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NL-91 (3-74)

THE IMPACT OF TEGULA PULLIGO, GMELIN
ON TISSUE LOSS FROM MACROCYSTIS INTEGRIFOLIA, BORY
IN BARKLEY SOUND, VANCOUVER ISLAND
BRITISH COLUMBIA

by

GLYN JOHN SHARP

B.Sc. Honours, 1969

Dalhousie University, Halifax

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

in the Department

of

Biological Sciences

Simon Fraser University

August 1974

APPROVAL

Name: Glyn John Sharp

Degree: Master of Science

Thesis Title: The Impact of *Tegula pulligo* Gmelin on Tissue Loss from *Macrocystis integrifolia* Bory in Barkley Sound, Vancouver Island, British Columbia.

Examining Committee:

Chairman: Dr. R. Brooke

L. D. Druehl
Senior Supervisor

W. C. Austin
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T. H. Carefoot
Supervisory Committee

R.M.F.S. Sadleir
Departmental Examiner

Date Approved: March 1, 1976

APPROVAL

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The impact of Tegula pulligo, Gmelin on tissue loss from Macrocystis integrifolia, Bory in Barkley Sound, Vancouver Island, British Columbia

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August 20, 1974
(date)

ABSTRACT

Macrocystis integrifolia, Bory (kelp) beds in Barkley Sound, Vancouver Island contain numerous invertebrate herbivores. A prosobranch gastropod, *Tegula pulligo* Gmelin was found to be numerically dominant throughout the year in all surveyed kelp beds. It was highly motile but did not make any mass migrations within the study period.

Laboratory feeding experiments with *T. pulligo* indicated that consumption of tissue was not a satisfactory indicator of grazing impact. A significant amount of tissue was lost due to the incidental effects of grazing. In the field grazing and water motion acted together to accelerate the loss of plant tissue.

Growth of *M. integrifolia* was assessed during a period of maximum growth in the kelp bed. The lamina was used to assess production, since grazing and erosion acted most directly on this frond structure. The laminae grew as a moving belt of tissue up to 24 days after they split from the apical scimitar.

In a small (100 m square) kelp bed the plant and herbivore population was surveyed twice over 60 days. Using this detailed study a value was calculated to reflect both the consumption of laminae production and grazing impact of *T. pulligo* over 30 days from the final survey. *Tegula pulligo* consumed 2.3 ± 1.6% of lamina production, but the interaction of its grazing with erosion caused a loss of 55 ± 38.5% of lamina production.

ACKNOWLEDGEMENTS

I would like to thank Dr. L.D. Druehl for his confidence, financial assistance and help with manuscript preparations; Dr. W.C. Austin and Dr. T.H. Carefoot for criticism of manuscript; Doug Kittle for help in the field and all my diving partners including Dan Pace, Chris Lobban and students of the Bamfield Marine Station, Summer session, 1973; Judy Murphy for assistance at various stages of my work; Karl Ostrom, Rol Ostrom and Frank Wick for help in the design and construction of underwater equipment; Ron Long for photographic work; Audio Visual Graphics department for drawn figures; and lastly, but not least, the people of Bamfield for their help and kindness.

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INTRODUCTION

The kelp bed (*Macrocystis*, C.A. Agardh, 1823) communities on the Pacific Coast of North America contain many separate plant-herbivore associations. I have investigated the relationship between the brown alga *Macrocystis integrifolia* Bory (Order Laminariales) and associated herbivores particularly the prosobranch gastropod *Tegula pulligo* Gmelin (Family Trochidae) in Barkley Sound on Vancouver Island, British Columbia, Canada.

Macrocystis integrifolia grows inshore from a meter above 0 tide level (Canadian Datum) to 7 meters below and ranges from Point Conception, California to Kodiak Island, Alaska, U.S.A. (Druehl, 1970; North, 1971; Womersley, 1954). *Tegula pulligo* is subtidal and ranges from Sitka, Alaska to lower California, U.S.A. (Griffith, 1967). Species related to this plant and this animal have received considerable attention from researchers.

North, (1957-1974) has led a research group investigating *Macrocystis pyrifera* (Linneaus) A. Agardh in California. These workers studied aspects of ecology, biochemistry, growth, physiology, reproduction and faunal associations. Independent studies were conducted earlier, for example investigations of faunal associations in the kelp beds (Andres, 1945; Aleem, 1956). Published studies concerning *M. integrifolia* have been largely limited to growth (Scagel, 1947; North, 1973), morphological variation (Pace, 1972), chemical composition (Wort, 1955), and a single calorific value (Paine and Vadas, 1969).

Tegula funebralis (A. Adams), an intertidal neighbour of T. pulligo has been the subject of many studies: physiology (Galli and Giese, 1959); growth (Frank, 1965); feeding rates (Best, 1964); energetics (Paine, 1966); predator prey interaction (Paine, 1969); and locomotion (Miller, 1974). The limited access to T. pulligo has restricted research to a few studies. A class at Hopkins Marine Station, California performed short projects on the following: respiration, predation and distribution (Pearse, 1972). Lowry (1974) studied the distribution of Tegula species in a M. pyrifera bed.

The major purpose of my study was to assess the impact of T. pulligo on the natural loss of M. integrifolia tissue. During this study I also noted the distributions of the other herbivores. The investigation was in four parts: local M. integrifolia distribution and growth; T. pulligo's distribution, population structure, movement and feeding behaviour; interaction of the plant and the herbivore and a detailed field assessment of T. pulligo's grazing impact.

The first part of the study involved obtaining production rates of plant laminae since the laminae were the most important frond structure in the plant-herbivore relationship. Further, I investigated distribution of the plant horizontally and vertically as well as the phenology of the kelp bed throughout the year.

The second part of my studies considered such questions as: what is the distribution of T. pulligo and other herbivores vertically and horizontally; do the herbivores remain in the kelp bed throughout the year? Further, to establish a feeding rate for the snail answers to the following questions were required: what is the feeding period, feeding frequency, the effect of light, temperature and food preference? Initial laboratory feeding experiments indicated the tissue consumed was only part of the total tissue lost to the plant.

This additional tissue loss led to part three of this study involving the interaction of the grazers and the plant in the field. Specifically, does grazing weaken tissue so it is more susceptible to erosion by water motion? What are the characteristics of grazing damage and its extent in the field?

The fourth part of the study was the calculation of a value to reflect the impact of T. pulligo grazing on M. integrifolia. Kelp bed complexity prevented the application of a general model for the plant-herbivore system over an extended period and area. Therefore, the value was calculated in reference to a 100 meter square area within a large kelp bed and applied to a one month period of maximum kelp growth.

This thesis is presented in four major sections, each consisting of specific methods, results and discussion. They are preceded by general methods and followed by a general discussion.

GENERAL METHODS

All statistics and statistical tests computed from my data with one exception used standing routines from STATPAK in the A.P.L. (A Programming Language) of Simon Fraser University Computing Centre. The exception was the t-test for the equality of means which was designed by Sokal and

Rohlf (1969). All tests for the equality of statistics were conducted at the 5 percent level of significance.

Laboratory studies were carried out in the Bamfield Marine Station, Bamfield, B.C. with one exception. Unless otherwise specified these experiments took place in an open seawater system. Organisms employed in laboratory experiments were transported to the open seawater system in plastic bags within 1 hour. All field studies were conducted in Barkley Sound, within a 5 Km radius of the Bamfield Marine Station and employed SCUBA.

STUDIES ON MACROCYSTIS INTEGRIFOLIA

METHODS

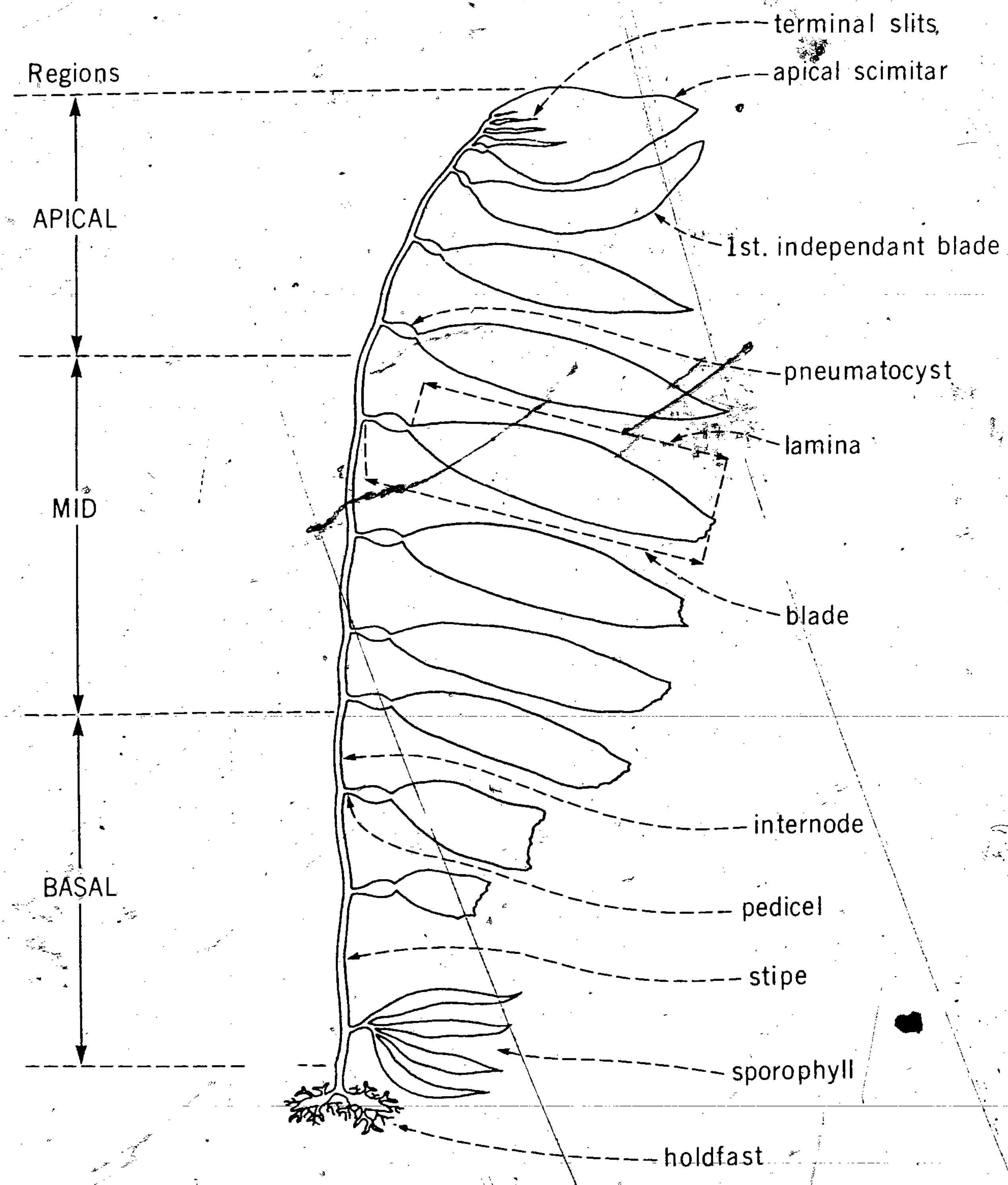
General distribution of M. integrifolia in Southeast Barkley Sound.

