

EPIPHYTISM AND ENDOPHYTISM OF
MACROCYSTIS INTEGRIFOLIA AND NEREOCYSTIS LUETKEANA:
SEASONALITY, SUCCESSION AND TACTICS ON
TEMPORARY, LIVING SUBSTRATE

by

William Roland
B.Sc.(Hons.), University of Victoria, 1975

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Biological Sciences

© William Roland 1980
SIMON FRASER UNIVERSITY
March, 1980

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

APPROVAL

Name: William G. Roland
Degree: Master of Science
Title of Thesis: Epiphytism and Endophytism of Macrocystis integrifolia
and Nereocystis luetkeana: seasonality, succession
and tactics on temporary living substrate

Examining Committee:

Chairman: Dr. Robert C. Brooke

Dr. L. D. Druehl, Senior Supervisor

~~Dr. G. R. Lister~~

Dr. E. B. Hartwick

Dr. P. V. Fankboner, Non-Supervisory Committee Examiner

Date approved

March 13, 1980

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis, ~~project or extended essay~~ (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution; on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/~~Project/Extended-Essay~~

Epiphytism and Endophytism of *Macrocystis integrifolia*
and *Nereocystis luetkeana*: seasonality, succession and tactics
on temporary living substrate

Author: _____

(signature)

William G. Roland

(name)

April 3, 1980

(date)

ABSTRACT

Epiphytism and endophytism of the stipes and blades of the large kelps Macrocystis integrifolia Bory and Nereocystis luetkeana (Mertens) Postels and Ruprecht were studied in a semi-exposed kelp bed in Bamfield Inlet, Vancouver Island, British Columbia. Major factors influencing epiphytism were seasonal immigration, specific features of the host, and the life spans of the blades and stipes. A spring increase in settlement of ectoprocts, hydroids, suctorians, and macroalgae was followed by summer or fall declines in species numbers and abundance. In contrast, diversity of diatoms on blades was lowest in spring and increased in fall and winter. Variations in densities of bacteria and endophytic algae were not seasonal. Growing tissue appeared to inhibit settlement and/or growth of organisms and host morphology effected positioning of organisms. The life span of the host tissue was important to the degree of development of organisms and assemblages of organisms. Abundant organisms on blades (life span of approximately 2 months) were restricted to bacteria, microalgae, and small animals. Only on stipes (life spans 6 - 14 months), did macroalgae become abundant.

Algae which were abundant had simple thalli with high surface to volume ratios, reproduced vegetatively on the host and had more rapid rates of development than less abundant seaweeds such as Fucales germlings and Laminariales which were solitary, complex, and failed to attain reproductive maturity within the host life span. Most abundant animals were small at maturity, reproduced by budding and produced disseminules within the life span of the host. Mortality mainly resulted from death of the host but also occurred from grazing (Druehl et al, 1977; Roland 1978). Density dependent mortality from competition for space occurred

seasonally and more rarely from overgrowth of certain organisms by others.

ACKNOWLEDGMENTS

I wish to thank my supervisor, Dr. Louis D. Druehl, for providing the opportunity to conduct this research. His direction and influence were invaluable.

I am grateful to my committee, Drs. Geoffry R. Lister and E. Brian Hartwick, for help throughout the study.

I wish to thank the staff of the Bamfield Marine Station and express appreciation for use of the facilities.

The research was principally funded through National Research Council of Canada grants to Dr. Louis Druehl. I am grateful to them for support during 1975 and 1976 with a Postgraduate Scholarship.

Mr. L. Michael Coon provided criticism of the final draft. Ms. Shirley Smith typed the defended manuscript and Pat Mash typed the final draft.

TABLE OF CONTENTS

	<u>Page</u>
APPROVAL	ii
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
LIST OF TABLES	viii
LIST OF FIGURES	ix
INTRODUCTION	1
DESCRIPTION OF STUDY SITE AND STUDIED HOST SPECIES	2
METHODS AND MATERIALS	6
Sampling Procedure	6
Treatment of Samples	6
Statistical Treatment	7
Artificial Substrate	8
Settlement of <u>Membranipora serrilamella</u>	9
Taxonomic Notes	9
RESULTS	9
Phylum Ectoprocta	10
Phylum Cnidaria	12
Phylum Protozoa	12
Division Phaeophyta	13
Order Ectocarpales	13
Order Laminariales	14
Division Chlorophyta	14
Family Ulvaceae	14
Family Chaetophoraceae	15

	<u>Page</u>
Division Rhodophyta	16
Diatoms on blades of <u>Macrocystis</u> and <u>Nereocystis</u>	32
Bacteria on blades of <u>Macrocystis</u> and <u>Nereocystis</u>	41
Epiphytism of Artificial Substrates	43
Glass Slides	43
Plastic "Plants"	43
DISCUSSION	44
Colonization	44
Host Effects	46
Host Life Span, Life Histories, and Succession	49
REFERENCES CITED	52

LIST OF TABLES

<u>Number</u>		<u>Page</u>
1	Epiphytes and endophytes, except diatoms and bacteria, of the stipes and blades of <u>Macrocystis</u> and <u>Nereocystis</u>	17
2	Seasonal occurrence of diatom taxa on blades of <u>Macrocystis</u>	34
3	Seasonal occurrence of diatom taxa on blades of <u>Nereocystis</u>	35

LIST OF FIGURES

<u>Number</u>		<u>Page</u>
1.	Locations of study sites	4
2.	Semi-diagrammatic sketches of <u>Macrocystis integrifolia</u> and <u>Nereocystis luetkeana</u>	5
3.	Colonization curves of stipes and blades of <u>Macrocystis</u> and <u>Nereocystis</u>	18
4.	Percent cover of the encrusting bryozoan, <u>Membranipora serrilamella</u> Osburn, on blades of <u>Macrocystis</u> from June 1976 through December 1977	19
5.	Size class histograms of <u>Membranipora serrilamella</u> Osburn colonies on blades of <u>Macrocystis</u>	20
6.	Percent cover of the encrusting bryozoan, <u>Membranipora serrilamella</u> Osburn from February 1977 through December 1977	21
7.	Density of the hydroid, <u>Obelia</u> sp., on <u>Macrocystis</u> blades from June 1976 through December 1977	22
8.	Density of suctorians on blades of <u>Macrocystis</u> from June 1976 through December 1977	23
9.	Percent chance of occurrence per mm ² for Ectocarps on stipes of <u>Nereocystis</u> from February 1977 through December 1977	24
10.	Density of the endophyte <u>Streblonema aecidioides</u> f. <u>pacificum</u> Setchell and Gardner from July 1976 through December 1977 in blades of <u>Macrocystis</u>	25
11.	Percent chance of occurrence per mm ² of the endophyte <u>Bulbocoleon piliferum</u> Pringsheim	26
12.	Photographs of <u>Membranipora serrilamella</u> Osborn and <u>Obelia</u> sp	27
13.	Photographs of suctorians	28
14.	Photographs of epiphytised stipes of <u>Macrocystis</u> and <u>Nereocystis</u>	29

<u>Number</u>		<u>Page</u>
15.	Photographs of <u>Streblonema aecidioides f. pacificum</u> Setchell and Gardner in blades of <u>Macrocystis</u>	30
16.	Photographs of <u>Bulbocoleon piliferum</u> Pringsheim in blades of <u>Macrocystis</u>	31
17.	Seasonal variation in diatom densities on blades of <u>Macrocystis</u>	36
18.	Seasonal variation in diversity (H') and equidability ($\frac{H'}{\log_2 S}$) of diatoms on blades of <u>Macrocystis</u> and <u>Nereocystis</u>	37
19.	Dendrograms derived from cluster analysis of sampling dates for diatoms on blades of <u>Macrocystis</u> and <u>Nereocystis</u>	38
20, 21	Scanning electron photomicrographs of diatoms and bacteria on <u>Macrocystis</u>	39, 40
22.	Density of bacteria on blades of <u>Macrocystis</u>	42

INTRODUCTION

The life history traits of colonizers of unstable environments (Southwood, et al, 1974; Nichols, 1976), and the significance of seasonality and substrate stability to community structure in temperate marine waters have been theoretically and experimentally examined (e.g. Emerson and Zelder, 1978; Osman, 1977). Epiphytes (organisms attached to plants) of benthic marine plants in temperate latitudes live in a seasonally changing environment and, since host tissue is typically short lived, inhabit unstable substrates. However, an epiphytic ecosystem is peculiar in that the substrate may have evolved responses to colonizers (e.g. Sieburth, et al, 1974), and the often continual formation of new substrate through plant growth creates a habitat for colonization which is predictable and not dependent on perturbations for creation of new space.

Epiphytism of seaweeds and seagrasses has been studied descriptively and experimentally (e.g. Sloan et al, 1957; Harlin, 1973a,b, 1975; Boaden et al, 1976); however, I am not aware of any comprehensive study of an epiphytic ecosystem. Markham (1969) described the vertical distribution of seaweed epiphytes on the stipes of Nereocystis luetkeana (Mertens) Postels and Repracht near San Juan Island, Washington, but epiphytism has not been described for plants on the west coast of British Columbia. Except for brief mention (Scagel, 1947; Tokida, 1960; Lobban, 1976) epiphytism of Macrocystis integrifolia Bory has not been studied. I have described the seasonal and within plant distributions of epiphytes and endophytes of the stipes and blades of the large kelps N. luetkeana and M. integrifolia. Succession of epiphytic and endophytic organisms was followed. Life history and natural history characters of

of the epiphytes and endophytes were noted. Artificial substrates were used to compare the seasonality and succession of biotic with abiotic substrates.

Description of Study Site and Studied Host Species

The main study site was a kelp bed in Bamfield Inlet on Vancouver Island, British Columbia (Fig. 1). Macrocystis, the most abundant of the two species, formed a fringing bed close to shore. Nereocystis was scattered throughout the bed of Macrocystis and along the outer perimeter. The depth range of the two species was from 0 to -4m below 0 tide. Monthly variations in temperature, salinity, and solar radiation throughout the period of this study have been reported by Lindsay and Saunders (1977, 1978). Surface water temperatures were 5 - 10°C in winter and over 15°C in summer. Salinities were between 25 and 28‰ in winter and around 30‰ in summer. Solar radiation in winter was less than 100 gcal/cm²/day and over 400 gcal/cm²/day in summer. In summer the kelp bed was fairly sheltered from waves but was semi-exposed in winter due to changing prevailing winds. Mean higher high water and mean lower low water were 3.3 and 0.9 m respectively above 0 tide.

These kelps were unique for a study of epiphytism due to their large size (length of mature stipes 3-4 m) and pattern of growth (Fig. 2). The main intercalary meristematic region is near the apex of the frond (stipe plus blades) of Macrocystis and at the junction of the stipe and blades of Nereocystis. These meristems continually produce new tissue, although the rate varies seasonally (Lobban, 1978; Foreman, R.E., Dept. of Botany, University of British Columbia). The holdfast

of Macrocystis is perennial and new fronds are produced throughout the year. The stipe, which bears the blades, is present approximately 6 months and any blade lives about 2 months (Lobban, 1978). The Nereocystis sporophyte is an annual which begins growth in March and April, ceases growth by late summer and dies during spring and early summer of the following year. The stipe is present 12-14 months and any piece of blade tissue probably remains about 2 months. The blades of Macrocystis are covered with furrows and ridges and blades of Nereocystis are smooth. Because new tissue is added at the meristems with progressively older tissue found distal to the meristems, certain successive events can be followed without the passing of time. Each species has tissues of widely varying ages throughout all seasons, allowing the importance of the state of tissue maturity to be examined. In this study I recognized three qualitative ages or states of tissue maturity: growing tissue, mature tissue (not growing but healthy) and senescent tissue (decaying).

Figure 1. Locations of study sites.

4b

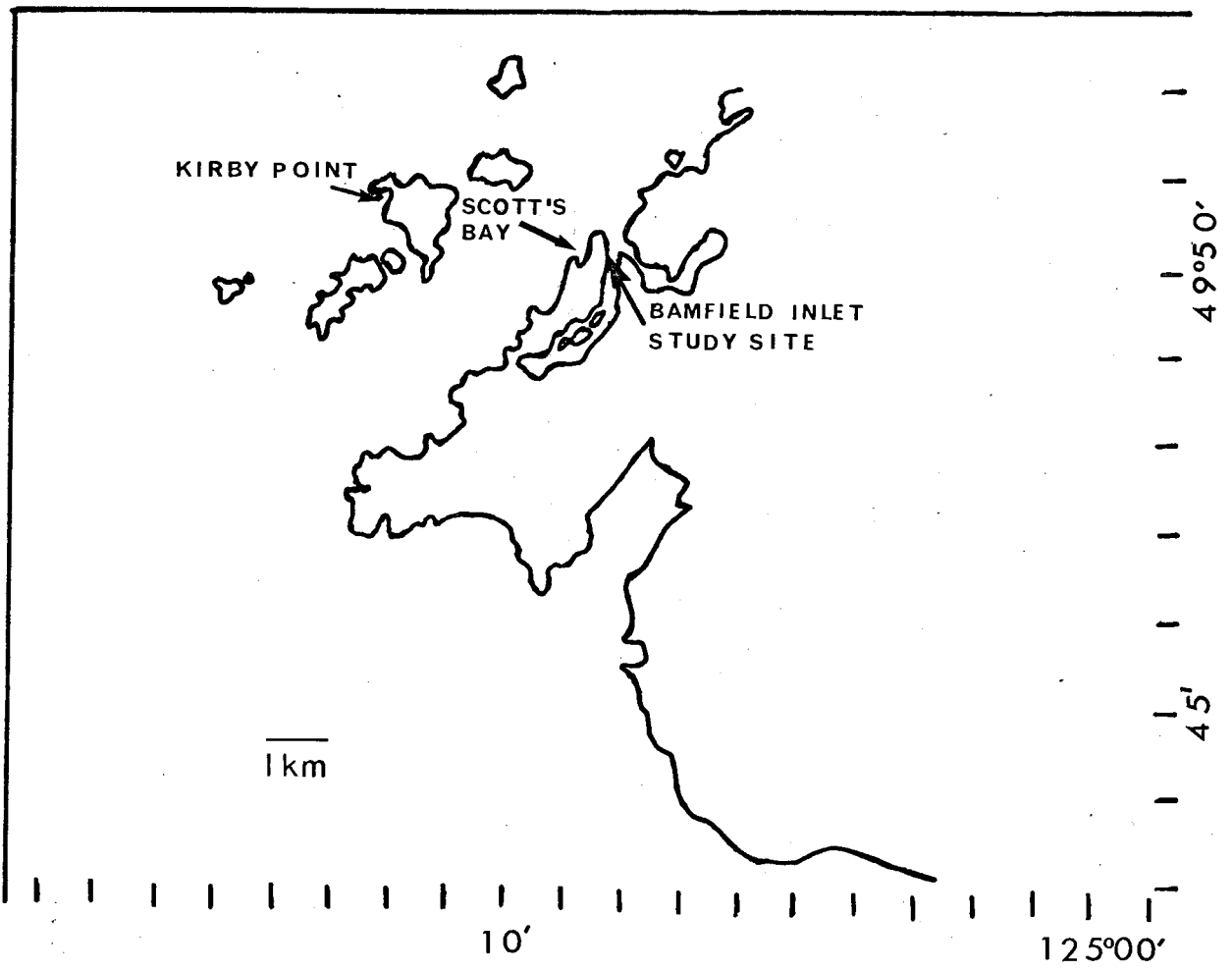
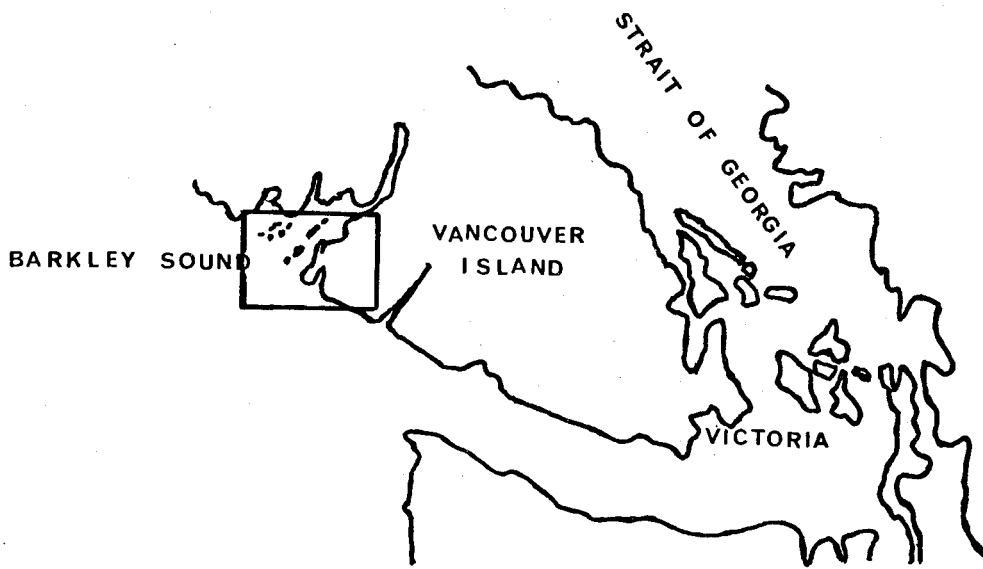
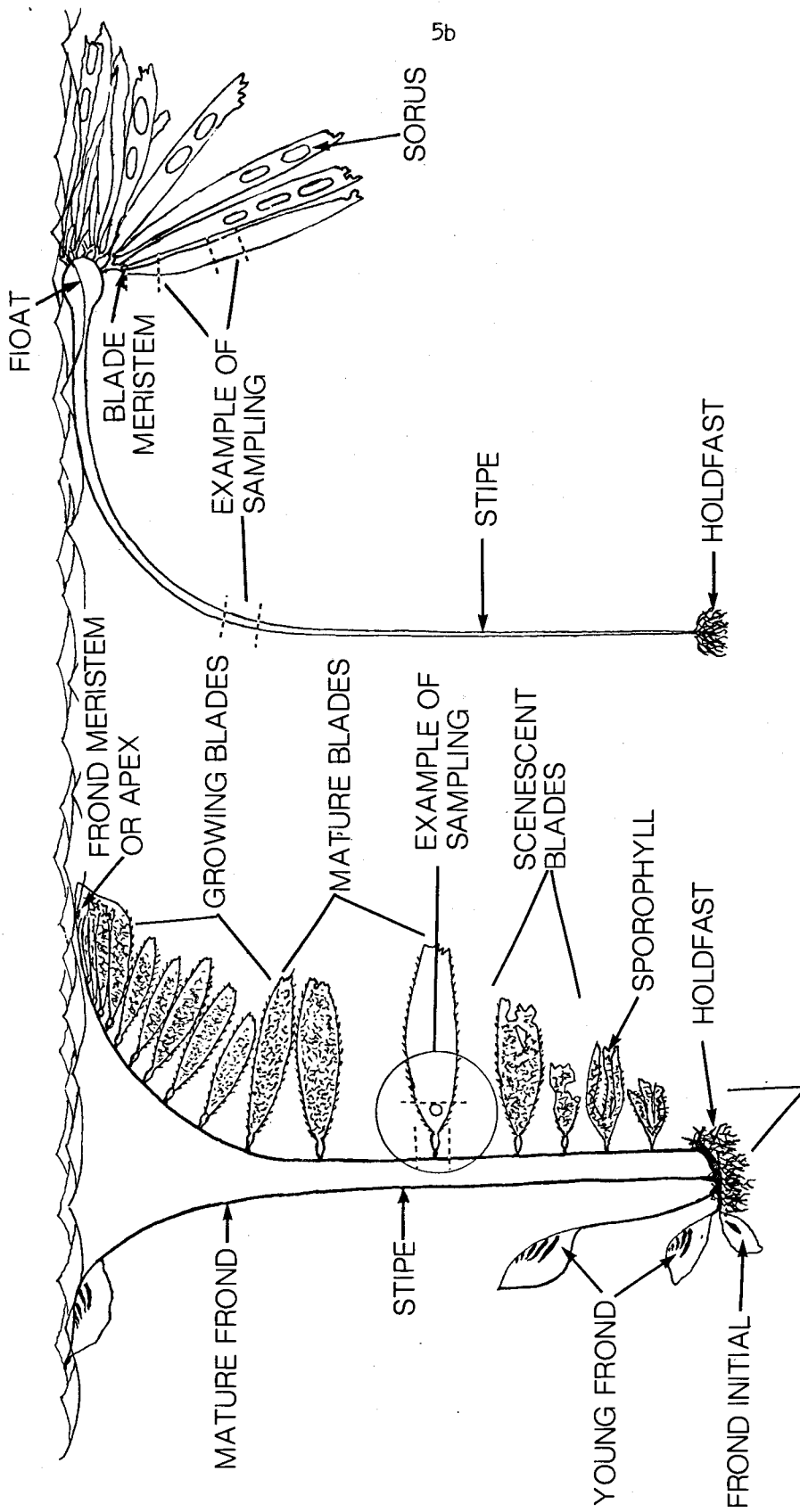


Figure 2. Semi-diagrammatic sketches of Macrocystis integrifolia (left) and Nereocystis luetkeana (right).



