Thalli

Maturation Data

= Thallus Identification Number

Size = Size (cm^2) at Maturity

LHS = Life History Stage

T = Tetrasporangial

C = Cystocarpic

M = Male

- = No Measurement Taken

Appendix 18, continued

Iridaea cordata Maturation Data

#	Date Tagged	Date Mature	Size (cm^2)	Days to Maturation	LHS
	1974	1974			
29	Mar 5	May 23	276.4	79	T
32	"	Aug 17	295.1	165	T
33	"	May 23	187.4	79	T
36	"	"	132.3	79	T
37	"	"	68.2	79	T
40	"	"	-	79	T
45	Apr 25	Oct 15	573.5	173	C
51	"	Oct 16	45.3	174	M
52	"	"	84.1	174	M
54	"	"	46.6	174	T
56	"	"	98.6	174	T
57	"	"	20.0	174	T
58	"	"	42.2	174	T
60	"	June 20	-	56	T
61	"	Oct 16	71.0	174	C
67	"	"	175.2	174	M
72	"	"	156.3	174	C
73	"	Nov 29	69.6	218	C
75	May 24	"	55.6	190	T
76	"	"	53.5	190	T
77	"	"	334.7	190	C
79	"	Jan 9,1975	12.8	231	T
83	"	"	107.1	231	T
84	"	Nov 29,1974	48.4	190	T
86	"	Oct 16,1974	292.2	145	T
96	July 21	Jan 9,1975	14.0	172	T
98	"	"	13.3	172	T
99	"	Nov 30,1974	22.8	131	T
100	"	"	42.9	131	T
102	"	Jan 9,1975	-	172	T
112	Oct 16	"	24.3	85	T
113	"	"	24.4	85	T
114	"	"	23.1	85	T
115	"	"	11.4	85	T
116	"	Nov 28,1974	28.2	44	T
117	"	"	35.0	44	T
118	"	"	33.8	44	T
119	Nov 30	Dec 12,1974	16.5	12	T
122	"	Jan 9,1975	13.9	40	T
123	"	Dec 12,1974	23.0	12	T
124	"	"	25.3	12	T
125	"	Jan 24,1975	42.8	55	C

Appendix 18, continued

#	Date Tagged	Date Mature	Size (cm^2)	Days to Maturation	LHS
	1975				
127	Jan 25	Mar 29	200.5	66	C
128	"	"	-	66	C
129	"	Apr 27	286.6	95	C
130	"	"	79.3	95	T
131	"	Mar 29	35.3	66	T
133	"	"	41.8	66	T
134	"	"	89.0	66	T
135	"	"	52.9	66	M
136	"	"	91.3	66	M
137	"	Apr 27	92.0	95	T
142	"	Mar 29	17.7	66	T
143	"	May 26	218.1	125	T
147	"	Apr 27	316	95	C
151	Feb 23	"	231.7	66	T
152	"	"	229.5	66	T
155	Feb 24	May 26	273.9	94	T
156	"	"	191.7	94	T
157	"	"	241.5	94	T
158	"	"	-	94	M
160	"	"	154.2	94	M
162	"	"	366.2	94	T
163	"	"	183.6	94	T
165	"	Apr 27	169.9	66	T
167	"	May 26	110.3	94	T
168	"	"	134.9	94	T
169	"	"	163.2	94	T
170	"	Apr 27	189.0	66	T

APPENDIX 19

Iridaea cordata Tagged Thalli

-Senescence Data-

= Thallus Identification Number

Size (cm ^{2}) = Size at senescence

LHS = Life History Stage

NR = Non-Reproductive

T = Tetrasporangial

C = Cystocarpic

M = Male

Appendix 19, continued

Iridaea cordata Senescence Data

#	Date Tagged	Date of Senescence	Size (cm^2)	# Days to Senescence	LHS
32	Mar 5 1974	Dec 11 1974	370.3	281	T
33	"	Aug 17 1974	278.1	165	T
36	"	"	250.5	165	T
51	Apr 25	Oct 16	45.3	174	M
52	"	Nov 29	53.3	218	M
61	"	"	57.0	218	C
62	"	"	5.2	218	NR
63	"	Oct 16	15.5	174	NR
68	"	"	45.1	174	NR
69	"	"	32.9	174	NR
71	"	Dec 11	31.9	240	NR
72	"	"	156.1	240	C
73	"	Nov 29	69.6	218	C
77	May 24	Dec 11	306.0	202	C
79	"	Nov 29	11.9	190	T
83	"	Feb 23 1975	67.1	276	T
84	"	"	47.9	276	T
86	"	Nov 29 1974	78.1	190	T
98	July 21	Mar 29 1975	6.8	251	T
102	"	Oct 15 1974	11.7	87	T
103	"	"	16.7	87	NR
112	Oct 16	Jan 24 1975	23.4	100	T
113	"	Jan 9	24.4	85	T
116	"	"	27.1	85	T
118	"	"	34.8	85	T
119	Nov 30	"	15.0	40	T
122	"	"	13.9	40	T
123	"	"	18.9	40	T
124	"	Dec 12 1974	25.3	12	T
125	"	Apr 26 1975	42.9	127	C
127	Jan 25 1975	"	46.4	91	C
130	"	July 9 1975	93.1	165	T
135	"	"	121.7	165	NR
142	"	May 26	293.1	121	T
170	Feb 24	"	165.0	91	T
171	"	Mar 29	5.8	33	NR

CHAPTER FOUR: IRIDAEA CORDATA, PHYSIOLOGICAL STUDIES

INTRODUCTION

Field determined production rates of Iridaea cordata give realistic estimates of growth under the natural limitations of the complex of environmental variables. To estimate the potential productivity of this species and related genera and to discern the limiting ranges of critical environmental factors, production must be measured under controlled conditions. Since many benthic red algae grow very slowly in the laboratory without considerable agitation simulating wave action, production has more accurately been determined by measuring the rates of selected physiological processes. Numerous such studies have been conducted on photosynthesis and respiration of genera in the Order Gigartinales (Newton et al., 1959; Blinks and Givan, 1960; Majak et al., 1960; Kanwisher, 1966; Mathieson and Burns, 1971; Buggeln and Craigie, 1973; Brinkhuis and Jones, 1974; Johnson et al., 1974; Littler and Murray, 1974; Mathieson and Burns, 1974; Mathieson and Dawes, 1974; Mathieson and Norall, 1974), but rarely have similar studies been done on aspects of benthic algal production in terms of nitrogen (Topinka, 1975; Bird, 1976).

I. cordata grows poorly in the laboratory and never approximates average 'field-grown' size. Therefore, physiological experiments on field-grown material were designed to provide estimates of production in terms of carbon and nitrogen by measuring photosynthesis, respiration, and nitrogen uptake kinetics. These physiological studies were based on the following questions. 1. What is the respiration rate and is it affected by thallus size or seawater nitrogen concentration? 2. What is the photosynthetic rate and is it similar for all life history stages and non-reproductive thalli? 3. What is the irradiance saturation level for photosynthesis and how does this compare to the actual irradiance at -1 m? 4. Is photosynthetic rate affected by seawater nitrogen concentration? 5. Are ammonium, nitrate, and nitrite taken up by this species? 6. Are nitrogen uptake rates, in relation to substrate concentration, hyperbolic in nature as has been described for many phytoplankton species? 7. Is nitrogen taken up in the dark? 8. Is there a nitrogen ion uptake differential? 9. What is the total nitrogen and carbon content/unit dry wt. of an _I. cordata_ thallus? 10. How do the _in vitro_ production rates in terms of carbon and nitrogen, compare to the field-derived production rates?

METHODS AND MATERIALS

Iridaea cordata thalli were collected during low tide periods from three central California populations (El Jarro Point, Scott Creek, and Año Nuevo Point) for photosynthesis, respiration, and nitrogen-uptake experiments. These experiments were conducted from April, 1975 to January, 1976.

The thalli collected were healthy in external appearance, intact with no mechanical rips or extensive holes, and free of macro-epiphytes and obvious endophytes (e.g. *Endophyton ramosum*). The thalli were carefully removed from the basal crusts with the stipe intact or the total plant was collected and the stipe disengaged from the crust in the laboratory. The thalli were transported in an ice-cooled container, transferred to filter-sterilized seawater (FSSW) at near ambient temperature within two hours of collecting, and kept in the dark. Prior to the experiment the thalli were incubated for 12-24 hours in an aliquot of the seawater to be used and kept in subdued light. When the same thalli were to be tested under varying experimental conditions, incubation duration between tests was two hours. All experiments were run between 0900 and 1600 within thirty-six hours of sample collection.

Specimens were prepared for experiments in one of two ways. 1. Thalli were submerged and agitated for ten seconds in a dilute (0.5 - 5.0%) solution of sodium hypochlorite (CLOROX) and seawater at near ambient temperature, the surfaces wiped clean, and rinsed four to five times in FSSW. 2. The thallus surfaces were scrubbed gently with Kimwipes (slightly abrasive tissue), soaked in FSSW and then highly agitated in four to five rinses of FSSW. Method 1. was used only for experiments designed to test the effects of sodium hypochlorite treatment. Cleansing method 2 was used for all comparative experiments.

All I. cordata photosynthesis - nitrogen uptake experiments were done in an Environator (trade name) controlled temperature room. The experimental system (Figure 33) included facilities for up to seven replicates and one control experiment to be run concurrently. The room temperature varied ± 2.5°C due to heat radiated from the lighting system. Temperature fluctuations within the experimental chambers were kept to a minimum by submerging the chambers in aquaria, or by placing 2.5 cm wide water baths between the lights and chambers to function as infra-red wavelength filters. Seawater temperature within the chambers was recorded before and after experiments.

Low light intensities were provided by two opposing banks (one not shown in Figure 33) of cool white fluorescent lights (total 240 watts). High light intensities were supplied

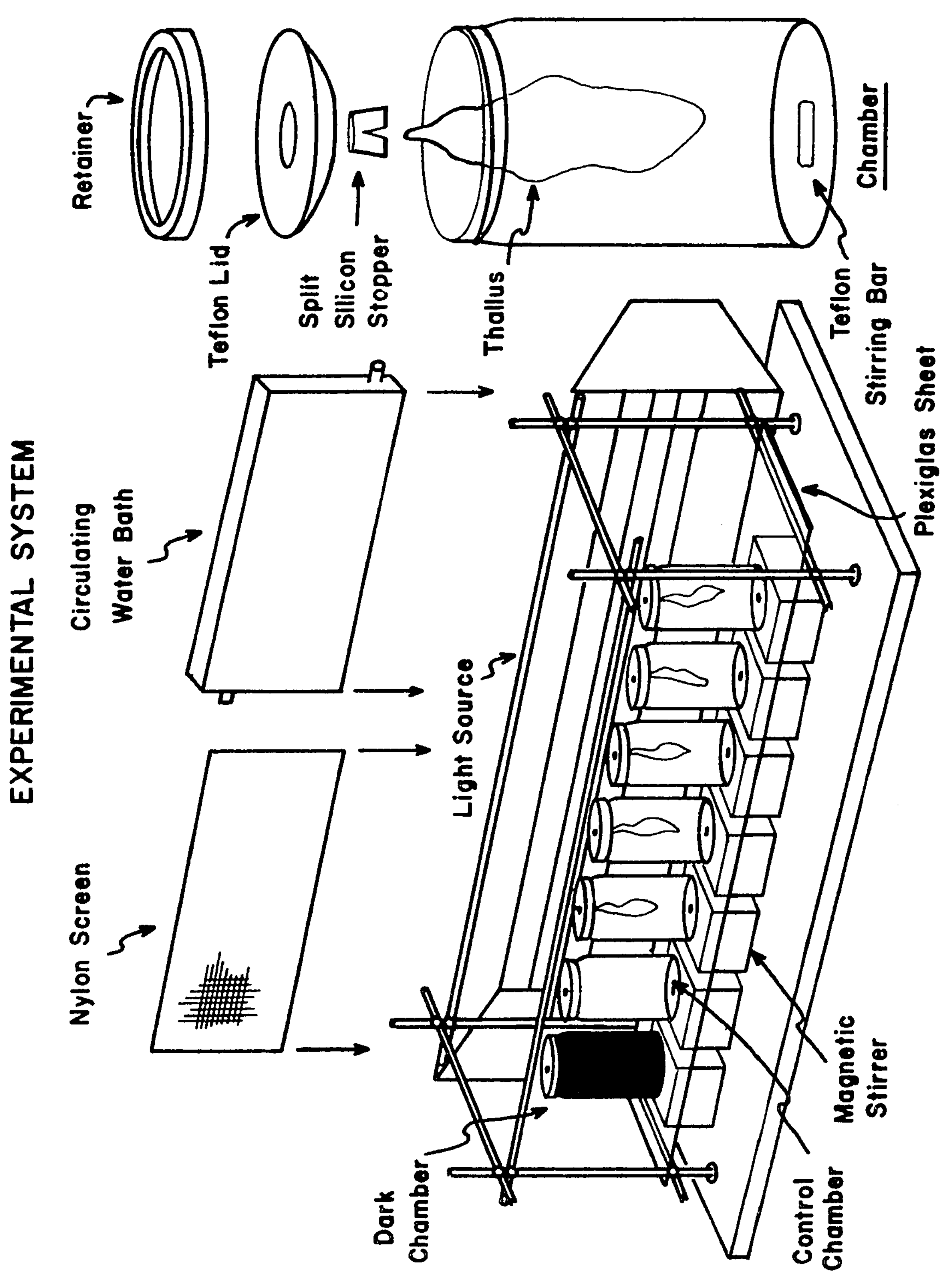

EXPERIMENTAL SYSTEM
Nylon Screen
Circulating Water Bath
Light Source
Dark Chamber
Retainer
Teflon Lid
Split Silicon Stopper
Thallus
Chamber
Teflon Stirring Bar
Plexiglas Sheet
Magnetic Stirrer
Control Chamber

FIGURE 33

by two 500 watt tungsten iodide lights that required cooling by circulating water baths. Sheets of 1 mm mesh plastic screen were placed between the experimental chambers and the lights to reduce the light intensity when required. Irradiance was measured using a Lambda LI-185 Photometer with a Quantum Sensor LI-190S. The sensor is a silicon photodiode that measures quanta (microeinsteins m^{-2} sec^{-1} = 6.02 X 10^{17}photons) of the 400 - 700 nm spectral region. The relative error of the instrument is less than 5% with a cosine error of less than 2% from 0 to 82° angles of incidence.

Water agitation was facilitated by placing a 4 cm Teflon stirring bar in the bottom of each experimental chamber and the chamber was positioned on a magnetic stirrer separated from the chamber by a 5 mm thick sheet of Plexiglass. This separation was required due to heat generated by the stirring motors.

The experimental chambers (Figure 33) were nearly cylindrical in shape and the volume ranged between .942 and .953 1 after algal displacement (approximately 2 cm^3). A Teflon lid was designed to hold a split, silicon stopper in the center (for securing the thallus) and to fit so that no bubbles remained within the closed chamber. Silicon vacuum grease was used to insure a perfect seal, and the lid was secured with a screw-on metal retainer. The thallus to be tested was secured by pinching the stipe in the split stopper. Thus the thallus hung upside-down in the chamber above the stirring rod.

The magnetic stirrer was adjusted so that the thallus undulated back and forth to minimize the surface boundary layer and thus optimize diffusion conditions (Neushul, 1972).

Seawater to be used for the experiments was collected in 150 1 black polyethylene containers from two miles off either Monterey or Santa Cruz, California. The seawater was pumped from -15 m in an attempt to reduce surface water particulates (e.g.: plankton, organic aggregates, debris). The seawater was filtered using a sterile Millipore filtering apparatus with HA .45 μM glass fiber filters. The filtered water was stored in 15 1 sterile containers at 10°C in the dark. All experiments were carried out for less than 2.5 hours to avoid oxygen saturation. In no case did bubbles form within the chambers.

If respiration rate was also to be determined, a chamber was wrapped with aluminum foil to completely eliminate light. For each experiment, a 'light' control was also run. This experimental chamber was treated identically to the others, but an _I. cordata_ thallus was not included.

To determine _I. cordata_ photosynthetic and respiration rates under various controlled conditions, dissolved oxygen was measured using the Winkler method (Carritt and Carpenter, 1966). In this chemical method, the oxidizing potential of molecular oxygen dissolved in the seawater sample is stoichometrically transferred to iodine through the oxidation of iodide. The iodine produced is titrated with sodium thiosulfate to a starch endpoint.

At the beginning of each experiment, replicate water samples were siphoned from the reservoir into 125 ml iodine titration flasks, immediately fixed with 1 ml manganese chloride and 1 ml alkaline iodide solution, shaken, the precipitate allowed to settle, then shaken and settled again, acidified, and titrated for dissolved oxygen within two hours. The same reservoir water was used for all experimental chambers. At the end of an experiment, duplicate water samples were taken from each chamber, treated as above, and the dissolved oxygen determined.

The dissolved oxygen concentration before and after the experiment was calculated as follows.

$$\text{Oxygen (ml/l)} = (R_{sam} - R_{blk})\,(F_{std})\,(F_b) - 0.02$$

Where: R_{sam}= titration value (ml) for the sample

R_{blk}= titration value (ml) for the reagent blank

$F_{std} = \frac{4.209}{(R_{std} - R_{blk})}$ where R_{std} is the mean of three titrations

$$F_b = \frac{132.70}{\text{Bottle Volume (ml)} - 2.00}$$

0.02= the amount of oxygen (ml/l) introduced by the reagents

The photosynthetic or respiration rate was taken as the amount of oxygen produced or consumed (ml O_2/l) between the beginning and the end of an experiment and was converted to mg O_2/l and mg equivalents of carbon. This conversion was done so that laboratory results could be more easily compared to field-determined growth rates.

$$\frac{\underline{\text{ml } O_2\text{/l/gm dry weight/hr X chamber volume}}}{22.4} \text{X } 32 = \text{mg } O_2$$

$$\frac{\underline{\text{mg } O_2\text{/gm dry weight/hr}}}{32} \text{ X } 12 = \text{mg Carbon/gm dry weight/hr}$$

At the end of each experiment, the individual thalli were briefly rinsed in fresh water to remove external salt, dried at 50°C to constant temperature, and the dry weight determined.

The percentage of organic carbon in selected I. cordata thalli was determined using a LECO Carbon Analyzer. The dried thallus was pulverized, the fine powder dried at 50°C to constant temperature, and dessicated. The percentage of total carbon was calculated as follows (Leco, 1959).

$$\text{\% Total Carbon} = \frac{\text{organic carbon (gm)}}{\text{sample weight (gm)}} \text{ X } 100$$

Doubling time for I. cordata, in terms of carbon fixed, was calculated using the experimental net photosynthetic rate (mg C/gm dry wt./hr), effective daylength, and thallus carbon content ($\overline{X}$ = 27.35% by dry weight). Seasonal doubling times were calculated for non-reproductive and reproductive thalli, and for the combined life history stages (population doubling time) by using the corresponding mean photosynthetic rates of 2.49, 1.49, and 1.99 mgC/gm DW/hr respectively. Calculations were based on the relative growth rate equation (Evans, 1972) and expressed in terms of doubling time (days).

$$R_E(\text{carbon}) = \frac{\log_2 X_2 - \mathrm{lo}_2 X_1}{t_2 - t_1} \quad \text{or} \quad \frac{\log_{10}\cdot\left(\frac{X_2}{X_1}\right) 3.32}{\Delta t}$$

where: $R_E(\text{carbon})$ = relative growth rate in terms of carbon

$$X_1 = 1.0000$$

$$X_2 = \frac{\text{net photosynthetic rate(mg/mgDW/hr)}}{\text{thallus carbon content (mg/gm/DW)}}$$

X effective daylength (season_i)

$t_2 - t_1$, $\Delta t = 1.0$ day

$\log_2 = \log_{10}(3.32)$

And: $t/R_E t$ or $1/R_E(\text{carbon})$ = Doubling Time (days)

For complete calculations see Appendix 20.

Since photosynthetic rate, respiration rate and time may be experimentally controlled, seasonal daylength is a critical variable. Therefore, considerable effort was given to obtaining an accurate estimate of daylength within an I. cordata field population (effective daylength). Effective daylength is defined here as: the time (hours) that an I. cordata population at -1.0 m (DATUM: mean sea level: +.92 m) is irradiated with light of the 400 - 700 nM spectral range with an intensity of 150 µE or greater. The experimentally estimated saturation level of photosynthesis for this species is 150 µE.

Intertidal Irradiance

Intertidal irradiance was measured 11 July 1976 at the Almar Street-University of California Sea Grant Station at the 17.7 m marker rod. This stainless steel marker rod is permanently located within a Phyllospadix torreyi, I. cordata, Egregia menziesii community at approximately 0.0 m (DATUM: mean lower low water). A Lambda-LICOR Photometer 185 system was used to measure concurrently, sea surface and subsurface irradiance between 400 - 700 nM. The surface sensor (LI-COR 182) and recording instruments were established at approximately +1.8 m (DATUM; mean lower low water) from which the submarine cable connected the subsurface sensor to the 17.7m marker rod. Readings from both sensors were taken every fifteen minutes from 0900 to 1300 over a tidal height range of 0.52 m to 1.19 m (DATUM: mean lower low water).

The light attenuation coefficients for the seventeen readings were calculated according to Beers Law as follows:

$$I_Z = I_O^{-kz} \quad \text{(Riley, 1957)}$$

Where: I_z = Irradiance at depth z

I_o = Irradiance at sea surface

k = light attenuation coefficient

z = depth (m) (Table 8).

The light attenuation at -1 m was used to calculate the effective daylength (for complete calculations see appendices

TABLE 8

Intertidal Irradiance

Time	Z (m)	I_o (μE)	I_z (μE)	$\ln\left(\frac{I_z}{I_o}\right)$	K
0900	0.520	1290	510	.928	1.78
0915	0.642	1350	750	.588	0.92
0930	0.734	1440	750	.652	0.89
0945	0.826	1500	690	.777	0.94
1000	0.917	1200	600	.693	0.76
1015	0.979	1020	600	.531	0.54
1030	0.917	1020	450	.818	0.89
1045	1.101	1050	390	.990	0.90
1100	1.162	2040	750	1.000	0.86
1115	1.193	2070	600	1.238	1.04
1130	1.223	2100	960	.783	0.64
1145	1.254	2160	750	1.058	0.84
1200	1.254	2190	600	1.295	1.03
1215	1.254	2205	600	1.302	1.04
1230	1.250	2220	750	1.085	0.87
1245	1.223	2220	840	.972	0.79
1300	1.193	2220	900	.903	0.76

N = 17 $\bar{X}$ K = 0.91

$I_z = I_o{}^{e-kz}$ where (e-kz) = 0.406 for z = -1m

∴ light attenuation at - 1m (datum:mean sea level (3.0 ft.) = 59.4%

Z = depth (m)

I_o = sea surface irradiance (microeinsteins/cm^2/sec)

I_z = irradiance at depth z

K = attenuation coefficient

21 and 22). Graphic examples of seasonal effective daylength are given in Figure 3, Chapter One and Figure 34.

The uptake rate of ammonium-nitrogen (NH_4-N) or nitrate-nitrogen (NO_3-N) or both were measured concurrently with photosynthetic rates.

Either ambient (low NH_4-N) FSSW or FSSW enriched with ammonium was used (high NH_4-N). Extreme precautions were taken to avoid ammonium contamination. All glassware, sampling bottles and equipment were sterilized and washed with warm 5% HCl solution to solubilize any ammonium residues adhering to the container walls.

Two replicate 60-125 ml samples were taken from the reservoir at the onset of an experiment and from each chamber when the experiment was terminated. Care was exercised to not touch the sample bottle rim or top. Samples were immediately either: 1) frozen at -7°C, 2) preserved with Hg_2Cl and refrigerated, or 3) quick frozen in a solution of ethyl alcohol and dry ice, and stored at -7°C. Comparison of these three methods showed the third to be the best, offering the most accurate results and was therefore used for the majority of the experiments. An inconsistent amount of ammonium may be lost prior to sample analysis using methods 1) and 2) (Hansen, J. C., unpublished). Samples were analyzed for ammonium and nitrate by J. C. Hansen using a Technicon II Autoanalyzer (Technicon 1972).