During July 1971, a presence-absence survey was conducted for the distribution of M. integrifolia (Druehl, pers. comm.). Presence or absence was established by surface and underwater reconnaissance.

Growth Measurements

Figure 1 illustrates the morphological terminology employed for M. integrifolia in this thesis.

Figure 1 A schematic diagram of a M. integrifolia frond showing the nomenclature of structures and regions


terminal slits
apical scimitar
Regions
APICAL
1st. independant blade
pneumatocyst
lamina
MID
blade
internode
BASAL
pedicel
stipe
sporophyll
holdfast

Stipe Length and Blade Number

All stipe and blade measurements were made underwater with a meter stick or 30 centimeter rule. Stipes and associated blades were identified with surveyor's marker tape lettered with waterproof ink. The tape was tied loosely at the base of each stipe or at an internode to prevent tissue damage. The groups of fronds used in stipe elongation and blade number measurements with dates or measurements are listed on Table (I). Stipe length was defined as the distance from the most recent terminal slit to the juncture of the stipe and holdfast. Blade number was defined as the total number of independent blades plus the number of terminal slits per frond. Accuracy in measuring underwater decreased with the size of the frond. Blade counts were estimated to be approximately within 10% of the true number and length to within 10% of the stipe length.

Lamina Length and Width Increment, Duration and Pattern of Growth

A paper punch was used to cut 1 cm diameter holes 2-3 cm inside the periphery of the lamina. Width increment was defined as the change in centre to centre distance between two opposite holes. Length increment was defined as the change in distance between a hole centre and the base of the lamina (Cribb, 1954). When holes were punched in the meristematic area of the lamina, the holes grew in diameter but did not move along the lamina. To avoid this problem the holes were subsequently punched at least 5 cm from the base of the lamina. Four separate groups of fronds were used for the study of lamina growth. The sample groups and procedures

TABLE I

Frond Sample Groups Used in Growth Rate Experiments Ross Islets Plateau Kelp Bed

Plant Structure	Purpose	Dimension	Method	Position of Holes on Lamina	Sample Number	Dates of Measurement
Stipe	Rate of Elongation	Length	Distance from the base of the stipe to the last terminal slit	None	80	18/7/73 - 19/8/73
Blade	Number per unit length	Total number	All independent blades plus terminal slits counted	None	65	13/8/73 & 10/9/73
Blade	Rate of addition	Total number	All independent blades plus terminal slits counted	None	65	18/7/73, +4, +8, +14, +20, +24
Lamina	Duration of growth and mean rate	Length & width	Holes in pairs on laminae of the mid to basal region of frond	Base	80	24/6/73, +21
Lamina	Duration of growth and mean rate	Length & width	Holes in pairs on first independent laminae	Base	65	18/7/73, +4, +8, +14, +20, +24
Lamina	Relative growth of adjacent lamina	Length & width	Holes in triangle of 4-5 adjacent laminae	Base	50	13/8/73, +4, +7
Lamina	Pattern of growth	Length & width	3, hole pairs on first independent laminae	Middle & Base	20	11/9/73 - 16/9/73

used to assess the pattern, relative growth and mean growth rate of laminae are listed in Table (I).

Biomass Per Unit Area of the Lamina

Twenty-three fronds ranging from 0.25 cm to 6.0 m in length were collected from the Ross Islets Plateau kelp bed in June, 1973 (Fig. 2). The apical lamina, first independent lamina, a mid region lamina and basal lamina were removed from each frond. The fresh blotted weight of each lamina was measured on a toploading Mettler model ph200 balance to 0.1 gm. The perimeter of each lamina was traced on newsprint for later reference. No attempt was made to include holes in the lamina, unless they exceeded one third of the width. The area of each tracing was calculated by a Salmoiraghie Model 236 planimeter (Salmoiraghie Instruments, Milan, Italy) to 0.1 cm^2. The weight per unit area was then calculated for each lamina grouping.

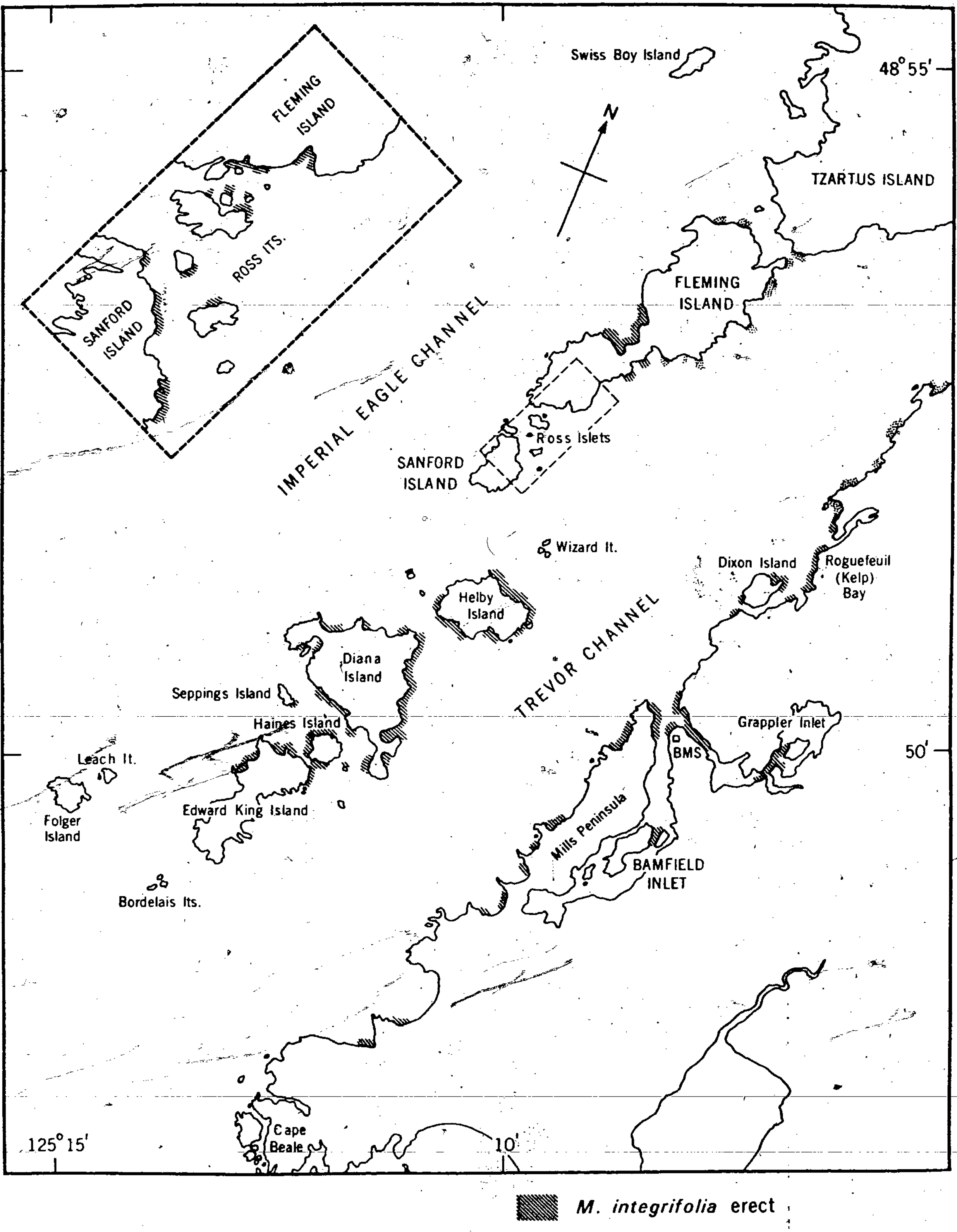
RESULTS

General distribution of M. integrifolia in Southeast Barkley Sound.

Two forms of M. integrifolia were distinguished in the 1971 survey (Fig. 2, Druehl, pers. comm.). There was an erect form which floated at the surface and a low-lying form which laid along the bottom. The prostrate form was restricted to the sheltered northern end of the Trevor channel on silt covered bottoms. Macrocystis integrifolia was present in moderately exposed to sheltered areas where there was a stable substrate and good water circulation.

Figure 2 The distribution of two forms of *M. integrifolia* as observed in a survey covering southeast Barkley Sound in July 1971 (Druehl, pers. comm.)

Scale: 1 cm = 1 km


FLEMING ISLAND
ROSS ITS.
SANFORD ISLAND
Swiss Boy Island
48°55′
N
TZARTUS ISLAND
FLEMING ISLAND
IMPERIAL EAGLE CHANNEL
Ross Islets
SANFORD ISLAND
Wizard It.
Dixon Island
Roguefeuil (Kelp) Bay
Helby Island
TREVOR CHANNEL
Diana Island
Seppings Island
Haines Island
Grappler Inlet
BMS
50′
Leach It.
Folger Island
Edward King Island
Mills Peninsula
BAMFIELD INLET
Bordelais Its.
Cape Beale
125°15′
10′
▨ *M. integrifolia* erect
░ *M. integrifolia* prostrate

Growth Measurements

Stipe Length and Blade Number

The rate of stipe elongation increased with the stipe length up to approximately 200 cm. Then the rate of growth decreased by 30 percent for each additional 100-150 cm of stipe length (Fig. 3). A linear regression line for the data had an R value of 0.16 and accounted for 2% of the data variation indicating a poor linear relationship. Therefore a curved line was fitted by hand. Although a decrease in growth is suggested beyond the 200 cm length position of the line is in doubt due to the paucity of measurements.