METHODS AND MATERIALS

Sampling Procedure

Plants of Macrocystis and Nereocystis were randomly sampled each 4-7 weeks from July 1976 to December 1977. Fronds of Macrocystis (n=10-18) were subsampled at 0.1 m below the frond meristem, then at 0.5 m intervals to the frond base. At each interval, 10 cm of the stipe and the first 10 cm of the blade from the float were sampled (Fig. 2). For low magnification work and diatom study by acid clearing, 3.5 cm diameter subsamples were taken 10 cm from the float. For scanning electron microscopy (SEM), five 1 cm diameter subsamples, cut 10 cm from the float, were taken at 0.1, 1.0, and 2.0 m from the frond meristem.

Blades of Nereocystis (n=5) were subsampled 5-15 and 45 - 55 cm from the float (Fig. 2). Stipes (n=2-6) were sampled at each 0.5 m interval from the float from February to December 1977. Each sample was 10 cm long.

Taxa missed due to sampling error were calculated with a species area curve, where area was the number of stipes or blades. Virtually all sample sizes taken were well into the asymptote of the curves.

Epiphytes and endophytes were occasionally observed on Macrocystis and Nereocystis in other areas, over a range of wave exposures.

Treatment of Samples

Plant tissue was preserved in 10% formalin in seawater. The preserved tissue was examined for epiphytes and endophytes at three levels of magnification. 1. Epiphytes clearly discerned with the unaided eye (e.g. bryozoans and macro-algae) were quantified on the entire piece of tissue sampled. 2. Epiphytes requiring low (X45) magnification (e.g. suctorians and hydroids) were quantified with a dissecting microscope by

counting organisms occurring in 100 randomly chosen 1 mm^2 quadrats on the tissue sampled. 3. Epiphytes requiring high (500-10,000 X) magnification (e.g. diatoms and bacteria) were examined with light or scanning electron (SEM) microscopy.

Tissue for SEM observations was preserved in 5% glutaraldehyde in 1:1 sea water and fresh water. Tissue was refrigerated up to two months, then dehydrated in a series of acetone washings, critical point dried with CO_2 , mounted onto stubs with silver paint, gold coated by vacuum diffusion (NRC 3115) and viewed with the SEM (ETEC Corp.). Diatoms were counted and identified in 10 random quadrats at 900X (0.81 mm^2). Epiphytic diatoms were also examined by dissolving samples of plant tissue, after removal of large epiphytes, with 1:1 sulfuric and nitric acids. The resultant suspension was allowed to settle for 24 hr, the supernatant poured off, and the settled diatoms diluted with distilled water. This was repeated several times to dilute the acid to a low concentration. Measured amounts of the final volume of suspended diatoms were spread evenly onto coverslips, dried and mounted in Hyrax. Random transects on 3 slides were counted to quantify the number of diatoms per unit area of host tissue. Typically 500 diatoms were counted in each sample, as this number was always into the asymptote of species versus sample size curves (Saunders, 1968) indicating that a large change in sample size added very few species.

Statistical Treatment

Diversity of diatoms sampled was estimated by the information measure (H') (Shannon and Weaver, 1949) where n_i is the number of

individuals in the i th species, N is the total number of individuals in the sample, and s is the number of species in the sample.

$$H' = - \sum_{i=1}^s \left(\frac{n_i}{N} \right) \log_2 \left(\frac{n_i}{N} \right)$$

Evenness of distribution of individuals among the species was calculated as $\frac{H'}{\log_2 s}$ (Pielou, 1975). This measure aids in interpreting the calculated diversity index since a community with a few evenly distributed species can have the same H' as one with many unevenly distributed species (Pielou, 1975).

The niche breadth of diatom taxa were calculated by the expression

$$B_i = \exp \left[- \sum_{r=1}^Q \left(\frac{n_{ir}}{N_i} \right) \log_e \left(\frac{n_{ir}}{N_i} \right) \right]$$

where n_{ir} is the number of individuals of the i th taxon in the r th sample in all Q samples (Levins, 1968; McIntire and Overton, 1971; Main and McIntire, 1974). This measures the evenness of distribution of a taxon throughout the samples considered (Main and McIntire, 1974).

Cluster analysis of cases (Biomedical Program series at Simon Fraser University computing center) was used to cluster sampling dates of diatoms. The chi-square test of equality defined the distance between data of any two cases and was used to form clusters.

Artificial Substrate

"Plants" composed of plastic 5 cm x 50 cm strips tied at 0.5 m intervals to tygon tubing, and of open boxes tied to a rope at 0.5 m intervals, containing glass slides held in place with elastic bands, were suspended in the kelp bed. Glass slides were replaced at 1-2 month intervals from May 1976 to April 1977, and the plastic was sampled without replacement each 1-2 months from May 1976 to June 1977.

Settlement of Membranipora serrilamella

Larvae and colonies in small size classes were counted on proximal (youngest) and distal (oldest) portions of growing and senescent blades (5x15 cm samples of blades, n = 3 - 5). Assuming that growth of colonies on young and old tissue was similar, areas of preferred settlement could be determined.

Taxonomic Notes

Invertebrates were identified using Light (1975) and Kozloff (1975). Suctorians were identified using Kudo (1971) and Ricketts and Calvin (1968). Seaweeds were identified in Setchell and Gardner (1920, 1925), and Widdowson (1974). Dr. R.F. Scagel confirmed the identification of Streblonema acidoides f. pacificum. Dr. C. Tanner identified species of Ulva. Diatoms were identified by using van Heurk (1962) and Rao and Lewin (1976), and certain identifications were confirmed by Drs. J. Lewin and M. Taylor. Dr. M. Hawkes identified the Porphyras.

RESULTS

All epiphytes and endophytes, except diatoms and bacteria, found through sampling or by casual observation on the stipes and blades of Macrocystis and Nereocystis are listed in Table 1; Tables 2 and 3 list diatoms found on blades of Macrocystis and Nereocystis respectively. Colonization curves of epiphytes and endophytes recorded through the sampling procedure (not casual occurrences) of the stipes and blades of the two host kelps are in Fig. 3, and diversity indices (H') of diatoms on the blades of both hosts are in Fig. 18. Colonization curves show most immigration during June, July and August for blades of both host

species with more taxa on blades of Macrocystis, but diversity of diatoms was lowest in early spring and summer on blades of both plants. Mortality of organisms was mainly due to death of the host, and post summer immigration of organisms, except for diatoms, was low. The result is seen as a decrease in the number of epiphytic taxa after summer in Fig. 3.

Stipes of Nereocystis along the perimeter of the bed were epiphytised only by diatoms and bacteria until August when host growth ceased. From that point on several additional epiphytes were present through December; in the spring additional species settled. None of these epiphytes became extinct until death of the plants. Nereocystis inside the bed of Macrocystis became senescent by June and were heavily epiphytised until their death in August (Table 1). Stipes of Macrocystis had one epiphyte other than diatoms and bacteria during the summer months but occasionally a senescent stipe was discovered which bore several large epiphytes (Table 1).

Phylum Ectoprocta

Membranipora serrilamella settled on the stipes and blades of both hosts during summer but persisted through winter only on stipes of Nereocystis. Hippothoa hyalina occurred rarely on blades of Macrocystis and stipes of Nereocystis, and Tricellaria occidentalis occurred rarely on blades of Macrocystis.

Membranipora serrilamella was present on the blades of Macrocystis from May to August 1976 and in June and August 1977 (Fig. 4); stipes were more rarely encrusted at these times. Larvae settled on the newest tissue but blades less than 1.5 m from the frond meristem rarely had more than 5% cover. Heaviest coverages occurred during May and June 1976 when most blades 2.5 and 3.0 m from the apex were 25 to 100% encrusted

(Fig. 12a). By August 1976 the older zooids of colonies were gone, leaving only an outer perimeter of young zooids (Fig. 12b). Two encrustations occurred in 1977, a small one in June and one much larger in August; however, neither was the magnitude which occurred in 1976. In 1976, abundance was significantly correlated with distance of the blade from the apex, but in 1977 the correlation coefficients were not significant. Median densities closely paralleled the means but variance to mean ratios were high indicating that coverage was clumped for blades of similar distance from the apex within the bed.

The larvae of Membranipora settled only in the furrows of the blades of Macrocystis, but would settle and grow on the relatively smooth stipe. Larvae appeared to settle indiscriminately on young and older blades. The frequency of colonies in the same small size classes were distributed fairly equally on the proximal (growing) and distal (not growing) ends of growing blades (about 0.6 m from the meristem), and fairly equally apportioned between growing and nearly senescent blades about 1.6 m from the frond meristem (Fig. 5). During spring settlement I have observed dense numbers of larvae on the youngest and oldest blades of Macrocystis. Colonies grew by radiating from the larvae, encrusting the blade surface. Eventually they would grow over the edge of the blade, covering the spinules along the edge of the blades and continue growth on the other side of the blade. Colonies were never observed to overgrow one another.

From June to August 1976 Membranipora serrilamella heavily encrusted the stipe of Nereocystis and persisted until February 1977 when quantitative measurements were initiated (Fig. 6). Senescent plants in February and April 1977 had encrustations of less than 25% cover in the

upper 0.5 m of stipe. Membranipora was absent from the stipes of plants which began growing in spring 1977 until October 1977. Colonies occurred from the holdfast to the blades but highest percent covers were between the float and 0.5 m of stipe. Blades were only rarely epiphytised by this bryozoan and only during summer.

Phylum Cnidaria

Obelia sp. (Hydrozoa) was common on blades of Macrocystis but occurred rarely on stipes of Macrocystis. One specimen of the anemone Metridium sp. occurred on a Macrocystis stipe.

Obelia colonies were present on blades of Macrocystis from June 1976 to October 1976 and from June 1977 to October 1977 (Fig. 7). Maximum densities exceeding $0.30 \text{ colonies/mm}^2$, occurred during the summer of both years, on blades 1m or more from the apex (Fig. 12c,d). Mean densities on the plants ranged from around 0.025 to $0.10 \text{ colonies/mm}^2$. Colonies were never observed at 0.1 m and only rarely at 0.5 m from the apex. Abundance was positively correlated with distance from the apex at 5% confidence level for 7 of 8 months. Median densities were nearly always less than the mean, and variance to mean ratios were much greater than one indicating a clumped distribution within the bed on similarly positioned blades. Colonies of Obelia 3 to 4 cm in length could possess gonozooids. Densities could be reduced from overgrowth by Membranipora.

Phylum Protozoa

Suctorians (Acineta sp. and Ephelota sp.) were found on blades of both hosts. Folliculina sp. Vorticella sp. and Zoothamnion sp. rarely occurred on blades of Macrocystis.

Suctorians were present on blades of Macrocystis from June 1976 to December 1977 (Fig. 8, 15). Maximum mean densities of $2 - 4/\text{mm}^2$ occurred on blades 1 or 2 m from the frond meristem during June, 1976 to April, 1977. At these times they formed a visible layer on the blades. During the other months of both years the densities were visibly lower and typically less than $1/\text{mm}^2$. Abundance was not significantly correlated with distance from the apex but maximum densities were never observed on growing tissue. Variance to mean ratios were high, indicating a clumped distribution within the bed on similarly positioned blades. Distribution on the blades was clumped as they were present only in the furrows.

Suctorians were present on blades of Nereocystis during June and July of both years but densities never exceeded $0.25/\text{mm}^2$ on blade tissue 0.5 m from the float. They were never observed on the stipes. Densities of suctorians on blades of Macrocystis and Nereocystis could be reduced from overgrowth by Membranipora (Fig. 13a).

Division Phaeophyta

Members of the Order Ectocarpales were present on the stipes and blades of both hosts. Members of the Order Laminariales were found in spring on stipes of both species, and germlings of the Order Fucales occurred on blades of Macrocystis during summer.

Order Ectocarpales

Ectocarpales were present throughout the year on senescent blade tissue of Nereocystis, but did not appear on the stipes of plants which began growth early in the spring until August. They totally covered the stipe by December (Fig. 9, 14c). Distribution was not significantly correlated with distance from the float. Nereocystis growing inside the bed of Macrocystis developed heavy mats by July. Epiphytic Ectocarpales

occurred only on stipes of Macrocystis which were aging.

The brown algal endophyte, Streblonema aecidioides f. pacificum, was present in the blades of Macrocystis from July 1976 through December 1977 with the exception of August 1977, when none were found among the 11 sampled fronds (Fig. 10). Maximum density of eruptions of the thallus through the epidermis (Fig. 16a, b, c, d) appeared to occur during the summer with mean densities reaching 1 - 2/mm². Mean abundance of eruptions tended to be positively correlated with distance from the frond meristem, 5 to 10 linear correlation coefficients being significant at the 5% confidence level. No eruptions were seen on blades 0.1 and 0.5 m from the apex. Young unerupted thalli were occasionally seen by sectioning blades close to the apex (Fig. 11c). Median densities were typically less than the mean and variance to mean ratios were greater than one, indicating a clumped distribution within the bed on similarly positioned blades.

Order Laminariales

Alaria sp. occurred on stipes of Nereocystis in April and persisted until death of the host in densities of approximately 0.1/cm². During summer 1976 a senescent stipe of Macrocystis was found with Laminaria groenlandica (Fig. 14a). None of these epiphytic kelps were reproductive.

Division Chlorophyta

Family Ulvaceae

Nereocystis outside the bed of Macrocystis which began growing in the spring of 1977 had Ulva on the float by August and through October and December the distribution remained restricted to the float. In February, 1977 the previous generation of plants had Ulva present on the upper 0.5 m

of stipe (approx. $20/\text{cm}^2$) most of which were less than 0.5 cm in length. By April 1977 Ulva occurred as low as 1.5 m from the float on these host plants and were present in lesser densities of approximately $5/\text{cm}^2$; many of the plants were 5-10 cm in length. All Ulva large enough to be identified were U. stenophylla or U. fenestrata.

Enteromorpha linza occurred on the upper 0.5 m of the stipe of Nereocystis in February 1977 and on the upper 1 m in April 1977 and respective densities were approximately $10/\text{cm}^2$ and $3/\text{cm}^2$.

Family Chaetophoroaceae

The endophyte Bulbocoleon piliferum was present between the epidermal blade cells of Macrocystis from July 1976 through December 1977 (Fig. 11, 16). Presence or absence/ mm^2 was recorded as individual plants were difficult to discern. Seasonal trends were not evident. From December 1976 through December 1977 mean occurrence/ mm^2 on blades 1 m or more from the frond meristem ranged from approximately 25 to 100%, and median frequencies were nearly always greater than the mean indicating the commonness of the alga. Variance to mean ratios were nearly always greater than one, indicating a clumped distribution of the endophyte on similarly positioned blades on stipes within the bed, but occasionally (e.g. February 1977) variance to mean ratios were less than one, indicating a more uniform distribution. Frequency of occurrence was positively and significantly associated with increasing distance from the apex meristem. The alga occurred only rarely in stipes of Nereocystis and blades and in stipes of Macrocystis.

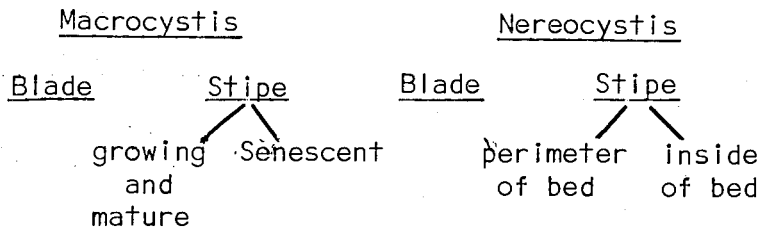
Cells with spores occurred in blades of Macrocystis 2 m or more from the frond meristem. Occasionally Bulbocoleon became so dense that

the host epidermal cells eroded (Fig. 16b).