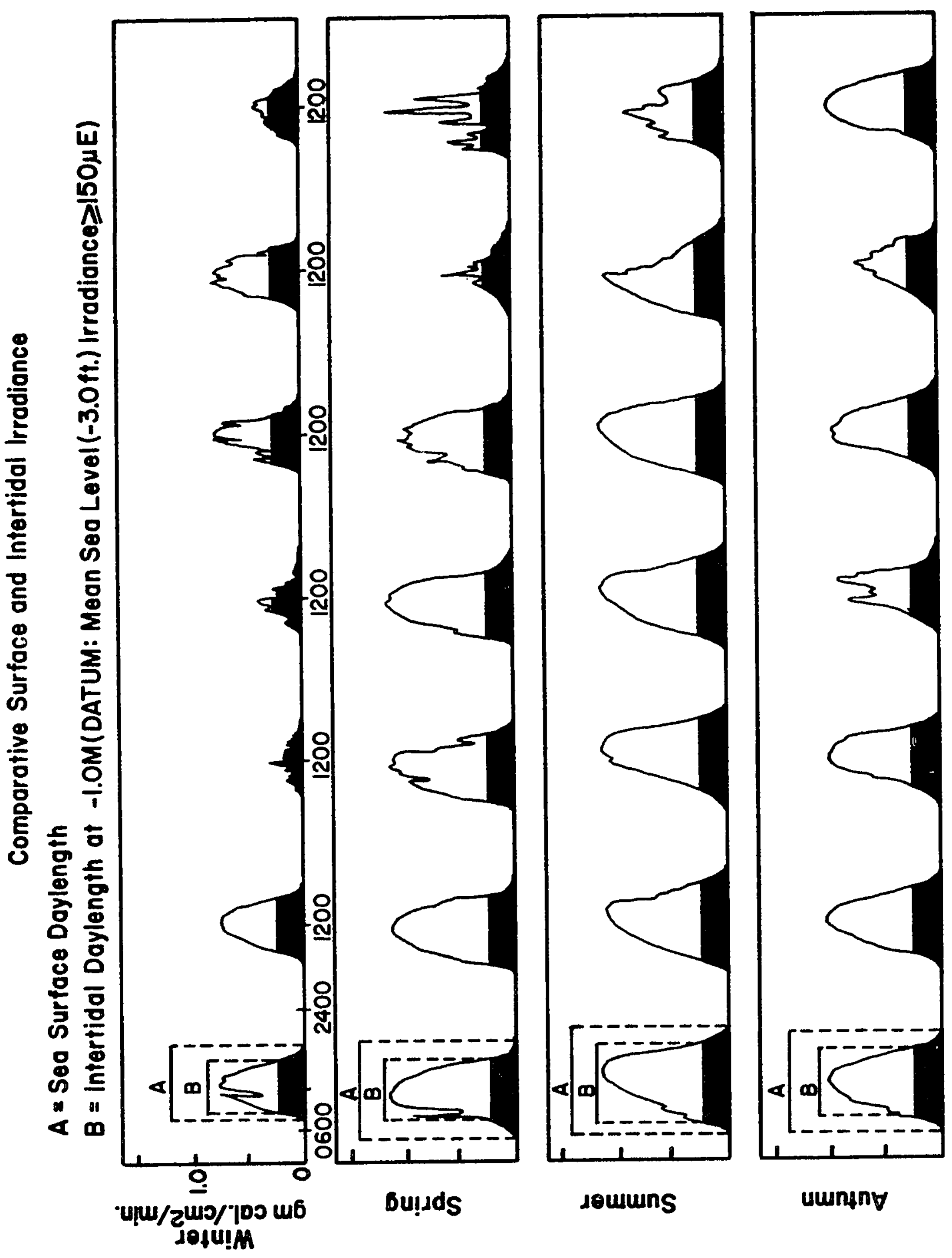

Comparative Surface and Intertidal Irradiance
A = Sea Surface Daylength
B = Intertidal Daylength at -1.0M(DATUM: Mean Sea Level(-3.0ft.) Irradiance≥150μE)
A
B
0600
2400
1200
1200
1200
1200
1200
1200
0
1.0
Winter
gm cal./cm2/min.
Spring
Summer
Autumn

FIGURE 34

Ammonium and nitrate uptake (μM/gm dry weight/hr) by I. cordata was calculated from the difference between the control value and the value determined for each chamber at the end of an experiment X chamber vol./dry wt/time. The saturation level, half-saturation constant (K_s), and uptake velocities (v and V_{max} - μM/gm dry weight/hr) for ammonium as described by the Michaelis-Menten equation, were estimated from the hyperbola.

$$v = V_m \ S/K_s + S$$

where: v = rate of nitrogen uptake (μM/gm dry weight/hr)

S = concentration of substrate (NH_4-N, NO_3-N μM)

K_s = half-saturation constant (the substrate concentration supporting half the maximum uptake rate).

The nitrogen uptake data were linearly transformed using the equation suggested by Dowd and Riggs (1965).

$$(S/v) = (K_s/V_{max}) + (1/V_{max})S.$$

Total thallus nitrogen was determined using the Kjehldahl digestion method (Strickland and Parsons, 1968). Samples for analysis were taken from batches of dried and pulverized I. cordata thalli of the same life history stage. The percentage of thallus nitrogen by dry weight was determined for reproductive life history stages and non-reproductive juvenile thalli collected from Año Nuevo Point 20 May, 21 July and 11 September, 1974.

_I_. _cordata_ doubling times, in terms of nitrogen, were calculated as described for carbon but using the mean daily ammonium plus nitrate uptake rate (based on 1. ammonium K_s, and 2. the mean seasonal seawater ammonium concentration), mean seasonal effective daylength, and mean total N content of _I_. _cordata_. See Appendix 20 for complete calculations.

The statistical analyses employed: t-test, paired data test, Kendall's tau test for correlation and linear regression are described in Sokal and Rolf (1969).

RESULTS

Respiration

Iridaea cordata respiration was measured for non-reproductive thalli (Table 9). All experiments were run at 11.5°±2.0°C which corresponded closely to local, ambient seawater conditions, and the water was continuously agitated as described for the experimental procedure. Variation in respiration rate within the non-reproductive stage was low ($\bar{X}$ = 0.07 ± .02 mg C/gm dry wt/hr) and the rate did not vary with the seasons considered (May, September, 1975; January, 1976). Further, there was no enhancement of the rate by either increasing the ammonium or nitrate concentration (Table 10). Neither was there a correlation between respiration rate and the experimental thallus size range. However, larger sizes were excluded since the thallus size was limited by the size of the experimental chamber.

Photosynthesis

Photosynthetic rate was measured for non-reproductive (n = 54), male (n = 14), cystocarpic (n = 26), and tetrasporangial (n = 17) thalli under consistent temperature conditions (11.5°C±2.5°C) and varying irradiance (23-420 µE; see Appendix 23).

Saturation levels for all life history stages were at approximately 150 µE or 7.5% of full surface sunlight. Some

TABLE 9

Iridaea cordata Respiration

Exp.#	Time (hrs)	Vol (l)	Dry Wt (gm)	mlO_2/g/hr	mgO_2/g/hr	mgC/g/hr
27	1.88	.953	.23	.20	.29	.11
29	3.25	.946	.28	.03	.04	.02
30	2.00	.946	.47	.07	.10	.04
31	2.67	.948	.34	.12	.17	.06
32	1.62	.953	.35	.05	.07	.03
33A	2.08	.953	.54	.11	.16	.06
33B	2.40	.953	.54	.15	.21	.08
43	3.00	.949	.58	.22	.31	.12
			Mean	= 0.12	= .17	= .07
			Standard Error	= 0.02	= .03	= .01
			Variance	= 0.005	= .007	= .0015
			Sample Number	= 8	= 8	= 8

TABLE 10

Iridaea cordata Respiration versus Nitrogen Concentration and Dry Weight

Exp.#	Respiration Rate (mgC/gm DW/hr)	Dry Weight (Gm)	NH_4-N (μM)	NO_3-N (μM)	$NH_4 + NO_3$ -N (μM)
27	0.11	.23	4.52	7.1	11.62
29	0.02	.28	3.46	4.0	7.46
30	0.04	.47	2.38	11.3	13.68
31	0.06	.34	1.64	17.5	19.14
32	0.03	.35	4.98	11.0	15.98
33A	0.06	.54	-	18.3	-
33B	0.08	.54	-	18.3	-
43	0.12	.58	2.51	3.4	5.91

Kendall's Tau Test for Correlation

	Tau	Probability
Resp/Dry wt (gm)	.43	$p = .20$
Resp/NH_4-N	.2	$p > .20$
Resp/NO_3-N	.14	$p > .20$
Resp/NH_4-N+NO_3-N	.2	$p > .20$

TABLE 11

Iridaea cordata Photosynthesis versus Irradiance

Photosynthetic Rate (mgC/gm dry wt/hr)

Life History Stage	Irradiance (Microeinsteins/cm^2/sec)				
	420	225	150	67	23
NR	2.25	-	2.21	1.24	-
NR	2.48	-	2.10	1.16	0.36
NR	3.09	2.94	2.60	1.35	-
M	1.62	-	1.33	0.79	0.29
C	1.11	1.23	1.03	0.57	0.09
T	1.50	1.24	1.66	0.86	0.30
T	1.91	1.88	1.71	-	-

NR - Non Reproductive
M - Male
C - Cystocarpic
T - Tetrasporangial

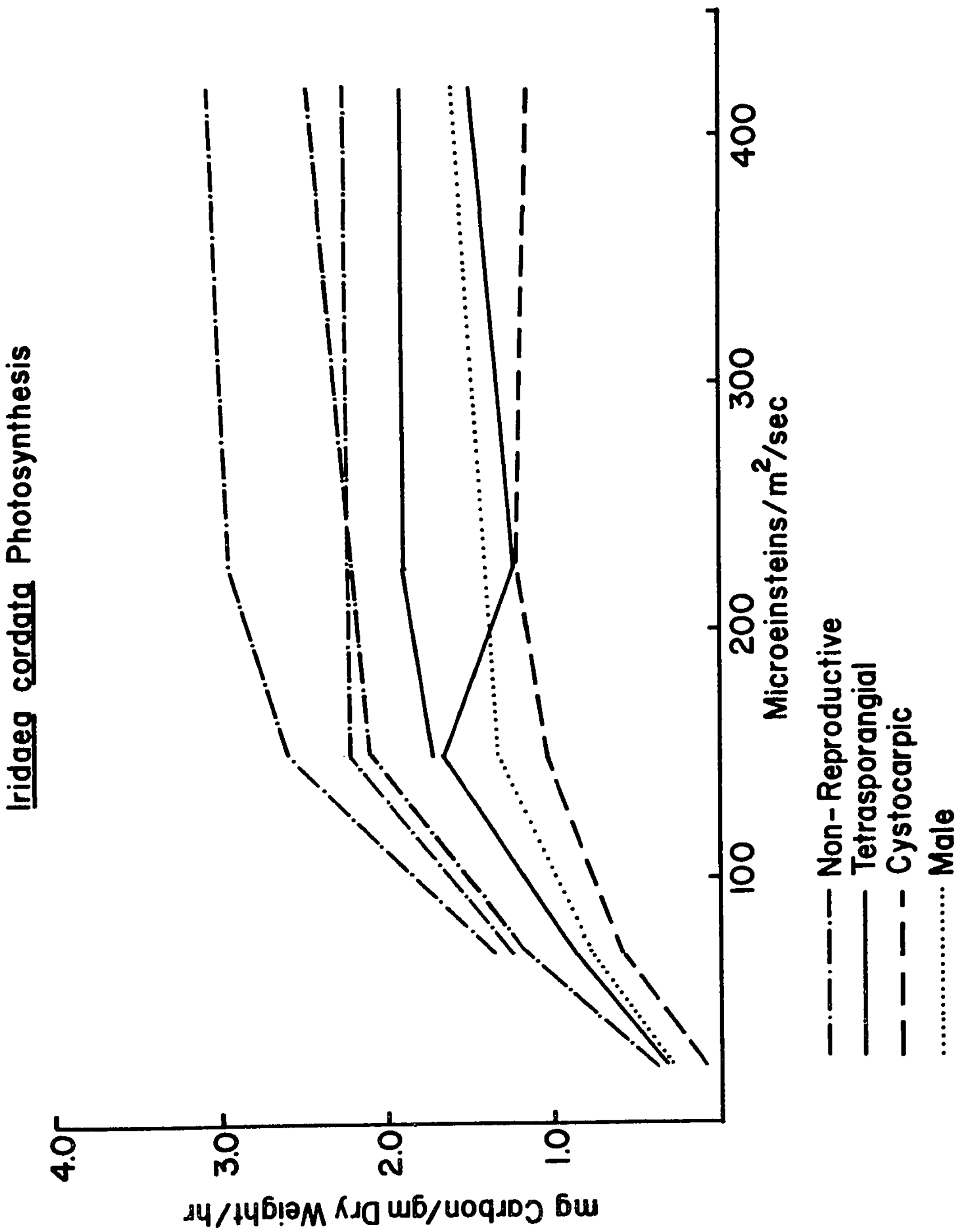

Iridaea cordata Photosynthesis
mg Carbon/gm Dry Weight/hr
4.0
3.0
2.0
1.0
100
200
300
400
Microeinsteins/m²/sec
Non-Reproductive
Tetrasporangial
Cystocarpic
Male

FIGURE 35

variation in the saturation level does occur, especially in the non-reproductive stage (Table 11, Figure 35). At and above the saturation level, the photosynthetic rate for all reproductive stages (male, cystocarpic and tetrasporangial) were similar ($\overline{X} = 1.51 \pm 0.15$; $\overline{X} = 1.48 \pm 0.10$; $\overline{X} = 1.47 \pm 0.09$ mg C/gm dry wt/hr, respectively). However, rates for the non-reproductive thalli ($\overline{X} = 2.49 \pm 0.08$ mg C/gm dry wt/hr) were significantly greater than those of the combined reproductive thalli ($p \ll .001$). Correspondingly, the mean photosynthesis to respiration ratio for non-reproductive thalli was 35 : 1 while the mean gametangial and tetrasporangial ratios were 21 : 1. To determine whether this dichotomy in photosynthetic rate between non-reproductive and reproductive thalli was dependent upon size (dry weight), photosynthetic rate and thallus size for each life history stage were compared (Figure 36). Statistical analyses of these results indicate that the rates for all reproductive stages are inversely correlated with size. There is no correlation between photosynthetic rate and thallus size for the non-reproductive plants ($p = .26$). However, when non-reproductive and reproductive thalli of similar size were compared, a highly significant difference was apparent ($p < .001$) indicating that this difference is inherent and not a function of size.

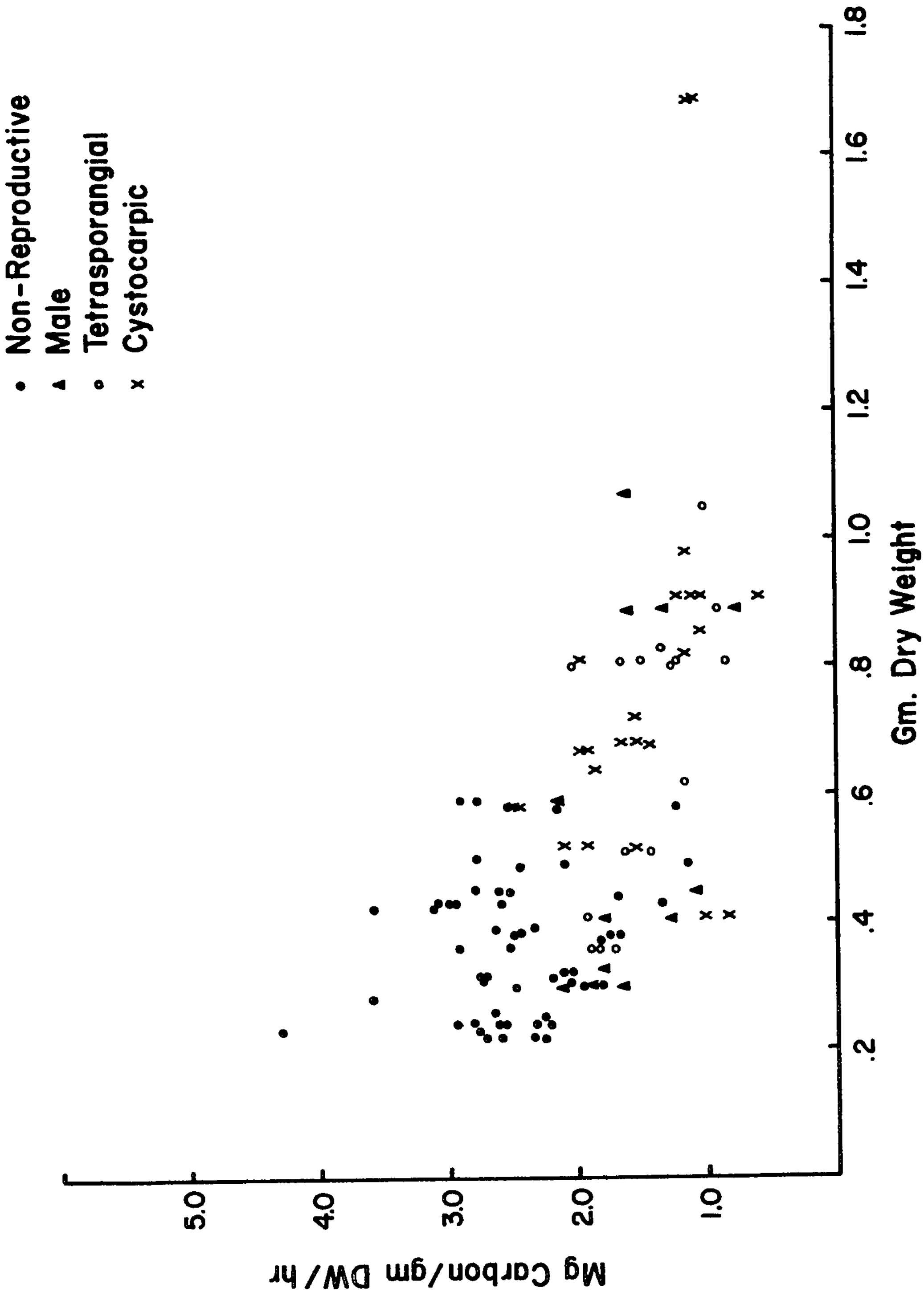

● Non-Reproductive
▲ Male
○ Tetrasporangial
× Cystocarpic
Mg Carbon/gm DW/hr
5.0
4.0
3.0
2.0
1.0
Gm. Dry Weight
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8

FIGURE 36

Photosynthetic rates of non-reproductive and the combined reproductive thalli under saturating irradiance conditions, were compared to 1) NH_4-N, 2) NO_3-N, and 3) NH_4-N + NO_3-N levels by regression analyses (Table 12). These analyses indicate that significant linear relationships do not occur between I. cordata photosynthetic rate and seawater nitrogen in the molecular forms and substrate levels used in these short-term experiments.

The mean percentage of total organic carbon in I. cordata thalli was 27.19 ± 0.46% (Appendix 24). This value was used for the basic comparison between field and laboratory determined results and for calculating doubling times in terms of carbon.

The photosynthesis, respiration, and thallus carbon results provide the necessary data to calculate doubling times, in terms of carbon for this species. Doubling time is the number of days required for one doubling of thallus carbon under the specified experimental conditions. Doubling times were based upon photosynthetic rates of 1) reproductive thalli, 2) non-reproductive thalli, and 3) a mean of 1 and 2 which represents the population doubling time (Table 13). The critical value, intertidal daylength of irradiance at -1 m greater than 150 μE (effective daylength) was calculated using the experimentally determined intertidal light attenuation of 59.4%.

TABLE 12

Iridaea cordata Photosynthesis and Nitrogen Levels

Linear Regression Analyses

Variables		Equation	t	Probability
(X)	(Y)			
Non-Reproductive Photosynthetic Rate	NH_4-N μM	$y = 1.5 \times -1.85$	$t_{43} = 1.67$	$p > .10$
Non-Reproductive Photosynthetic Rate	NO_3-N μM	$y = 1.19 \times +17.66$	$t_{47} = 1.45$	$p > .10$
Non-Reproductive Photosynthetic Rate	NH_4-N + NO_3-N μM	$y = 1.14 \times +10.78$	$t_{42} = 1.01$	$p > .10$
Reproductive Photosynthetic Rate	NH_4-N μM	$y = 1.02 \times +1.83$	$t_{44} = 1.42$	$p > .10$
Reproductive Photosynthetic Rate	NO_3-N μM	$y = 1.79 \times +16.95$	$t_{48} = 1.92$	$.1 > p > .05$
Reproductive Photosynthetic Rate	NH_4-N + NO_3-N μM	$y = 0.37 \times +16.99$	$t_{43} = .29$	$p > .10$

TABLE 13

Season	Doubling Times (Days) Population	Non-reprod.	Reprod.	Effective $\bar{X}$ Intertidal Daylength(-1.0m)
Winter	24.3	18.7	34.7	4.83
Spring	14.2	11.1	19.6	7.75
Summer	10.7	8.5	14.6	10.07
Autumn	14.3	11.2	19.8	7.68

Nitrogen Uptake

Three preliminary experiments were carried out to determine the basic patterns of nitrogen uptake in Iridaea cordata (Figure 37a, b, c).

Replicate, individual I. cordata thalli were incubated in low (1.16 μM NH_4-N) and subsequently ammonium enriched (4.98 - 15.16 μM NH_4-N) seawater under saturating irradiance conditions. A two hour acclimation period separated the treatments. The results demonstrated a highly significant increase in ammonium uptake rate with increased substrate concentration in all experiments ($p < .001$, $p < .001$, $p < .01$). Further, ammonium uptake occurred in the dark and was enhanced with increased substrate concentration (Figure 37a, c).