There was a constant relationship between the length of stipes and the number of blades (Fig. 4). The linear regression line was a good fit to the data with an R value of 0.9 accounting for 81% of the data variation.

There was a slight increase in the rate of blade addition over the range of stipe lengths (Fig. 5). The mean rate of blade addition for the sample qas 0.4 SD ± 0.2 blades/day. A curvilinear relationship may be argued for the variation in the rate of blade addition with initial stipe length. However, the previous blade number results showing there is a constant number of blades per unit length regardless of length indicate a linear relationship exists between the two sets of data. The R value for these data is 0.35 and accounts for only 12% of the variation. This is a poor fit and for any stipe length the rate of addition can range from .1 to .8 blades per day. Additional data beyond 200 cm stipe length is required to prove this relationship.

Figure 3 Variation in the rate of stipe elongation with the length of 56 stipes measured over 30 day periods, during July, August and September at the Ross Islets Plateau kelp bed. The curved line was drawn by hand

- - - - line in doubt due to lack of points

11b

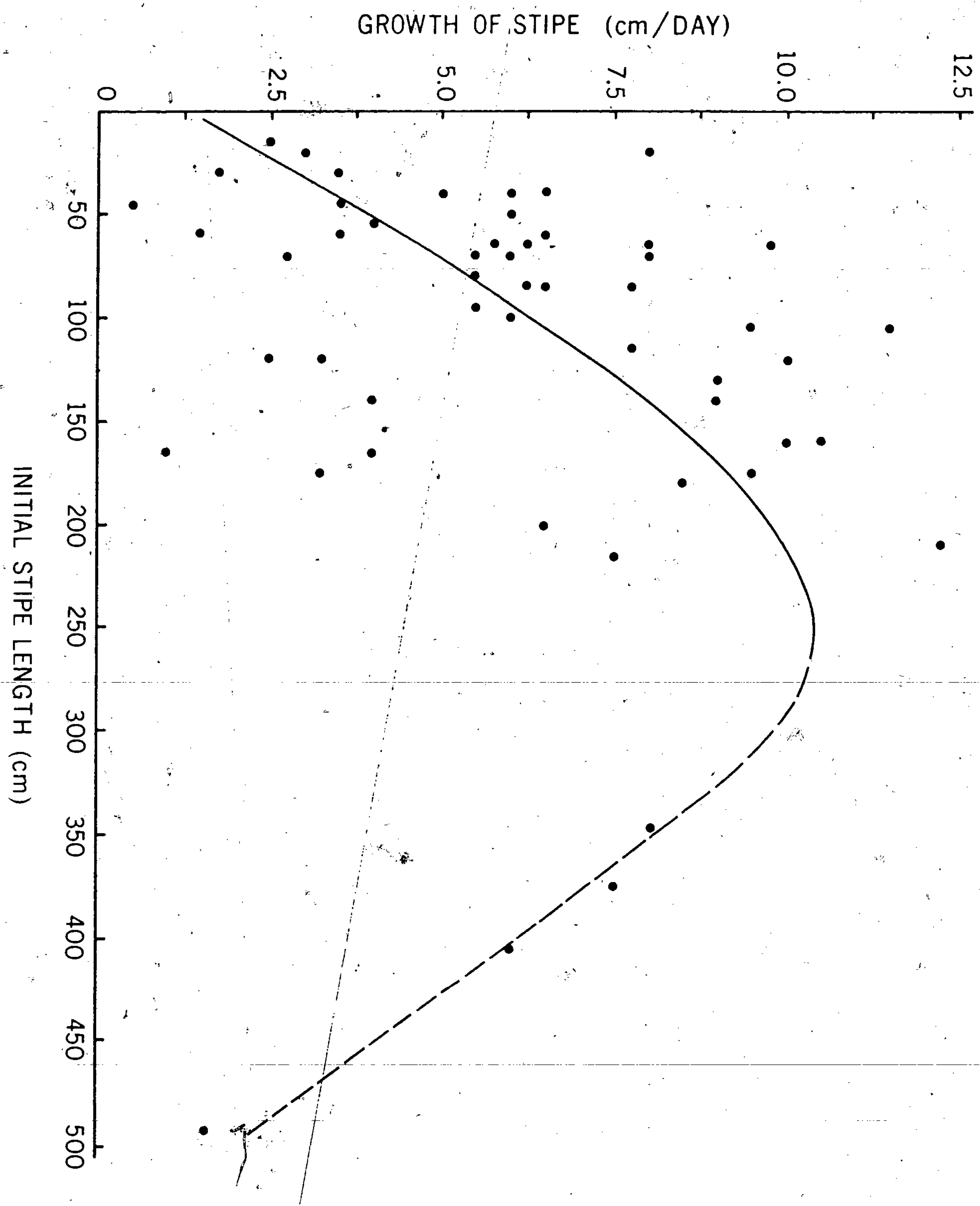

GROWTH OF STIPE (cm/DAY)
0
2.5
5.0
7.5
10.0
12.5
INITIAL STIPE LENGTH (cm)
50
100
150
200
250
300
350
400
450
500

Figure 4 Variation in the number of blades on a stipe with the length of the stipe. Blade counts were made in the Ross Islets kelp bed on 56 fronds during July, August and September, 1973. The formula describes the line through the points

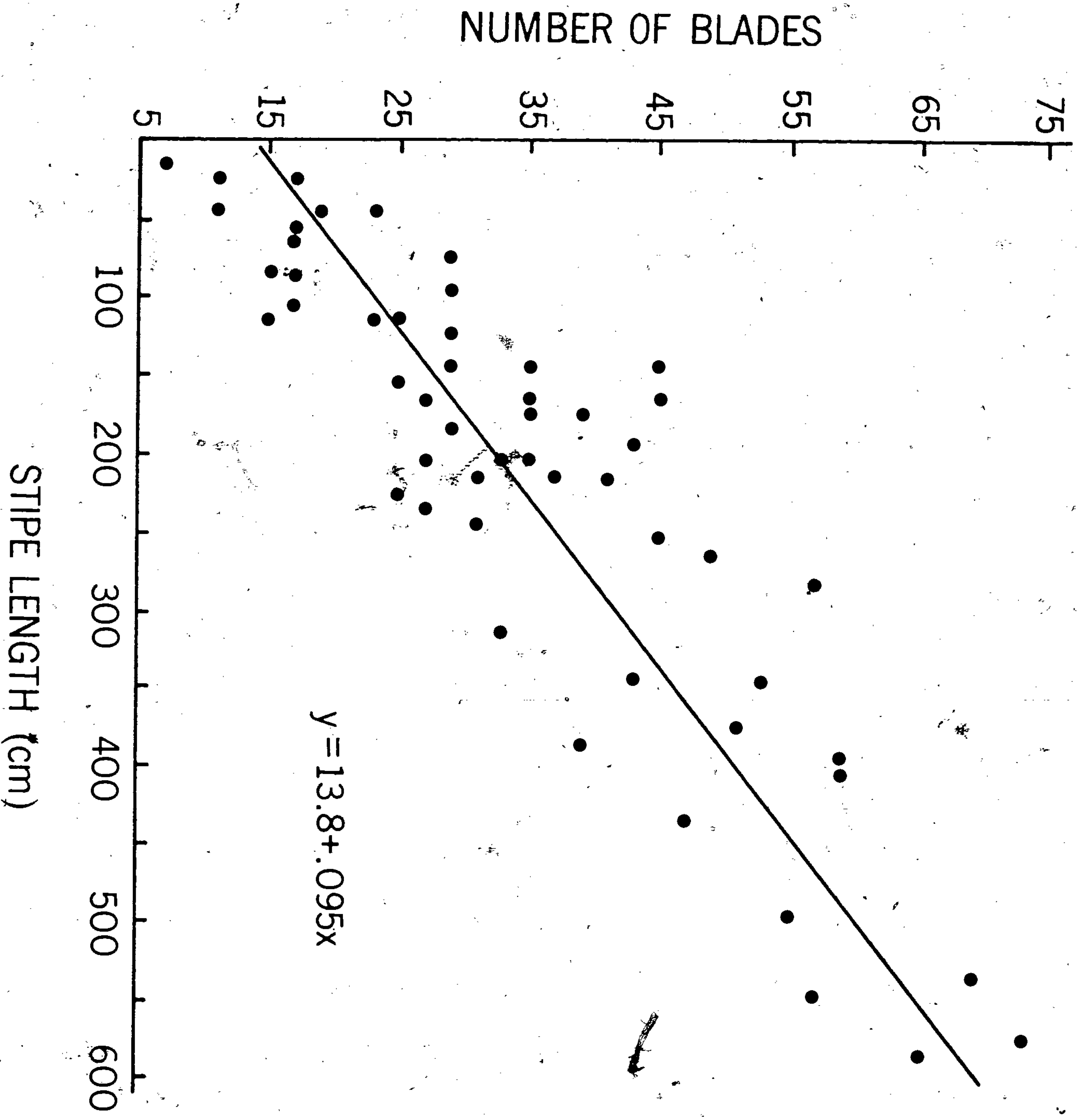
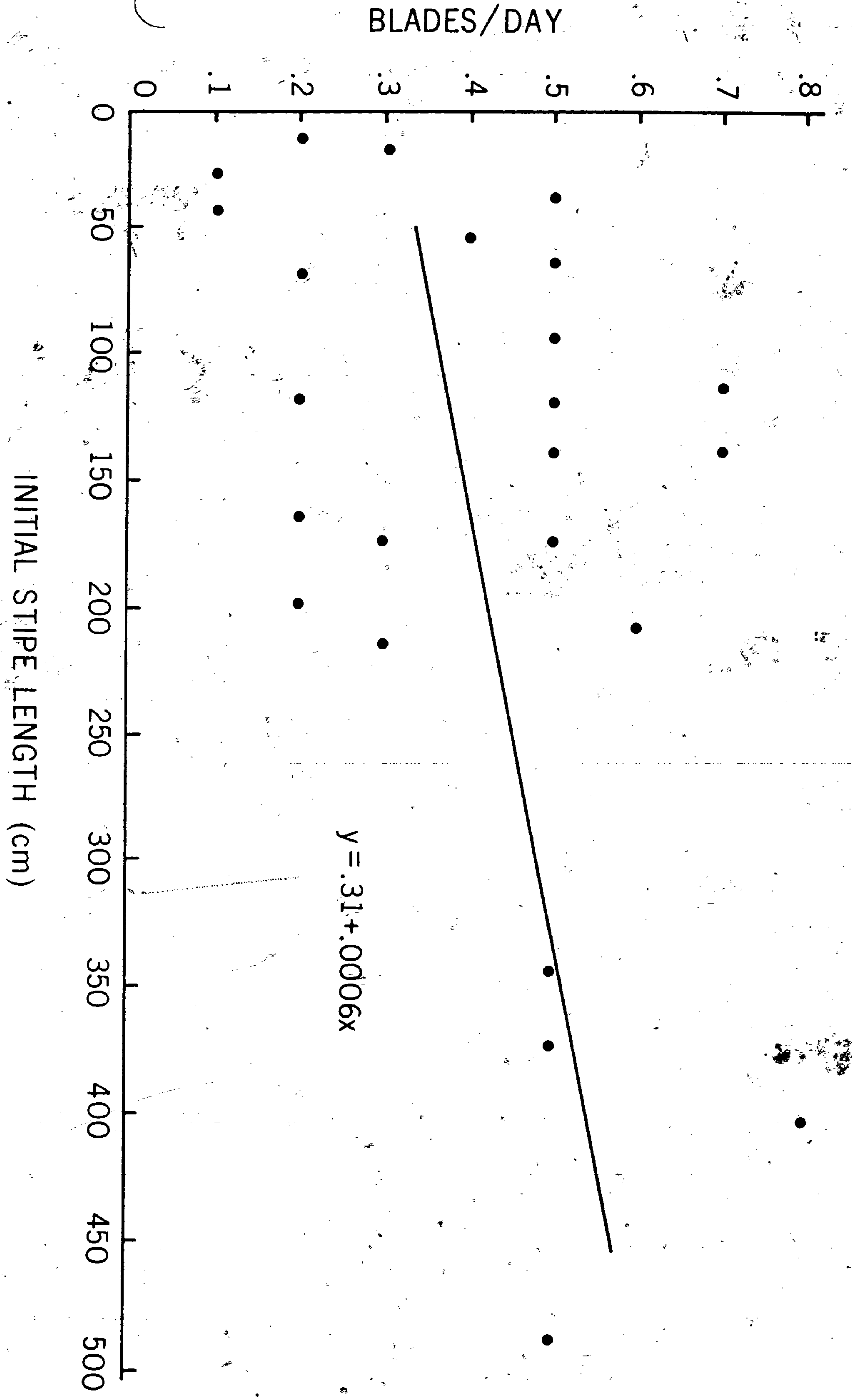