Division Rhodophyta

Porphyra (less than 1 cm long) occurred in February 1977 on Nereocystis from 0.1 to 2 m below the float in respective maximum densities of $5/\text{cm}^2$ and $35/\text{cm}^2$ ($n=4$). By April, Porphyra occurred in maximum densities of $0.01/\text{cm}^2$ and $5/\text{cm}^2$, 0.1 m and 1.0 m respectively from the float ($n=2$). All large enough to identify were P. nereocystis; and blades in April could be fertile. Nonreproductive, less than 1 cm long Antithamnion-type filaments were present in February and April with maximum densities ($25/\text{cm}^2$ and $55/\text{cm}^2$ respectively) 1 to 2 m from the float of Nereocystis.

Table 1. Epiphytes and endophytes, except bacteria and diatoms, found through sampling (X) and casual observation(*) on the stipes and blades of Macrocystis and Nereocystis. Senescent stipes of Macrocystis which were rarely observed are distinguished from growing and mature stipes found through the regular sampling procedure. Stipes of Nereocystis from inside the bed of Macrocystis are distinguished from those along the perimeter of the bed due to differences in sampling procedure.



CHLOROPHYTA

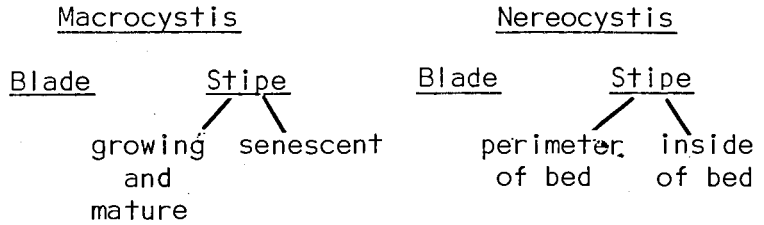
<u>Cladophora</u> sp.						X
<u>Enteromorpha</u> sp.						X
<u>E. linza</u> Agardh			X			X
<u>Bulbocoleon piliferum</u> Pringsheim	X		X	X	*	
<u>Ulva fenestrata</u> Postels and Ruprecht			X			X
<u>Ulva stenophylla</u> Setchell and Gardner			X			

PHAEOPHYTA

<u>Alaria</u> sp.			X			
Ectocarpales			X	X	*	X
Fucales (germlings)	X					
<u>Streblonema aecidioides</u> Setchel and Gardner	X					
<u>Laminaria groenlandica</u> Rosenvinge					*	

RHODOPHYTA

<u>Antithamnion</u> sp.			X			
-------------------------	--	--	---	--	--	--



Porphyra nereocystis
Anderson

X

PROTOZOA

Folliculina sp. *

Suctorians X

Vorticella sp. *

Zoothamnion sp. *

X

CNIDARIA

Coryne sp. *

Obelia sp. X *

Metridium sp. * *

ECTOPROCTA

Membranipora serrilamella Osburn X X * X X X

Hippothoa hyalina Linnaeus * *

Tricellaria occidentalis Trusk *

Figure 3. Colonization curves for blades and stipes of Macrocystis and Nereocystis.

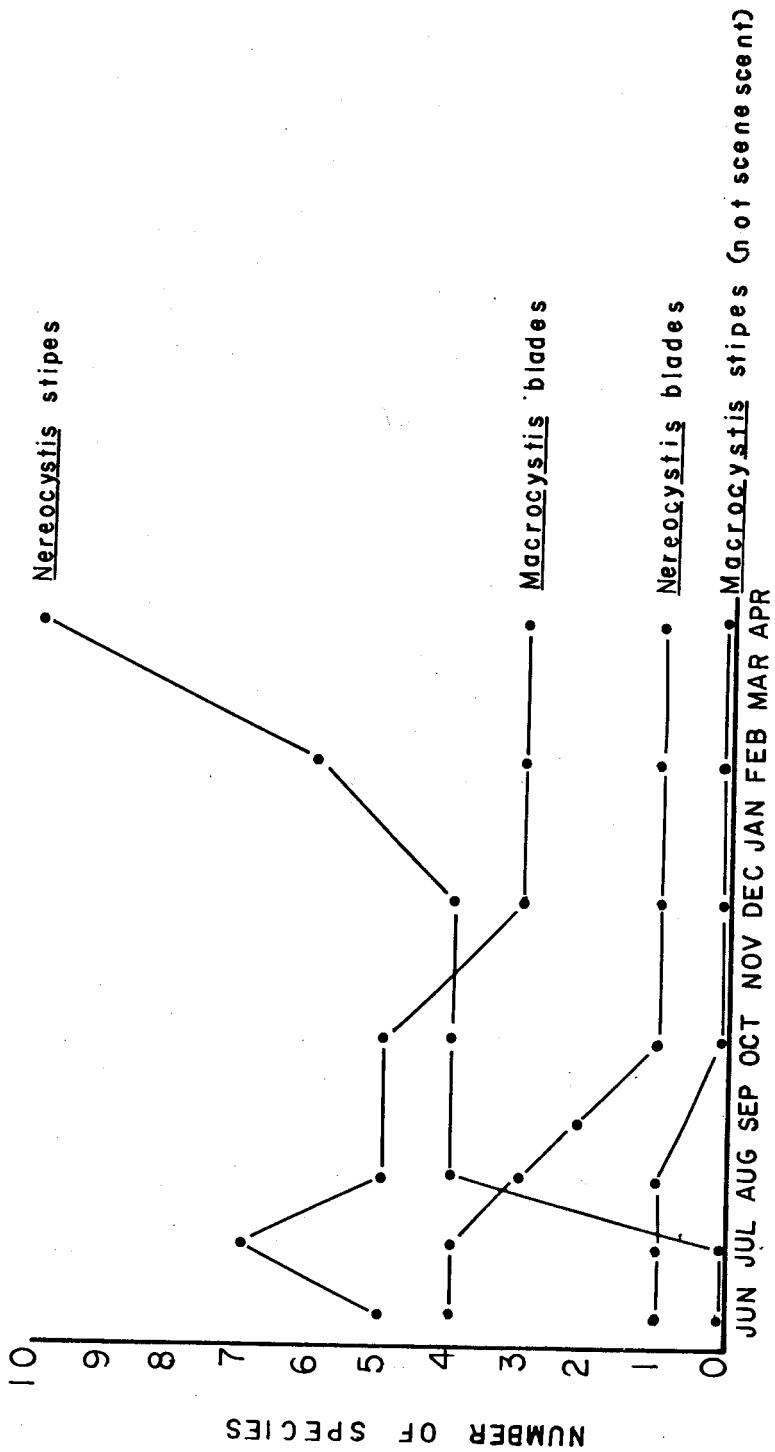
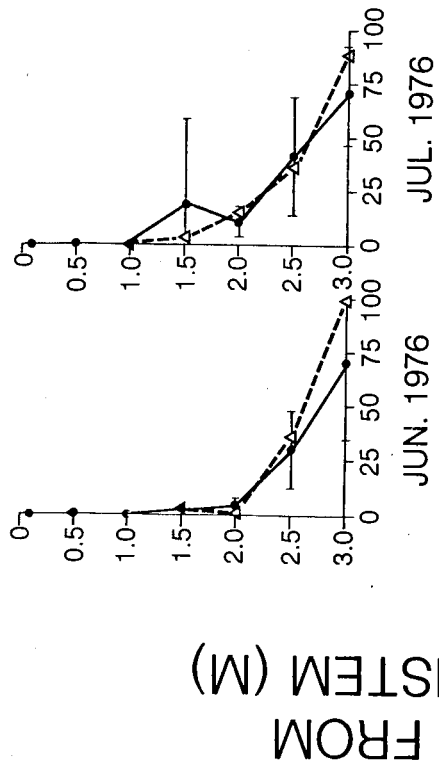
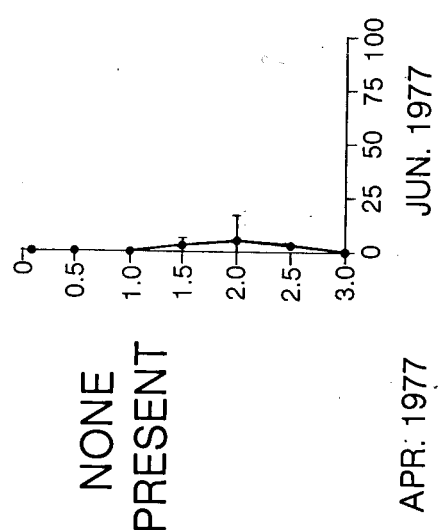


Figure 4. Percent cover of the encrusting bryozoan, Membranipora serrilamella Osburn, on blades of Macrocystis, from June 1976 through December 1977. Solid lines indicate mean values with standard deviations and dashed lines indicate median values.



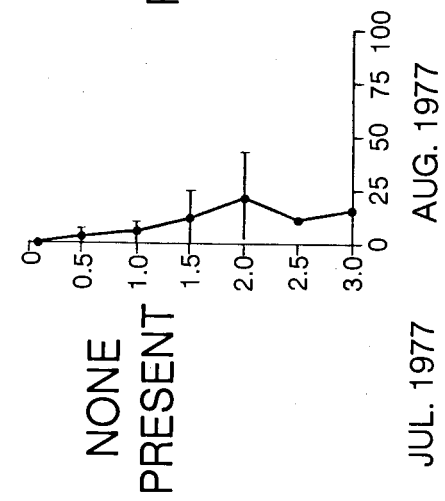
ONLY TRACES < 1% COVER NONE PRESENT NONE PRESENT NONE PRESENT

JUN. 1976 JUL. 1976 OCT. 1976 DEC. 1976 FEB. 1977



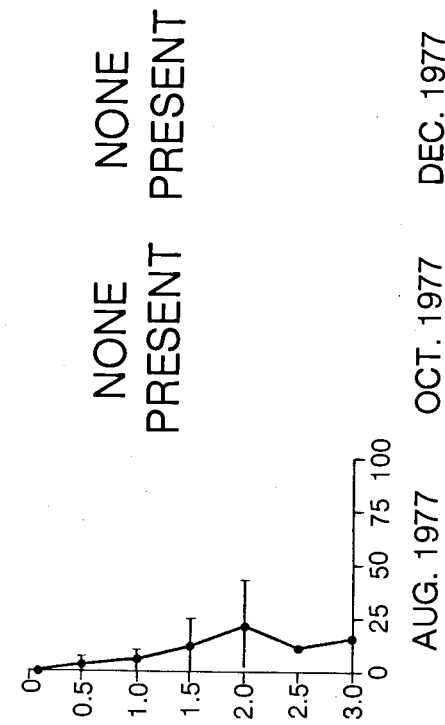
NONE PRESENT

APR. 1977



NONE PRESENT

JUL. 1977



NONE PRESENT

OCT. 1977

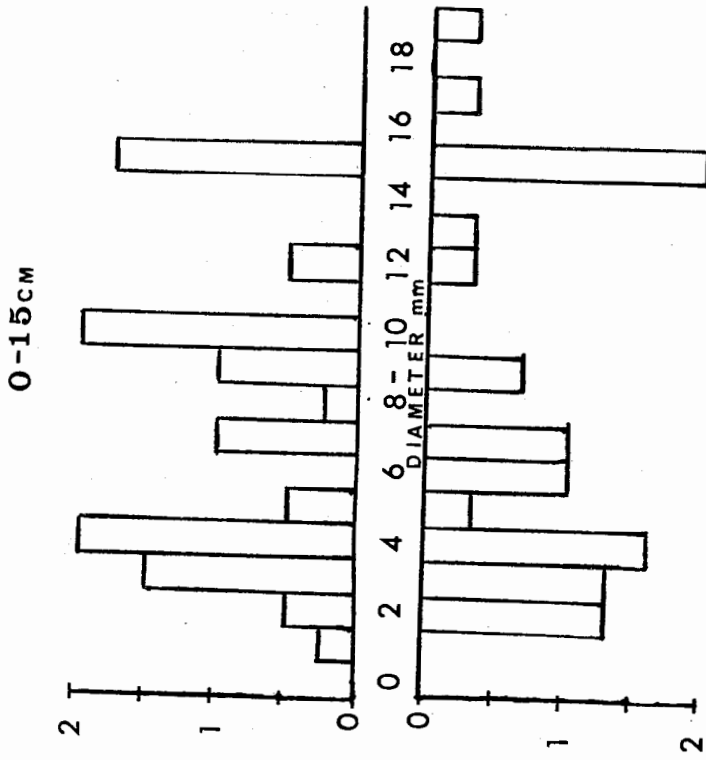
NONE PRESENT

DEC. 1977

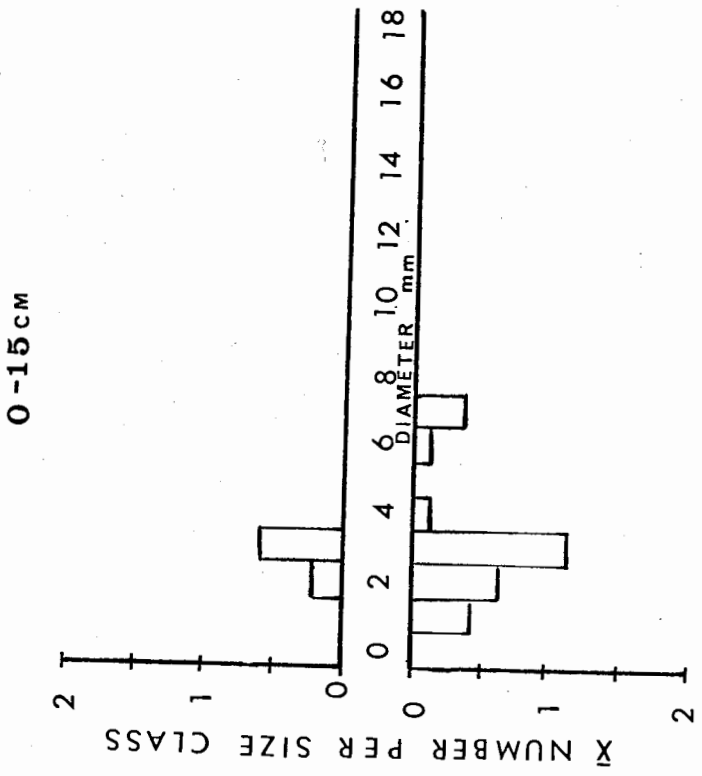
% COVER

DISTANCE FROM FROND MERISTEM (M)

Figure 5. Size class histograms of Membranipora serrilamella Osburn colonies on blades of Macrocystis. 15 x 5 cm samples of blade were taken between 0 and 15 cm from the blade float (n=5), and 25 and 40 cm from the float (n=5) on growing blades between 0.6 and 0.7 m from the apex meristem. Mature to senescent blades were similarly sampled from 1.7 - 1.8 m from the apex meristem at 0 - 15 cm (n=4) and 25 - 40 cm (n=3) from the blade float.



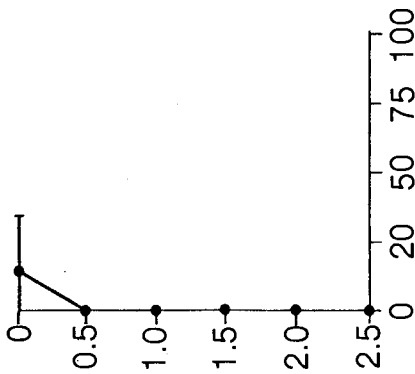
25-40cm
MATURE BLADES



25-40cm
GROWING BLADES

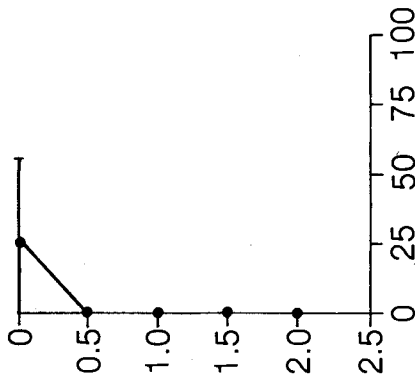
Figure 6. Percent cover of the encrusting ectoproct, Membranipora serrilamella Osburn, on stipes of Nereocystis February 1977 through December 1977. Solid points indicate mean values with standard deviations and triangular points indicate median values. The number of stipes sampled is indicated by n.