Nitrate uptake at substrate concentrations of 7.0 and 20.0 μM NO_3-N was measured in the presence of low and high ammonium concentrations (Figure 37b, c). Nitrate and

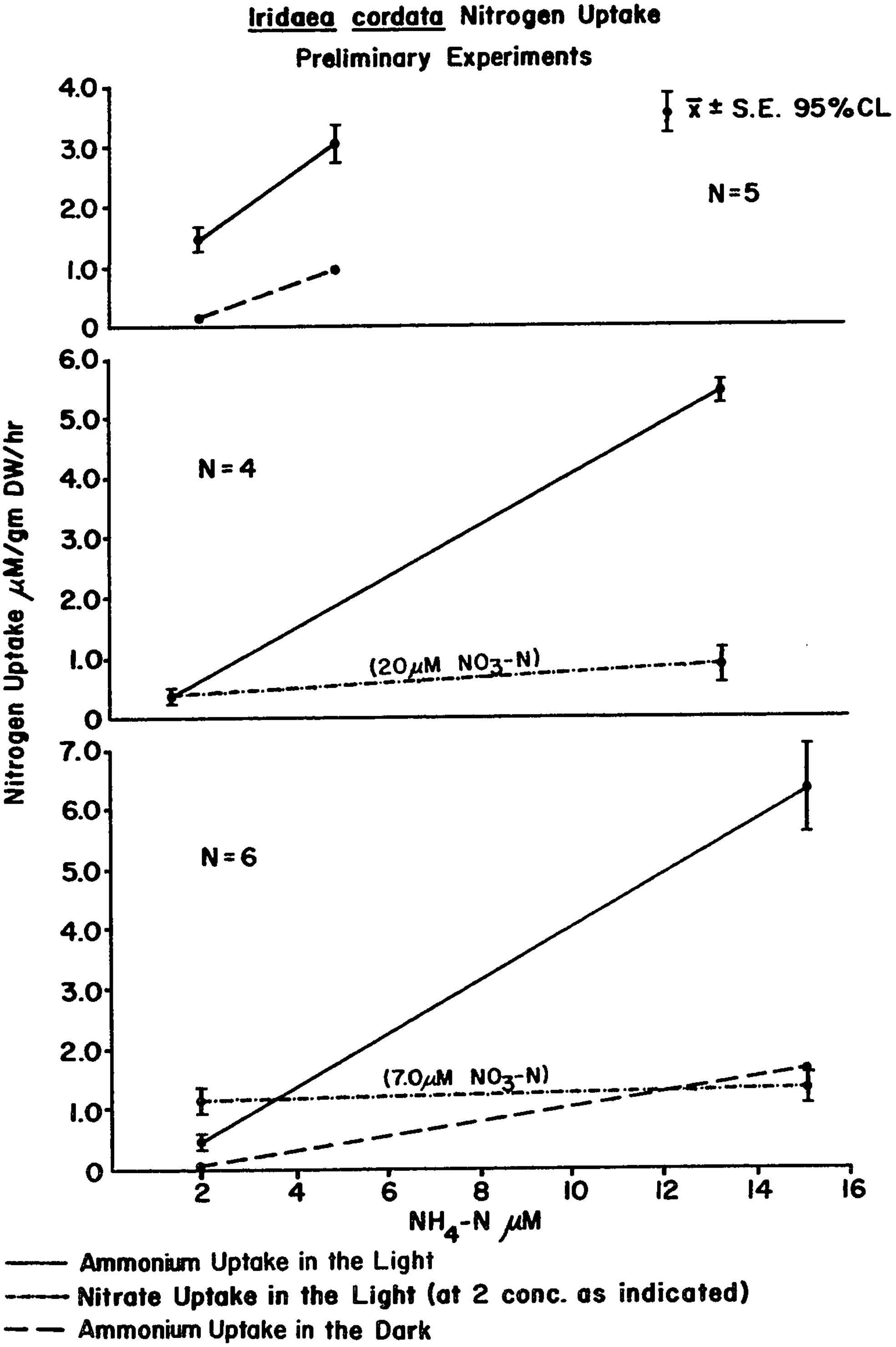

Iridaea cordata Nitrogen Uptake
Preliminary Experiments
x̄ ± S.E. 95%CL
N=5
N=4
N=6
(20μM NO3-N)
(7.0μM NO3-N)
Nitrogen Uptake μM/gm DW/hr
NH4-N μM
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
2
4
6
8
10
12
14
16
Ammonium Uptake in the Light
Nitrate Uptake in the Light (at 2 conc. as indicated)
Ammonium Uptake in the Dark

FIGURE 37

ammonium uptake rates were similar at low ammonium concentrations. When the rates were subsequently determined for these same thalli in ammonium enriched seawater, there was no significant increase in nitrate uptake. Therefore, there was no effect of ammonium concentration on the rate of nitrate uptake.

Further experiments were carried out to verify these nitrogen uptake patterns and to determine whether they were consistent among life history stages.

Nitrogen uptake rates were measured for non-reproductive ($n = 73$), male ($n = 13$), cystocarpic ($n = 27$), and tetrasporangial ($n = 18$) _L. cordata_ thalli with concentrations ranging from 1.16 to 21.34 μM NH_4-N and 3.4 to 20.0 μM NO_3-N (Appendix 25). Analyses of the results indicate that both ammonium and nitrate uptake rates are similar for all life history stages including the non-reproductive thalli. The ammonium uptake values for the combined life history stages give a hyperbolic curve (Figure 38A). However, when a linear transformation of the data was made using the equation suggested by Dowd and Rigg (1965), $(S/V) = (K_s/V_{max}) + (1/V_{max})\,S$ (Figure 38B, Appendix 26), small uptake values at correspondingly low substrate levels were quite variable and gave extremely high S/V values. Accentuation of the S/V values is an inherent drawback of this equation (op. cit.). Therefore, a hyperbola was fitted to the data by eye giving an estimated Ks of 2.5 μM NH_4-N, a mean v of 2.5 μM NH_4-N/gmDW/hr,

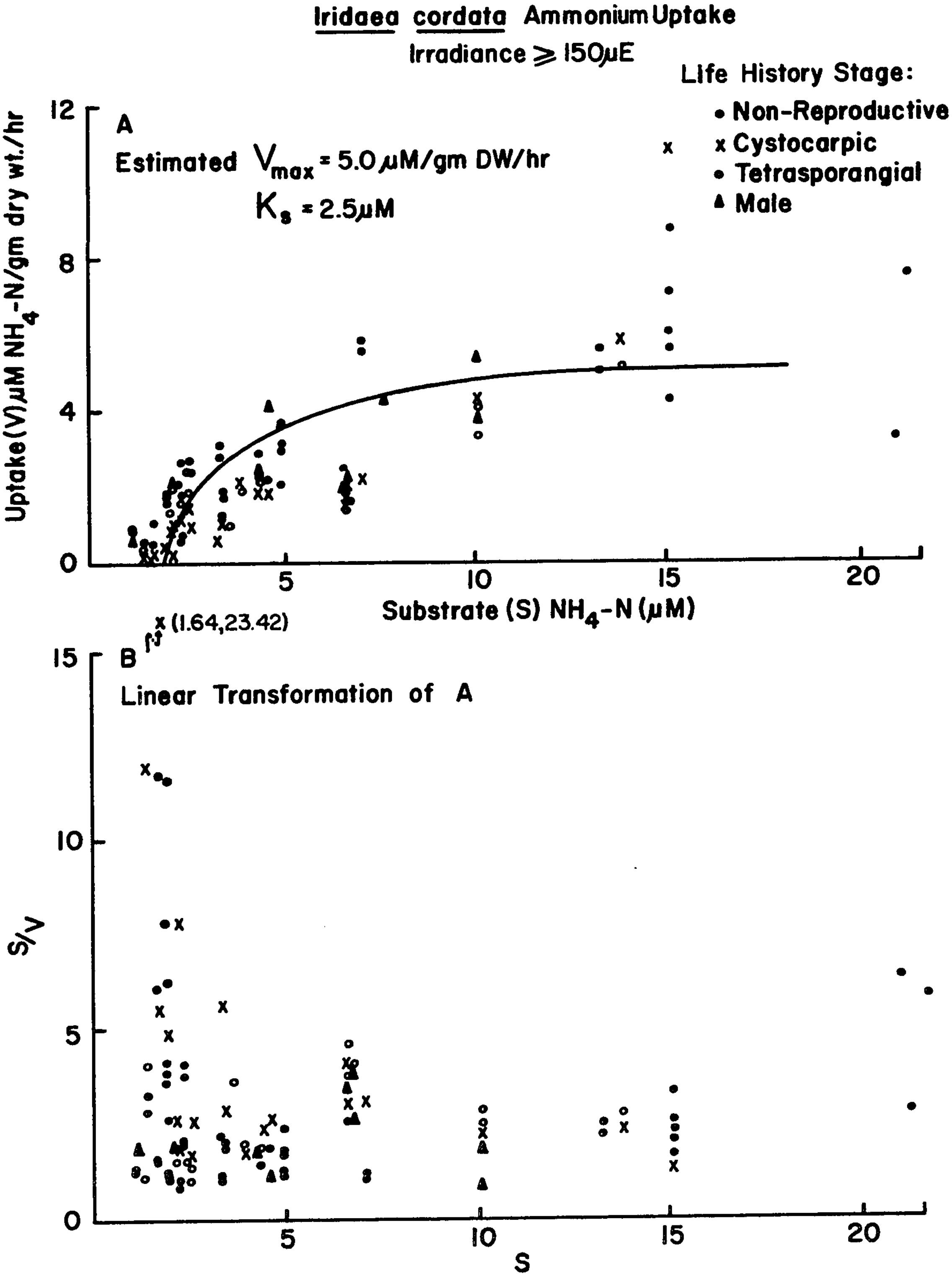

Iridaea cordata Ammonium Uptake
Irradiance ≥ 150μE
Life History Stage:
• Non-Reproductive
x Cystocarpic
• Tetrasporangial
▲ Male
A
Estimated V_{max} = 5.0μM/gm DW/hr
K_s = 2.5μM
Uptake (V) μM NH_4-N/gm dry wt./hr
0
4
8
12
5
10
15
20
Substrate (S) NH_4-N (μM)
x (1.64,23.42)
B
Linear Transformation of A
S/V
0
5
10
15
5
10
15
20
S

FIGURE 38

and a mean V_{max} of 5.5 μM NH_4-N gmDW/hr.

Nitrate uptake was highly variable and is not hyperbolic in nature with respect to the substrate levels considered (Figure 39, Appendix 26). Only uptake rates for natural seawater levels were determined (3.4 - 20.0 μM NO_3-N). Rates below a substrate level of 3.4μM NO_3-N may be critical to describing and understanding the uptake for this species. The mean nitrate uptake rate ($n = 122$) for all substrate levels used in these experiments was 1.68 ± .13μM/gm dry wt/hr.

Uptake of ammonium and to a lesser extent, nitrate, occurred in the dark. Paired data analyses indicate that both ammonium ($.02 < p < .05$) and nitrate ($p < .01$) uptake were significantly less in the dark than in the light (Appendix 27). Dark uptake of ammonium occurred in all experiments and the rate is positively correlated ($.02 < p < .01$) with increasing substrate concentration (Figure 40). Dark uptake of nitrate was highly variable, being zero in 50% of the experiments ($n = 10$) and was not correlated with substrate concentrations ($p > .20$) used in this study.

Simultaneous uptake of the three nitrogen sources (ammonium, nitrate, and nitrite) was compared for the different life history stages. Nitrite concentration was less than 0.6 μM NO_2-N in all experiments with a mean of 0.3 μM NO_2-N. At these low concentrations there was no significant uptake of nitrite by thalli of any life history stage. Ammonium and nitrate uptake rates were measured

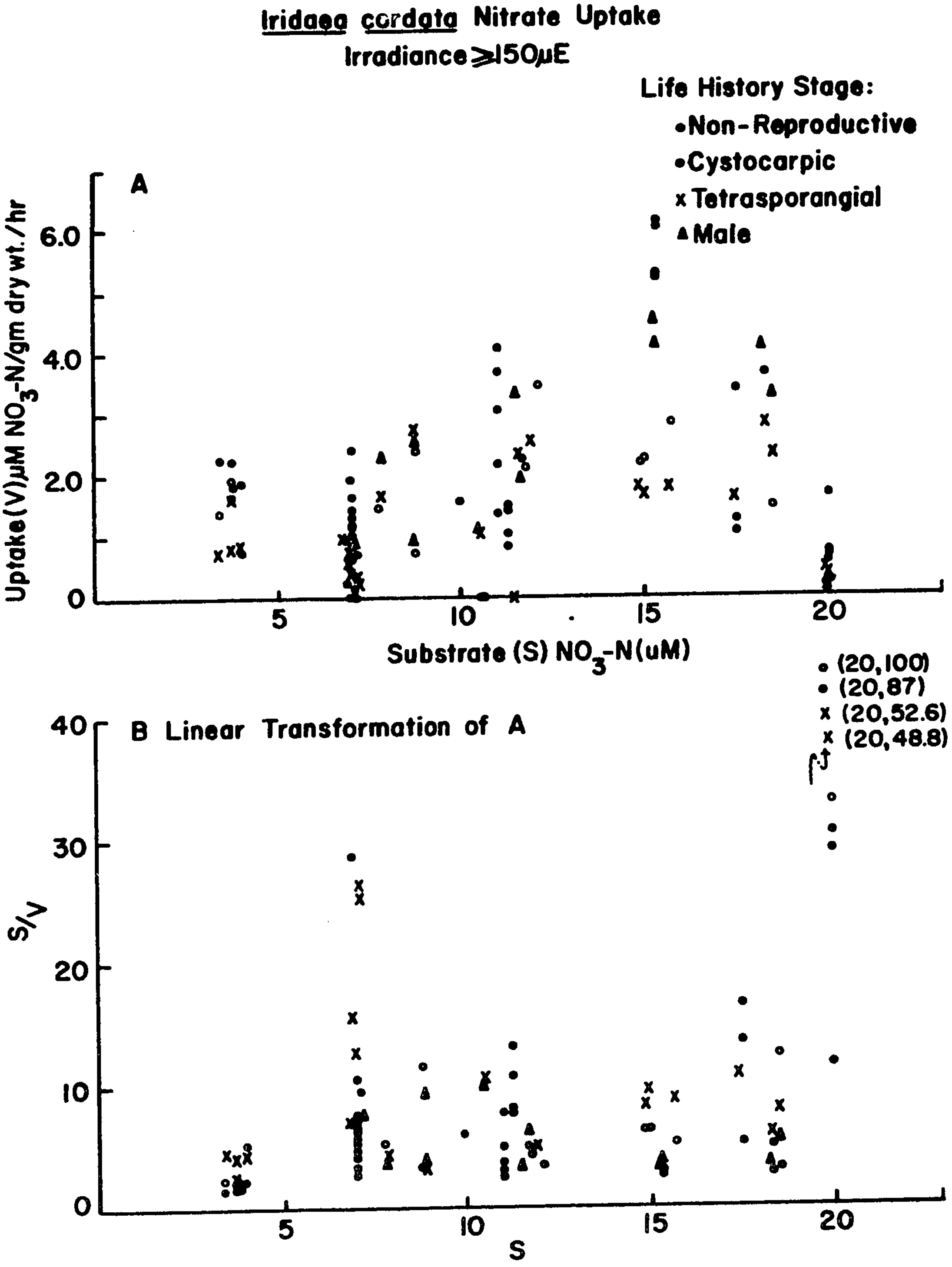
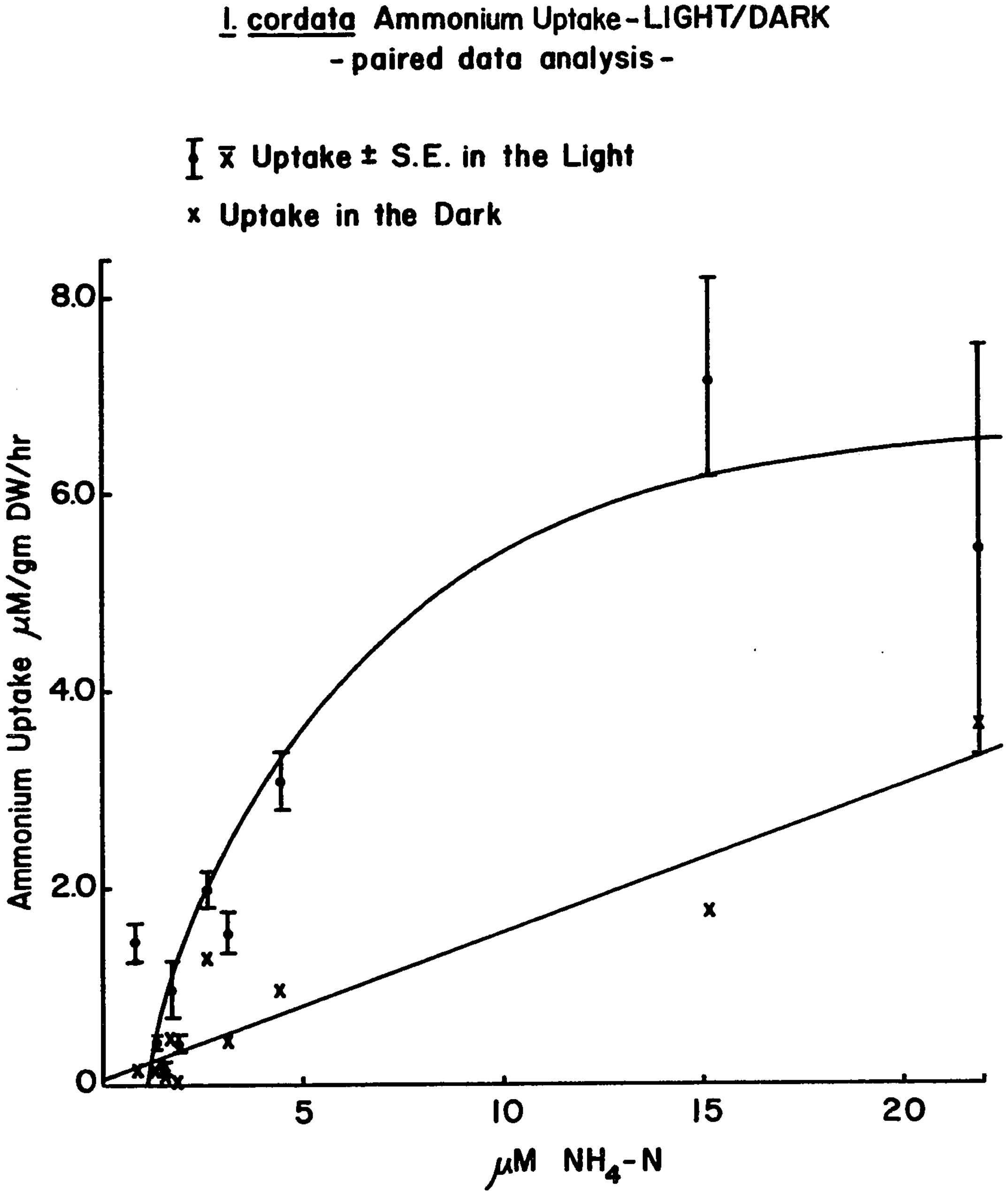

Iridaea cordata Nitrate Uptake
Irradiance ≥150µE
Life History Stage:
• Non-Reproductive
○ Cystocarpic
x Tetrasporangial
▲ Male
A
Uptake (V) µM NO3-N/gm dry wt./hr
6.0
4.0
2.0
0
5
10
15
20
Substrate (S) NO3-N(uM)
○ (20,100)
• (20,87)
x (20,52.6)
x (20,48.8)
40
B Linear Transformation of A
30
S/V
20
10
0
5
10
15
20
S

FIGURE 39



(.02>p>.05) Dark uptake significantly less than light uptake

(.02>p>.05) Dark uptake positively correlated with µM NH_4-N

FIGURE 40

concurrently for 91 *I. cordata* thalli in the light. Both forms of nitrogen were taken up simultaneously by 92% of the thalli tested representing all life history stages. The regressions of ammonium uptake to nitrate uptake (Fig. 41) and the corresponding S/V values (to normalize for substrate concentration)(Fig. 42) indicate that there is no linear relationship between the uptake rates, as was evident from the results of the preliminary experiments. In addition, the simultaneous ammonium and nitrate uptake rates were examined to detect whether there was an ion uptake differential in *I. cordata* thalli. The percentages of ammonium and nitrate uptake of the total uptake rate (Table 14) were compared for the individual thalli. A significant differential occurred for non-reproductive ($p < .001$), cystocarpic ($.10 < p < .02$), and tetrasporangial ($p = .05$), but not for male ($p < .10$) thalli. For the stages in which a differential occurred, the percentage of ammonium uptake was greater than nitrate uptake. In male thalli, the percentage uptake of the two sources was similar. A more descriptive comparison considering both ammonium and nitrate uptake rates in relation to concentrations was not included, as nitrate uptake is not correlated with the nitrate substrates considered. Therefore, further comparisons to the nitrate uptake data would be meaningless.

Kjehldahl nitrogen analyses of field-grown *I. cordata* thalli indicate that approximately 2.35 ± .07% of a thallus