NUMBER OF BLADES
5
15
25
35
45
55
65
75
100
200
300
400
500
600
STIPE LENGTH (cm)
y=13.8+.095x

Figure 5 Variation in the rate of blade addition with the stipe length of 26 fronds measured over 30 day periods in August and September in the Ross Islet Plateau Kelp bed. The formula describes the line through the points


BLADES/DAY
0
.1
.2
.3
.4
.5
.6
.7
.8
INITIAL STIPE LENGTH (cm)
0
50
100
150
200
250
300
350
400
450
500
y=.31+.0006x

Lamina Length and Width Increment, Duration and Pattern of Growth

The results of the two approaches to the problem of frowth duration replicate one another to some extent but illustrate clearly the interrelationship of blade position on the stipe and the growth activity of the lamina.

The more basal a blade's position on the stipe the slower was the rate of lamina elongation (Fig. 6). After 22 days there was no lamina elongation on any of the tagged blades. Assuming a blade addition rate of 0.4 blades per day; at seven days following the initial measurement at least 2 blades were added above the tagged blade. The diameter of the punched holes also showed dramatic differences in the growth of adjacent lamina (Fig. 7).

Holes punched near the meristematic region of the first independent blades ceased distal movement between 21 and 24 days (Fig. 8). The mean rate of elongation was 1.9 SD ± 1.5 cm per day over 22 days. The changes in the rate of hole movement over time can be related to the lamina growth pattern measurements.

The pattern of growth in length along the lamina was slow in the meristematic region and increased toward the middle region of the lamina (Fig. 9). Only one lamina was initially punched beyond 22 cm; (at 29.5 cm) its distal movement relative to the base was less than 1 cm per day. This single measurement suggests a trend to the cessation of growth in the distal region of the lamina as shown in the previous elongation data. The overall rate of elongation was 1.9 SD ± .9 cm/day.

Figure 6 Variation in the distal movement of holes punched in the lamina with initial blade position on five fronds over a 7 day period in August at Ross Islets Plateau kelp bed. The most apical blade is the first independent blade. The distal movement of punched holes is interpreted as the minimum rate of lamina elongation

Vertical lines	range cm/day
Horizontal lines	mean cm/day
Rectangle, vertical axis	SD cm/day

N = 5 per blade position

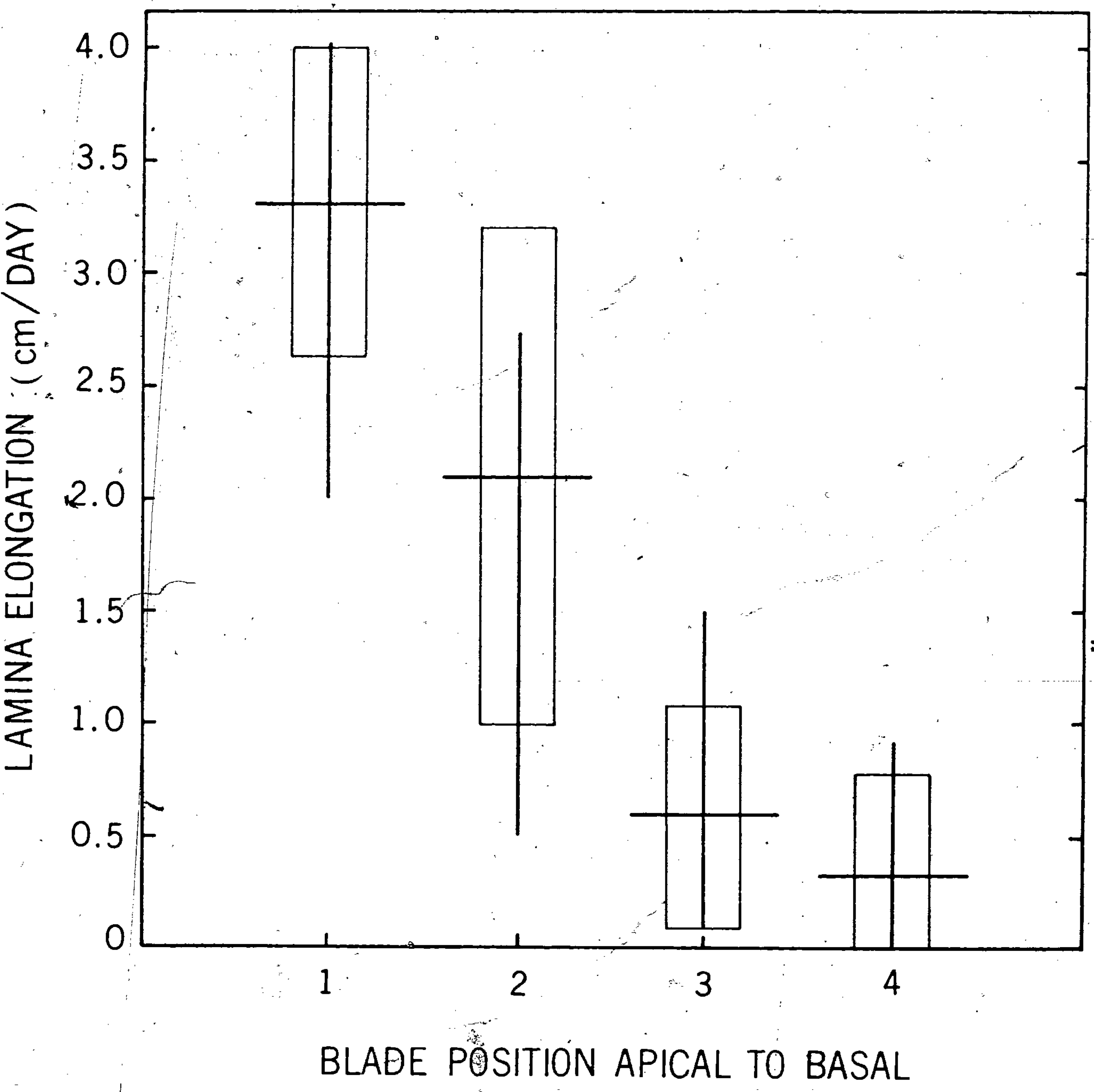
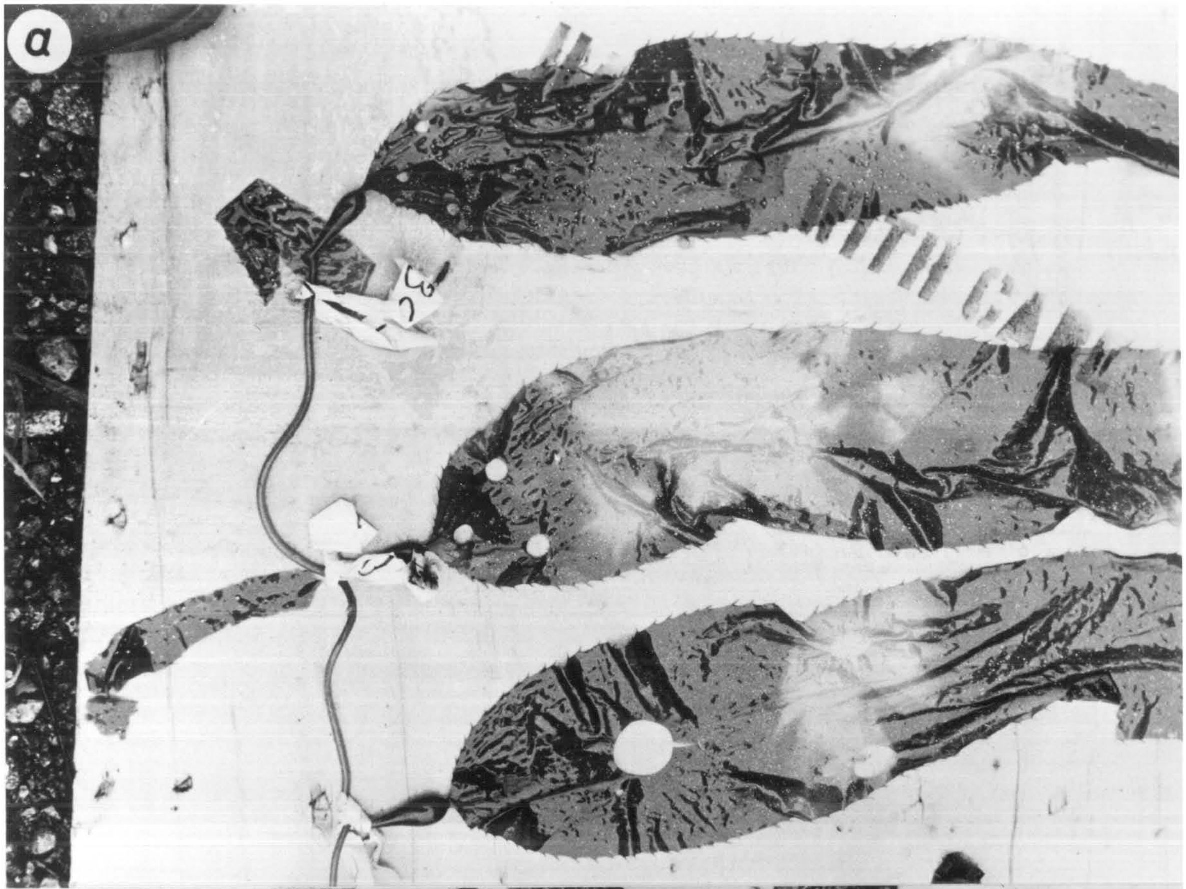