DISTANCE FROM FLOAT (M)



Feb. 1977

n=4



Apr. 1977

n=2

NONE
PRESENT

Jun. 1977

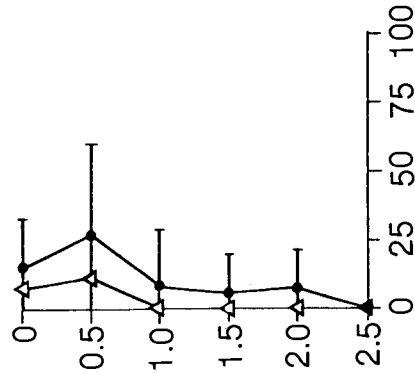
n=6

NONE
PRESENT

Aug. 1977

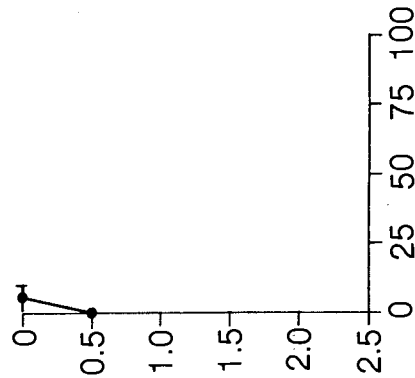
n=6

21b



Oct. 1977

n=6

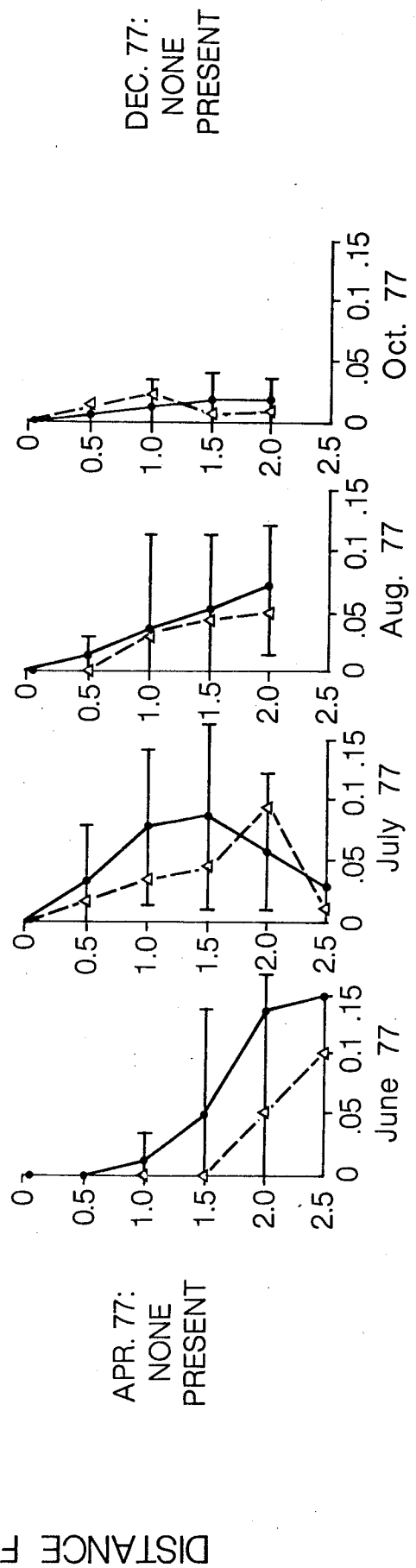
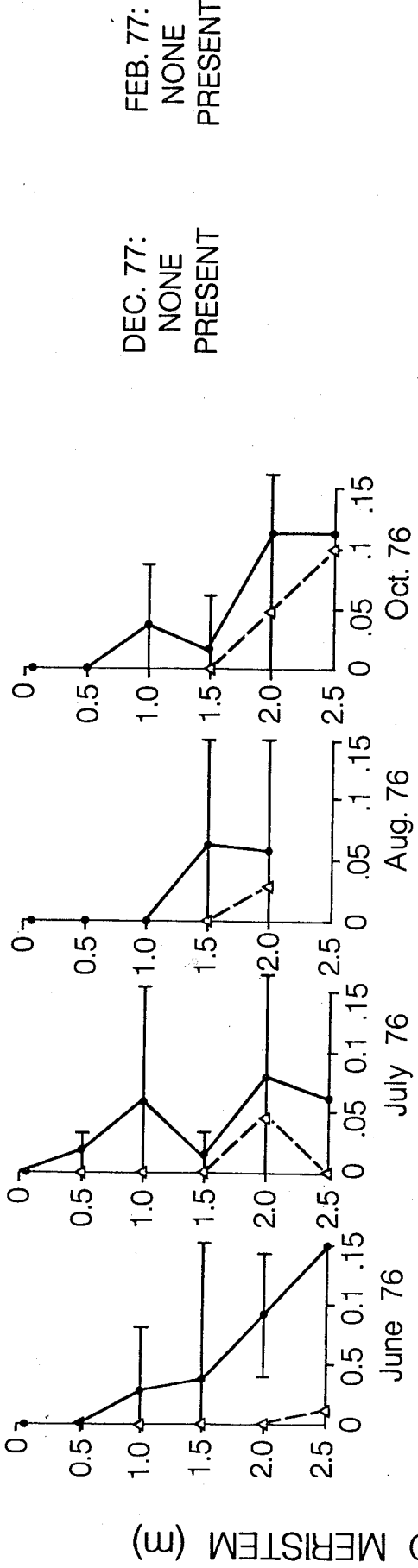


Dec. 1977

n=4

% COVER

Figure 7. Density of the hydroid, Obelia sp. (colonies/mm²), on blades of Macrocystis from June 1976 through December 1977. Solid lines indicate mean values with standard deviations and dashed lines indicate median values.

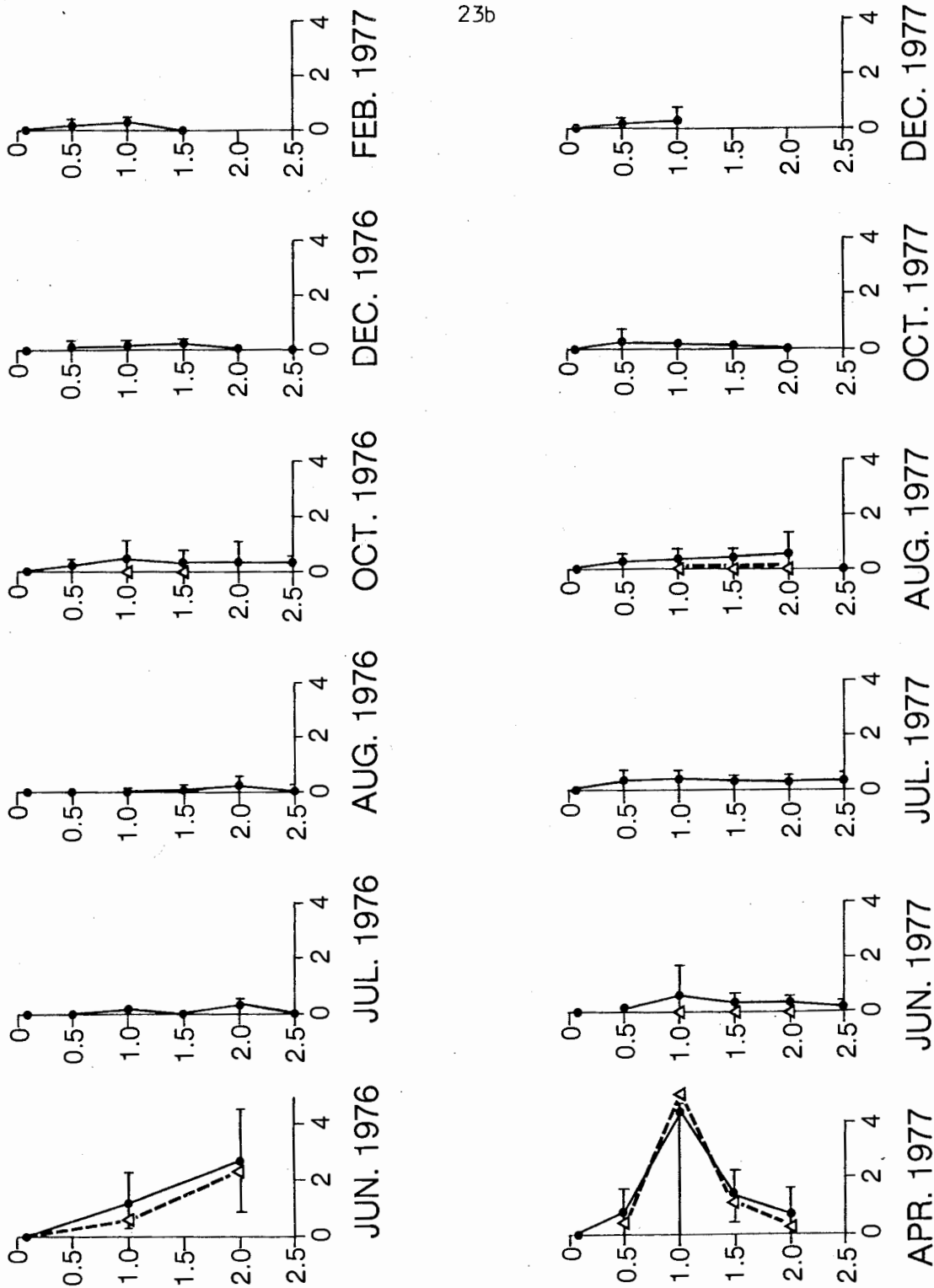


COLONIES PER mm²

DISTANCE FROM FROND MERISTEM (m)

Figure 8. Density (nos./mm²) of suctorians on blades of Macrocystis from June 1976 through December 1977. Solid lines indicate mean values with standard deviations and dashed lines indicate median values.

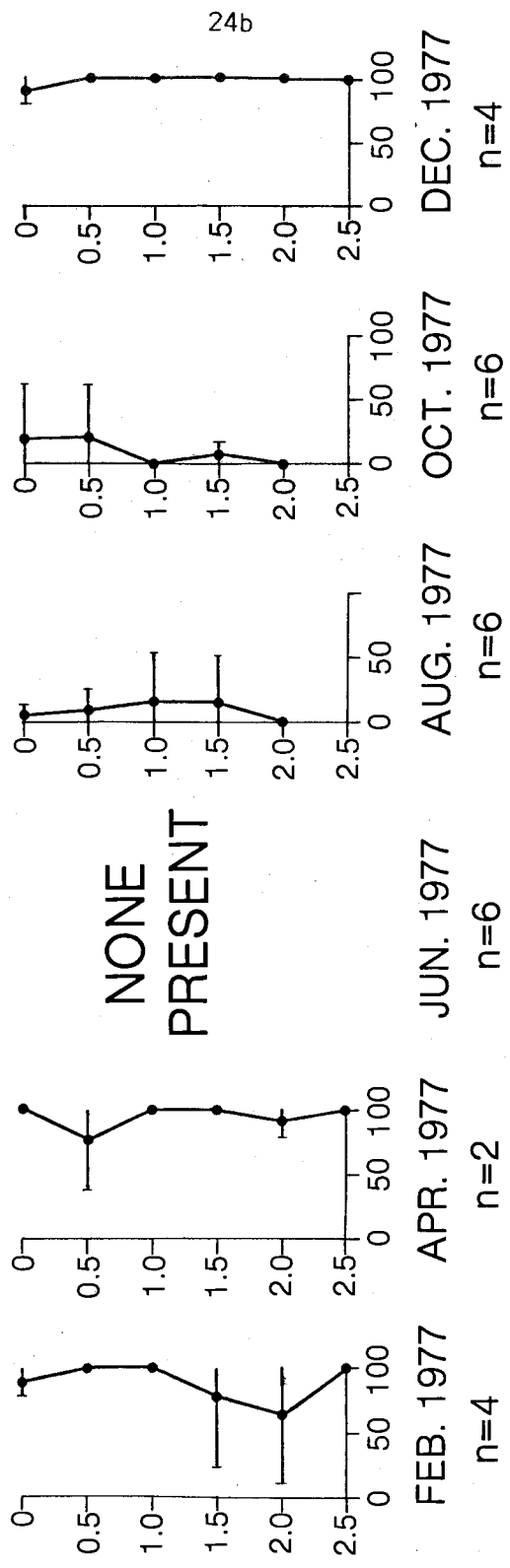
DISTANCE FROM FROND
MERISTEM (M)



NO. PER mm²

Figure 9. Percent chance of occurrence per mm^2 for Ectocarpales on stipes of Nereocystis from February 1977 through December 1977.

DISTANCE FROM
FLOAT (M)



% CHANGE OF OCCURRENCE PER mm²

Figure 10. Density (eruptions/mm²) of the endophyte Streblonema aecidioides f. pacificum Setchell and Gardner from July 1976 through December 1977 in blades of Macrocystis. Solid lines indicate mean values with standard deviations and dashed lines are median values.

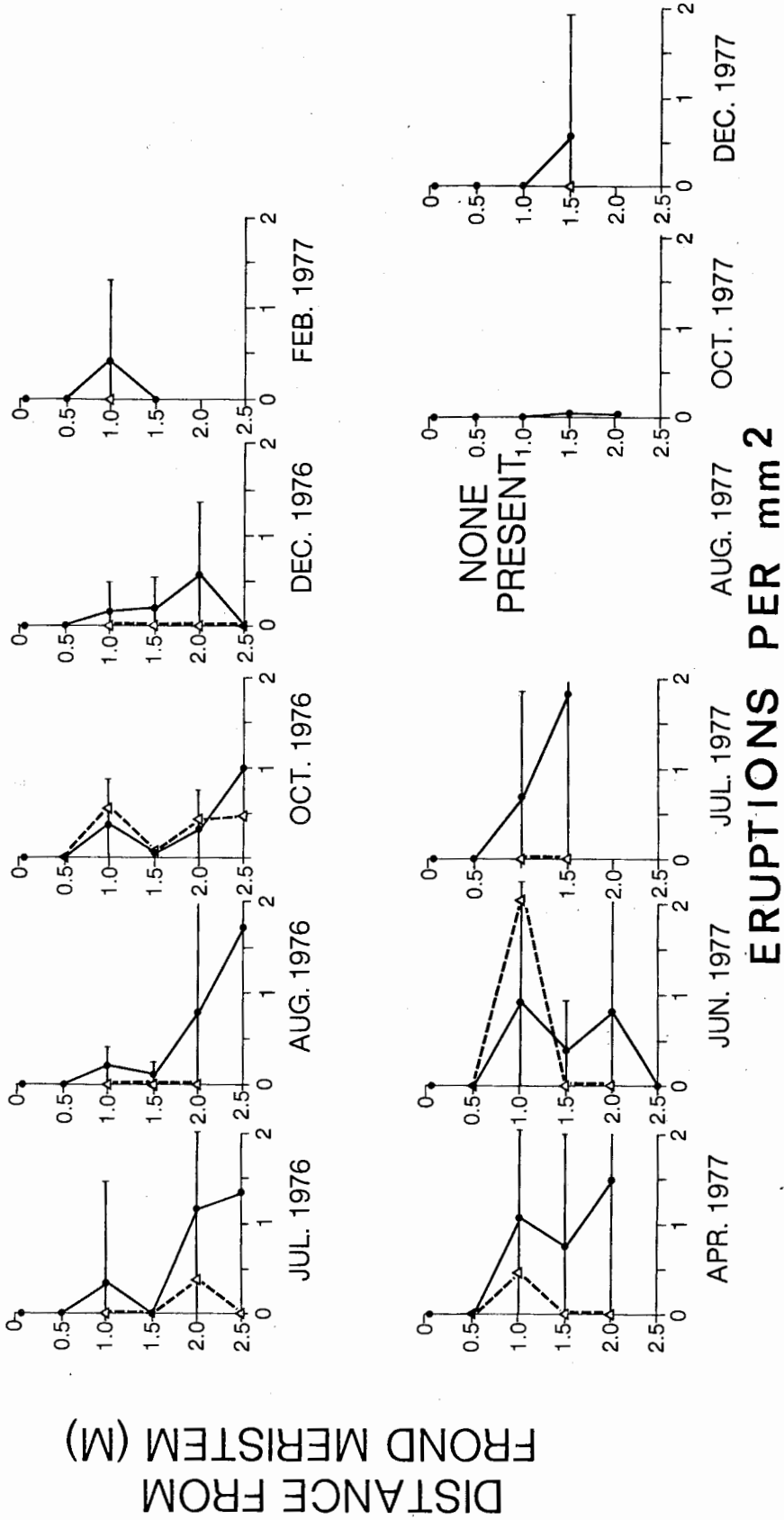
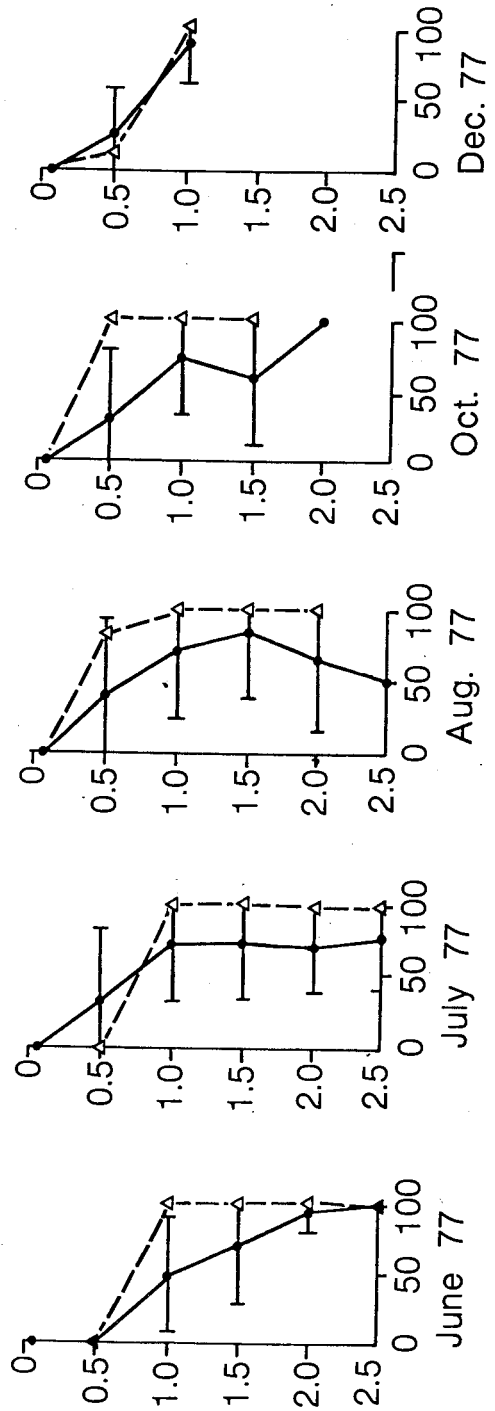
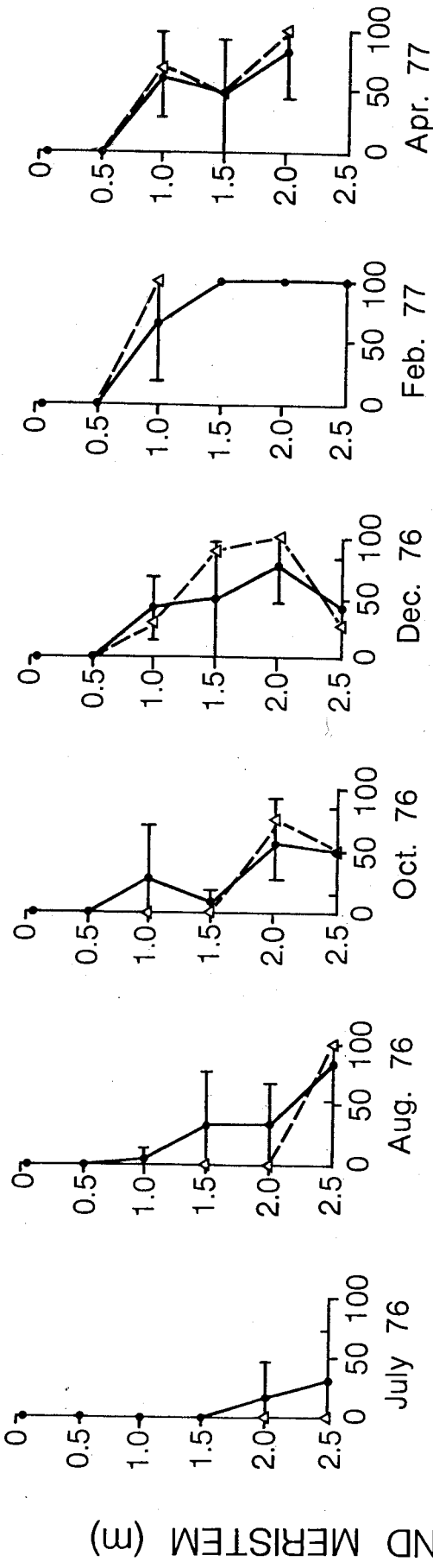
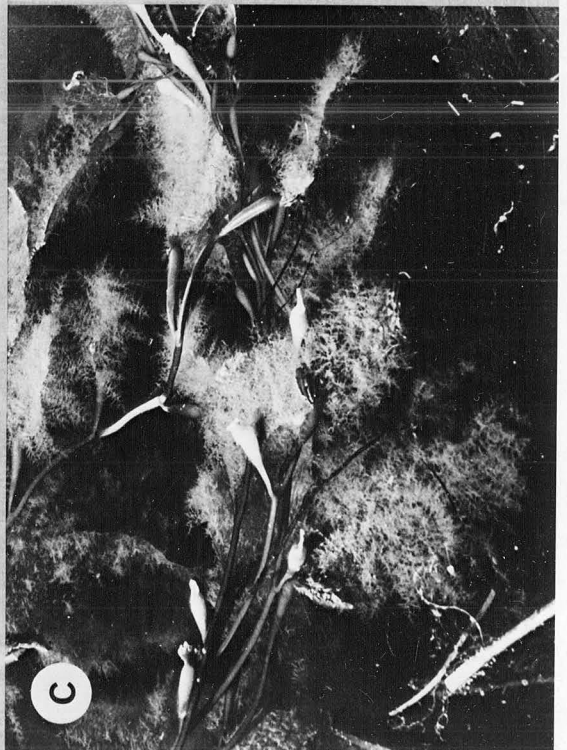
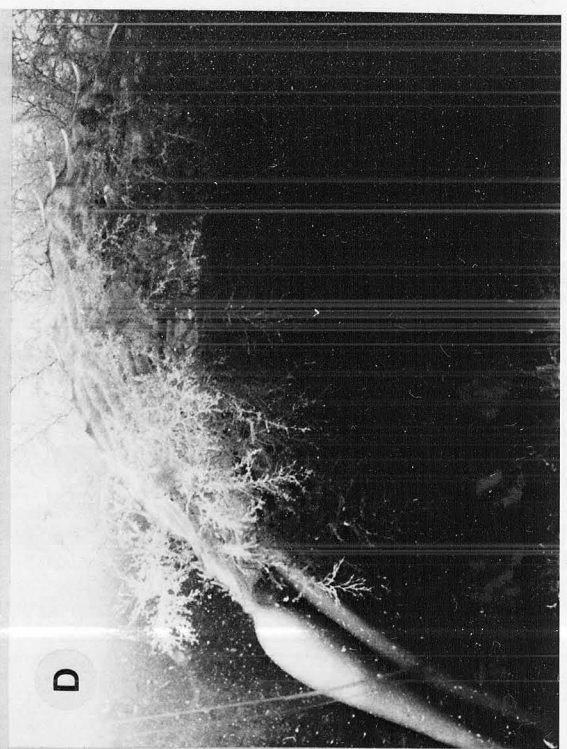
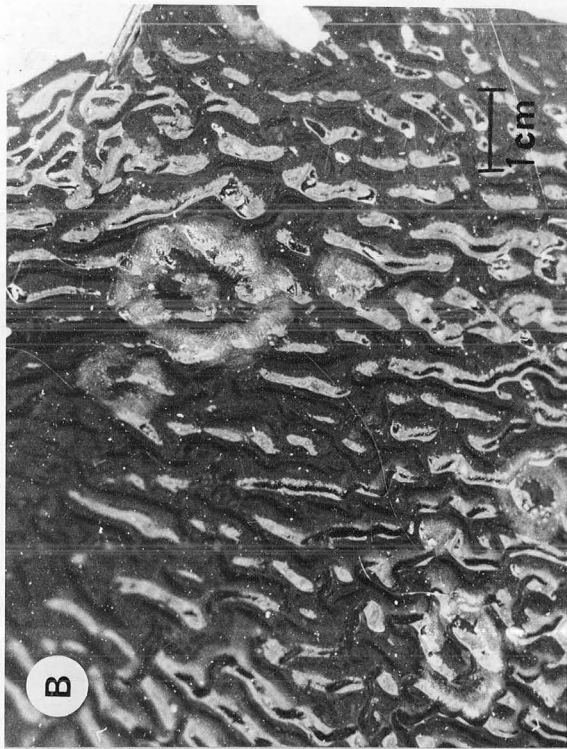