Ammonium Uptake Versus Nitrate Uptake

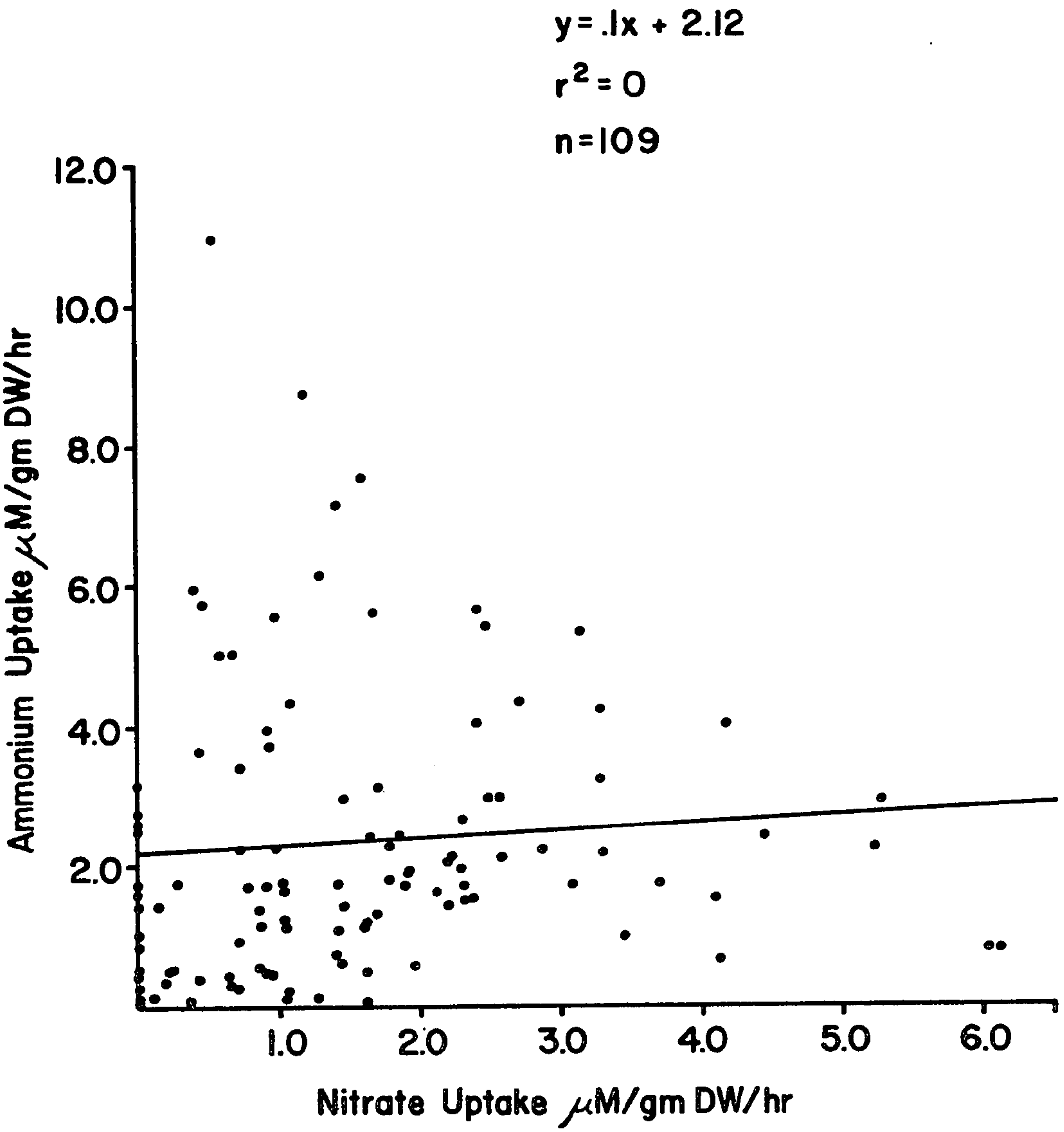


FIGURE 41

Nitrate $^{s}/_{v}$ vs. Ammonium $^{s}/_{v}$

s = nitrogen substrate concentration
v = nitrogen uptake rate

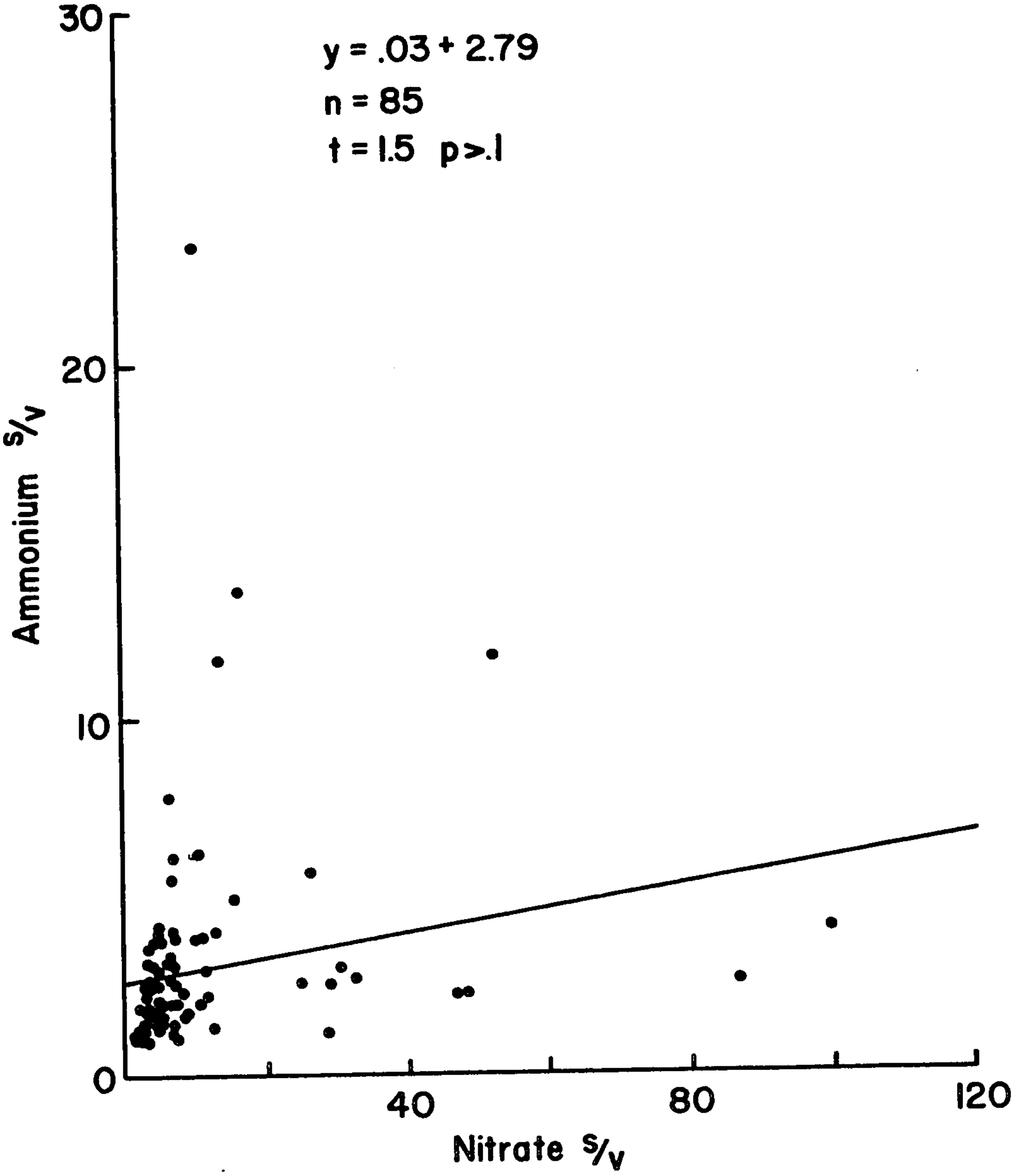


FIGURE 42

TABLE 14

Iridaea cordata Nitrogen Ion Uptake Differential

		Percentage of Total Nitrogen Uptake	
		$\%NH_4$-N	$\%NO_3$-N
Non-Reproductive	$\bar{X}$ =	60.74	39.26
	N =	58	58
		$t_{114} = 3.93$	
	Probability $p < .001$*		
Cystocarpic	$\bar{X}$ =	58.58	41.42
	N =	24	24
		$t_{46} = 2.44$	
	Probability $.01 < p < .02$*		
Male	$\bar{X}$ =	53.64	46.36
	N =	11	11
		$t_{20} = .85$	
	Probability $p > .10$ (not significant)		
Tetrasporangial	$\bar{X}$ =	57.31	42.75
	N =	16	16
		$t_{30} = 2.05$	
	Probability $p = .05$		

* NH_4-N is taken up at a significantly greater rate than NO_3-N in all stages of this species, except the males.

TABLE 15

Iridaea cordata - Thallus Nitrogen Content

Date Sampled	Life History Stage	%Kjeldahl N (by dry wt.)
5,6 February 1974	Non-Reproductive	2.35
		2.30
7, 8 May 1974	Non-Reproductive	2.87
	Cystocarpic	2.41
	Tetrasporangial	2.46
	Male	2.50
		2.49
21 July 1947	Non-Reproductive	1.92
	Cystocarpic	2.29
	Tetrasporangial	2.18
	Male	2.53
11 September 1974	Non-Reproductive	1.93
	Cystocarpic	2.10
	Tetrasporangial	2.30
	Male	2.62

$\overline{X} = 2.35$

Standard Error = 0.07

is nitrogen (Table 15).

Doubling times in terms of thallus nitrogen were calculated based on 1) the K_s for ammonium plus the mean nitrate uptake rate, and 2) the mean seasonal seawater ammonium concentrations (field-determined) and the mean nitrate uptake rate (Table 16). The calculations are similar to those for carbon doubling times and are included in Appendix 20.

TABLE 16

Doubling Times (days)

Season	(1) K_s	(2) Seawater N	Effective Daylength (hrs)
Winter	24.9	43.3	4.83
Spring	21.2	56.4	7.75
Summer	19.0	48.5	10.07
Autumn	22.7	36.9	7.68

Thallus Sterilization

Surface sterilization of *I. cordata* thalli with sodium hypochlorite (CLOROX) solutions was done in an attempt to control possible bacterial nitrogen uptake in these experiments. Table 17 and 18 demonstrate that both photosynthesis and nitrogen uptake rates of treated thalli were significantly lower than rates of non-treated thalli ($p < .001$, $.001 < p < .01$).

TABLE 17

Iridaea cordata Photosynthesis and Surface Sterilization

Exp	*Treatment	PHS-	PHS+	PHSΔ	LHS
35	5%	1.19	0.12	-1.07	T
35	5%	1.17	0.65	-0.52	C
35	5%	1.18	0.39	-0.79	M
40	2%	1.94	0.96	-0.98	T
40	2%	0.88	0.81	- .07	C
40	2%	1.89	1.27	-0.62	M
40B	2%	1.35	1.23	-0.12	T
40B	2%	1.99	0.93	-1.06	C
40B	2%	1.38	1.05	-0.33	M
39	1.5%	1.13	0.81	-0.32	G
39	1.5%	1.02	0.69	-0.33	G
38	1.5%	1.97	1.36	-0.61	C
37	1.5%	1.32	1.01	-0.31	G
36	1.0%	0.91	0.88	-0.03	T
				$n = 14$	

* Sodium hypochlorite treatment as described in Materials and Methods.

PHS- Photosynthetic rate (mgC/gm Dry Wt/hr) with no sodium hypochlorite treatment

PHS+ Photosynthetic rate with treatment.

t-test

$t_{13} = 5.38$

Probability = $p < .001$

Photosynthetic rate was significantly lowered by the sodium hypochlorite treatments.

LHS = Life history stage
T = Tetrasporangial
C = Cystocarpic
M = Male
G = Gametangial

TABLE 18

Iridaea cordata Nitrogen Uptake and Surface Sterilization

Exp	*Treatment(+)	NH_4-N-	NH_4-N+	Δ	NO_3-N-	NO_3-N+	Δ
35	5%	1.95±.04	1.46±.11	-0.49±.15	1.91±.95	1.10± 0	- .81±.95
35	5%	1.72±.47	0.86±.04	-0.86±.51	-	-	
35	5%	1.58±.18	0.57±.07	-1.01±.25	2.37±.82	0.42± 0	-1.95±.82
40	2%	1.37±.21	1.00±.01	-0.37±.22	1.46	1.00	- .46
40	2%	1.38±.15	1.14±.07	-0.24±.22	1.70	0.55	-1.15
40	2%	2.10±.13	2.20±.16	+0.10±.29	2.23	2.37	+0.14
39A	1.5%	0.27±.01	0.53±.15	+ .26±.16	-	-	
39B	1.5%	0.81±.02	0.70±.08	- .11±.10	-	-	
38	1.5%	3.74±.27	2.66±.04	-1.08±.31	0.94	0.86	- .08
37	1.5%	1.33±.10	0.54±.16	- .79±.26	1.89	1.31	- .58
36	1.0%	1.44±.06	1.00±.45	- .44±.51	-	-	
36	1.0%	1.44±.06	1.51±.38	+ .07±.44	-	-	
				$\bar{X}_\Delta$ = .413			$\bar{X}_\Delta$ = .699
				n = 12			n = 7

* Sodium hypochlorite treatment as described in Materials and Methods.

NH_4-N- Ammonia and nitrate-nitrogen uptake rates (μM/gm Dry Wt/hr) with
NO_3-N- no treatment

NH_4-N+ Ammonia and nitrate-nitrogen uptake rates with treatment
NO_3-N+

T-test

	NH_4-N uptake vs treatment	NO_3-N uptake vs treatment
t =	3.18	2.64
Probability =	$.001 < p < .01$	$.05 < p < .02$

NH_4-N and NO_3-N uptake rates are significantly less with treatment.

These data suggest that a critical metabolic step in both these processes was effected by the surface sterilization treatment. Therefore, this technique was discontinued; subsequently, the thalli were mechanically cleaned. Only those data derived from mechanically cleaned thalli were comparatively analyzed.

DISCUSSION

Respiration

Respiration, that reaction sequence by which carbohydrate is oxidized to CO_2 and H_2O,is more than the downhill phenomenon which dissipates part of the organic matter built up during photosynthesis. The respiratory process produces two kinds of products: 1) cellular energy reduced di- and triphosphopyridine nucleotide coenzymes (PNH) and ATP and 2) respiratory intermediates which provide the carbon skeletons for the assemblage of proteins, lipids, nucleic acids, storage reserves, and cell walls. The ideal plant, in terms of efficiency, would be one in which photosynthate and ATP and PNH consumption all would be directed only toward growth and maintenance. Plant parts not contributing directly to these constructive processes would be eliminated (e.g., the underground system)(Beevers, 1970).

The very low respiratory rates measured for *Iridaea cordata* in this study and the morphology of the plant itself promote this species as a candidate for the "ideal plant". Not only is the respiratory rate extremely low, but the thallus is analogous to a single photosynthetic leaf with only a small basal structure and no underground parts to act as a photosynthate "sink". Moreover, relatively little tissue is produced during reproduction compared to angiosperms (e.g., the flower).

Further, the respiration rates of non-reproductive I. cordata thalli are consistently low throughout the year in comparison with other red algal species, and are at least an order of magnitude lower than that of flowering plants (Table 19). The higher rates of related genera in the Order Gigartinales (e.g., Chondrus, Eucheuma, Gigartina) may be due to wound respiration as pieces, rather than whole thalli were used. Increased respiration rates (increases of 20 to 180%) in flowering plants due to wounding or even bending of leaves have been reported (Salisbury & Ross, 1969). Interpretation of interspecific rate differences in red algae must await until comparable experiments incorporating whole thalli and adequate medium agitation are carried out.

I. cordata respiration rate was not correlated with thallus dry weight (0.23-0.58 gm) as has been predicted for macroalgae by Kanwisher (1966) and demonstrated for unicellular algae by Banse (1976). However, the size range used in this study was quite small in order to allow for proper weight to volume ratio in the one liter chambers; a difference might have been detected had larger thalli been used. Because of the increase in volume of non-photosynthetic structural tissue (medulla) as the plant grows and matures, it seems reasonable that respiration rate should increase with size.

Respiration rate was not affected by ammonium, nitrate or ammonium plus nitrate concentrations in the experimental

TABLE 19

RESPIRATION

* Value estimated from graph

Species	Comments	Rate	Reference
Iridaea cordata (C. California) Whole thalli 11.5±2.5°C	Non-Reproductive Thalli $\overline{X}$ Annual	0.12±.02ml O_2/gmDW/hr 0.17±.03mg O_2/gmDW/hr 0.07±.01mg C/gmDW/hr	J. E. Hansen
Chondrus crispus pieces, 10°C	Subtidal, non-reproductive thalli	0.45 mg O_2/gmDW/hr	Newton et al. (1957)
	$\overline{X}$ Intertidal non-reprod. N = 32	0.68 mg O_2/gmDW/hr	
	$\overline{X}$ Intertidal, tetrasporangial thalli, N = 24	0.51 mg O_2/gmDW/hr	
C. crispus	pieces, $\overline{X}$ winter	200 mm^3/gmDW/hr	Kanwisher (1966)
*C. crispus**	14°C, pieces	13µl O_2/gmDW/min	Mathieson & Burns (1971)
C. stellata	14°C, pieces	7µl O_2/gmDW/min	
Eucheuma sp. *	18°C, pieces	0.5µl O_2/gmDW/10min	Mathieson & Dawes (1974)
Gelidium amansii	15°C, pieces, agitated	1µl O_2/mgDW/hr	Yokohama (1973)

Table 19 , cont., Respiration

Species	Comments	Rate	Reference
*Polysiphonia lanosa**	10°C	5µl O_2/gmDW/min	Fralick & Mathieson (1975)
*P. subtilissima**	15°C	8µl O_2/gmDW/min	
*P. elongata**	10°C	10µl O_2/gmDW/min	
*P. nigresens**	10°C	14µl O_2/gmDW/min	
Enteromorpha linza	Whole thalli, 15°C, no agitation	2mg O_2/gmDW/hr	Kjeldsen & Phinney (1971)
Laminaria sp.*	discs, 10°C	2µl O_2/mg/hr	
*Alaria marginata**	whole thalli, 15°C	39mg O_2/gmDW/hr	
Hordeum vulgare (barley) leaves	23°C	266µl O_2/gmFW/hr	Salisbury & Ross (1969)
Quercus ilva (oak)*		1.0mg CO_2/dm^2/hr	Nishioka & Nagamo et. Cooper (1973)
*Helianthus annuus** (sunflower)	whole young plants	3.0mg CO_2/gmDW/hr	Kidd et al. (1921)
	whole flowering plants	0.8mg CO_2/gmDW/hr	

medium. This may indirectly indicate that no short-term relationship exists between inorganic nitrogen concentration and immediate respiratory metabolism (e.g., carbohydrate breakdown), or that the plants used were not nitrogen starved prior to experiment initiation. Nitrogen deficient microalgae and _Fucus spiralis_, on the other hand, have been found to exhibit increased respiratory rates upon exposure to ammonium (Syrett, 1962; Topinka, 1975).

The results discussed indicate that the respiration rate of non-reproductive thalli in this species is fairly constant under the experimental conditions imposed. However, whether this rate varies during thallus development, with life history stage, or with more long-term experiments in _I. cordata_ was not determined. Newton et al. (1959) reported higher rates for non-reproductive than for tetrasporangial thalli of intertidal _C. crispus_. Similar differences between vegetative and flowering stages have been noted some time ago for such plants as the sunflower (Kidd, 1921).

Comparatively, and under the experimental conditions described, _I. cordata_ is an efficient plant in terms of respiration. The nature of this efficiency is probably due in large part to the morphology of the thallus.

Photosynthesis

Photosynthetic rate has been measured for numerous red algae encompassing species of diverse life forms and

TABLE 20

NET PHOTOSYNTHESIS OF RED ALGAE

* - value estimated from graph

SPECIES	COMMENTS	SAT.PT.	PHS RATE	REFERENCE
Iridaea cordata (*C. California*) 11.5±2.5° $\overline{X}$ Annual rate Winkler method	(Resp=0.7mgC/ gm DW/hr) Non-Reprod. Thalli	150μE	4.64±.15ml O_2/gmDW/hr 6.64±.21mg O_2/gmDW/hr 2.49±.08mg C^2/gmDW/hr	J. E.Hansen
	Male Thalli	150μE	2.81±.27ml O_2/gmDW/hr 4.02±.39mg O_2/gmDW/hr 1.51±.15mg O_2/gmDW/hr	
	Cystocarpic Thalli	150μE	2.77±.19ml O_2/gmDW/hr 3.96±.27mg O_2/gmDW/hr 1.48±.10mg C^2/gmDW/hr	
	Tetrasporangial Thalli	150μE	2.75±.18ml O_2/gmDW/hr 3.93±.26mg O_2/gmDW/hr 1.47±.09mg C^2/gmDW/hr	
	$\overline{X}$ Population Rate	150μE	1.99 mgC/gmDW/hr 2.15 mgC/100cm^2/hr (see App.28)	
Iridaea flaccida *C. California* Winkler method	15°C 800 ft.c. (no agitation)		$\overline{X}$ 0.37 cc^3O_2/gmFW/hr ≅ (1.70 ml O_2/gmDW/hr)	Blinks & Givan (1960)

Table 20, cont., Photosynthesis of Red Algae

SPECIES	COMMENTS	SAT.PT.	PHS RATE	REFERENCE
I. flaccida *C. California* Winkler method (pieces)	15±.05°C, 43,000 lux agitated		(water) 1.7±.35 $mgCO_2$/gmDW/hr (air) 5.2±.25 $mgCO_2$/gmDW/hr	Johnson et al. (1974)
Chondrus crispus *Nova Scotia (N)* C^{14} method (pieces) no agitation	15°C, 1600 ft-c.		0.65 mg CO_2/gmFW/hr	Bidwell (1958)
*C. crispus** *Woods Hole*, Mass. 20°C manometric method	vegetative	1000 ft-c. (~250μE)	7,500 mm^3O_2/gmDW/hr	Kanwisher (1966)
*C. crispus** *New Hampshire* 15°C manometric method	pieces	1000 ft-c	50μl O_2/gmDW/hr	Mathieson & Burns (1971)
C. crispus	15°C	$\left[\frac{mgCO_2}{44} = mM\times 32 = mgO_2\right]$	6.36 $mgCO_2$/gmDW/hr	Buggeln & Craigie (1973)
C. crispus *Long Is., New York*, C^{14} method	10-12°C whole thalli	no sat. obs. up to 2000 ft-c.	0.33 mgC/gmDW/hr	Brinkhuis & Jones (1974)

Table 20 , cont., Photosynthesis of Red Algae

SPECIES	COMMENTS	SAT.PT.	PHS RATE	REFERENCE
*C. crispus**	15°C 0m		36µl O_2/gmDW/min	Mathieson & Norall (1975)
New Hampshire	-6m		30µl O_2/gmDW/min	
manometric method	-12m		25µl O_2/gmDW/min	
pieces	5°C cystocarpic	1080 ft-c (~263µE)	37µl O_2/gmDW/min	
	Tetrasporangial	1080 ft-c	50µl O_2/gmDW/min	
Eucheuma sp. * Florida manometric method	18°C pieces	300-900 ft-c	2.8-3.0µl O_2/gmDW/10 min	Mathieson & Dawes (1974)
Gigartina stellata Nova Scotia C^{14} method	15°C, 15,000 lux		3.5 mg CO_2/gmDW/hr	Majak et al. (1960)
*G. stellata** New Hampshire manometric method pieces	15°C	~2,100 ft-c	50µl O_2/gmDW/min	Mathieson & Burne (1971)
G. canaliculata S. California	21,500-64,000 lux 15°C		1.61 mg C/gmDW/hr	Littler & Murray (1974)

Table 20, cont., Photosynthesis of Red Algae

SPECIES	COMMENTS	PHS RATE	REFERENCE
Rhodoglossum affine S. California	21,500-64,500 lux, 15°C	0.92 mg C/gmDW/hr	Littler & Murray (1974)
Agardhiella tenera Puget Sound, Wash. in situ Winkler method	natural light clear day incub. at 1 M 8-12 m form	2.80 ml O_2/gmFW/hr	Gail (1922)
Halosaccion glandiforme	Intertidal form clear	4.548ml O_2/gmFW/hr	
	12-20 m form clear	.421 ml O_2/gmFW/hr	
	12-20 m form cloudy	.147 ml O_2/gmFW/hr	
	12-20 m form choppy sea	.228 ml O_2/gmFW/hr	
	12-20 m form choppy/cloudy	.003 ml O_2/gmFW/hr	
Prionitis lyalli	tidepool form clear	1.041 ml O_2/gmFW/hr	
Rhodymenia pertusa	12 m form clear	.556 ml O_2/gmFW/hr	
	12 m form cloudy	1.487ml O_2/gmFW/hr	
Polysiphonia lanosa Nova Scotia C^{14} method	15°C, 1600 ft-c no agitation	3.90 mg CO_2/gmFW/hr	Bidwell (1958)
Halosaccion ramentaceum		0.985mg CO_2/gmFW/hr	
Rhodymenia palmata		3.60 mg CO_2/gmFW/hr	
Porphyra umbilicalis Nova Scotia C^{14} method	15°C 15,000 lux	31 mg CO_2/gmDW/hr	Majak et al. (1960)
Ahnfeltia plicata		3.8 mg CO_2/gmDW/hr	

Table 20, cont., Photosynthesis of Red Algae

SPECIES	COMMENTS	PHS RATE	REFERENCE
Cystoclonium purpureum		20 mg CO_2/gmDW/hr	Majak et al. (1960)
Ceramium rubrum		28 mg CO_2/gmDW/hr	
Phycodrys rubens		6.4mg CO_2/gmDW/hr	
Polysiphonia nigrescens		4.4mg CO_2/gmDW/hr	
Corallina officinalis		1.8mg CO_2/gmDW/hr	
Odonthalia floccosa*	15°C, whole thalli Oregon Winkler method	8.0mg O_2/gmDW/hr	Kjeldsen & Phinney (1971)
Porphyra suborbiculata*	30 Klux 15°C Japan manometric method	35µl O_2/mgDW/hr	Yokohama (1971)
Gloiopeltis complanata*		6.5µl O_2/mgDW/hr	
Gymnogongrus flabelliformis*		5.0µl O_2/mgDW/hr	
Gelidium amansii*		8.0µl O_2/mgDW/hr	
Endocladia muricata	15±.05°C 43,000 lux C. California Winkler method (water) Infrared gas analysis (air)	water 2.1±1.0mg CO_2/gmDW/hr air 3.4±2.1mg CO_2/gmDW/hr	Johnson et al. (1974)
Porphyra perforata		water 6.3±1.1mg CO_2/gmDW/hr air 17.7±.95mgCO_2/gmDW/hr	

Table 20, cont., Photosynthesis of Red Algae

SPECIES	COMMENTS	PHS RATE	REFERENCE
Prionitis lanceolata		water 1.2±.10mg CO_2/gmDW/hr air 1.1±.04mg CO_2/gmDW/hr	
Gelidium robustum Winkler method *in situ* So. California	15°C, 21,500-64,500 lux	2.64mg Cfixed/gmDW/hr	Littler & Murray (1974)
Pterocladia capillacea		2.50±.37mg C/gmDW/hr	
Gelidium pusillum		1.87±.78mg C/gmDW/hr	
Lithothrix aspergillum		1.63±.32mg C/gmDW/hr	
Corallina chilensis		1.63±.26mg C/gmDW/hr	
Lithophyllum decipiens		0.50±.11mg C/gmDW/hr	
Pseudolithoderma nigra		0.26±.05mg C/gmDW/hr	
Polysiphonia lanosa New Hampshire manometric method	Intertidal 10°C Sat. pt. = 850 ft-c	180µl O_2/gmDW/min	Fralick & Mathieson (1975)
P. subtilissima	upper subtidal 15°C Sat. pt. = 1000 ft-c	125µl O_2/gmDW/min	
P. elongata	Shady, 10°C Sat. pt. = 185-250 ft-c	120µl O_2/gmDW/min	
P. nigrescens	Subtidal, 10°C Sat. pt. = 1000 ft-c.	30µl O_2/gmDW/min	