LAMINA ELONGATION (cm/DAY)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
1
2
3
4
BLADE POSITION APICAL TO BASAL

Figure 7 The relative growth of 1 cm diameter holes punched in the laminae of adjacent blades over 22 days.

a. The most apical blade is the lower blade in this figure

b. The most apical blade is the blade on the right in this figure


a
3C

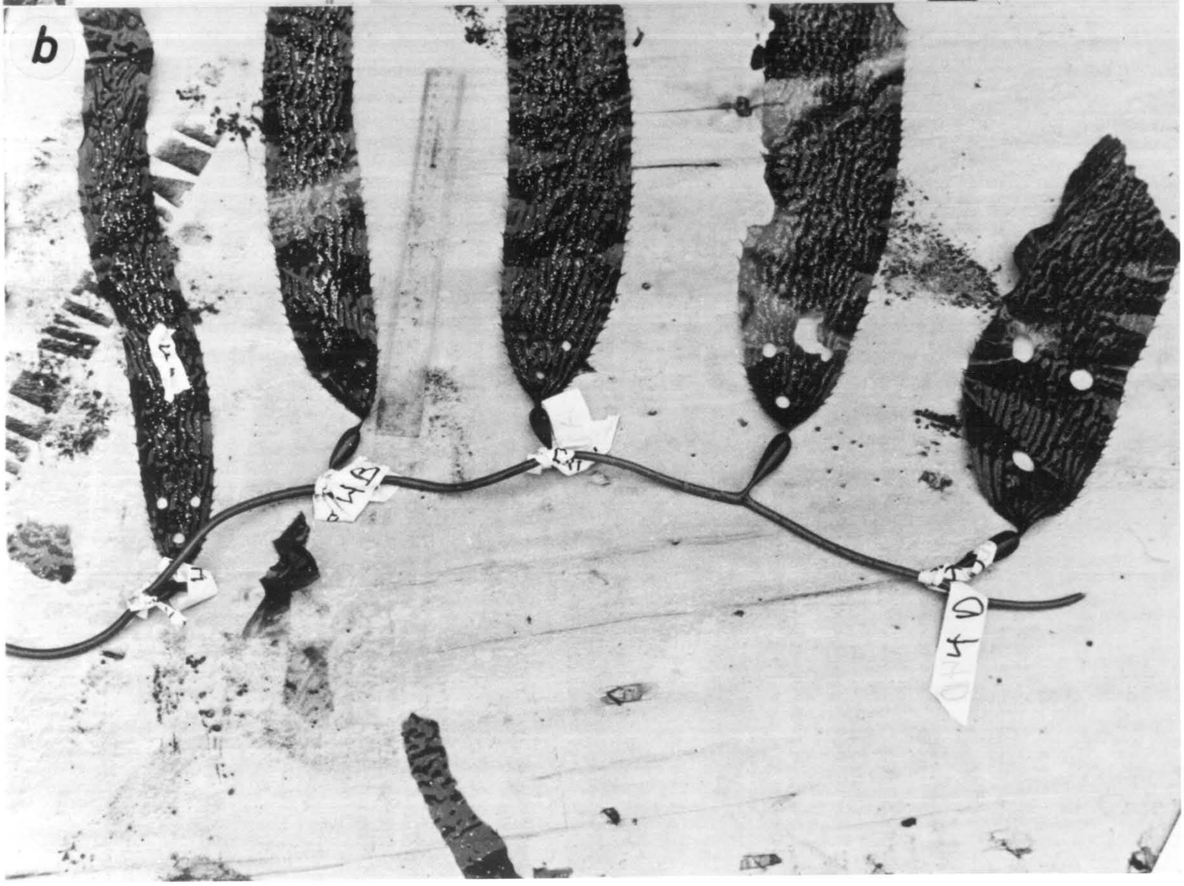

b
WB
4D

Figure 8 The distal rate of movement of holes punched in the laminae of the first independent blades with 4 - 8 day intervals from first measurement. Distal movement of basal holes was interpreted as the minimum rate of lamina elongation

time period	N
0 - 4	16
4 - 8	13
8 - 14	11
14 - 22	8
22 - 24	8

vertical lines	range in cm/day
horizontal lines	mean in cm/day
rectangle vertical axis	SD in cm/day

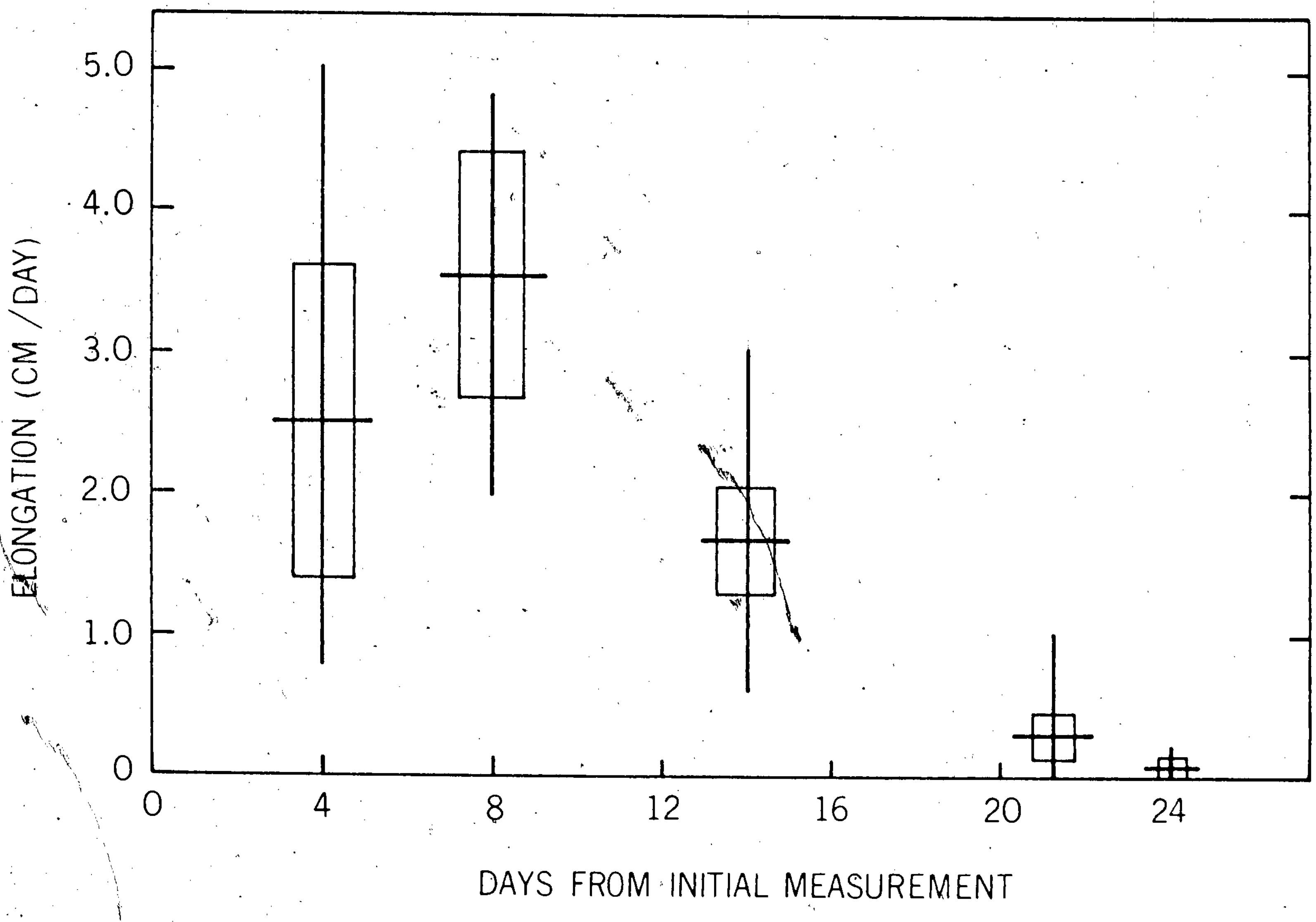
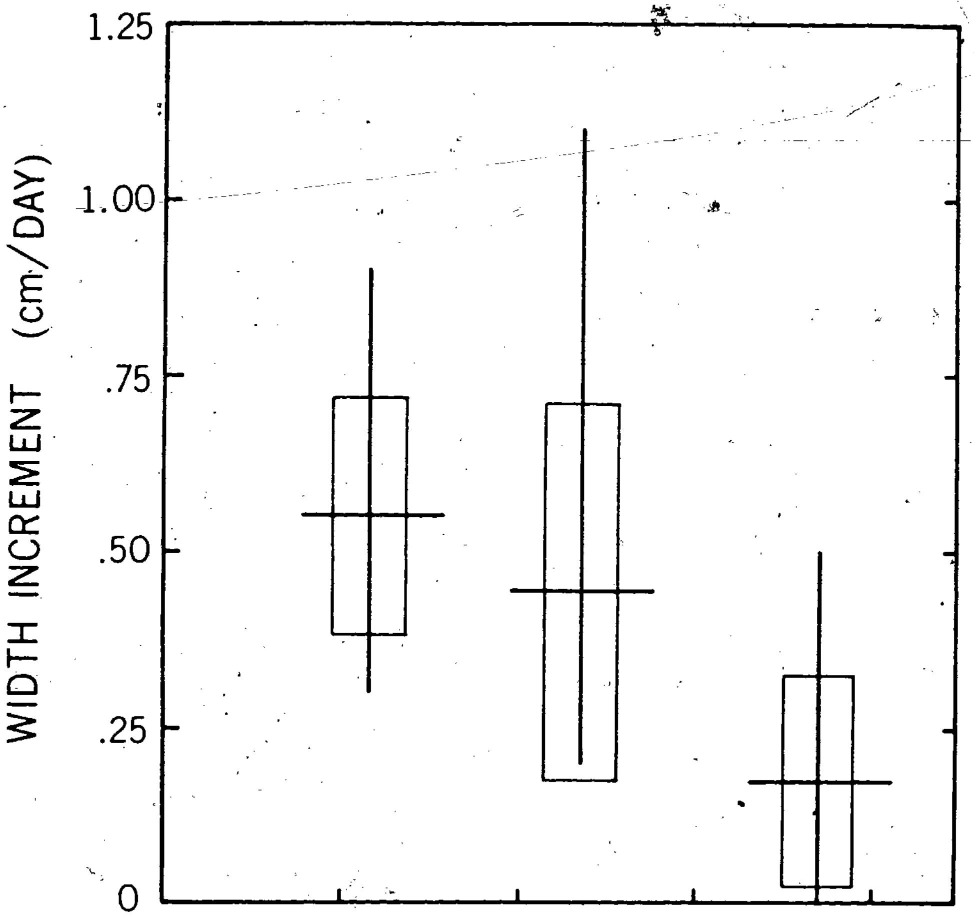