Figure II. Percent chance of occurrence per mm² of the endophyte Bulbocoleon piliferum Pringsheim. Solid lines indicate mean values with standard deviations and dashed lines are median values.

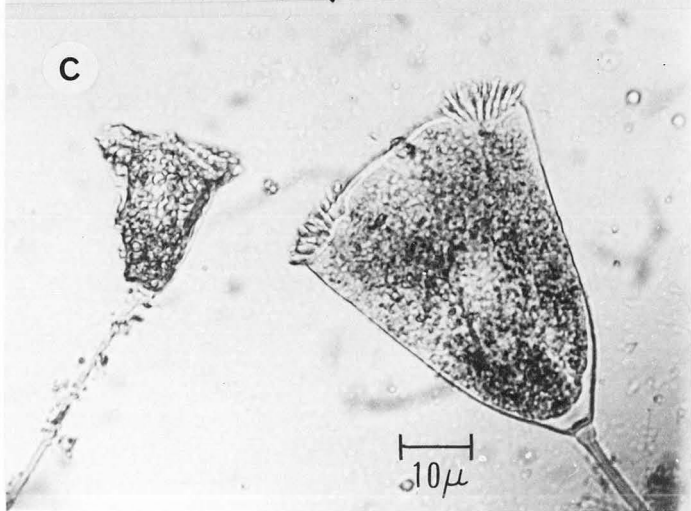
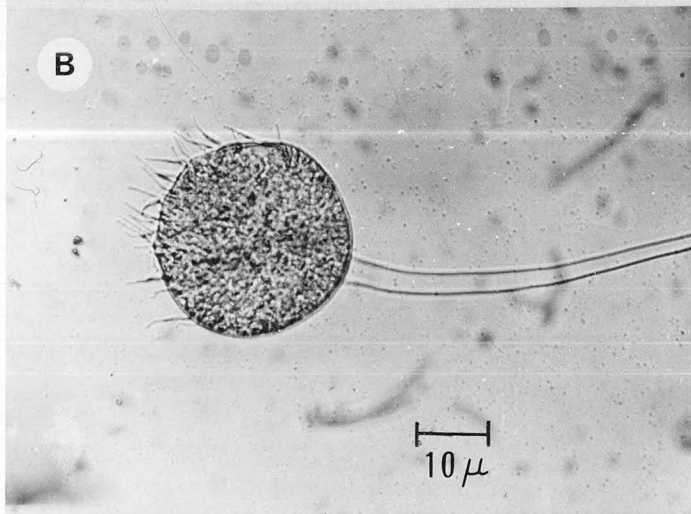
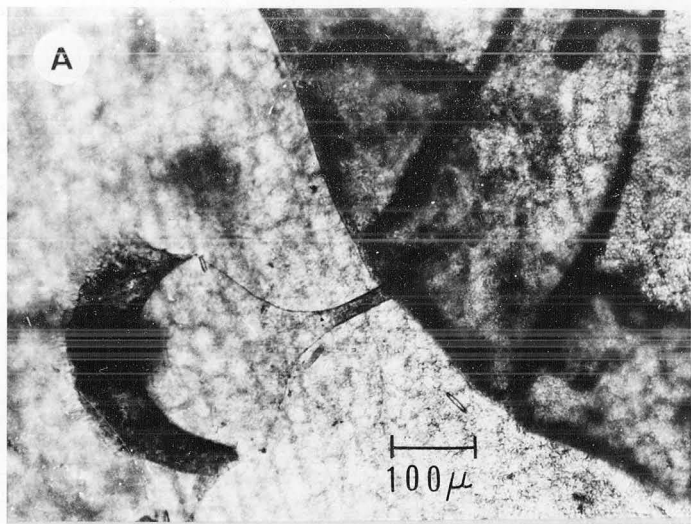


% CHANCE OF OCCURRENCE PER mm²

- Figure 12. A. Several colonies of Membranipora serrilamella Osburn encrusting a blade of Macrocystis.
- B. Colonies of Membranipora serrilamella on Macrocystis with central zooids eroded, possibly from being eaten by the nudibranch Doridella.
- C. In situ photograph of Obelia colonies on blades of Macrocystis.
- D. Dense cover of Obelia on blades of Macrocystis.



- Figure 13. A. Suctorian, probably Ephelota sp. being overgrown by Membranipora.
- B. Suctorian, probably Ephelota sp.
- C. Suctorians, probably a species of Acineta.



- Figure 14.
- A. Senescent stipe of Macrocystis collected in July, 1976 epiphytised with Laminaria groenlandica (arrow) and several other seaweeds.
 - B. Senescent stipe of Nereocystis growing inside the bed of Macrocystis, epiphytised with Membranipora (arrow) and several seaweeds. Collected in July, 1976.
 - C. Mature float and upper portion of a stipe of Nereocystis, epiphytised with Ulvales (arrow) on top of float, and Ectocarpales (appearing as a rough layer) below. This pattern of epiphytism was seen during winter.
 - d. Senescent stipe of Nereocystis collected in April, 1977, epiphytised with Ulvales (solid arrow) and Porphyra nereocystis Anderson (open arrow).

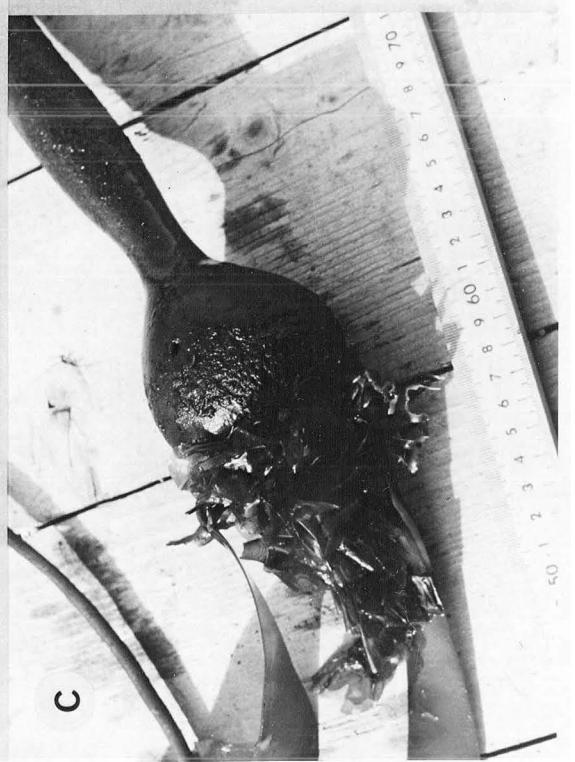
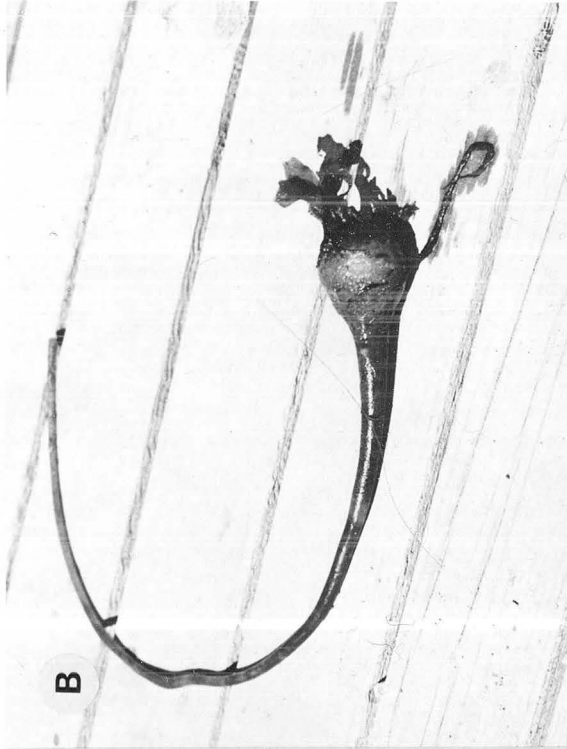
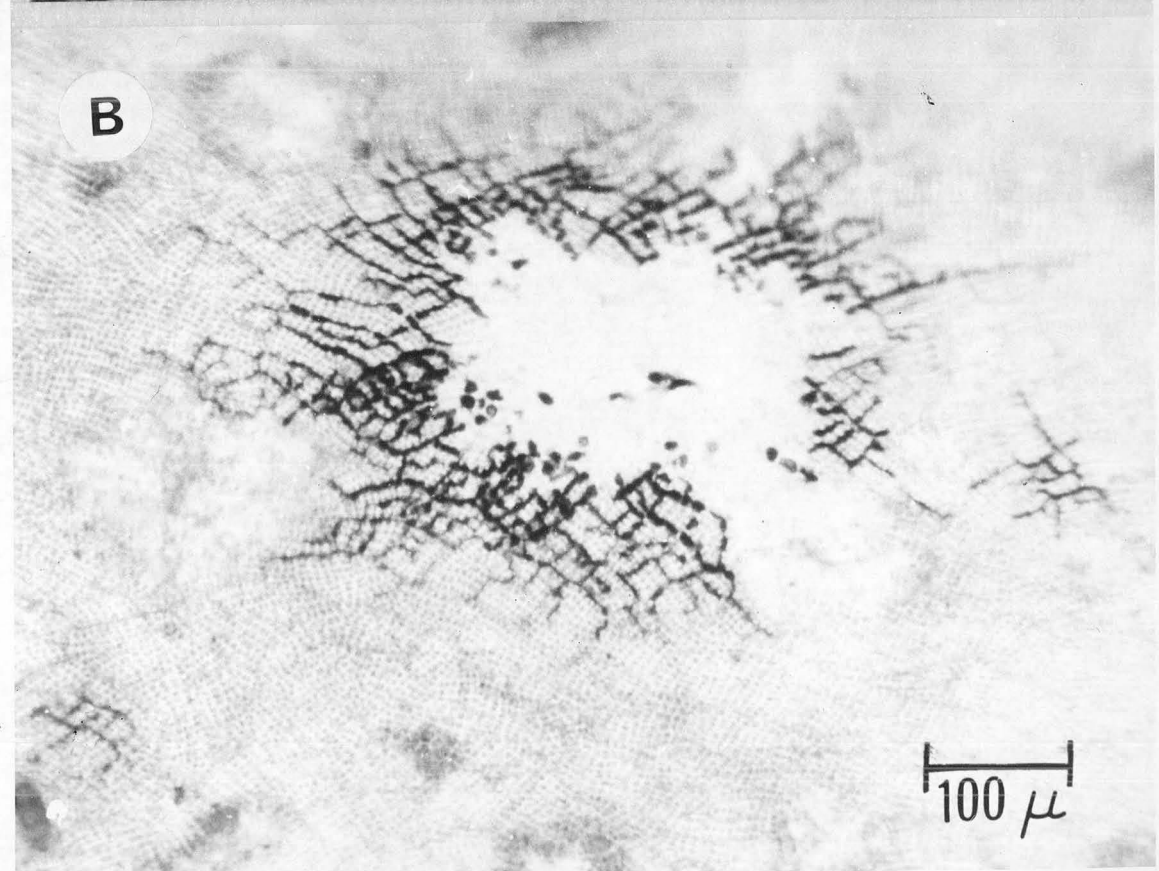
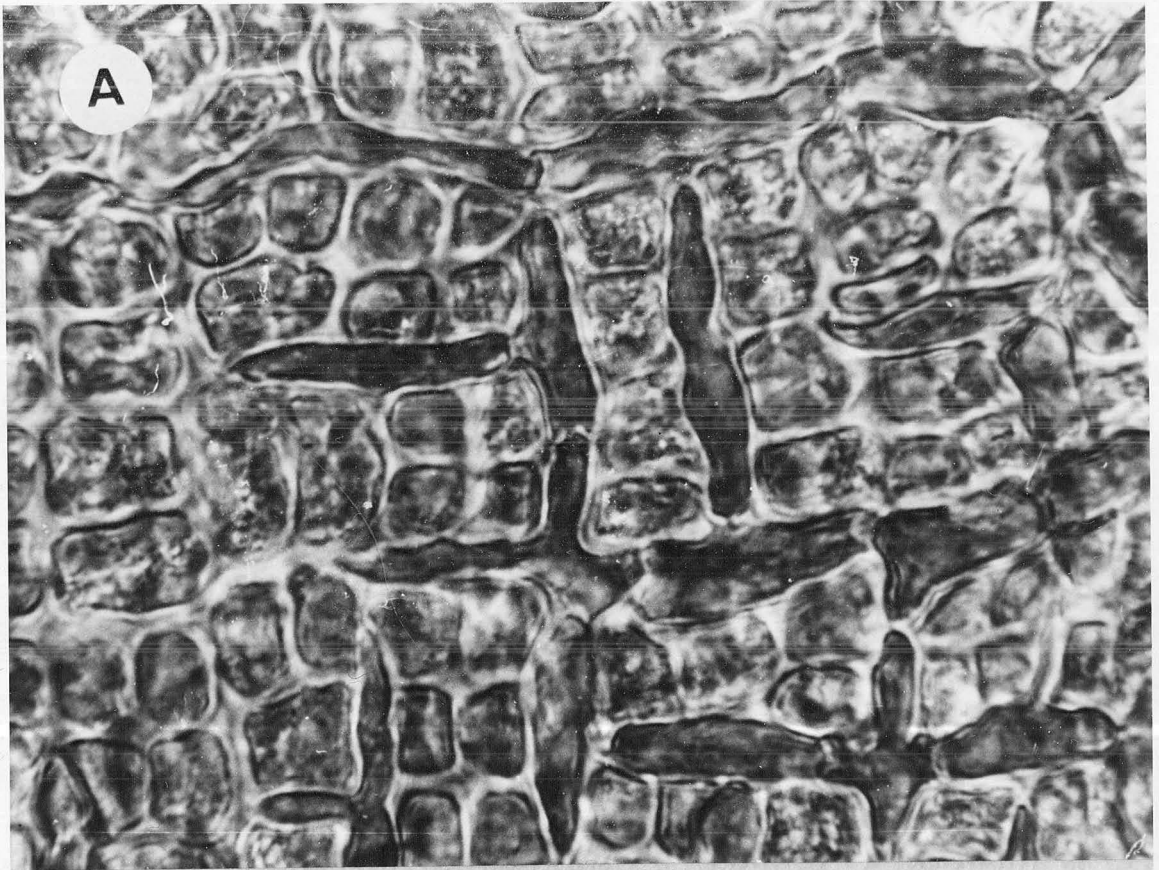


Figure 15. Streblonema aecidioides f. pacificum Setchell and Gardner, an endophytic alga, in blades of Macrocystis. A. Cross section of a plant about to erupt through the epidermis showing penetration of rhizoidal filaments into cortex. B. SEM micrograph of mature plant. C. Cross section of immature plant before eruption. D. Cross section of a newly erupted plant.