Table 20, cont., PHOTOSYNTHESIS OF PLANTS

SPECIES	COMMENTS		PHS RATE	REFERENCE
Blue-green algae California	15°C, 21,500-64,500 lux		0.26±.05mg C/gmDW/hr	Littler & Murray (1974)
Ulva expansa *California*	15±.05°C, 43,000 lux	(water)	16.7±.12mg CO_2/gmDW/hr	Johnson et al. (1974)
		(air)	12.2±3.0mg CO_2/gmDW/hr	
U. californica *California*	15°C, 21,500-64,500 lux		3.31±.59mg C/gmDW/hr	Littler & Murray (1974)
*Enteromorpha linza** *Oregon*	15°C	whole thalli	10mg O_2/gmDW/hr	Kjeldsen & Phinney (1971)
Laminaria sp.*	15°C	whole thalli Winkler method	6.0mg O_2/gm/hr	
	10°C	discs manometric method	2.0µl O_2/mgDW/hr	
*Alaria marginata**	15°C	whole thalli	3.9mg O_2/gmDW/hr	
*Sargassum muticum**	15°C	whole thalli Winkler method	5.5mg O_2/gmDW/hr	
	15°C	pieces manometric metod	3.0µl O_2/mg/hr	
Nereocystis luetkeana Puget Sound, Washington	incub. at 1 M	clear	1.207ml O_2/gmFW/hr	Gail (1922)
		choppy	.966 ml O_2/gmFW/hr	
		cloudy	.844 ml O_2/gmFW/hr	

Table 20, cont., Photosynthesis of Plants

SPECIES	COMMENTS	PHS RATE	REFERENCE
Fucus distichus California	15°±.05°C water air	.9±.13mg CO_2/gmDW/hr 5.8±.19mgCO_2/gmDW/hr	Johnson et al. (1974)
Egregia laevigata subsp. *borealis* California	15°, 21,500-64,500 lux	1.46±.17mg C/gmDW/hr	Littler & Murray (1974)
Sargassum agardhianum		1.34±.04mg C/gmDW/hr	
Eisenia arborea		0.90±.14mg C/gmDW/hr	
Colpomenia sinuosa		0.54±.08mg C/gmDW/hr	
Macrocystis pyrifera		2.94±.70mg C/gmDW/hr	
Phyllospadix torreyi c. *Melobesia*	15°C, 21,500-64,500 lux	1.45±.55mg C/gmDW/hr	Littler & Murray (1974)
P. torreyi		1.31±.19mg C/gmDW/hr	
Submerged freshwater angiosperms		2-10mg C/gmDW/hr	Westlake (1975)
Maize		15-70mg CO_2/dm^2/hr	Chmura (1967)
Alnus rubra (Elm)	peak, whole leaves	30mg CO_2/gmDW/hr	Schaedle (1975)
Pinus silvestris		25mg CO_2/gmDW/hr	
Picea abies (fir)		20mg CO_2/gmDW/hr	

Table 20, cont., Photosynthesis of Plants

SPECIES	COMMENTS	PHS RATE	REFERENCE
Glycine max (soybean) maximum	sun plant, Sat. pt. = 2,500 ft-c, comp. pt. = 100-150 ft-c	17mg $CO_2/100cm^2/hr$	Böhning & Bornside (1956)
Helianthus annuus (sunflower)		19mg $CO_2/100cm^2/hr$	
Nicotiana tabacum (tobacco)		15mg $CO_2/100cm^2/hr$	
Oxalis rubra	Shade plants, sat. pt. = 1000 ft-c; comp. pt. = 50 ft-c.	4mg $CO_2/100cm^2/hr$	
Dryopteris sp.		3mg $CO_2/100cm^2/hr$	
Sun plants (gen.)		10-20mg $C/100cm^2/hr$	Tranquillini (1964)
Shade plants (gen.)		4-16mg $C/100cm^2/hr$	
Cultivated plants (gen.)		20-30mg $C/100cm^2/hr$	
mosses	maximum rates 28 sp.	.6-3.5mg $CO_2/gmDW/hr$	Kallio, P. & L. Kärenlampi (1975)
lichens	max.	.3-1.5mg $CO_2/gmDW/hr$	

and habitats. For perspective, Table 20 gives a comparison among species in the Order Gigartinales and selected representatives from unrelated taxa.

The photosynthetic rates of intertidal central California *I. cordata* thalli are similar to some reported for *C. crispus* (Kanwisher, 1966; Bugglen and Craigie, 1973; Mathieson and Burns, 1974; Mathieson and Norall, 1975), *Gigartina stellata* (Mathieson and Burns, 1971; Majak et al., 1960), *Gigartina canaliculata* and *Rhodoglossum affine* (Littler and Murray, 1974). However, *I. cordata* rates are slightly higher than those reported for *Iridaea flaccida* from California, both in air and water (Blinks and Givan, 1960; Johnson et al., 1974). Brinkhuis and Jones (1974), using the ^{14}C method, report values an order of magnitude lower for *C. crispus* than those measured for *I. cordata*. Similarly, lower rates have been reported for various *Eucheuma* spp. from Florida (Mathieson and Dawes, 1974).

The intraspecific and intergeneric differences in photosynthetic rates of closely related taxa may be due in part to the "Doty Effect" by which the rate varies according to the time of day. Large differences between morning and afternoon phytoplankton photosynthetic rates have been demonstrated (Doty and Oguri, 1957; Yentsch and Ryther, 1957; Shimada, 1958). Similar variation in synchronous

Chlorella cultures (Tamiya, 1957; Sorokin, 1960) however, have been attributed to age, younger cells showing a higher rate than older cells. The absence of a daily photosynthetic rhythm in twelve California intertidal . algal species, including *I. flaccida* (Blinks and Givan, 1960), suggests that the "Doty Effect" may not be an important consideration in some macroalgae. However, a daily photosynthetic rhythm has recently been demonstrated in *Ulva* (Britz & Briggs, 1976). Since a study of daily rhythms was not undertaken for *I. cordata* nor for the other species cited in Table 20, the implications of the "Doty Effect" in relation to photosynthetic rate differentials among closely related taxa remains unknown.

Photosynthetic rates of red algae in general seem to be a reflection of life form, as suggested by Littler and Murray (1974). *I. cordata* photosynthetic rates are comparable to those of other foliose or robust genera, e.g., *Rhodymenia* (Gail, 1922), *Gloiopeltis*, *Gymnogongrus*, *Gelidium* (Yokohama, 1971), *Endocladia*, *Prionitis* (Johnson et al., 1974), *Gelidium* and *Pterocladia* (Littler and Murray, 1974), but are considerably lower than those for the filamentous or membraneous forms, e.g.: *Polysiphonia* and *Ceramium* (Majak et al., 1960; Fralich and Mathieson, 1975), *Phycodrys* (Majak et al., 1960) and *Porphyra* (Yokohama, 1971; Johnson et al., 1974).

The surf zone flowering plant *Phyllospadix torreyi*, a co-dominant within the central California *I. cordata* communities studied, has a photosynthetic rate quite similar to

I. cordata (Littler and Murray, 1974). The rates of terrestrial gymnosperms and angiosperms such as elm, pine, fir (Schaedle, 1975), soybean (Böhning and Burnside, 1956), maize (Chmura, 1967), and other sun plants in general (Tranquillini, 1964) are considerably higher than that of *I. cordata*. Terrestrial shade plants such as *Oxalis rubra* and a fern, *Dryopteris* sp. not only have photosynthetic rates comparable to those of *I. cordata* but are photosynthetically saturated at only slightly higher irradiance levels (Böhning and Bornside, 1956). The striking similarity between the primary production rates of the shade plants and *I. cordata* has undoubtedly resulted from adaptations to comparable irradiance regimes, i.e., in the deep redwood forest or damp coastal woodland and the surf zone at -1 m (DATUM: mean sea level). Moreover, all three genera are extremely successful in their shady habitats.

I. cordata photosynthetic rate is directly related to developmental stage. Rates of non-reproductive thalli are significantly higher (40.2%) than those of both gamatangial (male and cystocarpic) and tetrasporangial reproductive thalli. Since life history stage was not considered in most photosynthesis studies cited in Table 10, this rate differential,along with the "Doty Effect", could quite possibly be a source of intra- and interspecific variability in rates. This developmental stage rate differential was alluded to by Kanwisher (1960) when he reported that only vegatative algal parts were used in experiments because accessory (e.g., pneumatocysts) and reproductive parts gave variable results. Photosynthetic rates for tetrasporangial _C_. _crispus_ and _Ptilota_ _serrata_,but not _Euthora_ _cristata_,were higher than for respective cystocarpic stages (Mathieson and Norall, 1975a, 1975b). Unfortunately, it was not reported whether these differences were statistically significant.

The difference between non-reproductive and reproductive _I_. _cordata_ photosynthetic rates is reflected in the field-determined growth rates of individually tagged thalli (Table 21). Growth rates of _in_ _situ_ thalli were greater when non-reproductive than when reproductive in all months but July - October at which time the overall growth rates were very low and the thalli were undergoing seasonal senescence.

This rate differential may simply be due to the reduction in actively photosynthesizing cortical cells when thallus surface area is dominated by reproductive structures. Additionally, photosynthetic rates of reproductive thalli are inversely related to increasing thallus size (dry weight). This is most likely the effect of a decreasing ratio in the weights of non-photosynthetic (medulla) to photosynthetic (cortical) tissue as more structural tissue is added. The rate differential could also be due to an increased respiratory rate for reproductive thalli as was noted for _C_. _crispus_ (Newton et al., 1959); this was not measured in

TABLE 21

Iridaea cordata - Comparative Developmental Growth Rates

$(cm^2/cm^2/day)$

Date Tagged	$\bar{X}$ Rate-Non-Reprod.		$\bar{X}$ Rate-Reprod.		t	Probability
5 March 1974	.33	.15	.02	.004	3.40	$p < .05$
	.04	.21	.02	.02		
25 April	.01	.02	.002	.001	3.28	$p < .05$
	.044	.031	.008	.001		
6 June	.018	.026	.007	.003	3.34	$p < .05$
	.008	.026	.004	.004		
21 July	.0017	.0041	.0019	.0025	0.84	$p > .10$
	.0032		.0126			
17 August	.0042	.0055	.0018	.0018	4.69	$p > .10$
25 January 1975	.071	.0378	.0082	.0008	7.04	$p < .001$
	.1314	.1558	.0414	.0416		
	.0839	.044	.003	.0097		
	.075		.0078			
23 February	.1193	.1079	.0122	.0056	8.24	$p < .001$
	.1076	.1272	.0071	.0025		
	.1355	.1252	.0251	.115		
	.1676	.1265	.0148	.0101		
	.1265	.14	.0101	.0319		
	.0498	.1261	.0325	.0126		
	.121		.0066			

Table 21 , continued

_I_. _cordata_ Photosynthetic Rate - non-limiting conditions

Non-Reproductive Thalli -$\overline{X}$ - 2.49 ± .08 mgC/gm DW/hr

Reproductive Thalli (male, -$\overline{X}$ = 1.49 ± .01 mgC/gm DW/hr
Tetrasporangial, Cystocarpic)

this study. If true for I. cordata, this rate differential effect could also be attributed to an increasing ratio of photosynthetic to non-photosynthetic tissue.

Despite the photosynthesis rate differential for this species, all of the life history stages, including the non-reproductive stages, become photosynthetically saturated at approximately 150 μE. The compensation point was not reached by an irradiance of 23 μE, nor was inhibition observed by 420 μE (the highest irradiance used). Similar saturation points have been measured for subtidal Eucheuma sps. (Mathieson and Dawes, 1974) and for Polysiphonia elongata from shady habitats (Fralick and Mathieson, 1975), while slightly higher saturation points have been reported for east coast C. crispus (Kanwisher, 1966; Mathieson and Burns, 1971; Mathieson and Norall, 1975) and a number of terrestrial shade plants (Börning and Bornside, 1956). In one study of east coast C. crispus, no saturation was observed up to 2000 ft-c (approx. 400 μE) (Brinkhuis and Jones, 1974). It should be noted that photosynthetic rates reported in this study (op. cit.) were an order of magnitude less than all other reports for C. crispus. The saturation point for G. stellata, an upper intertidal inhabitant, was 2 to 2.5 times that of the above mentioned species and similar to terrestrial sun plants (Börning and Bornside, 1956).

These results indicate that plants from the lower intertidal, subtidal, and shady habitats in general, are just as efficient in terms of net production as are plants from habitats of greater irradiance.

The magnitude of I. cordata photosynthetic rate was not related to the nitrogen concentration of the seawater medium. This suggests that either nitrogen was never limiting, or the experiments were too short-term to reflect photosynthetic changes. Based upon the nitrogen uptake results to be discussed, the latter was most likely the case.

I. cordata doubling times in terms of carbon, were calculated from photosynthetic and respiration rates, thallus carbon content, and effective intertidal daylength. A doubling time indicates the number of days required for one doubling in thallus carbon under optimal laboratory conditions and actual effective mean seasonal daylength. The doubling times were shorter for non-reproductive thalli than for reproductive thalli reflecting the difference in photosynthetic rates of the two groups. Since natural populations are composites of all life history stages, a population doubling time is more representative than one for either non-reproductive or reproductive thalli alone. The doubling times varied seasonally due to effective daylength changes. The population doubling time for summer (10.7 days) was shorter than for any other season indicating annual light limitation, especially during winter.

Reported doubling times for phytoplankton and some macroalgae, have been based upon a twelve hour daylength of saturating irradiance. The results of submarine irradiance measurements in this study demonstrate that not only is irradiance attenuated by approximately 60% in the surf zone, but the effective daylength is truncated at both ends of the day, the extent of which is determined by the surface light intensity. Therefore, previously reported doubling times, with the possible exception of open ocean surface phytoplankton, may be inaccurate.

If effective daylength is accurately known for a specific algal habitat, algal doubling time can be extremely useful for interspecific comparisons and for predicting crop dynamics and development.

Nitrogen Uptake

The essential nutrient nitrogen can be limiting to plant growth in the oceans (Ketchum et al., 1958; Ryther, 1966; Thomas, 1969) just as it is on land, though relatively few studies describe the kinetics of nitrogen uptake for land plants (e.g., van den Honert and Hooymans, 1955; Becking, 1956; Fried et al., 1965; Picciurro et al., 1967; Berlier et al., 1969; Joseph et al., 1975; Hassan and Hai, 1976). The small number of studies on nitrogen uptake kinetics, relative to similar studies of other plant nutrients, has been attributed to 1) the lack of a convenient stable nitrogen isotope, and 2) the fact that nitrogen is metabolically very active and does not accumulate for assay purposes (Epstein, 1972). Uptake has been measured either by N-15 mass spectroscopy or by chemical analysis of the form of nitrogen in the medium before and after incubation of a particular plant species. Both of these methods have been used to measure nitrogen uptake in some phytoplankton species (Zobell, 1935; Dugdale and Goering, 1967; Eppley and Thomas, 1969; Eppley et al., 1969; Eppley and Rogers, 1970; Eppley and Sournia, 1971; Carpenter and Guillard, 1971; Caperon, 1972; McCarthy, 1972; McCarthy et al., 1972; McIsaac and Dugdale, 1972; Eppley and Renger, 1974; McIsaac et al., 1974; Thayer, 1974; Carpenter and McCarthy, 1975). Nitrogen uptake kinetics of a benthic alga, Fucus spiralis have recently been described (Topinka, 1975) and represent the only study on macroalgae.

The results of this study are the first to describe aspects of nitrogen uptake kinetics by Iridaea cordata, though such studies have been made on another red alga., Chondrus crispus (Craigie, unpublished, personal communication).

The following discussion should be predicated by the fact that the experimental thalli used were not axenic and some bacterial uptake of nitrogen may have occurred. However, I. cordata respiration measurements were very low, the error in the measurements due to bacterial respiration was much smaller than that due to analytical procedure. Therefore, any bacterial uptake or release of nitrogen in these experiments was considered to be negligible. Also rigorous thallus cleansing methods were employed to reduce bacterial contamination. Moreoever, non-axenic and axenic Gelidium nudifrons thalli exhibited (Bird, personal communication) similar nitrogen uptake rates suggesting that the bacterial uptake, compared to thallus uptake, was indeed negligible.

The results from the three preliminary experiments conducted on 15 I. cordata thalli indicated that: 1) both ammonium and nitrate are taken up, 2) ammonium is taken up in the dark, and 3) ammonium concentration has no effect on nitrate uptake. Further experiments carried out on 131 thalli verified and expanded upon these results.

Uptake rates of both ammonium and nitrate are similar for all life history stages including the non-reproductive thalli. This suggests that the I. cordata population as a whole, all life history stages as well as developmental stages, have uptake systems with a homogeneous affinity for these two nitrogen sources.

The ammonium/uptake substrate concentration curve for this species is hyperbolic in nature as described by the Michaelis-Menten equation or Langmuir absorption isotherm. To interpret the hyperbolic nature of the ammonium uptake data, analogy with enzyme kinetics must be made as follows:

$$S + C \underset{k_2}{\overset{k_1}{\rightleftarrows}} SC \quad \underset{k_4}{\overset{k_3}{\rightleftarrows}} C + S$$

where S represents the ion, C the carrier, and k_1, k_2, k_3 and k_4 the rate constants of the reaction where k_4 is negligible. To elaborate on the nature of ion uptake in terms of the Michaelis-Menten equation, it must be assumed that ammonium uptake is carrier-mediated. It should be noted however, that the carrier concept is only one possibility and alternate mechanisms (e.g., structural changes within the membrane resulting in electrical potential differences) have been proposed (Baker and Hall, 1975).

Evaluation of these conceptual mechanisms from the ion uptake data for I. cordata is beyond the scope of the present study.

The K_S (substrate concentration at which the uptake velocity is half maximal) and the V_{max} (maximum uptake velocity) for ammonium uptake by I. cordata were estimated from a rectangular hyperbola fitted by eye. These values were estimated from the hyperbola because a direct approximation from the linear transformation (S/V vs S) could not be made. This transformation tends to accentuate the smallest uptake values resulting in very large S/V values. Additionally, the greatest experimental error is likely to be made at the smallest substrate levels which would result in large S/V values.

It has been suggested that the K_S is an ecologically significant constant for organisms and is a reflection of ability to take up nutrients at specific concentrations, whereas the V_{max} is subject to the effects of environmental conditions (e.g., irradiance, daylength, temperature) (Eppley et al., 1968; Eppley et al., 1969).

Ammonium uptake (V) by I. cordata is linear at the lower substrate (S) levels used (1.16 to 5 μM NH_4-N) and the uptake system becomes saturated at higher levels (5-20 μM NH_4-N).

The estimated ammonium K_s for *I. cordata* (≅ 2.5 μm) is in the high range of those values reported for some marine phytoplankton species: *Skeletonema costatum* = 0.8-3.6 μM, *Rhizosolenia robusta* = 0.5 μM, *Ditylum brightwellii* = 1.1 μM, *Coscinodiscus lineatus* = 1.2-2.8 μM (Eppley et al., 1969), natural populations = 1.4 μM (McIsaac et al., 1974) and *Thalassiosira pseudonana* = .02-.66 μM (Eppley and Renger, 1975). The K_S reported for *Fucus spiralis* is higher (K_S = 9.6 ± 2.6) but within the same order of magnitude (Topinka, 1975). Ammonium K_S values for vascular plants such as corn, 23 μM (van den Honert and Hooynans, 1955), 13 μM (Becking, 1956), soybean, 5.2-19 μM (Joseph et al., 1975), and barley 110 μM (Rao and Rains, 1976) are quite variable, but in general high compared to those of the algae. Low ammonium K_S values represent a high affinity for this ion. Species with low values are able to utilize ammonium at lower concentrations in seawater or soil.

The estimated K_S for central California *I. cordata* is slightly high, but well within the normal concentration range (Broenkow, 1976) of coastal seawater ammonium. However, if the ammonium concentration fell well below the K_S, as it did at the study site during 1974-75, uptake would be considerably below $\frac{1}{2}V_{max}$. Therefore ammonia concentration could be limiting to growth of this species.

The variable ammonium V_{max} for *I. cordata* is most likely a reflection of previous history of the thalli used, as they were collected, and experiments were done throughout the year. Therefore, experimental thalli were subject to seasonally different environmental variables, e.g., photoperiod, irradiance, temperature, and nutrient regime, all of which have been reported to influence the V_{max} for phytoplankton (Eppley et al., 1968; Eppley et al., 1969). If there is an inherent difference in ammonium uptake among life history stages, it too may be obscured by previous-history influences. This will always be a limitation when field-grown thalli are used and V_{max} results should be evaluated accordingly.

The total V_{max} range for I. cordata is less than half that measured for F. spiralis ($V_{max} = .292 \pm .027$ $\mu M/cm^2/hr$). This would indicate that F. spiralis has a greater capability to utilize high ammonium levels when they are available. However, this comparison is subject to large confidence limits because one cm^2 of I. cordata is not comparable to one cm^2 of a Fucus apex. The values for F. spiralis would have been more useful if given on a volume or dry weight basis. Inherently high uptake velocities would be advantageous when ephemeral nitrogen sources were present. Such an opportunistic nitrogen uptake system suggests that algae may be able to store nitrogen and utilize it when needed. If present, such a storage capability would be highly important as it has been proposed that the internal nitrogen content (q) or the cell quota has more influence on nutrient uptake kinetics than the external nutrient concentration (Caperon and Meyer, 1972; Droop, 1973, 1974). This proposal is basic to nutrient uptake kinetic theory and should be tested for _I_. _cordata_ and other algae.

The graph of the ammonium uptake/substrate concentration relationship for _I_. _cordata_ is interesting in that the curve does not pass through the origin. That is, ammonium uptake appears to stop before the substrate concentration reaches zero somewhere between 1-2 μM (see Fig. 38A). Moreover, it is at these low substrate concentrations that the very high S/V values are found (see Fig. 38B). These ammonium uptake results at low substrate concentrations are not described by the Michaelis-Menten equation. Similar results have been reported for phytoplankton specific growth rate/substrate concentration curves for other ions (Caperon and Meyer, 1972; Paasche, 1973; Droop, 1974). Topinka (1975) found similar results for nitrogen uptake by _F_. _spiralis_, but regarded the data as anomalous and possibly due to contamination since it did not fit the Michaelis-Menten theory.

This threshold phenomenon could be due to contamination or experimental error as it is at very low substrate concentrations that such error is likely to occur. But in this study, extreme precautions were taken to control for such experimental error. Also, nitrogen leakage could account for the low residual substrate concentrations measured. Moreoever, for reasons related to the complex chemistry of seawater, some fraction of the NH_3+NH_4-N may be unavailable to the plant, just as binding of vitamin B_{12} and phosphate renders these nutrients unavailable to some phytoplankton species (Droop, 1973).

Caperon and Meyer (1972) and Paasche (1973) have introduced a substrate correction factor into the Michaelis-Menten equation to compensate for the uptake threshold. Droop (1973) argues that to introduce this factor "knocks away any theoretical foundations the equation may have had." Alternatively, Droop (op. cit.) hypothesizes that if some type of "product-control" were formulated into:

$$S + C \underset{k_2}{\overset{k_1}{\rightleftharpoons}} SC \underset{\boxed{k_4}}{\overset{k_3}{\rightleftharpoons}} S + C\ ,$$

that is a substantial k_4, the velocity of the reaction is no longer proportional to the concentration of the intermediate but is also influenced by the concentration of the product (cell quota). The overall reaction now has an equilibrium state where net uptake is zero with a finite substrate concentration, a phenomenon resulting from product breakdown (k_4). Consequently, the uptake or growth rate/ substrate curve would no longer pass through the origin, thus, the threshold effect. This hypothesis most certainly will be subject to rigorous radioisotopic testing. The threshold concept counterpart for fresh water microalgae and vascular plants has been observed for some time as the internal critical nutrient concentration below which growth ceases (e.g.: Gerloff and Skoog, 1957; Ingestad, 1960; Chapman, 1961; Gerloff and Krombholz, 1966).