ELONGATION (CM / DAY)
0
1.0
2.0
3.0
4.0
5.0
DAYS FROM INITIAL MEASUREMENT
0
4
8
12
16
20
24

Figure 9 Variation in the rate of hole movement (elongation and widening of the laminae) with the position of the hole from the base of the lamina over a 5 day period, on the laminae of the first independent blades of 16 fronds.

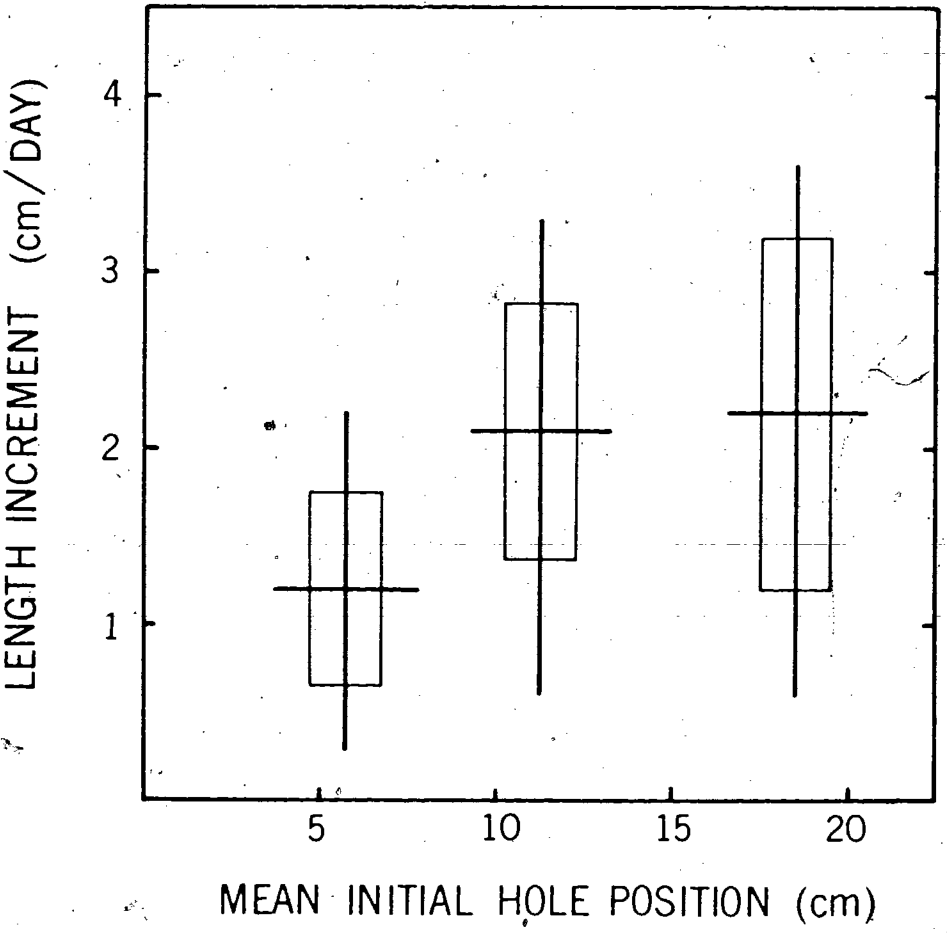
a. widening of the laminae

b. elongation of the laminae

vertical lines	range in cm/day
horizontal lines	mean in cm/day
vertical axis, rectangle	SD cm/day


WIDTH INCREMENT (cm/DAY)
1.25
1.00
.75
.50
.25
0

a.


LENGTH INCREMENT (cm/DAY)
4
3
2
1
5
10
15
20
MEAN INITIAL HOLE POSITION (cm)

b.

The movement of opposite holes away from each other decreases as the holes move toward the distal end of the lamina (Fig. 9). However, to translate the movement of punched holes into actual width increments of the lamina, I assumed the lamina to be a moving belt of tissue. Therefore the mean rate of width increment of 0.43 SD ± 0.3 cm/day was applied over the total linear growth period of the laminae.

From the preceding growth studies I concluded there are three types of laminae on a frond at the beginning of any measurement period exceeding 22 days.

1. The lamina which has grown for part of the 22 days growth period and will cease growth before 22 days.
2. The laminae added during the measurement period and will complete their growth before the end of the calculation period.
3. The laminae that are formed less than 22 days from the termination of the calculation period and will not cease growth before the end of the calculation period. The following formula includes formulae to calculate the total area increment (A) of all 3 previous categories of laminae:

$$
\begin{aligned}
A = S\,(\quad & (La \times 1.9) \quad (La \times .4) + Lc\,(364) \\
& + S \quad (Lb \times 1.9) \quad (Lb \times .4)\ ) \qquad (1)
\end{aligned}
$$

Where S is the sum of laminae area increment for each blade position from 1 thru 9 and 364 is the total area increment for a lamina over 22 days cm^2. La is the duration of lamina growth for a blade present at the beginning of the study period.

$$La = 22 - (Ba \times 2.5) \qquad (2)$$

Where Ba is the blade position relative to the apical scimitar and 1 blade is formed every 2.5 days. Lb is the duration of lamina growth for a blade formed during the calculation period but without a complete growth period.

$Lb = 22 - (Bd \times 2.5)$ (3)

Where Bd is the blade position relative to the last blade with a complete growth period. Lc is the number of laminae growing for 22 days in the calculation period.

$Lc = (T - 22)/2.5$ (4)

Where T is the calculation period.

Biomass Per Unit Area of Lamina

The fresh weight of lamina tissue (gm/cm^2) increased toward the basal region of the frond (Fig. 10). The mean fresh weight of sporophyll tissue was significantly greater than for all other laminae. The variation and range of values were extreme for the sporophylls (Fig. 10). The mean area of the first independent lamina obtained from tracings used for the calculation of lamina weight (N = 10) was 414 SD ± 199 cm^2. The mean area of all independent lamina (N = 45) on the collected fronds was 660 SD ± 116 cm^2.