- Figure 16. A. Cells of Bulbocoleon piliferum Pringsheim (arrows) between the epidermal cells of a blade of Macrocystis. 1 cm = 5 μ .
- B. Bulbocoleon cells (arrow) which have become so dense the epidermal blade cells of Macrocystis were destroyed.



Diatoms on Macrocyctis and Nereocystis Blades

Diatoms separated into 27 taxa on blades of Macrocyctis and 18 on blades of Nereocystis (Tables 2 and 3). Cocconeis scutellum had the highest average occurrence (50.8% on Macrocyctis and 47.0% on Nereocystis). Niche breadth values (Tables 2 and 3) indicated that Cocconeis scutellum and Synedra tabulata were most evenly distributed on Macrocyctis and C. scutellum, S. tabulata and Gomphonema no. 1 were distributed most evenly on Nereocystis.

Densities of diatoms were measured only on blades of Macrocyctis (Fig. 17). Total densities on blades 0.1 m from the frond meristem were relatively low (less than $70/\text{mm}^2$), during all seasons, but increased during June of 1976 and 1977 when C. scutellum formed a dense unialgal mat. On blades 1 and 2 m from the apex low densities (approx. 100 - $200/\text{mm}^2$) occurred during August - October 1976 and July - August 1977. These were periods of heightened diversity following a dominance by C. scutellum. Densities were higher at all other times (more than $400/\text{mm}^2$). Small standard deviations indicate that the counting procedure was very repeatable. Diatoms were counted using SEM (n=5 tissue samples) and variance to mean ratios were much larger than one indicating a clumped distribution of diatoms on similarly positioned blades within the bed.

The summer of 1976 and 1977 were similar for both host kelps due to a high abundance of C. scutellum and low species diversity. Diatom assemblages in December 1976 and 1977 were similar with C. scutellum, Achnanthes no. 1, and C. costata var pacificum present on both kelps. The seasonal patterns of diversity (Fig. 18) were fairly similar for both kelps ($r=0.74$, $r_{(10,0.1)}=0.71$) with low diversity in late spring

and/or summer and increased diversity in other seasons. Equitability ($\frac{H'}{\log_2 N}$) followed trends in diversity (H') indicating that increases in $\log_2 N$ diversity mainly resulted from a more even distribution of species rather than an increase in numbers of species. However, an increase in species number was responsible for some of the increased diatom diversity during July, August and October 1977 where Macrocystis was the host.

Analysis indicated three clusters of diatom distributions on blades of Macrocystis 1.0 m from the frond meristem (Fig. 19a). June, July and August 1976 and June 1977 assemblages consisted of over 95% C. scutellum with 1 - 3% S. tabulata. Taxa in December 1976, 1977 and February 1977 formed a distinct cluster with a diverse assemblage: C. costata var pacificum (27 - 42%), Achnanthes no. 1 (22 - 45%), C. scutellum (8 - 26%) and S. tabulata (0.2 - 11%). July 1977, August 1977, April 1977 and October 1976 were joined with summer months of both years (when C. scutellum was abundant). This cluster had 20 - 40% C. scutellum in common, but within this cluster associations were not close.

Taxa in June, July, and August 1976 formed a cluster on Nereocystis, all having 70 to 90% Coconeis scutellum in common (Fig. 19b). April and February 1977 taxa were clustered together with 75 and 92% C. costata in common. December 1976 and 1977 taxa formed another cluster with similar abundances of C. scutellum (10 - 11%), Achnanthes no. 1 (26 - 52%), and C. costata var pacificum (23 - 44%).

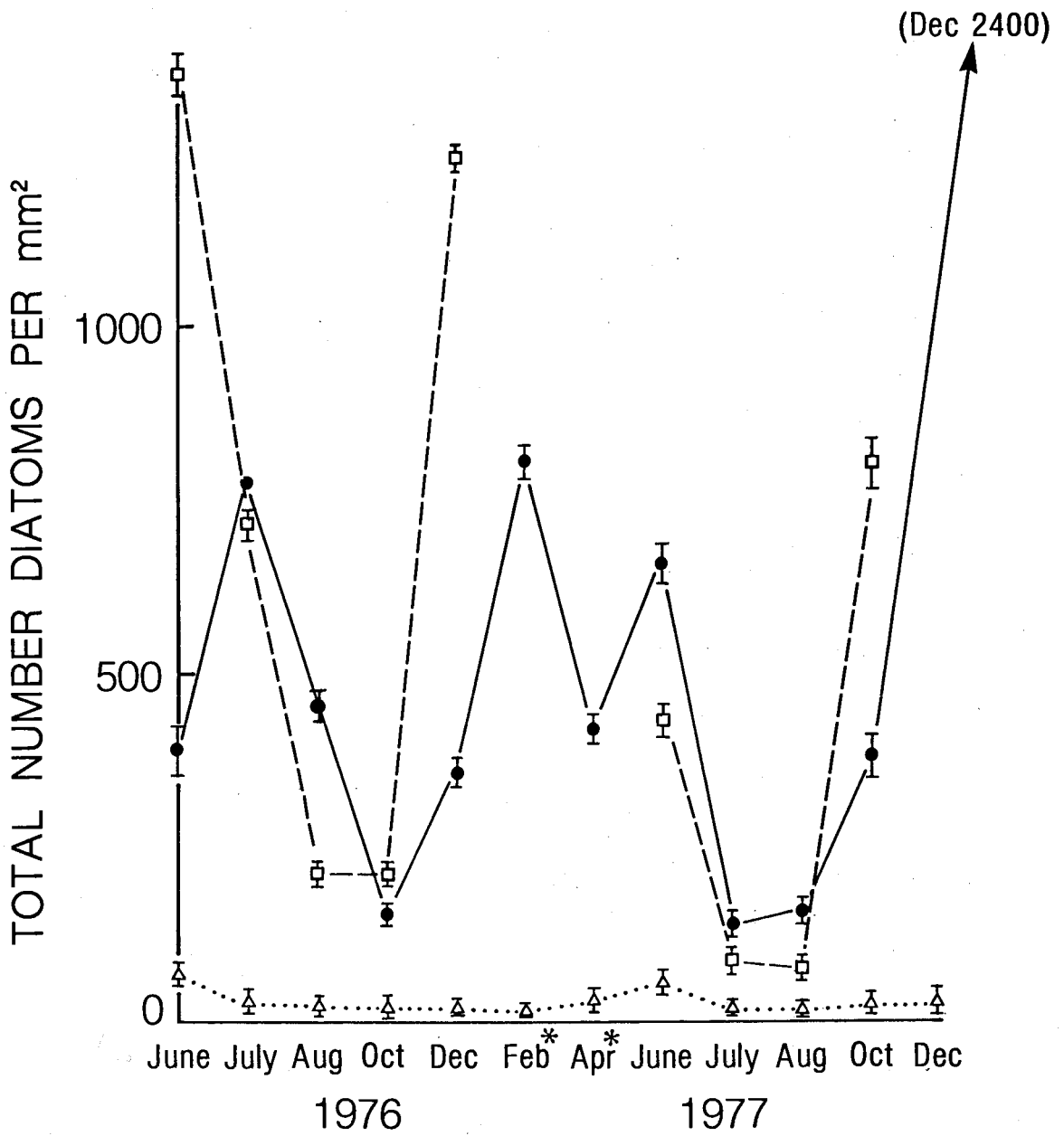
Table 2. Seasonal occurrence of diatom taxa on blades Macrocystis
0.1, 1.0, and 2.0 m from the frond meristem.

Table 3. Seasonal occurrence of diatom taxa on blades of Nereocystis 0.5 m from the float.

% OCCURRENCE

TAXON	Niche Breadth	\bar{X} % ± SD	% OCCURRENCE												
			Jun 76	Jul 76	Aug 76	Oct 76	Dec 76	Feb 77	Apr 77	Jun 77	Jul 77	Oct 77	Dec 77		
<i>Achnanthes longissipes</i> Ag.	1.0	0.2 ± 0.4	0	0	1.0	0	0	0	0	0	0	0	0	1.2	0
<i>Achnanthes</i> no 1	3.13	8.5 ± 16.4	0	0	0	0	51.6	11.6	1.4	0.6	0	1.86	26.0		
<i>Achnanthes</i> no 2	2.75	1.1 ± 2.1	0	0	0.2	0	3.6	6.4	0	1.4	0	0	0	0	0
<i>Amphora</i> spp	1.0	0.03 ± 0.09	0	0	0	0	0	0	0	0	0	0.3	0	0	0
<i>Chaetoceros</i> no 1	1.0	0.02 ± 0.06	0	0	0	0	0	0	0	0	0	0.2	0	0	0
<i>Cocconeis costata</i> Gregory	3.63	23.6 ± 34.8	0	0	0	58.4	0	74.4	92.2	27.8	1.6	0.8	4.4		
<i>Cocconeis costata</i> var <i>pacificum</i> Grun.	2.61	6.7 ± 14.0	0	0.4	0.2	0.6	23.0	1.6	0	0	0.6	0.2	43.8		
<i>Cocconeis scutellum</i> Ehr.	6.40	47.0 ± 38.4	97.0	90.8	97.0	27.8	11.4	2.6	3.2	67.0	60.6	56.2	10.2		35b
<i>Gomphonema</i> no 1	3.13	5.0 ± 9.6	1.6	0	0	0	1.6	0	0.4	0	21.6	26.6	3.6		
<i>Grammatophora marina</i> (Lyngb.) Kutz.	4.81	0.6 ± 0.9	0	0.4	0.2	0.2	0	0	0	0	1.4	2.8	1.2		
<i>Hyalodiscus subtilis</i> Ehr.	1.0	0.02 ± 0.06	0	0	0	0	0	0	0	0	0.2	0	0		
<i>Licmophora ehrenbergii</i> (Kutz.) Grun.	1.0	0.1 ± 0.24	0	0	0	0.8	0	0	0	0	0	0	0		
<i>Licmophora gracilis</i> Grun.	2.32	0.4 ± 0.8	0	0	0	2.2	0	0	0.2	0	0	1.6	0		
<i>Navicula</i> spp	7.10	1.9 ± 1.8	0.4	5.0	0	0.4	1.6	0.4	0.8	1.7	4.5	3.8	1.8		
<i>Nitzschia</i> no 1	1.0	0.05 ± 0.18	0	0	0	0.6	0	0	0	0	0	0	0		
<i>Nitzschia</i> no 2	1.0	0.02 ± 0.0.6	0	0	0.2	0	0	0	0	0	0	0	0		
<i>Rhoicosphenia curvata</i> (Kutz.) Grun.	5.31	0.6 ± 1.0	0	0	0	2.4	0	1.2	0	0.6	0.1	3.4	1.2		
<i>Synedra tabulata</i> (Ag.) Kutz	7.32	4.1 ± 4.1	0.8	2.0	0.6	12.2	3.2	1.4	0	1.4	7.6	9.2	7.0		

Figure 17. Seasonal variation in diatom densities on blades of Macrocystis 0.1 m (dotted line), 1.0 m (solid line), and 2.0 m (dashed line) from the frond meristem.



* NO PLANTS WITH 2M BLADES

Figure 18. Seasonal variation in diversity (H') of diatoms on blades of Macrocystis (solid line), 1 m from the frond meristem and on blades of Nereocystis (dashed line), 0.5 m from the float. Equitability ($\frac{H'}{\log_2 S}$) is plotted above.

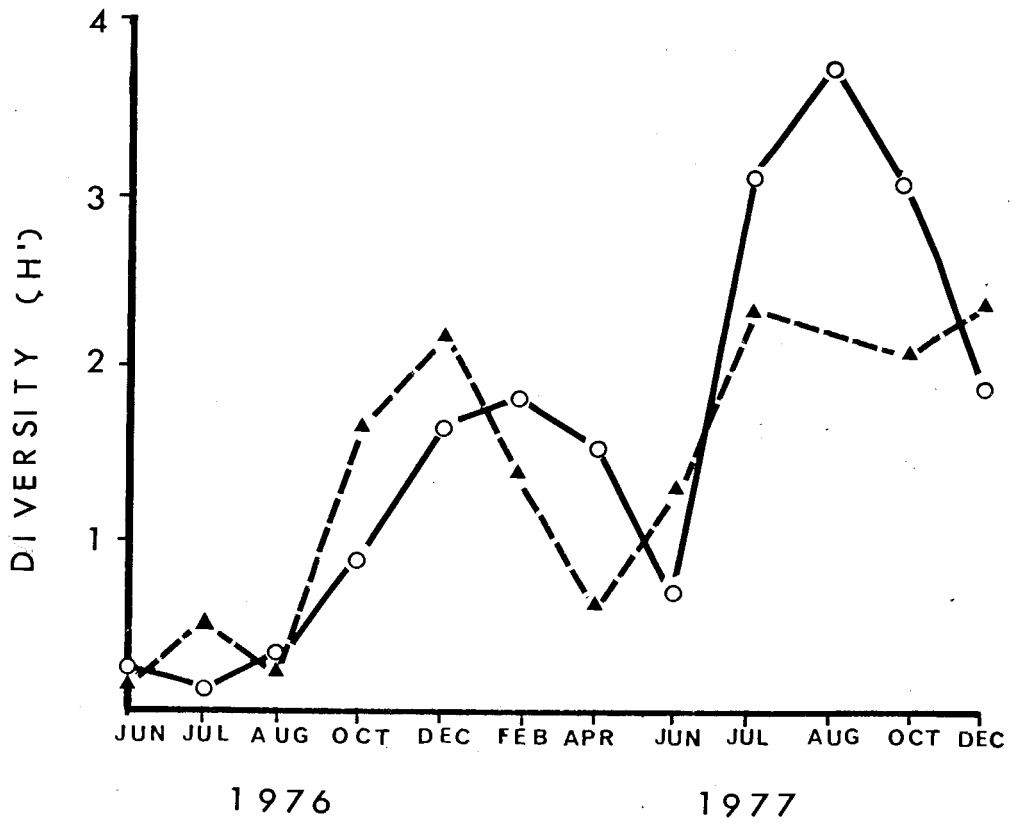
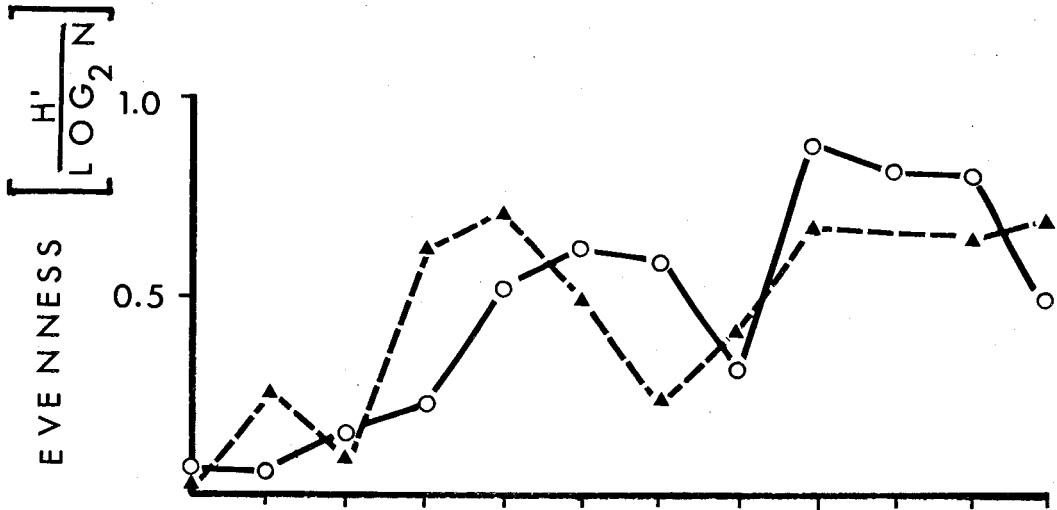


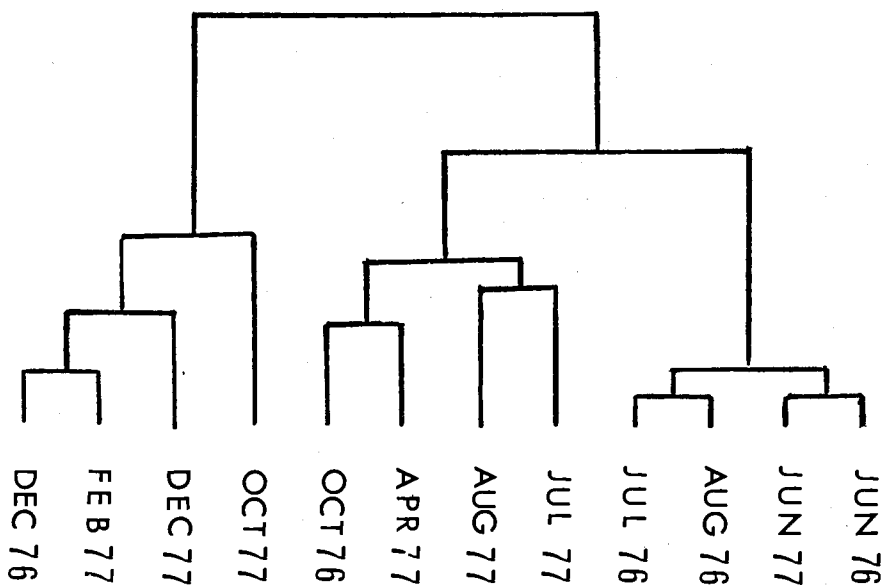
Figure 19. Dendrograms derived from cluster analysis of sampling dates for diatoms on A, Blades of Macrocystis 1 m from the frond meristem and B, on blades of Nereocystis 50 cm from the float.