If the ammonium uptake threshold for I. cordata is chemically accurate, the ecological implications could be far-reaching. The threshold occurs between 1-2 μM NH_4^+-N. Mean seawater ammonium concentrations near the study site ranged between 0.10 and 3.35 μM during 1974 (although levels can be much higher in normal coastal waters). If ammonium were the only nitrogen source available and seawater concentrations fell below 1 μM, this nitrogen source would be limiting to growth of I. cordata. If the internal nitrogen concentrations were measured for thalli growing on ammonium concentrations of threshold levels, that concentration would be equivalent to the critical nutrient level observed for vascular plants, or the cell subsistence quota described for phytoplankton (Droop, 1973). Therefore, the threshold value is that below which uptake and presumably growth would cease and the V_{max} occurs at the ammonium concentration for which the uptake system of I. cordata is saturated.

The above discussion is complicated of course by the fact that I. cordata and probably the algae in general do not take up only ammonium as a nitrogen source. The observation that I. cordata does not take up nitrite at the levels normally found in coastal seawater provides some simplification to the overall nitrogen uptake kinetics for this species. Nonetheless, nitrate is taken up and the rates are in general less, but similar to those of ammonium uptake.

Nitrate uptake for concentrations between 3.4 and 20.0 μM was extremely variable (see Fig. 39A) and no single line described the data. Variability was so large as to obscure any differences that may have existed between uptake at lower and higher concentrations, and the data are therefore not described by the Michaelis-Menten equation. This large variability, compared to that for ammonium uptake, suggests that the nitrate uptake mechanism may be very sensitive to changes in experimental conditions or "previous history" influences. Only a mean nitrate uptake value of 1.68 ± .13 μM/gm DW/hr over all concentrations used could be extracted from these data. The nitrate concentrations used were those normally found in seawater. It is probable that the critical concentrations needed to provide values for the linear section of the uptake/concentration curve are below 3.4 μM (the lowest concentration used). Therefore, further interpretation of these data must await further experiments. The mean nitrate uptake value used in the subsequent discussions of light/dark uptake, ion uptake differentials, and doubling times should be considered an approximation at best.

Uptake of ammonium by *I. cordata* and to a lesser extent nitrate, occurred in the dark. Dark uptake was approximately 40% and 19% respectively, of light uptake. Since the mean effective dark periods (at -1 m DATUM: mean sea level, + 3.0 ft.) ranged from 13.9 to 19.2 hrs/day, a significant proportion of total nitrogen (31-57%), especially ammonium, is taken up by *I. cordata* in the dark. No light/dark differences were observed for either ammonium or nitrate uptake by *F. spiralis* (Topinka, 1975), whereas reduced nitrogen uptake under low light or dark conditions has been observed for marine phytoplankton (Grant, 1967; Grant and Turner, 1969; McIsaac and Dugdale, 1972). In the diatom *Ditylum brightwellii* nitrate uptake occurred in the dark, and analyses demonstrated that nitrate remained unchanged within the cells, indicated that the energy required for nitrate reduction was not adequate (Eppley and Coatsworth, 1968). Similar results have been reported for *Fucus* sp. (Larsen et al., 1957).

The present results also demonstrate that ammonium and nitrate are taken up simultaneously by *I. cordata* thalli. However, regression analyses indicate that there is no linear relationship between uptake rates of these two nitrogen sources. Simultaneous uptake has also been reported for the macroalgae *F. spiralis* (Topinka, 1975), *Gelidium nudifrons*

(Bird, 1976) as well as natural phytoplankton populations (McIsaac et al., 1974). However, increases in ammonium concentration or uptake rate have been shown to inhibit nitrate uptake or nitrate reduction in some phytoplankton species (Dugdale and McIsaac, 1971; McCarthy and Eppley, 1972; Strickland et al., 1970; Eppley et al., 1969) and vascular plants (Lycklama, 1963; Minotti et al., 1969; Rao and Rains, 1976).

Further, the present results indicate that all I. cordata life history stages except the male thalli exhibited a nitrogen ion uptake differential. That is, the percentage of ammonium uptake was greater than that of nitrate uptake. This most likely indicates that ammonium uptake and assimilation requires less energy expenditure than does nitrate uptake. The exception of the male thalli may be a reflection of the small sample size tested. Similar results describing ion uptake differentials have been reported for phytoplankton (Syrett, 1962; Strickland et al., 1969; McIsaac and Dugdale, 1972; Bienfang, 1975) but were not observed for the benthic alga Gelidium nudifrons (Bird, 1976).

I. cordata growth (doubling time) in terms of thallus nitrogenous composition was calculated in two ways in order to verify whether or not the nitrogen (ammonium) uptake rates measured could reliably contribute the required amount of nitrogen necessary to support the I. cordata populations observed in the field. The first calculated doubling times were based upon the ammonium uptake rate at K_S (the substrate concentration at which the uptake rate was half maximal) plus the mean nitrate uptake rate. The second calculations were based upon ammonium uptake rates for the actual mean seasonal seawater concentrations measured at the study site plus the mean nitrate uptake rate. Even with the inclusion of the highly variable nitrate uptake rate, the first calculations are surprisingly similar to doubling times calculated for 1) the actual biomass of the natural population, and 2) thallus carbon (Table 22), whereas the second calculated doubling times are two to three times longer.

TABLE 22

Iridaea cordata Doubling Times (days)

SEASON	BIOMASS	CARBON	NITROGEN(K_S)	NITROGEN (SEAWATER)
Winter	23±2.7	24.3	24.9	43.3
Spring	11±0.5	14.2	21.2	56.4
Summer	15±3.3	10.7	19.0	48.5
Autumn	64±28.8	14.3	22.7	36.9

The biomass doubling times indicate the actual number of days required for the natural population to double in dry weight during a specified season. The doubling times in terms of thallus carbon were calculated from the experimentally determined net photosynthetic rates. These seasonal doubling times are nearly identical to the biomass-determined times and indicate that the natural populations measured were photosynthesizing at peak levels given the actual daylength and irradiance conditions present at -1 m (DATUM: mean sea level), except during autumn. The natural population doubled very slowly during autumn as the larger blades within the population senesced. The longer biomass doubling time for autumn suggests that growth was limited by effective irradiance, nitrogen, some other physical or chemical variable, or the function of a biological clock which triggers annual senescence.

The nitrogen doubling times based on the actual ammonium levels in the field were much longer than biomass determined times. These results suggest: 1) that thallus nitrogen content is lower than that measured or quite variable, 2) that the actual nitrogen uptake rates are higher than those measured (e.g., the mean nitrate uptake rate is higher), 3) that the ammonium levels within the population, either intermittent or continual, are higher than those measured (e.g., from invertebrate/vertebrate excreta), 4) that the thalli may be utilizing additional nitrogen sources (e.g., urea, amines, amides), and/or 5) that *I. cordata* is able to rapidly take up large amounts of nitrogen when it is available and store it until needed. This last possibility has been described by Droop (1973) as nutrient luxury consumption.

Since the nitrogen doubling times calculated from the ammonium K_s, are quite similar to both the biomass and carbon times, I. cordata thalli in natural populations are taking up more nitrogen than was measured in the laboratory under controlled conditions. That is, the measured ammonium uptake, extrapolated for actual seawater concentrations plus the estimated nitrate uptake, would not provide an adequate amount of nitrogen to support the thallus growth observed in the field and are, therefore, conservative in nature.

The results from this study have answered some important questions and in the process have raised a great many more regarding the physiological ecology of nitrogen uptake and its ultimate utilization by Iridaea cordata.

APPENDIX 20

Doubling Time Calculations - Photosynthesis (carbon)

$$R_E = \frac{\log_2 X_2 - \log_2 X_1}{t_2 - t_1} = \frac{\log_{10}\left(\frac{X_2}{X_1}\right) 3.32}{\Delta t}$$

$t/R_E t$ or $1/R_E$ = Doubling Time

Thallus carbon = 273.5 mg/gm DW

PHS mgC/gmDW/hr: $\bar{X}$ NR = 2.49
$\bar{X}$ R = 1.49
$\bar{X}$ Pop. = 1.99

RESP mgC/gmDW/hr: $\bar{X}$ = 0.07 × 24 hrs = 1.68 mg/day

$\Delta t = 1$ day

$x_1 = 1.0$

$$x_2 = \frac{\text{PHS (Effective Daylength) + RESP (24 hrs)}}{273.5}$$

Pop. Doubling Times

① Winter 1973-74 $\bar{X}$ daylength > 150 μE = 4.83 hrs

$$R_{E(pop)} = \log_{10}\left[1 + \frac{1.99(4.83)-0.07(24)}{273.5}\right]3.32$$

$$R_{E(pop)} = \log_{10}\left(1 + \frac{9.61-1.68}{273.5}\right)3.32 = \log_{10}(1.029)3.32$$

$$R_{E(pop)} = (.0124)(3.32) = .0412$$

$R_{E(pop)} = .0412$	$1/R_{E(pop)} = 24.27$ days
$R_{E(Reprod)} = .0288$	$1/R_{E(Reprod)} = 34.73$ days
$R_{E(NR)} = .0535$	$1/R_{E(NR)} = 18.68$ days

Appendix 20, Doubling Times-PHS (carbon) cont.

② Spring 1974 $\overline{X}$ Effective Daylength = 7.75 hours

$$R_{E(pop)} = \log_{10}\left[1 + \frac{1.99(7.75)-0.07(24)}{273.5}\right]3.32$$

$$R_{E(pop)} = (.0212720)(3.32) = .0706$$

$R_{E(pop)} = .0706$	$1/R_{E(pop)} = 14.16$ days
$R_{E(Reprod)} = .0510$	$1/R_{E(Reprod)} = 19.61$ days
$R_{E(NR)} = .0900$	$1/R_{E(NR)} = 11.11$ days

③ Summer 1974 $\overline{X}$ Effective Daylength = 10.07 hours

$$R_{E(pop)} = \log_{10}\left[1 + \frac{1.99(10.07)-0.07(24)}{273.5}\right]3.32$$

$$R_{E(pop)} = (1 + .067127)(3.32) = .0282051$$

$$R_{E(pop)} = .0936$$

$R_{E(pop)} = .0936$	$1/R_{E(pop)} = 10.68$ days
$R_{E(Reprod)} = .0685$	$1/R_{E(Reprod)} = 14.59$ days
$R_{E(NR)} = .1183$	$1/R_{E(NR)} = 8.45$ days

④ Autumn 1974 $\overline{X}$ Effective Daylength = 7.68 hours

$$R_{E(pop)} = \log_{10}\left[1 + \frac{1.99(7.68)-0.07(24)}{273.5}\right]3.32$$

$$R_{E(pop)} = (.0210652)(3.32) = .06993$$

$$R_{E(pop)} = .0699$$

Appendix 20, Doubling Times-PHS (carbon) cont.

$R_{E(pop)} = .0699$	$1/R_{E(pop)} = 14.30$ days
$R_{E(Reprod)} = .0504$	$1/R_{E(Reprod)} = 19.83$ days
$R_{E(NR)} = .0890$	$1/_{RE(NR)} = 11.23$ days

Doubling Time Calculations - Nitrogen

$$R_E \quad \frac{\log_2 X_2 - \log_2 X_1}{t_2 - t_1} \quad \text{or} \quad \frac{\log_{10} \frac{X_2}{X_1} \; 3.32}{\Delta t}$$

t/R_{Et} or $1/R_E$ = Doubling Time

$\Delta t = 1$ day

$X_1 = 1.0$

$$X_2 = \frac{\text{Light}\nu(\text{Effective Daylength}) + \text{Dark}\nu(\text{Dark hrs})}{23{,}500}$$

Thallus Nitrogen = 23,500 µgN/gmDW

a) Uptake rates (ν) based on NH_4-N K_S and NO_3-N $\bar{X}$ ν =

$\bar{X}$ Light NH_4-N ν = 2.5 µM/gmDW/hr x 14 = 35.0 µg

X Light NO_3-N ν = 1.76µM/gmDW/hr x 14 = 24.6 µg

$\bar{X}$ Dark NH_4-N ν = (35.0)(.416) = 14.7 µg

$\bar{X}$ Dark NO_3-N ν = (24.6)(.199) = 4.9 µg

Light ν = 59.6

Dark ν = 19.6

Appendix 20, Doubling Times - Nitrogen (cont.)

b) Uptake rates (ν) based on seasonal seawater substrate concentrations:

Winter

Light NH_4-N ν = 11.2 μg Light ν = 35.8
" NO_3-N ν = 24.6 μg

Dark NH_4-N ν = 4.7 μg Dark ν = 9.6
" NO_3-N ν = 4.9 μg

Summer

Light NH_4-N ν = 1.4 μg Light ν = 26.0
" NO_3-N ν = 24.6 μg
Dark NH_4-N ν = 0.6 μg Dark ν = 2.5
" NO_3-N ν = 4.9 μg

Spring

Light NH_4-N ν = 1.4 μg Light ν = 26.0
" NO_3-N ν = 24.6 μg
Dark NH_4-N ν = 0.6 μg Dark ν = 5.5
" NO_3-N ν = 4.9 μg

Autumn

Light NH_4-N ν = 14.0 μg Light ν = 38.6
" NO_3-N ν = 24.6 μg
Dark NH_4-N ν = 5.8 μg Dark ν = 10.7
" NO_3-N ν = 4.9 μg

<u>Winter</u> 1973-74 $\bar{X}$ Effective Daylength = 4.83 hrs,
Dark = 19.17 hrs

a) $$R_{E(pop)} = \log_{10}\left[1 + \frac{(59.6)(4.83) + (19.6)(19.17)}{23{,}500}\right]3.32$$

$$R_{E(pop)} = \log_{10}\left(1 + \frac{287.9 + 375.7}{23{,}500}\right)3.32$$

$$R_{E(pop)} = (.01258)(3.32) = .04178$$

Appendix 20, Doubling Times - Nitrogen (cont.)

Results:

a) R_E = .04178

$1/R_E$ = 24.9 days

b) R_E = .0231

$1/R_E$ = 43.28 days

Spring 1974 - $\bar{X}$ Effective Daylength = 7.75 hrs,
Dark = 16.25 hours

Results:

a) R_E = .047

$1/R_E$ = 21.23 days

b) R_E = .0177

$1/R_E$ = 56.38 days

Summer 1974 - $\bar{X}$ Effective Daylength = 10.07 hrs,
Dark = 13.93 hrs

Results:

a) R_E = .053

$1/R_E$ = 19.01 days

b) R_E = .0206

$1/R_E$ = 48.50 days

Autumn 1974 - $\bar{X}$ Effective Daylength = 7.68 hrs,
Dark = 16.32 hrs

Results:

a) R_E = .044

$1/R_E$ = 22.65 days

b) R_E = .0271

$1/R_E$ = 36.93 days

APPENDIX 21

IRRADIANCE CALCULATIONS

Interpretation of Weather measure Pyrheliograph charts.

1. Maximum chart reading = maximum units on chart(5) x instrument constant(0.37) = 1.85 ly

2. To measure $\overline{X}$ ly over a time period, multiply the area under the curve X instrument constant

3. $$\text{Chart constant} = \frac{\text{7 days} \times \text{1440 min/day} \times \text{1.85 ly}}{\text{area under 1.85 ly}}$$

$$= 125.75 \text{ gm cal/cm}^2\text{/cm}^2 \text{ of chart}$$

$$\overline{X} \text{ ly/day} = \frac{125.75 \times \text{area under curve for } x \text{ days}}{\text{\# days}}$$

Comparison between microeinsteins/m^2/sec and gm cal/cm^2/min (langley).

1) Regression equation: $y = 1831.1x - 55.1$ where $y = \mu E$ and x = ly (in terms of chart readings)

2) I. cordata is photosynthetically saturated at ~150 μE. Mean light attenuation at -1 m (Datum: mean sea level) = 59.4%. Therefore, saturating irradiance = 375 μE at the sea surface.

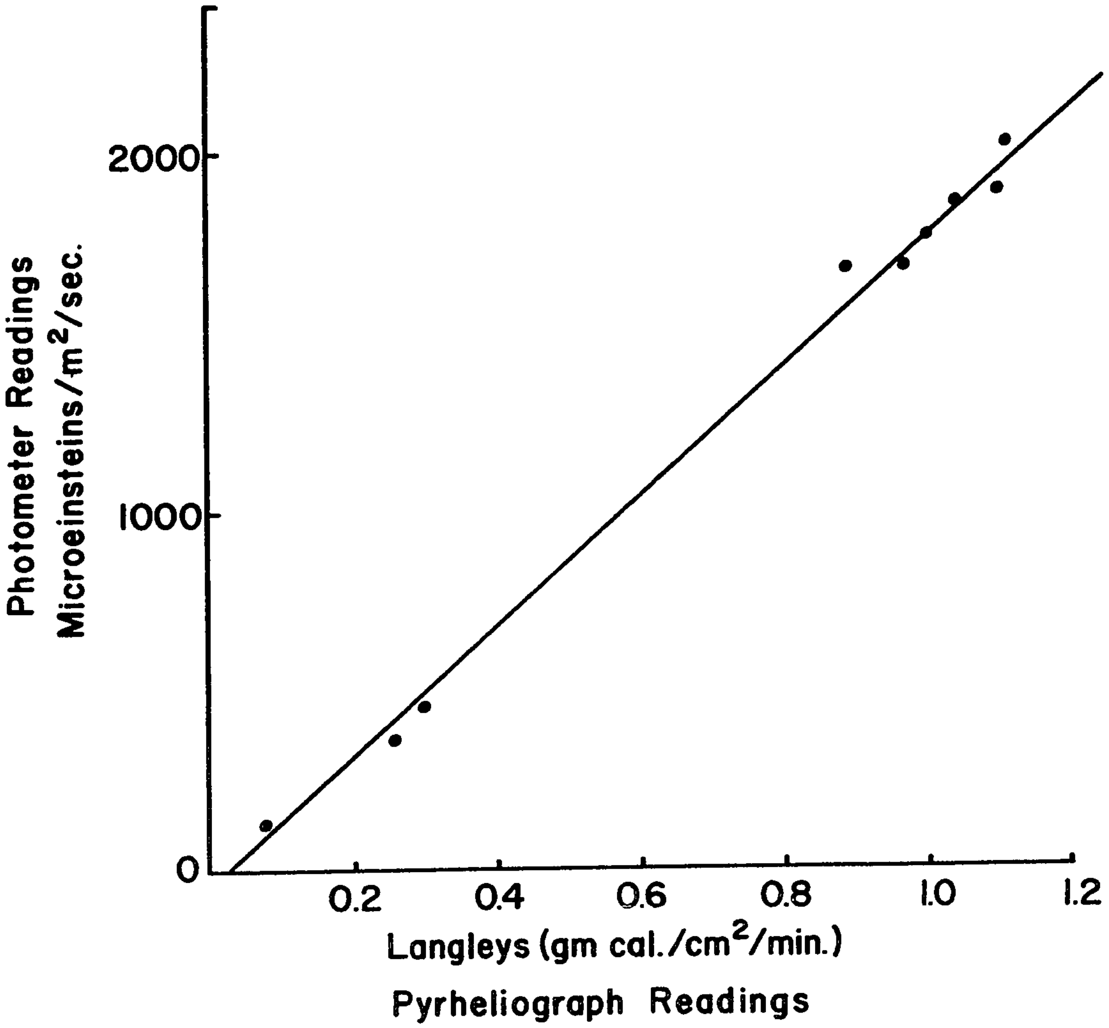
Thus: $375 = 1831.1x - 55.1$

$x = 0.24$

APPENDIX 21

Irradiance Comparison

$y = 1831.1x - 55.1$



APPENDIX 22

Año Nuevo Island, California

Daylength at -1 m (DATUM:MEAN SEA LEVEL)

Irradiance > 150μE (0.241 ly) = EFFECTIVE DAYLENGTH

Date	$\bar{X}$ hrs/day	Seasonal $\bar{X}$	Standard Error (Variance)
SPRING 1974 (5 February to 7 May, 1974)			
13 Feb-20 Feb	7.7	7.75	0.46
20 Feb-1 Mar	8.4		(1.29)
1 Mar-8 Mar	7.0		
9 Mar-15 Mar	7.0		
29 Mar-6 Apr	5.4		
12 Apr-19 Apr	8.0		
19 Apr-27 Apr	9.2		
27 Apr-6 May	9.3		
SUMMER 1974 (7 May to 19 July)			
6 May-13 May	9.6	10.07	0.31
13 May-19 May	10.7		(0.82)
19 May-26 May	10.7		
26 May-1 June	8.6		
1 June-10 June	11.0		
26 June-5 July	9.9		
5 July-15 July	10.0		
AUTUMN 1974 (19 July to 31 October)			
15 July-30 July	10.7	7.68	0.34
30 July-4 Aug	8.0		(1.33)
4 Aug-20 Aug	8.1		
21 Aug-26 Aug	8.8		
26 Aug-1 Sept	8.4		
27 Aug-3 Sept	7.1		
3 Sept-10 Sept	8.9		
10 Sept-17 Sept	7.7		
16 Sept-26 Sept	7.9		
29 Sept-1 Oct*	5.5		
1 Oct-7 Oct*	6.4		
8 Oct-14 Oct*	8.2		
15 Oct-22 Oct*	7.3		
22 Oct-29 Oct*	5.9		
29 Oct-31 Oct*	6.3		

Appendix 22, continued

Date	$\bar{X}$ hrs/day	Seasonal $\bar{X}$	Standard Error (Variance)
WINTER 1975			
29 Jan-6 Feb	4.8		

* Data from Hopkins Marine Station Instrument, Pacific Grove, California.

Effective daylength; the number of hours of irradiance > 150 µE at -1 m (DATUM: mean sea level) was measured directly from the Pyrheliograph data as the time (hrs) of irradiance ≥ 0.24 ly.