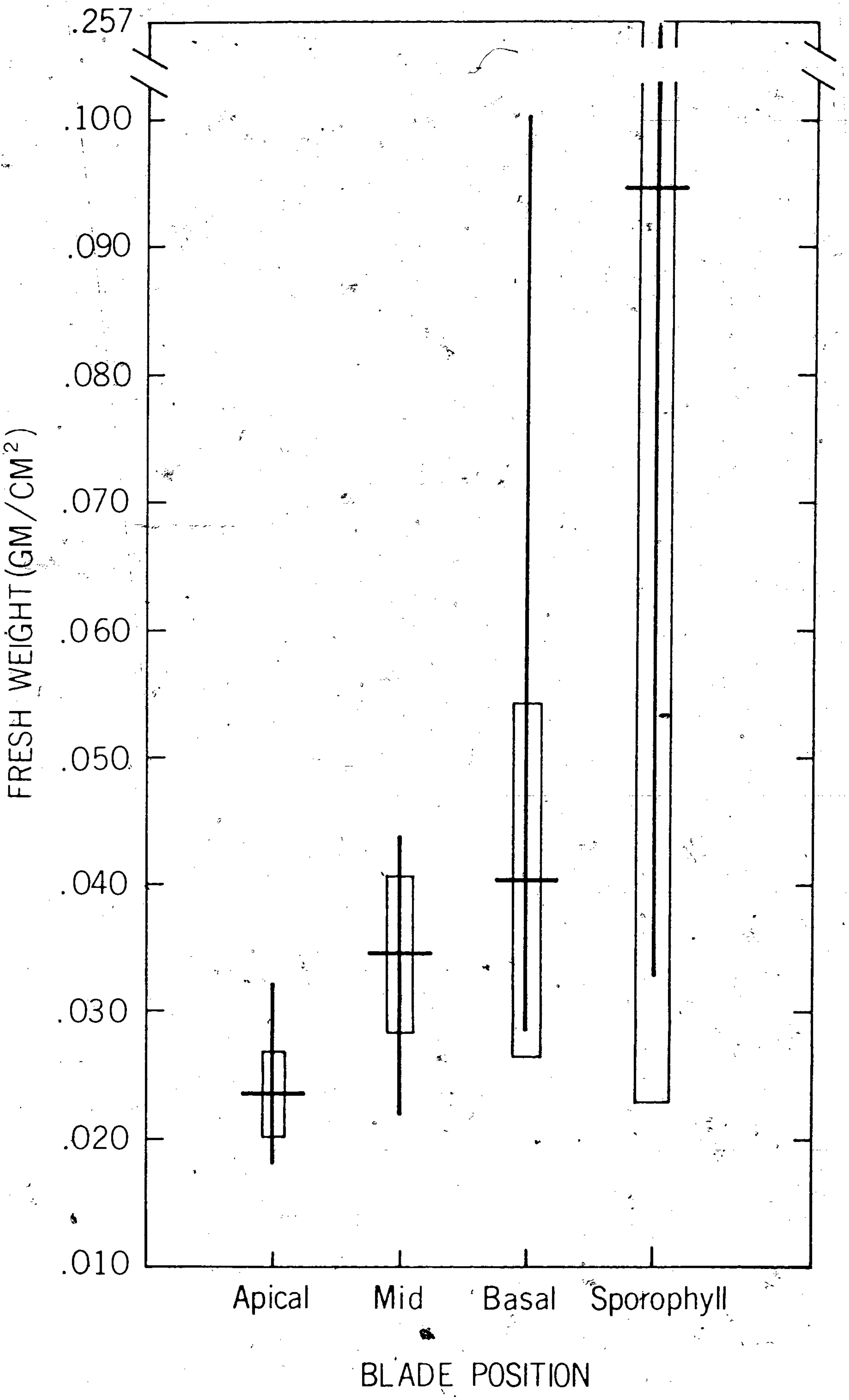
DISCUSSION

The two types of *M. integrifolia* encountered in the distributional survey may be accounted for by the tendency of the plant to develop larger laminae in sheltered areas (Pace, 1972). The laminae reach a weight

Figure 10 Variation in the fresh weight of *M. integrifolia* laminae with their position on the frond

vertical lines	range	gm/cm square
horizontal lines	mean	gm/cm square
rectangle, vertical axis	SD	gm/cm square

lamina position	N
apical	36
mid	21
basal	24
sporophyll	10


.257
.100
.090
.080
.070
.060
.050
.040
.030
.020
.010
FRESH WEIGHT (GM/CM^2)
Apical
Mid
Basal
Sporophyll
BLADE POSITION

which cannot be floated by the pneumatocysts and drag the frond downward. The observations on phenology, also vertical and horizontal distribution are presented with the description of herbivore distribution.

The growth of M. integrifolia laminae is a moving belt of tissue as with Laminaria laminae Mann (1972b). However, it is very different from Laminaria because instead of a single lamina growing continuously, laminae area growth is determinate, ceasing within approximately 20 days and frond growth continues with a more recent lamina (more apical laminae). That is, the whole frond acts as a belt of blades which are individually growing for a limited period.

Variation in the growth rate of fronds in terms of elongation of the stipe and blade addition for a given frond size will be discussed in two aspects relevant to the study period. First is the importance of translocation and the condition of other fronds on the plant. It has been shown that old M. integrifolia fronds translocate nutritive material to young fronds less than a meter in length (Lobban, pers. comm.). The loss of the primary apical scimitar appears to increase the transport of translocate to secondary fronds on the plant. Therefore, we could expect significantly different growth rates for a given frond size depending on the condition of its associated fronds.

Secondly, within a given kelp bed there are physical gradients which may influence the growth rate of fronds. For example, depth has been correlated with the frond weight of M. pyrifera (North, 1971).

In the case of M. integrifolia this factor may be significant since some of the plants in most M. integrifolia beds are intertidal (Scagel, 1947).

The morphological variation of wave-sheltered and wave-exposed fronds suggests that a wave-exposure gradient through a kelp bed may affect growth rates, in particular lamina width (Pace, 1972).

Lamina growth measurements depended on following the movement of holes punched in the laminae. The holes were usually placed near the base of the laminae and I did not measure growth beyond this point except in growth pattern studies. Growth did occur beyond the base, however, the error in the final calculation of area increment appeared to be reduced, because the first independent lamina was split from the apical scimitar due to unpredictable environmental factors such as wave action. As a result of these factors the size and overall growth rate of the first independent lamina was highly variable. Calculated from the movement of holes the total area increment was 364 SD ± 167 cm^2. This value was well within area increment measured from laminae tracing from the first independent lamina to the most basal laminae.

The cessation of growth or growth at a low uniform rate in lamina area was suggested by the relative size of laminae on the frond. Laminae reached a maximum area near the mid region of the frond and frequently were smaller in the basal region. This pattern was observed in *M. pyrifera* fronds by Sargent and Lantrip (1952). Aleem (1973), following hole movement to measure growth of *M. pyrifera* found laminae ceased growth after 4 to 6 days, in which time they were approximately 2 meters from the apical scimitar. Thickness was not included in these measurements but increasing weight per unit area of lamina toward the base of the frond suggests the meristoderm is actively adding tissue after surface area growth ceases.

In M. integrifolia the weight of tissue per unit could be an important factor in the strength of the lamina and in the survival of laminae. Sporophylls have a significantly higher weight per unit area than adjacent laminae and were observed to persist long after more apical laminae were lost. The mechanical strength of the heavier sporophyll tissue could be a deterrent to herbivore damage and erosion.

HERBIVORES

METHODS

A series of field studies were conducted on the distribution of *T. pulligo* in the southeast area of Barkley Sound. A number of problems were encountered in these surveys. Underwater observations were often limited by poor visibility. The snail presented problems due to its small size and cryptic colouration. The high-relief of the substrate and the large undulating surface of *M. integrifolia* created problems locating the snail.

General Distribution of *T. pulligo* in Southeast Barkley Sound

Seven sites were selected with a range of wave exposure (Table II, Fig. 11). These sites were surveyed using a compass transect perpendicular to the shoreline. A 1 m quadrat was laid every other meter along a weighted line. Plant cover, substrate type and herbivores within each quadrat were assessed on each transect. The end of each transect was determined by the lower limit of the sea urchin *Strongylocentrotus franciscanus* (A. Agassiz). The depth was recorded with a calibrated diver's depth gauge to .25 m. All data were transmitted to a surface tape recorder with a Sub-Com underwater communication system (Sub-Com System Ltd., North Vancouver, Canada). An additional two sites were surveyed using random quadrat placement.

TABLE II

Location and Wave Exposure of Temporary Transects in the General Survey of *T. pulligo* Distribution shown on Figure Number 11

Chart Number	Location	Date	Latitude Longitude	Open[a] Angle Degrees	Fetch[b] Min.	Km. Max	Exposure Index	M.i.[d]
1	Flemming I.	11/3/73	48°53 00 N 125°08 24 W	125°	13.7	2.6	M.S.[c]	-
2	Scott's Bay	21/3/73	48°50 06 N 125°08 54 W	175°	un-limited	2.6	E	-
3	Kelp Bay	12/3/73	48°51 18 N 125°06 30 W	90°	16.1	4.8	M.S. S.	+
4	Helby I.	9/3/73	48°51 24 N 125°09 54 W	180°	16.9	1.6	M.E.	+
5	Swiss Boy I.	23/3/73	48°55 00 N 125°07 48 W	180°	un-limited	1.2	E.	-
6	Grappler Mouth	20/4/73	48°50 30 N 125°08 00 W	110°	16.1	2.9	M.S. S.	+
7	Sanford I.	8/3/73	48°62 00 N 125°09 48 W	180°	un-limited	1.2	M.E.	-
8	Ross Islets	20/4/73	48°52 20 N 125°09 46 W	47°	5.6	.5	S.	+
9	Blue Stone Point	8/10/72	48°49 09 N 125°10 06 W	180°	un-limited	2.6	E.	-