60
50
40
30
20
10
0

AMALGAMATION DISTANCE

60
50
40
30
20
10
0

A



B

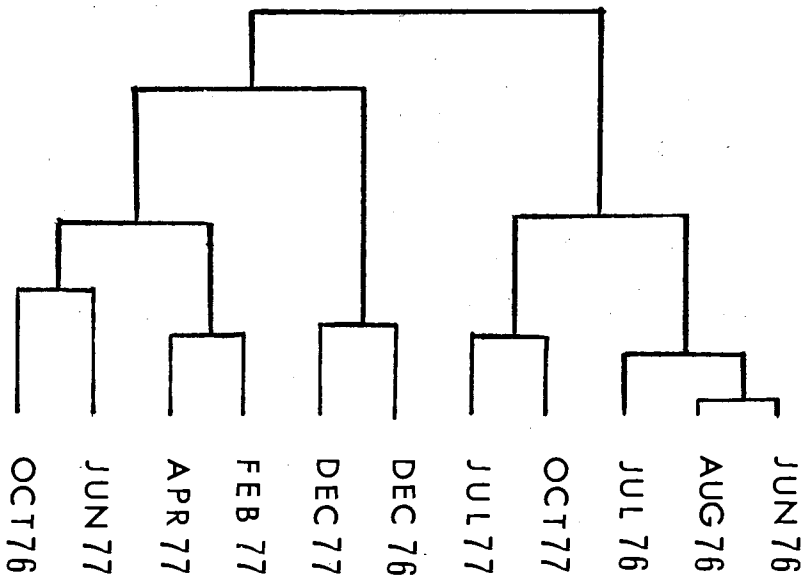


Figure 20. Diatoms on mature Macrocystis blades.

- A. Cocconeis scutellum Ehr. in a cluster.
Bacteria are visible.
- B. Dense cover of Cocconeis scutellum.
- C. Cocconeis costata var pacificum Grun.
(large and smaller diatoms with large costae), C. scutellum is in the upper right corner.
- D. Diatoms: Cocconeis costata Gregory, with punctate costae, (upper center), C. scutellum below, and Synedra tabulata (Ag.) Kutz. (long and narrow).

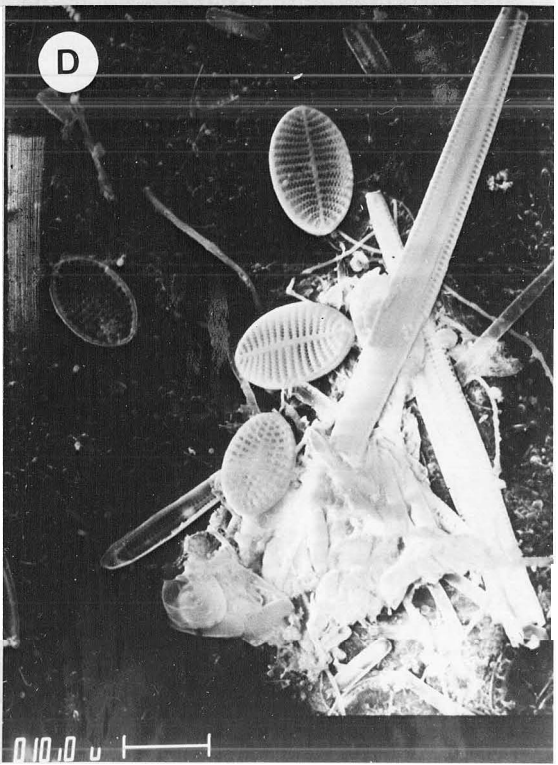
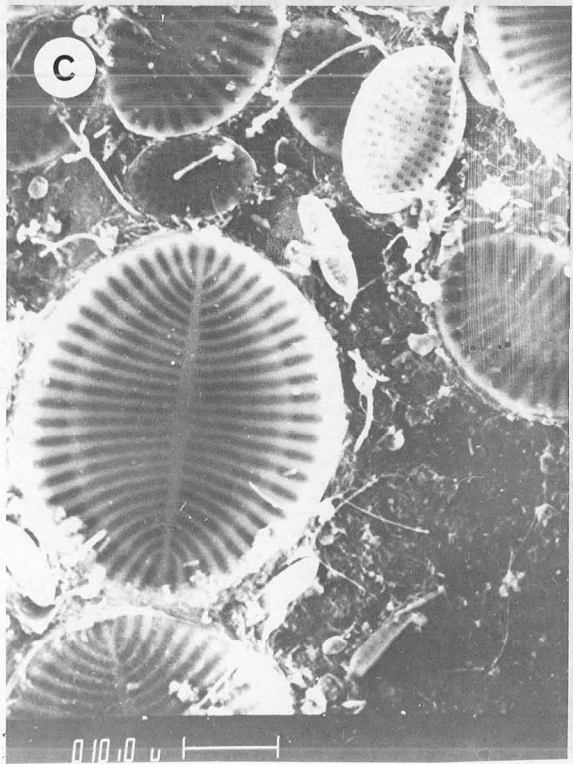
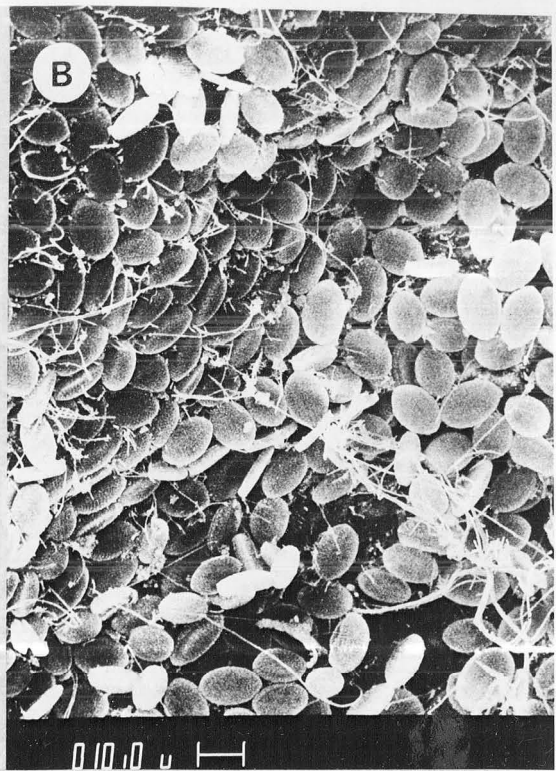
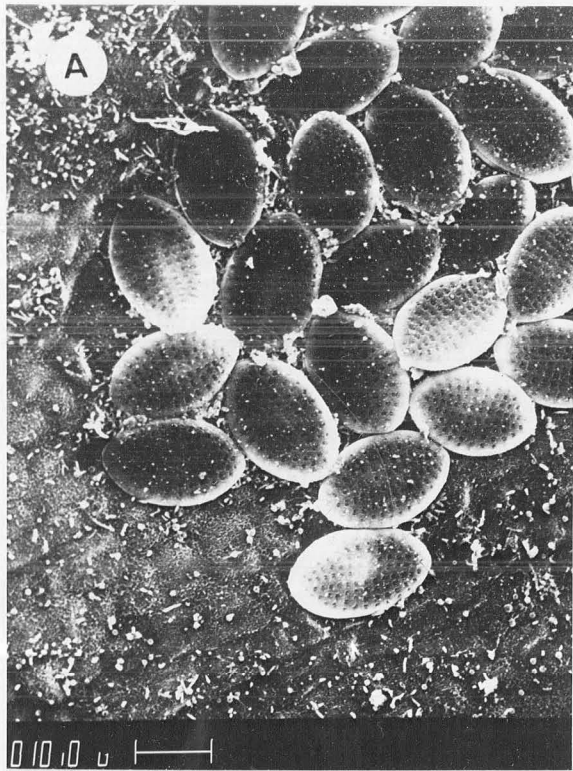


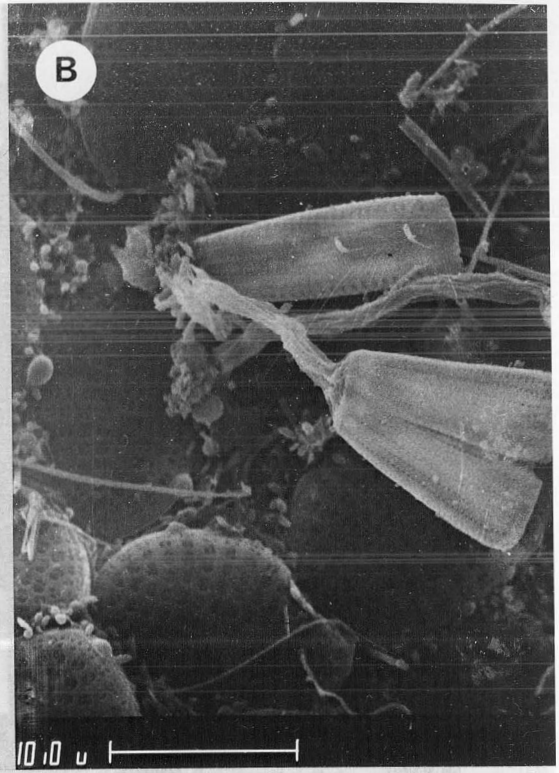
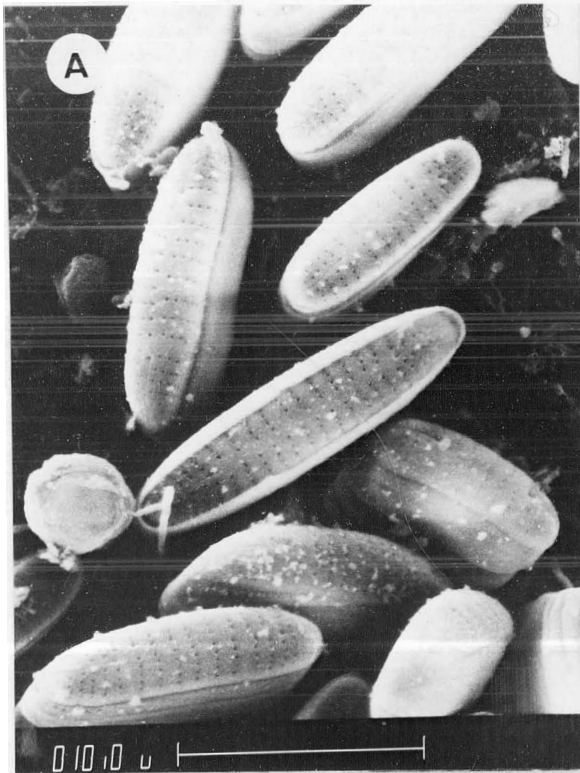
Figure 21. Diatoms and bacteria on Macrocystis.

A. Achnanthes no. 1.

B. Gomphonema sp. (stalked).

C. Rod form bacteria on a growing Macrocystis blade.

D. Rod and coccoid form bacteria on a senescent
Macrocystis blade.

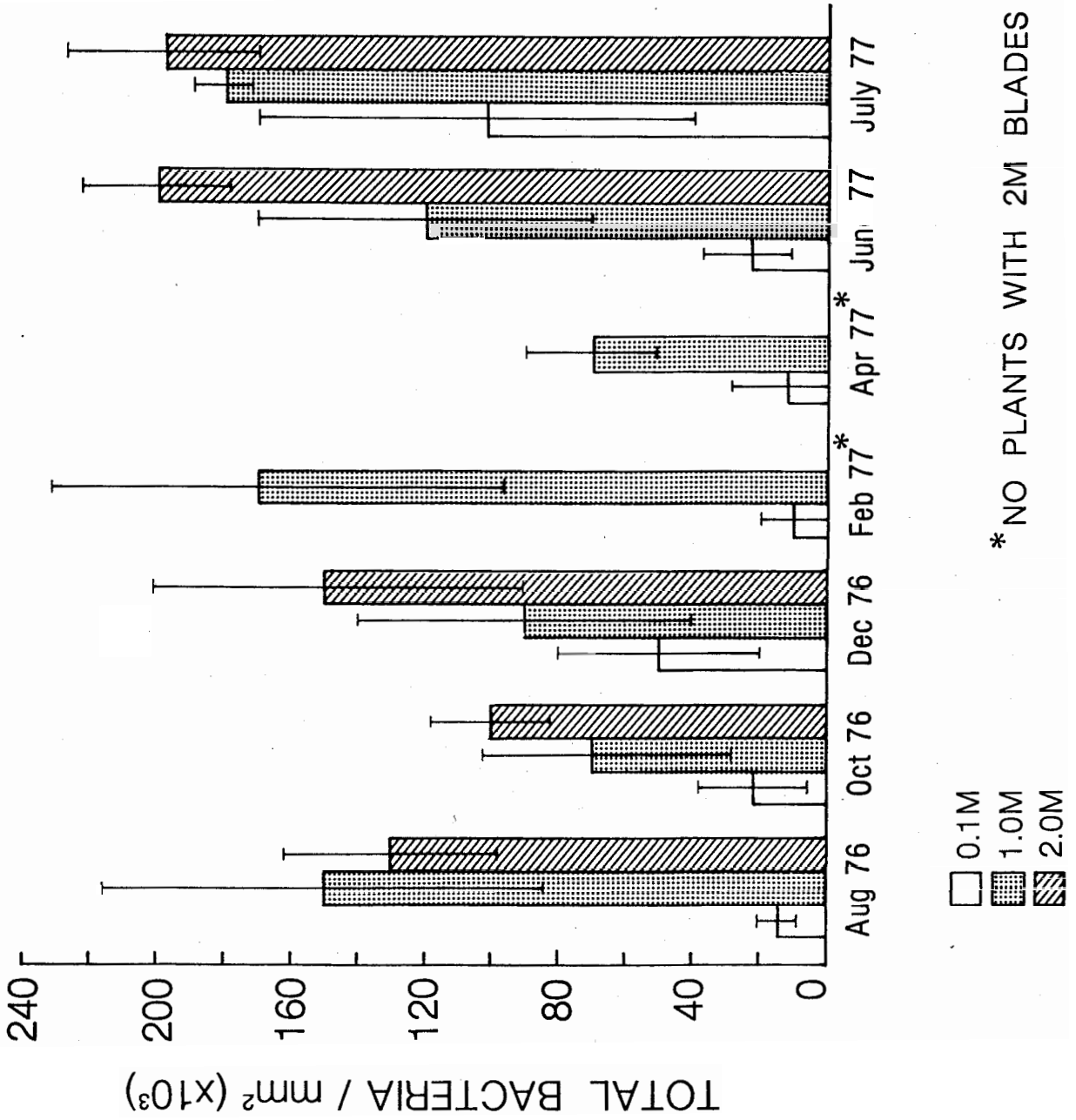


Bacteria on Macrocyctis and Nereocystis Blades

Blades of Macrocyctis 0.1 m from the frond meristem had an overall mean density of $32 \times 10^3 \pm 32 \times 10^3_s$ bacteria/mm² and approximately 10 times more rod than coccoid form bacteria (Fig. 21c, 22). Blades 1.0 m from the frond meristem had an overall density of $121 \times 10^3 \pm 46 \times 10^3_s$ bacteria/mm² and an approximate 1:1 ratio of rod and coccoid forms. Blades 2.0 m from the frond meristem had an overall mean density of $156 \times 10^3 \pm 43 \times 10^3_s$ bacteria/mm² and approximately a 0.6 rod to coccoid ratio (Fig. 21d). No seasonality in density or in rod to coccoid ratio was evident.

Blades of Nereocystis 0.1 and 0.5 m from the float had an overall mean of $9 \times 10^3 \pm 7 \times 10^3_s$ and $81 \times 10^3 \pm 54 \times 10^3_s$ bacteria/mm² respectively. Seasonal variations were not evident and the ratios of rod to coccoid form bacteria were approximately 1:1 for blade tissue at 0.1 and 0.5 m from the float.

Figure 22. Seasonal change in total numbers of bacteria/mm² on blades of Macrocystis 0.1, 1.0 and 2.0 m from the frond meristem ($\bar{X} \pm s.d.$)



* NO PLANTS WITH 2M BLADES

Epiphytism of Artificial Substrates

Glass Slides

Colonization of glass slides (sampled with replacement each collection date) was seasonal and development could be effected by competition. Suctorians were particularly dense from April to June and Obelia was dense from June through October; however the encrusting ectoproct Hippothoa hyalina from June through August could totally cover the slides in the sampling interval forcing suctorian and Obelia populations to extinction. Slides bore very reduced densities of suctorians, Obelia and diatoms through the winter months. Cocconeis scutellum, as on blades of Macrocystis and Nereocystis, formed a near unialgal mat on the slides in summer 1976.

Plastic "Plants"

Bacteria and diatoms initially colonized the plastic. Suctorians were present in relatively low densities throughout the year. An ectocarpalean mat began forming in July 1976. Colonies of Membranipora were rare but Obelia was dense through the summer and fall of 1976, and in winter and spring the colonies disappeared leaving only a network of stolons on the plastic. Ulva was present from July 1976 and Alaria and Porphyra nereocystis occurred in the spring and summer 1977. By October 1977 mussels were common and colonial tunicates covered most of the blades, overgrowing all preceding biota.

DISCUSSION

The pattern of succession on blades, stipes and artificial substrate was similar and proceeded in the following order: bacteria and diatoms, stalked ciliates and filamentous algae, hydroids and ectoprocts, structurally simple macro-algae, morphologically complex macro-algae. The population structure and degree of succession were subject to three major influences: 1. The time of year was important to colonization. 2. Effects of the host influenced spatial and temporal patterns of epiphytes. 3. Tissue life span was critical to the degree of community development.

Epiphytism and endophytism of Macrocystis and Nereocystis were described for a particular kelp bed. I briefly surveyed other locations through the year over a range of wave exposures and found that the phenomena do vary. Also, a more frequent sampling program would have provided a more complete picture of the seasonal pattern of succession.

Colonization of Hosts

Immigration of epiphytes onto Macrocystis and Nereocystis was seasonal. A spring increase in settlement of Membranipora, suctorians, and Obelia followed by summer or early fall declines in density was observed on blades of Macrocystis and glass slides. Most macroalgae appeared on the stipes of both host species and on plastic plants during spring and early summer. In contrast, total diatom densities did not increase in spring and the number of species markedly declined.