APPENDIX 23

Iridaea cordata Photosynthesis

Non-Reproductive Thalli

Exp.#	Time (hrs)	Dry Wt. (gm)	Irradiance (microeinstins/cm^2/sec)	mlO_2/gm/hr	mgO_2/gm/hr	mgC/gm/hr
22(1)	1.80	.36	150	4.61	6.59	2.52
22(2)	1.78	.23	150	8.13	11.63	4.32
23(1)	1.42	.50	150	5.29	7.56	2.88
23(2)	1.33	.43	150	5.54	7.92	3.00
23(3)	1.30	.28	150	6.77	9.68	3.60
24(A4)	1.83	.24	150	4.67	6.68	2.52
24(B3)	1.87	.45	150	4.72	6.75	2.52
24(B4)	1.88	.24	150	5.32	7.61	2.88
25(A1)	1.50	.42	150	6.79	9.71	3.64
25(A2)	1.50	.59	150	5.34	7.64	2.86
25(A3)	1.50	.45	150	5.28	7.55	2.83
25(A5)	1.50	.38	150	4.57	6.54	2.45

Appendix 23 continued , Non-Reproductive Thalli

Exp#	Time	Dry wt.	Irradiance	mlO_2/gm/hr	mgO_2/gm/hr	mgC/gm/hr
25(A6)	1.50	.22	150	4.70	6.72	2.52
25(B1)	1.52	.42	150	5.91	8.45	3.17
25(B2)	1.57	.59	150	5.21	7.45	2.79
25(B3)	1.55	.45	150	4.88	6.98	2.61
25(B5)	1.53	.38	150	4.62	6.61	2.48
25(B6)	1.55	.22	150	4.46	6.38	2.39
26(A1)	1.72	.24	150	4.36	6.23	2.34
26(A3)	1.72	.24	150	5.47	7.82	2.93
26(B1)	1.60	.24	150	4.15	5.93	2.22
26(B3)	1.67	.24	150	4.85	6.94	2.60
27(4)	1.63	.39	150	4.90	7.01	2.63
30(2)	2.00	.44	150	3.15	4.5	1.69
30(3)	2.00	.36	150	5.47	7.82	2.93
30(4)	2.00	.23	150	5.18	7.41	2.78
30(5)	2.00	.30	150	4.64	6.64	2.49
31(1)	2.17	.31	150	3.86	5.52	2.07

Appendix 23 continued, Non-Reproductive Thalli

Exp#	Time	Dry wt.	Irradiance	mlO_2/gm/hr	mgO_2/gm/hr	mgC/gm/hr
31(3)	2.17	.37	150	3.40	4.86	1.82
31(5)	2.12	.25	150	4.23	6.05	2.26
32(A1)	1.65	.26	150	4.94	7.06	2.65
32(A2)	1.68	.22	150	5.10	7.29	2.73
32(A3)	1.67	.38	150	3.26	4.66	1.75
32(A4)	1.67	.32	150	5.15	7.36	2.76
32(A5)	1.62	.31	150	5.09	7.28	2.73
32(B2)	1.50	.22	150	4.91	7.02	2.63
32(B3)	1.52	.38	150	3.15	4.5	1.69
32(B4)	1.45	.32	150	5.11	7.31	2.74
32(B5)	1.48	.31	150	4.12	5.89	2.21
33(A1)	2.00	.30	150	3.42	4.89	1.83
33(A4)	2.00	.32	150	3.88	5.55	2.08
33(B1)	2.00	.30	150	3.66	5.23	1.96
33(B4)	2.20	.32	150	3.94	5.63	2.11
41(2)	1.03	.57	420	4.19	5.99	2.25
41(3)	1.05	.49	420	4.63	6.62	2.48

Appendix 23 continued, Non-Reproductive Thalli

Exp#	Time	Dry Wt.	Irradiance	$mgO_2/gm/hr$	$mgO_2/gm/hr$	mgC/gm/hr
41(A2)	1.23	.57	150	4.12	5.89	2.21
41(A3)	1.25	.49	150	3.91	5.59	2.10
41(B2)	1.15	.57	67	2.31	3.30	1.24
41(B3)	1.17	.49	67	2.17	3.10	1.16
41(C3)	1.28	.49	23	0.67*	0.96	0.36*
43(1)	1.05	.43	420	5.76	8.24	3.09
43(A1)	1.07	.43	225	5.49	7.85	2.94
43(B1)	1.18	.43	150	4.85	6.94	2.60
43(C1)	1.23	.43	67	2.52	3.6	1.35
			Mean	= 4.64	= 6.64	= 2.49
			Standard Error	= 0.15	= .21	= 0.08
			Variance	= 1.17	= 1.67	= 0.33
			Sample Number	= 53	= 53	= 53

* value not included in mean calculations

Appendix 23, continued

Iridaea cordata Photosynthesis

Cystocarpic Thalli

Exp.#	Time (hrs)	Dry Wt. (gm)	Irradiance ($\mu E/cm^2/sec$)	$mlO_2/gm/hr$	$mgO_2/gm/hr$	mgC/gm/hr
24(A1)	1.87	.52	150	3.64	5.21	1.92
24(B1)	1.75	.52	150	3.93	5.62	2.10
25(A4)	1.50	.67	150	3.64	5.21	1.95
25(B4)	1.53	.67	150	3.61	5.16	1.93
26(A2)	1.77	.58	150	4.54	6.49	2.43
26(B2)	1.65	.58	150	4.61	6.59	2.47
27(1)	1.60	.64	150	3.44	4.92	1.87
29(3)	2.67	.52	150	2.82	4.03	1.51
31(4)	2.13	.72	150	2.88	4.12	1.54
33(A5)	2.00	1.69	150	1.99	2.85	1.06
33(B5)	2.00	1.69	150	2.00	2.86	1.07
35(5)	2.25	.82	420	2.19	3.13	1.17
36(B6)	1.52	.97	225	2.15	3.07	1.15
37(3)	1.92	.86	150	1.89	2.70	1.01

Appendix 23 continued, Cystocarpic Thalli

Exp#	Time	Dry Wt.	Irradiance	$ml O_2$/gm/hr	$mg O_2$/gm/hr	mgC/gm/hr
38(6)	1.25	.81	420	3.67	5.25	1.97
39(A1)	2.57	.41	<150	1.90	2.72	1.02
39(B1)	1.17	.41	>420	2.11*	3.02*	1.13*
40(A4)	1.22	.41	150	1.64	2.35	0.88
42(1)	1.03	.91	420	2.07	2.96	1.11
42(A1)	1.00	.91	225	2.30	3.29	1.23
42(B1)	1.00	.91	150	1.92	2.75	1.03
42(C1)	1.00	.91	67	1.05	1.50	0.57
42(D1)	1.07	.91	23	0.17*	0.24*	0.09*
43(3)	1.13	.68	420	2.65	3.79	1.42
43(A3)	1.15	.68	225	3.10	4.43	1.66
43(B3)	1.28	.68	150	2.91	4.16	1.56
			Mean =	2.77	= 3.96	= 1.48
			Standard Error =	0.19	= 0.27	= 0.10
			Variance =	0.90	= 1.29	= 0.26
			Sample Number =	24		= 24

Appendix 23 continued

Iridaea cordata Photosynthesis

Male Thalli

Exp.#	Time (hrs)	Dry Wt. (gm)	Irradiance ($\mu E/cm^2/sec$)	$mlO_2/gm/hr$	$mgO_2/gm/hr$	mgC/gm/hr
31(2)	2.20	.30	150	3.91	5.59	2.09
33(A2)	2.00	.30	150	3.10	4.43	1.66
33(B2)	2.00	.30	150	3.40	4.86	1.82
35(1)	2.40	.45	420	2.21	3.16	1.18
36(B5)	1.67	1.07	225	3.01	4.30	1.61
37(1)	1.95	.41	150	2.46	3.52	1.32
38(1)	1.22	.41	420	3.40	4.86	1.82
38(4)	1.22	.59	420	4.04	5.78	2.17
40(A6)	1.20	.32	150	3.52	5.03	1.89
41(1)	1.00	.89	420	3.02	4.32	1.62
41(A1)	1.17	.89	150	2.48	3.55	1.33

Appendix 23 continued, Male Thalli

Exp#	Time	Dry Wt.	Irradiance	$ml O_2$/gm/hr	$mg O_2$/gm/hr	mgC/gm/hr
41(B1)	1.10	.89	67	1.47	2.10	0.79
41(C1)	1.28	.89	23	0.54*	0.77*	0.29*
			Mean	= 2.81	= 4.02	= 1.51
			Standard Error	= 0.27	= .39	= 0.15
			Variance	= 0.96	= 1.37	= 0.28
			Sample Number	= 13		= 13

Appendix 23, continued

Iridaea cordata Photosynthesis

Tetrasporangial Thalli

Exp.#	Time (hrs)	Dry Wt. (gm)	Irradiance ($\mu E/cm^2/sec$)	$mlO_2/gm/hr$	$mgO_2/gm/hr$	mgC/gm/hr
24(A2)	1.88	.51	150	2.64	3.78	1.44
24(B2)	1.83	.51	150	3.22	4.6	1.68
33(B3)	2.00	1.05	150	1.87	2.67	1.00
35(3)	2.25	.62	420	2.22	3.17	1.19
36(B1)	2.05	.89	225	1.69	2.42	0.90
37(2)	1.92	.80	150	2.39	3.42	1.28
38(2)	1.17	.80	420	3.78	5.41	2.03
38(5)	1.23	.83	420	2.55	3.65	1.37
40(A2)	1.27	.41	150	3.62	5.18	1.94
42(2)	1.02	.81	420	2.80	4.0	1.50
42(A2)	1.03	.81	225	2.32	3.32	1.24
42(B2)	1.00	.81	150	3.09	4.42	1.66
42(C2)	1.03	.81	67	1.61	2.3	0.86

Appendix 23 continued, Tetrasporangial Thalli

Exp#	Time	Dry Wt.	Irradiance	$ml O_2$/gm/hr	$mg O_2$/gm/hr	mgC/gm/hr
42(D2)	1.10	.81	23	0.57*	0.82*	0.30*
43(2)	1.12	.36	420	3.57	5.11	1.91
43(A2)	1.12	.36	225	3.50	5.01	1.88
43(B2)	1.22	.36	150	3.19	4.56	1.71
			Mean =	2.75	= 3.93	= 1.47
			Standard Error =	0.18	= 0.26	= 0.09
			Variance =	0.49	= .7	= 0.14
			Sample Number =	16		= 16

APPENDIX 24

Iridaea cordata — Total Organic Carbon

Sample	Sample Weight (gm)	Barometric Pressure (mmHg)	Bar. T°C	Burrette T°C	$(\text{mgC} \times 10^{-2})$ Burrette Reading	Burrette Corr. Factor	Organic Content	% Org Carbon
24(L4)	.0221	74.38	23.8	29.0	.615	.910	.00560	25.3
22(D)	.0253	74.47	24.0	27.0	.724	.921	.00667	26.36
21(L1)	.0227	74.47	24.0	28.0	.735	.916	.00673	29.70
21(L2)	.0232	74.47	24.0	28.0	.685	.916	.00627	27.02
19(D)	.0210	74.40	24.0	28.0	.677	.916	.00620	29.50
24(D)	.0417	74.47	24.5	28.5	.760	.913	.00694	28.10
24(L1)	.0236	74.46	24.5	28.7	.753	.910	.00685	29.01
24(L3A)	.0254	74.46	23.5	27.8	.710	.916	.00650	25.60
24(L3B)	.0242	74.40	23.5	27.5	.694	.916	.00636	25.30
24(L2A)	.0234	74.46	24.5	28.0	.650	.916	.00595	25.44
24(L2B)	.0222	74.40	24.5	28.2	.640	.916	.00586	26.40

Appendix 24 continued, Total Organic Carbon

19(5A)	.0226	74.40	24.5	28.3	.667	.916	.00611	27.03
19(5B)	.0237	74.40	24.5	28.5	.747	.913	.00682	28.77

Mean = 27.19
Standard Error = 0.46
Variance = 2.69
Sample Number = 13

APPENDIX 25

Iridaea cordata Nitrogen Uptake

LHS = Life History Stage

NR = Non-Reproductive Thallus

C = Cystocarpic Thallus

T = Tetrasporangial Thallus

M = Male Thallus

* = Experiment carried out in the dark

± = Error range for replicate sample analyses

APPENDIX 25

Iridaea cordata Nitrogen Uptake

Exp#	Irradiance ($\mu E/cm^2/sec$)	NH_4-N (μM/gm/hr)	Orig. Conc. (μM)	End Conc. (μM)	NO_3-N (μM/gm/hr)	Orig. Conc. (μM)	End Conc. (μM)	Dry Weight (gm)	LHS
22(1)	150	3.31	21.02	12.48	-	-		.36	NR
22(2)	150	7.52	21.34	12.40	1.60	9.9	9.2	.23	NR
22D*	-	3.66	21.88	12.36	0.45	9.9	9.6	.34	NR
23(1)	150	1.60	2.49	1.18	0	22.6	22.6	.50	NR
23(2)	150	1.73	2.34	1.10	0	22.6	22.6	.43	NR
23(3)	150	2.60	2.34	1.12	0	22.6	22.6	.28	NR
24(A)	150	0.12	1.41	1.32	0.38	20.0	19.6	.52	C
24(A2)	150	0.35	1.41	.98	0.20	20.0	19.8	.51	T
24(A3)	150	0.51	1.41	.92	0.23	20.0	19.8	.45	NR
24(A4)	150	0.45	1.41	1.24	0.65	20.0	19.7	.24	NR
24(B)	150	5.90	13.86	7.76	0.41	20.0	19.6	.24	C
24(B2)	150	5.14	13.86	8.36	0.60	20.0	19.4	.24	T
24(B3)	150	5.08	13.26	8.72	0.68	20.0	19.4	.45	NR
24(B4)	150	5.66	13.26	10.16	1.68	20.0	19.2	.24	NR
24D*	-	0.13	1.29	1.28	0.11	20.0	19.9	.49	NR
25(A1)	150	0.52	1.97	1.62	1.64	7.0	5.9	.42	NR
25(A2)	150	0.48	1.97	1.52	0.96	7.0	6.1	.59	NR
25(A3)	150	0.60	1.97	1.54	1.96	7.0	5.6	.45	NR
25(A4)	150	0.40	1.97	1.54	0.45	7.0	.5	.67	C
25(A5)	150	0.31	1.97	1.78	0.66	7.0	6.6	.38	NR
25(A6)	150	0.25	1.97	1.88	1.13	7.0	6.6	.22	NR
25D*	-	0.02	1.97	1.96	0	7.0	7.0	.26	NR

APPENDIX 25

Iridaea cordata Nitrogen Uptake

Exp#	Irradiance (μE/cm^2/sec)	NH$_4$-N (μM/gm/hr)	Orig. Conc. (μM)	End Conc. (μM)	NO$_3$-N (μM/gm/hr)	Orig. Conc. (μM)	End Conc. (μM)	Dry Wt. (gm)	LHS
25(B1)	150	8.76	15.16	9.20	1.18	7.0	6.2	.72	NR
25(B2)	150	7.17	15.16	8.12	1.43	7.0	5.6	.59	NR
25(B3)	150	5.68	15.16	10.96	2.43	7.0	5.2	.45	NR
25(B4)	150	10.99	15.16	3.20	0.55	7.0	6.4	.45	C
25(B5)	150	6.17	15.16	11.36	1.30	7.0	6.2	.38	NR
25(B6)	150	4.36	15.16	13.56	1.09	7.0	6.6	.22	NR
25(BD)*	-	1.75	15.16	14.40	0.92	7.0	6.6	.26	NR
26(A1)	150	.50	1.64	1.52	0.91	7.0	6.6	.24	NR
26(A2)	150	0.29	1.64	1.32	0.73	7.0	6.2	.58	C
26(A3)	150	1.07	1.64	1.18	0	7.0	7.0	.24	NR
26(B1)	150	5.52	7.06	4.80	0.98	6.9	6.5	.24	NR
26(B2)	150	2.23	7.06	2.88	0.99	6.9	5.9	.24	C
26(B3)	150	5.73	7.06	4.66	0.24	6.9	6.8	.24	NR
27(1)	150	1.76	4.52	2.62	0.28	7.1	6.8	.64	C
27(4)	150	2.29	4.52	3.00	0.74	7.1	6.6	.39	NR
27(5)	150	4.06	4.52	2.78	0.93	7.1	6.1	.25	M
28(1)	150	3.18	3.36	1.96	0	7.1	7.1	.20	NR
28(2)	150	1.44	3.36	2.42	0.15	7.1	7.0	.29	NR
28(3)	150	0.59	3.36	2.04	0.27	7.1	6.5	1.00	C
28(4)	150	2.73	3.36	2.18	0	7.1	7.1	.19	NR
29(3)	150	1.18	3.46	1.72	0.88	4.0	2.7	.52	C
29(4)	150	1.71	3.46	1.70	0.78	4.0	3.2	.38	NR
29(5)	150	1.76	3.46	2.06	1.90	4.0	2.5	.29	NR
29(D)*	-	0.44	3.46	3.04	0	4.0	4.0	.28	NR
30(2)	150	0.58	2.38	1.84	0.86	11.3	10.5	.44	NR
30(3)	150	1.16	2.38	1.50	1.05	11.3	10.5	.36	NR
30(4)	150	0.62	2.38	2.08	1.45	11.3	10.9	.23	NR
30(5)	150	1.11	2.38	1.68	1.43	11.3	10.4	.30	NR
30(D)*	-	0.52	2.38	1.86	0	11.3	11.3	.47	NR

Appendix 25 continued, Nitrogen Uptake

Exp#	Irradiance ($\mu E/cm^2/sec$)	NH_4-N (μM/gm/hr)	Orig. Conc. (μM)	End Conc. (μM)	NO_3-N (μM/gm/hr)	Orig. Conc. (μM)	End Conc. (μM)	Dry Wt. (gm)	LHS
31(1)	150	0.14	1.64	1.54	1.26	17.5	16.6	.31	NR
31(3)	150	0.12	1.64	1.54	1.06	17.5	16.6	.37	NR
31(4)	150	0.07	1.64	1.54	1.62	17.5	14.9	.72	C
31(5)	150	-	-	-	3.40	17.5	15.6	.25	NR
31(D)*	-	0.10	1.64	1.54	0	17.5	17.5	.34	NR
32(A1)	150	1.46	1.98	1.32	2.20	11.0	10.0	.26	NR
32(A2)	150	1.74	1.98	1.30	3.07	11.0	10.2	.22	NR
32(A3)	150	0.77	1.98	1.46	1,40	11.0	10.2	.38	NR
32(A4)	150	1.73	1.98	1.00	3.71	11.0	8.9	.32	NR
32(A5)	150	1.51	1.98	1.10	4.10	11.0	8.9	.31	NR
32(AD)*	150	0.17	1.98	0.88	-	11.0	9.4	.35	NR
32(B1)	150	3.64	4.98	3.58	-	11.5		.26	NR
32(B2)	150	3.62	4.98	3.72	-	11.5		.22	NR
32(B3)	150	2.02	4.98	3.74	-	11.5		.38	NR
32(B4)	150	3.22	4.98	3.40	-	11.5		.32	NR
32(B5)	150	2.94	4.98	3.56	-	11.5		.31	NR
32(BD)*	150	0.97	4.98	4.48	-	11.5		.35	NR
33(A1)	150				3.63	18.3	16.0	.30	NR
33(A2)	150	-	-		4.14	18.3	15.7	.30	M
33(A4)	150				6.71	18.3	13.7	.32	NR
33(A5)	150				2.84	18.3	9.2	1.68	C
33(AD)*	-				0	18.3	18.3	.54	NR
33(B1)	150				-	18.5		.30	NR
33(B2)	150				3.34	18.5	16.4	.30	M
33(B3)	150				1.47	18.5	14.9	1.05	T
33(B4)	150				5.83	18.5	14.5	.32	NR
33(B5)	150				2.34	18.5	10.2	.32	C
33(BD)*	-				0.22	18.5	18.2	.54	NR
35(1)	420	1.95±.04	6.55	2.55	1.91±.95	11.6	8.33	.45	M
35(3)	420	1.72±.47	6.55	3.30	2.30	11.6	8.2	.62	T

Appendix 25 continued, Nitrogen Uptake

Exp#	Irradiance ($\mu E/cm^2/sec$)	NH_4-N ($\mu M/gm/hr$)	Orig. Conc. (μM)	End Conc. (μM)	NO_3-N ($\mu M/gm/hr$)	Orig. Conc. (μM)	End Conc. (μM)	Dry Wt. (gm)	LHS
35(5)	420	1.58±.18	6.55	3.48	2.37±.82	11.6	7.0	.82	C
36(A1)	640	1.44±.06	6.60	3.85	0	10.5	10.5	.89	T
36(A4)	640	2.50±.34	6.60	5.06	0	10.5	10.5	.25	NR
36(A5)	640	1.76±.02	6.60	1.90	1.05	10.5	7.7	1.07	M
36(A6)	640	1.66±.19	6.60	2.79	1.01	10.5	8.3	.97	C
36(B1)	225	1.66	6.66	3.46	2.13	11.7	7.6	.89	T
36(B5)	225	2.22	6.66	2.48	3.30	11.5	5.3	1.07	M
36(B6)	225	2.11	6.66	3.39	2.59	11.9	7.9	.97	C
37(2)	150	1.00±.15	3.63	2.01	3.45	12.1	6.5	.80	T
38(1)	420	3.74±.27	10.02	8.04	0.94	8.7	8.2	.41	M
38(2)	420	4.07±.25	10.02	6.00	2.4	8.7	6.3	.80	T
38(4)	420	5.42±.97	10.02	5.89	2.49	8.7	6.8	.59	M
38(5)	420	3.42±.32	10.02	6.34	0.74	8.7	8.0	.83	T
38(6)	420	4.36±.50	10.02	5.39	2.72	8.7	5.8	.81	C
39(A1)	150	0.27±.01	2.11	1.80	0	11.4	11.4	.41	C
39(B1)	>420	0.81±.02	2.11	1.70	0	11.4	11.4	.41	C
40(A2)	150	1.37±.21	2.05	1.30	1.46	7.8	7.0	.41	T
40(A4)	150	1.38±.15	2.05	1.32	1.70	7.8	6.9	.41	C
40(A6)	150	2.10±.13	2.05	1.20	2.23	7.8	6.9	.32	M
41(1)	420	0.64±.08	1.16	0.55	4.14	15.3	11.4	.89	M
41(2)	420	0.81	1.16	0.66	6.13	15.3	3.8	.57	NR
41(3)	420	0.81±.06	1.16	0.72	6.04	15.3	3.3	.49	NR
41(A1)	150	2.44±.06	4.32	1.63	4.45	15.3	10.4	.89	M
41(A2)	150	2.97±.07	4.32	2.12	5.27	15.3	3.9	.57	NR
41(A3)	150	2.29±.03	4.32	2.83	5.22	15.3	3.4	.49	NR
41(B1)	67	4.27±.11	7.67	3.25	3.29	15.3	11.9	.89	M
41(B2)	67	4.08±.07	7.67	4.85	4.19	15.3	12.4	.57	NR
41(B3)	67	3.29±.13	7.67	5.41	3.29	15.3	13.3	.49	NR
41(C1)	23	3.04±0	8.05	4.39	2.57	15.1	12.0	.89	M
41(C3)	23	5.39±.27	8.05	4.46	3.15	15.1	14.1	.49	NR

Appendix 25 continued, Nitrogen Uptake

Exp#	Irradiance ($\mu E/cm^2/sec$)	NH_4-N ($\mu M/gm/hr$)	Orig. Conc. (μM)	End Conc. (μM)	NO_3-N ($\mu M/gm/hr$)	Orig. Conc. (μM)	End Conc. (μM)	Dry Wt. (gm)	LHS
42(1)	420	1.24±.01	2.32	1.10	1.62	15.0	13.4	.91	C
42(2)	420	1.52±.01	2.32	1.00	2.31	15.0	13.0	.81	T
42(A1)	225	2.30±.02	3.93	1.73	1.77	14.9	13.2	.91	C
42(A2)	225	1.98± 0	3.93	2.20	2.28	14.9	15.6	.81	T
42(B1)	150	1.81±.12	4.35	2.62	1.77	15.6	13.9	.91	C
42(B2)	150	2.25±.02	4.35	2.44	2.88	15.6	15.1	.81	T
42(C1)	67	3.01±.09	5.8	3.01	1.46	15.5	14.1	.91	C
42(C2)	67	3.15±.06	5.80	3.04	1.71	15.5	14.1	.81	T
42(D1)	23	-	-	-	0.88	15.4	14.5	.91	C
42(D2)	23	-	-	-	0.96	15.4	14.5	.81	T
43(1)	420	2.68±.15	2.51	1.23	2.30	3.4	2.3	.43	NR
43(2)	420	1.79±.09	2.51	1.75	1.41	3.4	2.8	.36	T
43(3)	420	0.99±.10	2.51	1.70	0.73	3.4	2.8	.68	C
43(A1)	225	2.47±.22	2.51	1.42	1.85	3.7	2.8	.43	NR
43(A2)	225	2.49±.03	2.51	1.45	1.65	3.7	3.0	.36	T
43(A3)	225	1.40± 0	2.51	1.35	0.86	3.7	3.0	.68	C
43(B1)	150	2.18±.09	2.22	1.10	2.24	3.7	2.5	.43	NR
43(B2)	150	1.99±.19	2.22	1.30	1.94	3.7	2.8	.36	T
43(B3)	150	1.18± 0	2.22	1.13	1.62	3.7	2.2	.68	C
43(D)*	-	1.28±.02	2.51	.15	1.04	3.4	1.5	.58	NR