The studies of epiphytism in more temperate waters generally indicate the importance of seasonality. The importance of seasonality to colonization of abiotic marine substrates in temperate climates

similarly is recognized (Scheer, 1945; Aleem, 1950; Lee, 1966; Castenholz, 1967; Sutherland, 1974; Shoener, 1974; Neushal, et al, 1976; Osman, 1977; Sutherland and Karlson, 1977; Emerson and Zedler, 1978; Osman, 1978). Lobban (1976) found that bryozoans and hydroids settled on Macrocystis in Barkley Sound, British Columbia, during the spring and disappeared by September. Markham (1969) reported little change in the epiphytic assemblage on stipes of Nereocystis after December in the vicinity of Friday Harbor, Washington; Laminariales, however, were not present until April. Mukai (1971) found high spring and summer abundances of epiphytes on Sargassum in Japan. Penhale (1977) discovered that epiphyte biomass on eelgrass (Zostera) in North Carolina remained fairly constant through the year. Humm (1964) found a spring decrease in epiphytism on the seagrass Thalassia in Florida and considered this a result of rapid plant growth which allowed less time for the epiphytic assemblage to develop. In the present study highest growth rate of Macrocystis (Lobban, 1977) was during the time of heaviest epiphytism. No correlation between Macrocystis growth rate (from Lobban, 1976) and diatom densities was observed ($r=0.34$).

The unialgal mat of diatoms in spring (Cocconeis scutellum on Macrocystis and C. scutellum or, C. costata on Nereocystis) was preceded by more diverse assemblages and may have resulted from the superior ability of C. scutellum and other dominant benthic and pelagic primary producers to out-compete other plants in an environment which remained stable long enough for competitive exclusion to occur. Hutchinson (1961) and Titman (1976) discussed such exclusion from competition but I do not know the resources that were in demand. I do not believe that competition for space on the blades determined assemblages since diatoms settling on

newly formed tissue were very similar to assemblages on older tissue. This unialgal population may have declined from over exploitation resources in a previously nutrient enriched environment (Rozenweig, 1971). Such enrichment occurs in temperate climates during spring from high light intensities and nutrient concentrations (O'Brien, 1974). The subsequent assemblages of higher diversity and distantly related species compositions may result from failure of any assemblage to competitively exclude other diatoms before the environment changed significantly (Hutchinson, 1961). The role of grazing in increasing diversity (Paine, 1966; O'Brien, 1971; Connell, 1972; Dayton, 1975; Menge, 1976; and Menge and Sutherland, 1976) seemed unimportant as areas of blade grazed by invertebrates (Druehl, et al, 1977) were recolonized by the same species of diatoms already present on the blades.

Variations in bacterial and endophyte densities on blades of Macrocystis were not seasonal. Although most dense in spring, Cocconeis scutellum had the greatest niche breadth value on both hosts, indicating that it was more evenly distributed than any other diatom throughout all seasons. McIntire and Overton (1971) considered diatoms with broad realized niches to be ecological generalists, and Levins (1968) suggested that a broad niche is optimal in an uncertain environment. Perhaps these organisms have a broad tolerance to environmental factors and/or readily exploit disturbed habitats.

Host Effects

Settlement of organisms onto seaweeds has been related to anti-biotic properties of host tissue, (e.g. Sieburth, et al, 1974), age of tissue (Stebbing, 1972), the presence of attractive exudates (Crisp and Williams, 1960), loyalty of larvae (Doyle, 1976), preference for certain

host species (Ryland, 1959), and morphology of the host (Ryland, 1959; Edsbacke, 1966).

The importance of the state of tissue development was demonstrated by the stipes of both plants. Nereocystis growing inside the bed of Macrocystis were apparently at a competitive disadvantage and were senescent by June and became heavily epiphytised with bryozoans and seaweeds. In contrast, plants outside the bed Macrocystis reached maturity by August and only subsequently became epiphytised. Stipes of Macrocystis were epiphytised only by microbiota and Membranipora until senescent, after which Obelia and seaweeds could appear. The abundance of slippery exudates on growing tissue of both species compared to older tissue suggests that sloughing or exudates containing antibiotics may help keep tissue clean. McLachlan and Craigie (1964), Sieburth *et al* (1974), and Hornsey and Hide (1976) found highest antibiotic activity in the growing tissue of the seaweed species examined. The state of tissue development may have been responsible for the high ratio of rod to coccoid form bacteria on growing blades Macrocystis and the high number of coccoid forms on old and senescent blades.

Settlement onto younger tissue, as occurs with Spirobis settling on Laminaria (Stebbing, 1972), may maximise the length of time for development of an organism but my observations did not indicate such a preference for Membranipora serrilamella. Bernstein (per. comm.) found that larvae of Membranipora were positively phototactic and tended to settle on the younger tissue of Macrocystis pyrifera in southern California. This effect may be removed for M. integrifolia because this species grows in waters about three to six times shallower than M. pyrifera.

Absence of Obelia, Streblonema, and several diatom species from Nereocystis may have indicated a preference of these organisms for Macrocystis. The presence of exudates (Crisp and Williams, 1960) or blade morphology may have effected settlement on the two host species. Suctorians, larvae of Membranipora, larvae and primary axes of Obelia, larvae of Hippothoa, larvae of Tricellaria, and Spirorbis were all located in the furrows of Macrocystis blades. Absence of such furrows on blades of Macrocystis may have been the cause of the comparatively less diverse and abundant fauna. Similarly the broyozoan, Celleporelia, was shown by Ryland (1959) to preferentially settle into concavities of the blade of Laminaria saccharina.

None of the epiphytes present on either species were obligate epiphytes as all grew on glass slides or plastic. Harlin (1973a) found that the supposed obligate epiphyte Smithora would grow on plastic. The endophytes may have been obligate to plant tissue as no alternative morphology was known. Seasonality in occurrence cannot be exhibited by endophytes if no alternate epibenthic form, long lived planktonic phase, or other refuge exists. If plant tissue infected with these endophytes died and new tissue was not infected, extinction of the species would result. This is not the case and I suggest that endophytes have evolved as generalists in response to the short life span of seaweed substrate and to the predictability of formation of new substrate for colonization.

Possible antibiotic effects of host species were discussed earlier, but life history traits of hosts related to epiphytism were not mentioned. The rhizome production of Macrocystis provides a colonial growth strategy, and a single plant (colony of fronds) can prevent being overwhelmed with epiphytism by continually producing new fronds. The importance of

epiphytism in life histories is not known but this growth strategy may have evolved in response to epiphytism, thus allowing a perennial life history strategy. Nereocystis is solitary and becomes heavily epiphytised, thus epiphytism may have been important in the evolution of its annual life history strategy. This supports Jackson's (1977) conclusion that colonial organisms with continual indeterminate growth are less susceptible to fouling.

Host Life Span, Life Histories, and Succession

The life span of the host tissue was important in determining which organisms and assemblages of organisms developed. Abundant organisms on blades (life span of about 2 months) and glass slides were restricted to microbiota and small animals. Only on stipes (life span about 4 - 6 months for Macrocystis and 12 - 14 months for Nereocystis) and plastic did macroalgae become abundant. Osman (1977) discovered that as stability of rocks subject to turnover by waves increased, epifaunal assemblages changed from short lived species to assemblages with longer life spans and superior competitive tactics. Those organisms reproductively and competitively successful on blades and glass slides had more r-ish life history traits (Pianka, 1970) than certain major epiphytes on stipes. A life history trait associated with unstable environments where adult mortality is high is the large investment of energy into production of disseminules (Gadgil and Solbrig, 1972; Gaines, 1974; Giesel, 1976; Stearns, 1977). I did not directly measure energy allocation, however, the speed of development to reproductive maturity (a life history character used by McNaughton, 1975) was relatively rapid and within the host life span for all organisms except

Laminariales, Fucales, and mussels. Reproducing algal species had high surface to volume ratios, simple thalli, and indeterminate growth patterns. Animals were small at maturity and most were colonial. Littler and Murray (1975) reported similar r-type features for an algal assemblage subjected to a periodically toxic sewage outfall.

Mortality was mainly due to the death of the host, but could result from grazing. Diatoms on Macrocystis blades supported a year round population of harpacticoid copepods (Roland, 1978). Membranipora and Obelia were eaten by several species of nudibranchs (Druehl, et al, 1977), and both predator and prey occurred seasonally. Density dependent mortality resulted from the superior competitive ability of certain colonial animals to acquire space by overgrowing others. Solitary forms such as suctorians and Folliculina were overgrown by the colonial ectoprocts. The colonial hydroid Obelia was also overgrown by the ectoprocts Membranipora and Hippothoa but could produce primary axes from overgrown stolons at the interface of two of these encrusting colonies. Jackson (1977) concluded that the indeterminate growth of colonial animals allows continual substrate occupation eliminating the need for recruitment and making them less susceptible to fouling and overgrowth. For colonial animals in the epiphytic habitat recruitment is necessary only on young host tissue.

Studies of succession on marine substrates typically describe a microbial and diatom colonization which is succeeded by more complex organisms, (e.g. Wilson, 1925; Neushul, et al, 1976; Emerson and Zedler, 1978). I saw a similar progression in the epiphytic assemblages on Macrocystis and Nereocystis and Sieburth, et al (1974) noted the same trend in other seaweeds. A true succession where changes in

assemblages are dependent on the presence of other organisms (Connell, 1972) may occur in the epiphytic habitat. An assemblage of a limited biota not repulsed by antibiotic properties may form a crust nullifying antibiotic effects which may allow the colonization to proceed similar to that on inanimate objects (Sieburth, et al, 1974). I observed a succession from organisms with more r-type characteristics to organisms with more K-type life histories when I compared blades to senescent stipes.

REFERENCES CITED

- Aleem, A.A., 1950. Distribution and ecology of British marine littoral diatoms. *J. Ecol.*, 38: 75-106.
- Boaden, P.J.S. et al. 1976. The fauna of a Fucus serratus L. community: ecological isolation in sponges and tunicates. *J. Exp. Mar. Biol. Ecol.*, 21: 249-267.
- Castenholz, R.W. 1967. Seasonal ecology of non-planktonic marine diatoms of the western coast of Norway. *Sarsia*, 29: 237-256.
- Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.*, 3: 169-192.
- Crisp, D.J. and G.B. Williams. 1960. Effects of extract from fucoids in promoting settlement of epiphytic polyzoa. *Nature*, 196: 1206-1027.
- Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal community. *Ecol. Mon.* 45: 137-159.
- Doyle, R.W. 1976. Analysis of habitat loyalty and habitat preference in the settlement behavior of marine planktonic larvae. *Am. Nat.*, 110: 719-730.
- Druehl, L.D., W. Roland, and T. Tuominen. 1977. Food chains originating from Macrocystis integrifolia. *J. Phycol.*, 13 (supp): abst.
- Edsbagger, H. 1966. Some problems in the relationship between diatoms and seaweeds. *Bot. Mar.*, 11: 65-67.
- Emerson, S.E. and J.B. Zelder. 1978. Recolonization of intertidal algae: an experimental study. *Mar. Biol.*, 44: 315-324.
- Gadgil, M., and O.T. Solbrig. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *Am. Nat.*, 106: 14-31.
- Gaines, M.S. 1974. Reproductive strategies and growth patterns in sunflowers (Helianthus). *Am. Nat.*, 108: 889-894.
- Giesel, J.T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Ann. Rev. Ecol. Syst.*, 7: 57-59.
- Harlin, M.M. 1973a. "Obligate" algal epiphyte: Smithora naiadum grows on a synthetic substrate. *J. Phycol.*, 9: 230-232.
- _____. 1973b. Transfer of products between epiphytic marine algae and host plants. *J. Phycol.*, 9: 243-248.

- Harlin, M.M. 1975. Epiphyte-host relations in seagrass communities. *Aquatic Botany*, 1: 124-131.
- Heurck, van, H. 1962. A Treatise on the Diatomaceae. Cramer, Weinheim.
- Hornsey, I.S. and D. Hide. 1976. The production of antimicrobial compounds by British marine algae III. Distribution of antimicrobial activity within the algal thallus. *Br. Phycol. J.*, 11: 175-181.
- Humm, H.J. 1964. Epiphytes of the seagrass Thalassia testudinum, in Florida. *Bull. of Mar. Sci. of the Gulf and Caribbean*. 14: 306-341.
- Hutchinson, G.E. 1961. The paradox of the plankton. *Am. Nat.*, 95: 137-145.
- Jackson, J.B.C. 1977. Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Am. Nat.*, 111: 743-767.
- Kozloff, E.N. 1975. Keys to the Marine Invertebrates of Puget Sound, the San Juan Archipelago, and Adjacent Regions. University of Washington, Seattle.
- Kudo, R.R. 1971. Protozoology. Thomas, Springfield, Ill. pp. 1036-1056.
- Lee, R.K. 1966. Development of marine benthic algal communities on Vancouver Island, British Columbia. In The Evolution of Canada's Flora. Edited by R.L. Taylor and R.A. Ludwig. University of Toronto. pp. 100-120.
- Levins, R. 1968. Evolution in changing environments. Monographs in Population Biology. 2. Princeton University. pp. 41-47.
- Light, S.E. 1975. Light's Manual: Intertidal Invertebrates of the Central California Coast. Third Ed. University of California, Berkeley.
- Lindsay, J.G. and R.G. Saunders. 1977. Growth and enhancement of the agarophyte Gracilaria. Fisheries Management Report No. 8, British Columbia Marine Resources Branch.
- _____. 1978. Experiments on the agarophyte Gracilaria in an intensive floating culture system. Fisheries Management Report (in press), British Columbia Marine Resources Branch.

- Littler, M.M. and S.N. Marray. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macroorganisms. *Mar. Biol.*, 30: 277-291.
- Lobban, C.S. 1976. Growth, translocation and harvesting interactions in Macrocystis integrifolia. Report to Marine Resources Branch, British Columbia.
- Lobban, C.S. 1978. The growth and death of the Macrocystis sporophyte (Phaeophyceae, Laminariales). *Phycologia*, 17: 196-212.
- Main, S.P. and C.D. McIntire. 1974. The distribution of epiphytic diatoms in the Yaquina Estuary, Oregon (U.S.A.). *Bot. Mar.*, 17: 88-99.
- Markham, J.W. 1969. Vertical distribution of epiphytes on the stipe of Nereocystis luetkeana (Mertens) Postels and Ruprecht. *Syysis*, 2: 227-240.
- McIntire, C.D. and W.S. Overton. 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. *Ecology*, 52: 758-777.
- McLachlan, J. and J.S. Craigie. 1966. Antialgal activity of some simple phenols. *J. Phycol.*, 2: 133-135.
- McNaughton, S.J. 1975. r- and K-selection in Typha. *Am. Nat.*, 109: 251-261.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs*, 46: 355-393.
- Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of roles of predation, competition, and temporal heterogeneity. *Am. Nat.*, 110: 351-369.
- Mukai, H. 1971. The phytal animals on the thalli of Sargassum serratifolium in the Sargassum region, with reference to their seasonal fluctuations. *Mar. Biol.*, 8: 170-182.
- Neushul, M. et al. 1976. An in situ study of recruitment, growth and survival of subtidal marine algae: techniques and preliminary results. *J. Phycol.*, 12: 397-408.
- Nichols, J.D., et al. 1976. Temporally dynamic reproductive strategies and the concept of r- and K- selection. *Am. Nat.*, 110: 995-1005.
- O'Brien, W.J. 1974. The dynamics of nutrient limitation of phytoplankton algae: A model reconsidered. *Ecology*, 55: 135-141.

- Osman, R.W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs*, 47: 37-63.
- Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.*, 100: 65-75.
- Penhale, P.A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *J. Exp. Mar. Biol. Ecol.*, 26: 211-224.
- Pianka, E.R. 1970. On r- and K-selection. *Am. Nat.*, 104: 592-596.
- Pielou, E.C. 1975. Ecological Diversity. Wiley.
- Rao, V.N.R. and J. Lewin. 1976. Benthic marine diatom flora of False Bay, San Juan Island, Washington. *Syesis*, 9: 197-213.
- Ricketts, E.F. and J. Calvin. 1968. Between Pacific Tides. Stanford, Ca. p. 356.
- Roland, W. 1978. Feeding behavior of the kelp clingfish *Rimicola muscarum* residing on the kelp *Macrocystis integrifolia*. *Can. J. Zool.*, 56: 711-712.
- Rosenzweig, M.L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171: 385-387.
- Ryland, J.S. 1959. Experiments on the selection of algal substrates by polyzoan larvae. *J. Exp. Biol.*, 36: 613-631.
- Sanders, H.L. 1968. Marine Benthic diversity: a comparative study. *Am. Nat.*, 102: 243-282.
- Scagel, R.F. 1947. An investigation on marine plants near Port Hardy Bay, B.C. Prov. Dept. of Fish., Victoria, B.C., no. 1. 70 pp.
- Scheer, B.T. 1945. The development of marine fouling communities. *Biol. Bull.*, 89: 103-121.
- Shannon, C.E., and W. Weaver. 1949. The Mathematical Theory of Communication. University of Illinois, Urbana.
- Setchell, W.A. and N.L. Gardner. 1920. The Marine Algae of the Pacific Coast of North America. Part II Chlorophyceae. *U. of Ca. Pub. in Bot.* 8: 139-374.
- _____. 1925. The Marine Algae of the Pacific Coast of North America. Part III Melanophyceae. *U. of Ca. Pub. Bot.*, 8: 387-711.

- Shoener, A. 1974. Colonization curves for planar marine islands. *Ecology*, 55: 818-827.
- Sieburth, J. McN., et al. 1974. Microbial colonization of marine plant surfaces as observed by scanning electron microscopy. In Microbial Seascapes. Edited by J. McN. Sieburth.
- Sloan, J.F. et al. 1957. The ecology of the Lough Ine rapids with special reference to water currents. V. The sedentary fauna of the Laminarian algae in the Lough Ine area., *J. Anim. Ecol.*, 26: 197-211.
- Southwood, T.R.E., et al. 1974. Ecological strategies and population parameters. *Am. Nat.*, 108: 791-804.
- Stearns, S.C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.*, 8: 145-171.
- Stebbling, A.R.D. 1972. Preferential settlement of a bryozoan and serpulid larvae on the younger parts of Laminaria fronds, *J. Mar. Biol. Ass. U.K.*, 52: 765-772.
- Sutherland, J.P. 1974. Multiple stable points in natural communities. *Am. Nat.*, 108: 859-873.
- Sutherland, J.P. and R.H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecological Monographs*, 47: 425-446.
- Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*, 192: 463-465.
- Tokida, J. 1960. Marine algae epiphytic on Laminariales plants. *Bull. Fac. Fish. Hokkaido Univ.*, 11: 73-104.
- Widdowson, T.B. 1974. Keys to the Ratgor, Batgor and Gatgor of British Columbia. Mss. Bamfield Marine Station.
- Wilson, O.T. 1925. Some experimental observations of marine algal successions. *Ecology*, 6: 303-311.