APPENDIX 26

Iridaea cordata Nitrogen Uptake Kinetics

Non-Reproductive Thalli

Exp#	NH_4-N			NO_3-N			Total Uptake NH_4-N + NO_3-N	% of Total Uptake	
	V	S	S/V	V	S	S/V		NH_4-N	NO_3-N
22(1)	3.31	21.02	6.35	-	-	-	3.31	-	-
22(2)	7.52	21.34	2.84	1.6	9.9	6.2	9.12	82%	18%
22D*	3.66	21.88	5.98	0.45	9.9	22.0	4.11	89	11
23(1)	1.60	2.49	1.56	0	22.6	-	1.60	100	0
23(2)	1.73	2.34	1.35	0	22.6	-	1.73	100	0
23(3)	2.60	2.34	0.89	0	22.6	-	2.60	100	0
24(A3)	0.51	1.41	2.76	0.23	20.0	87.0	0.74	69	31
24(A4)	0.45	1.41	3.13	0.65	20.0	30.8	1.10	41	59
24(B3)	5.08	13.26	2.61	0.68	20.0	29.4	5.76	88	12
24(B4)	5.66	13.26	2.34	1.68	20.0	11.9	7.34	77	23
24D*	0.13	1.29	9.92	0.11	20.0	181.8	0.24	54	46
25(A1)	0.52	1.97	3.79	1.64	7.0	4.3	2.16	24	76
25(A2)	0.48	1.97	4.1	0.96	7.0	7.3	1.44	33	67
25(A3)	0.60	1.97	3.28	1.96	7.0	3.6	2.56	23	77
25(A5)	0.31	1.97	6.35	0.66	7.0	10.6	0.97	32	68
25(A6)	0.25	1.97	7.88	1.13	7.0	6.2	1.38	18	82
25D*	.02	1.97	98.5	0	7.0	-	.02	100	0
25(B1)	8.76	15.16	1.73	1.18	7.0	5.9	9.94	88	12
25(B2)	7.17	15.16	2.11	1.43	7.0	4.9	8.6	83	17
25(B3)	5.68	15.16	2.67	2.43	7.0	2.9	8.11	70	30
25(B5)	6.17	15.16	2.46	1.30	7.0	5.4	7.47	83	17
25(B6)	4.36	15.16	3.48	1.09	7.0	6.4	5.45	80	20
25(BD)*	1.75	15.16	8.66	0.92	7.0	7.6	2.67	66	34
26(A1)	0.50	1.64	6.07	0.91	7.0	7.7	1.41	35	65

Appendix 26 continued, Non-Reproductive

	NH_4N			NO_3-N			Total Uptake NH_4-N +	% of Total Uptake	
Exp#	V	S	S/V	V	S	S/V	NO_3-N	NH_4-N	NO_3-N
26(A3)	1.07	1.64	1.64	0	7.0	-	1.07	100%	0%
26(B1)	5.52	7.06	1.28	0.98	6.9	7.0	6.5	85	15
26(B3)	5.73	7.06	1.28	0.24	6.9	28.8	5.97	96	4
27(4)	2.29	4.52	1.97	0.74	7.1	9.6	3.03	76	24
28(1)	3.18	3.36	1.06	0	7.1	-	3.18	100	0
28(2)	1.44	3.36	2.33	0.15	7.1	47.3	1.59	91	9
28(4)	2.73	3.36	1.23	0	7.1	-	2.73	100	0
29(4)	1.71	3.46	2.02	0.78	4.0	5.1	2.49	69	31
29(5)	1.76	3.46	1.97	1.90	4.0	2.1	3.66	48	52
29(D)*	0.44	3.46	7.86	0	4.0	-	0.44	100	0
30(2)	0.58	2.38	4.10	0.86	11.3	13.1	1.44	40	60
30(3)	1.16	2.38	2.05	1.05	11.3	10.8	2.21	52	48
30(4)	0.62	2.38	3.84	1.45	11.3	7.8	2.07	30	70
30(5)	1.11	2.38	2.14	1.43	11.3	7.9	2.54	44	56
30(D)*	0.52	2.38	4.58	0	11.3	-	0.52	100	0
31(1)	0.14	1.64	11.71	1.26	17.5	13.9	1.40	10	90
31(3)	0.12	1.64	13.67	1.06	17.5	16.5	1.18	10	90
31(5)	-	-	-	3.40	17.5	5.1	3.4	-	-
31(D)*	0.10	1.64	16.4	0	17.5	-	0.1	100	0
32(A1)	1.46	1.98	1.36	2.20	11.0	5.0	3.66	40	60
32(A2)	1.74	1.98	1.14	3.07	11.0	3.6	4.81	36	64
32(A3)	0.77	1.98	2.59	1.40	11.0	7.9	2.17	35	65
32(A4)	1.73	1.98	1.14	3.71	11.0	3.0	5.44	32	68
32(A5)	1.51	1.98	1.31	4.10	11.0	2.7	5.61	27	73
32(AD)*	0.17	1.98	11.65	-	11.0	-	-		
32(B1)	3.64	4.98	1.37						
32(B2)	3.62	4.98	1.38						

Appendix 26 continued, Non-Reproductive

Exp#	NH_4-N V	NH_4-N S	NH_4-N S/V	NO_3-N V	NO_3-N S	NO_3-N S/V	Total Uptake NH_4-N + NO_3-N	% of Total Uptake NH_4-N	% of Total Uptake NO_3-N
32(B3)	2.02	4.98	2.47						
32(B4)	3.22	4.98	1.55						
32(B5)	2.94	4.98	1.69						
32(BD)*	0.97	4.98	5.13						
33(A1)				3.63	18.3	5.0			
33(A4)				6.71	18.3	2.7			
33(AD)*				0	18.3	-			
33(B1)				-	18.5	-			
33(B4)				5.83	18.5	3.2			
33(BD)*				0.22	18.5	84.1			
36(A4)	2.5±.34	6.6	2.64	0	10.5	-	2.5	100%	0%
41(2)	0.81	1.16	1.43	6.13	15.3	2.5	6.94	12	88
41(3)	0.81±.06	1.16	1.43	6.04	15.3	2.5	6.85	12	88
41(A2)	2.97±.07	4.32	1.45	5.27	15.3	2.9	8.24	36	64
41(A3)	2.29±.03	4.32	1.89	5.22	15.3	2.9	7.51	30	70
41(B2)	4.08±.07	7.67	1.88	4.19	15.3	3.7	8.27	49	51
41(B3)	3.29±.13	7.67	2.33	3.29	15.3	4.7	6.58	50	50
41(C3)	5.39±.27	8.05	1.49	3.15	15.1	4.8	8.54	63	37
43(1)	2.68±.15	2.51	0.94	2.30	3.4	1.5	4.98	54	46
43(A1)	2.47±.22	2.51	1.02	1.85	3.7	2.0	4.32	57	43
43(B1)	2.18±.09	2.22	1.02	2.24	3.7	1.7	4.42	49	51
43(D)*	1.28±.02	2.51	1.96	1.04	3.4	3.3	2.32	55	45

APPENDIX 26

Iridaea cordata Nitrogen Uptake Kinetics

Tetrasporangial Thalli

Exp#	NH_4-N V	NH_4-N S	NH_4-N S/V	NO_3-N V	NO_3-N S	NO_3-N S/V	Total Uptake NH_4-N + NO_3-N	% of Total Uptake NH_4-N	% of Total Uptake NO_3-N
24(A2)	0.35	1.41	4.02	0.20	20.0	100.0	.55	64%	36%
24(B2)	5.14	13.86	2.7	0.60	20.0	33.3	6.24	90	10
33(B3)	-			1.47	18.5	12.59	1.47	-	-
35(3)	1.72±.47	6.55	3.8	2.30	11.6	5.0	4.02	43	57
36(A1)	1.44±.06	6.60	4.58	0	10.5	-	1.44	100	0
36(B1)	1.66	6.66	4.01	2.13	11.7	4.7	3.71	43	57
37(2)	1.00±.15	3.63	3.63	3.45	12.1	3.5	4.45	22	78
38(2)	4.07±.25	10.02	2.5	2.4	8.7	3.6	6.47	63	37
38(5)	3.42±.32	10.02	2.9	0.74	8.7	11.8	4.16	82	18
40(A2)	1.37±.21	2.05	1.5	1.46	7.8	5.3	2.83	48	51
42(2)	1.52±.01	2.32	1.5	2.31	15.0	6.5	3.83	40	60
42(A2)	1.98± 0	3.93	2.0	2.28	14.9	6.5	4.26	46	54
42(B2)	2.25±.02	4.35	1.9	2.88	15.6	5.4	5.13	44	56
42(C2)	3.15±.06	5.80	1.8	1.71	15.5	9.1	4.86	65	35
42(D2)*	-	-	-	.96	15.4	16.04	-	-	-
43(2)	1.79±.09	2.51	1.4	1.41	3.4	2.4	3.20	56	41
43(A2)	2.49±.03	2.51	1.0	1.65	3.7	2.2	4.14	60	45
43(B2)	1.99±.19	2.22	1.1	1.94	3.7	1.9	3.93	51	49

APPENDIX 26

Iridaea cordata Nitrogen Uptake Kinetics

Male Thalli

	NH_4-N			NO_3-N			Total Uptake	% of Total Uptake	
Exp#	V	S	S/V	V	S	S/V	NH_4-N + NO_3-N	NH_4-N	NO_3-N
27(5)	4.06	4.52	1.11	0.93	7.1	7.6	4.99	81%	19%
33(A2)	-	-	-	4.14	18.3	4.4	-	-	-
33(B2)	-	-	-	3.34	18.5	5.5	-	-	-
35(1)	1.95±.04	6.55	3.36	1.91±.95	11.6	6.1	3.86	51	49
36(A5)	1.76±.02	6.60	3.75	1.05	10.5	10.0	2.81	63	37
36(B5)	2.22	6.66	2.68	3.30	11.5	3.5	5.52	40	60
38(1)	3.74±.27	10.02	1.85	0.94	8.7	9.3	4.68	80	20
38(4)	5.42±.97	10.02	0.98	2.49	8.7	3.5	7.91	69	31
40(A6)	2.10±.13	2.05	1.81	2.23	7.8	3.5	4.33	48	52
41(1)	0.64±.08	1.16	1.77	4.14	15.3	3.7	4.78	13	87
41(A1)	2.44±.06	4.32	1.80	4.45	15.3	3.4	6.89	35	65
41(B1)	4.27±.11	7.67	2.65	3.29	15.3	4.7	7.56	56	44
41(C1)	3.04± 0	8.05	3.0	2.57	15.1	5.9	5.61	54	46

APPENDIX 26

Iridaea cordata Nitrogen Uptake Kinetics

Cystocarpic Thalli

Exp#	NH$_4$-N			NO$_3$-N			Total Uptake	% of Total Uptake	
	V	S	S/V	V	S	S/V	NH$_4$-N + NO$_3$-N	NH$_4$-N	NO$_3$-N
24(A)	0.12	1.41	11.75	0.38	20.0	52.6	.50	24%	76%
24(B)	5.9	13.86	2.34	0.41	20.0	48.8	6.31	94	6
25(A4)	0.40	1.97	4.92	0.45	7.0	15.6	.85	47	53
25(B4)	10.99	15.16	1.38	0.55	7.0	12.7	11.54	95	5
26(A2)	0.29	1.64	5.66	0.73	7.0	7.0	1.02	28	72
26(B2)	2.23	7.06	3.17	0.99	6.9	7.0	3.22	69	31
27(1)	1.76	4.52	2.57	0.28	7.1	25.4	2.04	86	14
28(3)	0.59	3.36	5.69	0.27	7.1	26.3	0.86	69	31
29(3)	1.18	3.46	2.93	0.88	4.0	4.5	2.06	57	43
31(4)	0.07	1.64	23.42	1.62	17.5	10.8	1.69	4	96
33(A5)				2.84	18.3	6.4	-	-	-
33(B5)				2.34	18.5	7.9	-	-	-
35(5)	1.58±.18	6.55	4.15	2.37±.82	11.6	4.9	3.95	40	60
36(A6)	1.66±.19	6.60	3.98	1.01	10.5	10.4	2.67	62	38
36(B6)	2.11	6.66	3.16	2.59	11.9	4.59	4.70	45	55
38(6)	4.36±.5	10.02	2.3	2.72	8.7	3.2	7.08	62	38
39(A1)	0.27±.01	2.11	7.81	0	11.4	-	0.27	100	0
39(B1)	0.81±.02	2.11	2.60	0	11.4	-	0.81	100	0
40(A4)	1.38±.15	2.05	1.49	1.70	7.8	4.6	3.08	45	55
42(1)	1.24±.01	2.32	1.87	1.62	15.0	9.3	2.86	43	57
42(A1)	2.30±.02	3.93	1.71	1.77	14.9	8.4	4.07	57	43
42(B1)	1.81±.12	4.35	2.40	1.77	15.6	8.8	3.58	51	49
42(C1)	3.01±.09	5.80	1.93	1.46	15.5	10.6	4.47	67	33
42(D1)	-	-	-	0.88	15.4	17.5	-	-	-

Appendix 26 continued, Cystocarpic Thalli

	NH_4-N			NO_3-N			Total Uptake	% of Total Uptake	
Exp#	V	S	S/V	V	S	S/V	NH_4-N + NO_3-N	NH_4-N	NO_3N
43(3)	0.99±.10	2.51	2.53	0.73	3.4	4.7	1.73	57%	43%
43(A3)	1.40± 0	2.50	1.79	0.86	3.7	4.3	2.26	62	38
43(B3)	1.18± 0	2.22	1.88	1.62	3.7	2.3	2.80	42	58

APPENDIX 27

Light and Dark Nitrogen Uptake in *Iridaea cordata*

NH_4-N μM/gmDW/hr				NO_3-N μM/gmDw/hr			
Dark	Light	$\overline{X}$	% of $\overline{X}$ Light	Dark	Light	$\overline{X}$	% of $\overline{X}$ Light
3.66	3.31 7.52	5.42±2.11	68	.45	1.60		28
.13	.51 .45 .35	0.44±.05	30	.11	.23 .65 .20	.36±.15	31
.02	.52 .48 .60 .31 .25 .40	0.43±.05	5	0	1.64 .96 1.96 .66 1.13 .45	1.13±.24	0
1.75	8.76 7.17 5.68 6.17 4.36 10.99	7.19±.97	24	.92	1.18 1.43 2.43 1.30 1.09 .55	1.33±.25	69
.44	1.71 1.76 1.18	1.55±.19	28	0	.78 1.90 .88	1.19±.36	0

Appendix 27, cont., Light and Dark Nitrogen Uptake

NH_4-N µM/gmDW/hr				NO_3-N µM/gmDW/hr			
Dark	Light	$\overline{X}$	% of $\overline{X}$ Light	Dark	Light	$\overline{X}$	% of $\overline{X}$ Light
.52	.58	.87±.15	60	0	.86	1.20±.15	0
	1.16				1.05		
	.62				1.45		
	1.11				1.43		
.10	.14	.11±.02	91	0	1.26	1.84±.53	0
	.12				1.06		
	.07				3.40		
					1.62		
.17	1.46	1.44±.08	12	0	3.63	4.33±.84	0
	1.74				6.71		
	.77				4.14		
	1.73				2.84		
	1.51						
.97	3.64	3.09±.30	31	.22	5.83	3.25±.94	7
	3.62				3.34		
	2.02				1.47		
	3.22				2.34		
	2.94						
1.28	2.68	1.91±.20	67	1.04	2.30	1.62±.18	64
	2.47				1.85		
	2.18				2.24		
	.99				.73		
	1.40				.86		
	1.18				1.62		
	1.79				1.41		
	2.49				1.65		
	1.99				1.94		

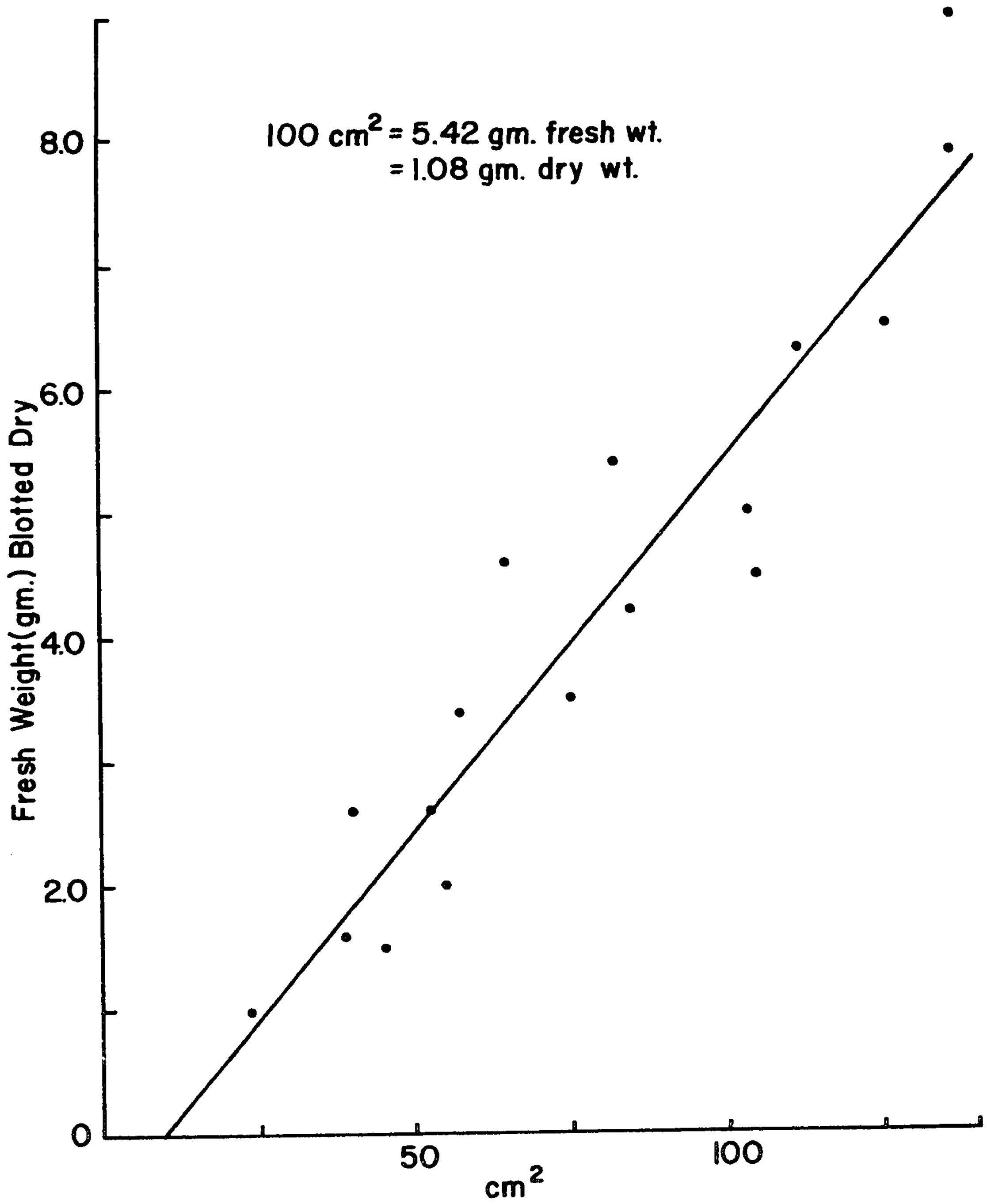
Appendix 27, cont., Light and Dark Nitrogen Uptake

$\overline{X}\%$ = 41.6±8.9	$\overline{X}\%$ = 19.9±8.6
N = 10	N = 10
Variance = 786.4	Variance = 744.4
Paired data dest = t_9 = 2.66	= t_9 = 3.77
Probability = $.02 < p < .05$	= $p < .01$

* Uptake of both NH_4-N and NO_3-N is significantly less in the dark than in the light.

APPENDIX 28

Iridaea cordata Area(cm²)/Blotted Fresh Weight(gm.)



CONCLUDING REMARKS

The present studies were designed to answer several questions regarding the *in situ* population structure, ontogeny, and growth of *Iridaea cordata* in relation to net photosynthesis and nitrogen uptake, aspects of its physiological ecology.

Iridaea cordata populations vary seasonally with peak crops during summer and lows in winter. The overall population density and biomass are dominated by the tetrasporangial stage. The biochemical results of carrageenan analyses indicate that this dominance is also present in the juvenile population. It is suggested that dominance arises either at the spore level or through highly successful vegetative reproduction of the diploid stage. The physiological results indicate that this dominance phenomenon is not the result of more efficient net photosynthesis or nitrogen uptake by the tetrasporangial stage.

Regrowth of *in situ I. cordata* populations following seasonal harvests occurs predominately from vegetative reproduction of annual erect blades from the basal, perennial crusts. The success and extent of both vegetative reproduction and perennation in this species suggests that the contribution of these processes to benthic algal production in general may be considerably underestimated. Furthermore, the perennating crust acts as a 'space-saver' following senescence and die-back of the erect blades —— an effective adaptation for successful competition where available substrate is limited.

Growth of *in situ I. cordata*, measured as a) cumulative growth from perennial crusts, b) discrete seasonal growth from crusts, and c) growth of individual thalli, is highly correlated with the season. The lowest growth rates, during winter,are followed by a spectacular 18 - 22 fold increase during spring. Those thalli that are initiated in winter and sustain the following spring burst of growth, continue to grow rapidly throughout the summer and attain the maximum growth potential observed. Those thalli initiated at other times of the year never realize the maximum growth potential and have shorter, more variable life spans. The majority of thalli begin to senesce during autumn, and die-back with the onset of winter storms. This overall pattern demonstrates that growth in *I. cordata* is synchronous and is characterized by distinct annual oscillations.

I. cordata reproductive maturation occurs throughout the year and within three to six months of blade initiation except during winter when the growth rate is slow. The majority of blades continue to grow following maturation, but at a slower rate. This rate differential is a reflection of the photosynthetic rate; the rate of non-reproductive thalli is approximately 42% higher than that of reproductive thalli of all life history stages. This rate differential is most likely due to a reduction in photosynthetically active cortical tissue as it is replaced by reproductive tissue.

These overall results demonstrate the chronological ontogenetic progression of this species. Initiation of juvenile thalli occurs predominately during winter followed by a burst of growth in spring which is associated with a three-fold increase in solar irradiance and a concurrent increase in daylength. Thallus maturation proceeds throughout the summer and the majority of the population is reproductively mature by autumn. General population senescence begins in autumn and a major component of the large senescing blades are torn loose with the onset of the first severe winter storms. This winter die-back leaves the population composed of basal perennial crusts with remnants of erect thalli and small, usually stunted thalli (that were initiated after spring and never reached the maximum growth potential), and juvenile blades less than 3 cm in length.

The results of the physiological studies of I. cordata demonstrate that the irradiance requirements for photosynthesis are very similar to those of terrestrial shade plants. The comparative doubling times (in situ biomass and in vivo carbon) for I. cordata, based on the measured effective daylength at -1 m (DATUM: mean sea level) indicate that growth is limited during winter by irradiance/daylength. That is, the calculated amount of carbon fixed at the peak photosynthetic rate based on the actual winter irradiance/daylength at -1 m, is equal to that produced in the natural population during winter. Growth is not limited by irradiance for the remainder of the year. Autumn growth is very slow and is complicated by the onset of annual thallus senescence.

The results of I. cordata nitrogen uptake kinetics demonstrate that both ammonium and nitrate, but not nitrite (at ambient seawater concentrations) are taken up. Ammonium uptake is hyperbolic in nature with an estimated K_s of 2.5 μM and a mean V_{max} of 5.0 μM/gm DW/hr. A significant proportion of ammonium uptake occurs in the dark. A notable uptake threshold for ammonium occurs between 1 and 2 μM NH_4-N. If ammonium were the only nitrogen source available to this species and levels fell below this critical threshold, growth would cease. Nitrate uptake was highly variable indicating that it may be very sensitive to previous history influences (e.g., irradiance, temperature, other nutrients) which have been shown to influence phytoplankton uptake rates. Additionally, both ammonium and nitrate are taken up simultaneously, but ammonium concentration does not appear to affect nitrate uptake.

A discrepancy existed between seasonal *in situ I. cordata* doubling times and calculated doubling times of its nitrogen content based on nitrogen uptake rates. The calculated doubling times, extrapolated for actual seawater nitrogen concentrations, were considerably longer than *in situ* times suggesting that nitrogen was limiting throughout the year. As this was probably not the case, these results indicate that *in situ* thalli take up more, and or different forms of nitrogen than were measured under experimental conditions.

This study incorporates the first detailed analysis of the natural population biology and physiological ecology of a red alga, *Iridaea cordata*. A number of questions were answered and many more were raised. This alone stresses the need for further, concurrent analytical field biology/ physiological studies of macroalgae.

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