[a] Open Angle - angle through which waves can travel unrestricted

[b] Fetch - maximum distance for unrestricted wave travel

[c] M.S. - moderately sheltered, M.E. - moderately exposed

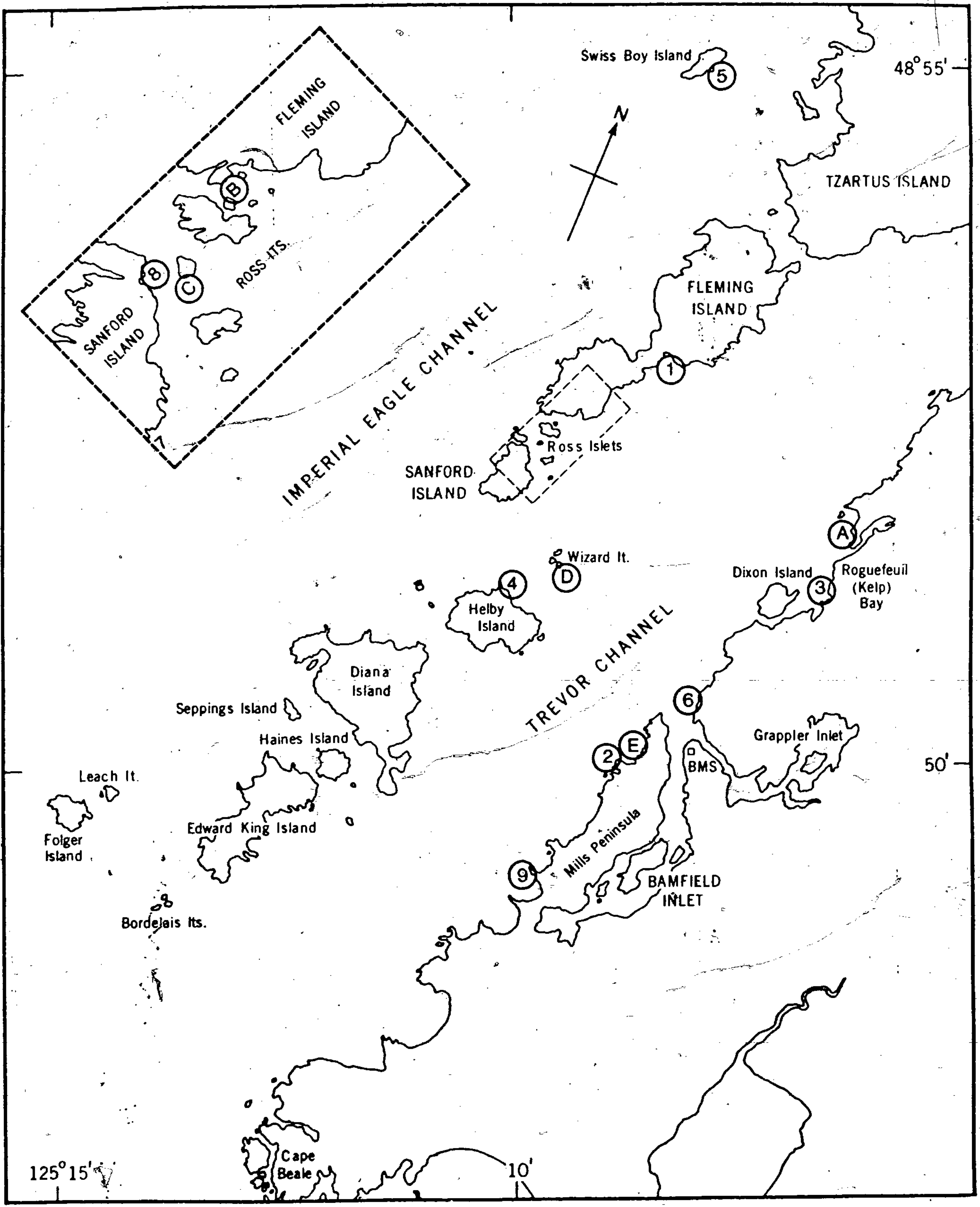
[d] *Macrocystis integrifolia*

Figure 11 Locations of study sites in Southeast Barkley Sound, Vancouver Island

numerals	Temporary survey sites
letters	Permanent transect sites and the detailed study site
BMS	Bamfield Marine Station
scale	1 cm = 1.2 km

From chart 3637 Barkley Sound

Compass variation 23 degrees 30 min East


Swiss Boy Island
5
48°55'
N
TZARTUS ISLAND
FLEMING ISLAND
B
ROSS ITS.
8
C
SANFORD ISLAND
IMPERIAL EAGLE CHANNEL
FLEMING ISLAND
1
Ross Islets
SANFORD ISLAND
A
Wizard It.
D
4
Dixon Island
3
Roguefeuil (Kelp) Bay
Helby Island
TREVOR CHANNEL
Diana Island
6
Seppings Island
Haines Island
Grappler Inlet
2
E
BMS
50'
Leach It.
Folger Island
Edward King Island
Mills Peninsula
9
BAMFIELD INLET
Bordelais Its.
Cape Beale
125°15'
10'

Seasonal Distribution of *T. pulligo* and Other Herbivores

Permanent transects were constructed at four sites chosen for their diversity of exposure, diversity of kelp bed, substrate type and herbivores (Table III, Fig. 11). Transects were set perpendicular to the shore line beginning at the edge of the intertidal zone (except at Scott's Bay) and ending at least 5 m beyond the outer limit of *M. integrifolia*. A 1/8 inch plastic line was tied to 3/8 inch rock bolts driven into bedrock or boulders. The line was used as a quide only, and on each survey a plastic surveyors chain (metric) was strung between the pins. A 0.5 m^2 quadrat was placed at 2 or 4 m intervals along the chain and plant cover, substrate type and herbivore concentrations were recorded.

At Scott's Bay the density of the kelp bed prevented the use of a quadrat. Instead, a line encounter method was used. The herbivores were counted on each plant that touched the line. Transect surveys all began in September 1972, but the Scott's Bay transect was abandoned in mid-winter, 1972, because large plants were drifting free in tangled masses along the transect. The data for the Wizard Islet transect were incomplete due to the difficulty of maintaining a transect line. The China Hat Pass and Kelp Bay transects were surveyed successfully each month from September 1972 to September 1973 excepting December 1972 and August 1973. During all surveys qualitative observations were made on the distribution and behaviour of *T. pulligo*.

TABLE III

Location and Wave Exposure of Permanent Transects and Detailed Study Site Shown on Figure 11

Chart Letter	Location	Latitude Longitude	Open Angle Degrees	Fetch Km		Exposure Index	*M. integrifolia*
				Min.	Max.		
A	Kelp Bay	48° 50 36 N 125° 06 12 W	105°	19.4	4.0	M.E.[a]	+
B	China Hat Pass	48° 52 33 N 125° 09 24 W	60°	13.0	4.2	M.S.	+
C	Ross Islet Plateau	48° 52 24 N 125° 09 36 W	80	13.7	4.0	M.S.	+
D	Wizard Islet	48° 51 27 N 125° 09 36 W	115°	4.4	2.1	M.E.	+
E	Scott's Bay	48° 50 09 N 125° 08 36 W	120°	12.3	1.8	M.S.- M.E.	+

[a] M.E. - moderately exposed; M.S. - moderately sheltered

The Population Structure of T. pulligo

In areas near the permanent transects, collections of T. pulligo were made from two distinct regions. One collection of 20-50 individuals from on or beneath M. integrifolia, and one collection from the substrate outside the beds were made after each month's transect survey. Degeneration of the kelp bed in the winter prevented successive collections from M. integrifolia. At China Hat Pass the sampling procedure for substrate collections was changed from a substrate surface collection to a complete removal of the upper 5 cm of the substrate, because I noticed individuals less than 10 mm basal diameter were absent in the previous samples.

The final collection at Kelp Bay was to distinguish the size of individuals upon the rocks and shell sand which had previously been grouped as a cobble collection. The basal diameter of each snail was measured to 0.1 mm with vernier calipers.

Motility

In all motility experiments T. pulligo was tagged by the following method. A portion of the shell spire was scraped clean of encrustation. A drop of non-toxic epoxy (Sea Go-In Poxy Putty, Permalite Plastics, Costa Mesa, Cal., U.S.A.) was placed on the clean area and a piece of labeled plastic tape was pressed into the epoxy (Rosenthall, 1969). Care was taken to prevent the loss of the label while the epoxy set. The specimens were held in running seawater prior to replacement in the field.

Motility and Substrate Preference of Tagged T. pulligo

The purpose of this experiment was to study the movement and substrate preference of *T. pulligo* in the kelp bed.

Tegula pulligo were collected from three distinct and adjacent areas: shell sand, bedrock and on or beneath *M. integrifolia* at the Ross Islets kelp bed. Each of the 138 animals was coded for individual identification and its substrate origin, then the basal diameter was measured to 0.1 mm. The collections from shell sand and *M. integrifolia* were switched when replaced in the field, and the bedrock collection was the control. Each collection was deposited in a permanent 0.5 m quadrat. A search was made within a 15 m radius for 0.5 hr at 3, 13, 30 and 48 days after replacement. The numbers within the deposit quadrats, distance from point of replacement and numbers of each type of substrate were noted using underwater writing slates.

Motility of Tagged T. pulligo on M. integrifolia

An isolated plant at the end of the Scott's Bay permanent transect was stripped of all *T. pulligo*. Twenty-nine snails were measured for basal diameter, tagged, then returned to the holdfast region. The plant was examined for the presence of tagged and untagged individuals at 5, 10, 15 and 88 days after deposition.

Kelp Bay Infestation Experiment

This experiment tested the rate of recruitment of *T. pulligo* to *M. integrifolia* in areas devoid of *M. integrifolia*. Two fronds 1.5 m long were attached to stones with rubber bands. One frond was placed in an area of cobble substrate adjacent to the permanent transect at Kelp Bay. The second frond was set 15 m from the first frond at the seaward end of the transect. I counted the number of herbivores on the fronds and noted the grazing damage after 2 and 4 days in June, 1972.

Motility as Related to Water Movement

To determine if *T. pulligo* motility was affected by water movement tidal current measurements were made inside and outside the Wizard Islet kelp bed using a Dumas Neypric current meter (Neypric, Grenoble, France). Qualitative observations were made of the *T. pulligo*'s position on *M. integrifolia* during the periods of maximum tidal flow and strong wave action.

Feeding Behaviour

Two general types of feeding experiments were conducted in the laboratory. The first type of experiment followed the fresh weight-loss method described by Leighton (1966). The procedure was to allow a conditioning period of one week. Snails were then subjected to a non-feeding period prior to the experiment. The fresh weight of algal pieces was determined to 0.01 gm and then the algae were placed in the holding containers. Leighton was dealing with subjects exceeding 50 gm body weight and used 1 or 2 individuals in 6 separate experiments. Since *T. pulligo* rarely exceeded 4 gm body weight, I put a minimum of 10 snails per container and 4 containers per experiment. Not all tissue which was lost from the algal pieces was due to consumption by *T. pulligo*. Fresh weight of all algal pieces greater than 1 cm in any dimension was weighed at the end of the experiment. A significant number of fragments were less than 1 cm.

The second type of feeding experiments was designed to eliminate this incidental tissue loss. These experiments followed the previous procedures except the lamina sections were glued to disposible petri dishes (100 mm diameter) with an organic glue Sico - Met (Sicdhel-Werke, GMBH, Hannover, Germany) (Fig. 12). This design significantly reduced tissue loss incidental with grazing and allowed weighing to 0.001 gm. Therefore, this method more accurately measured the actual consumption of algal tissue. The first day's results were left out of the final calculation of a mean feeding rate.

Feeding Experiment to Test Feeding Rates with Two Species of Algae

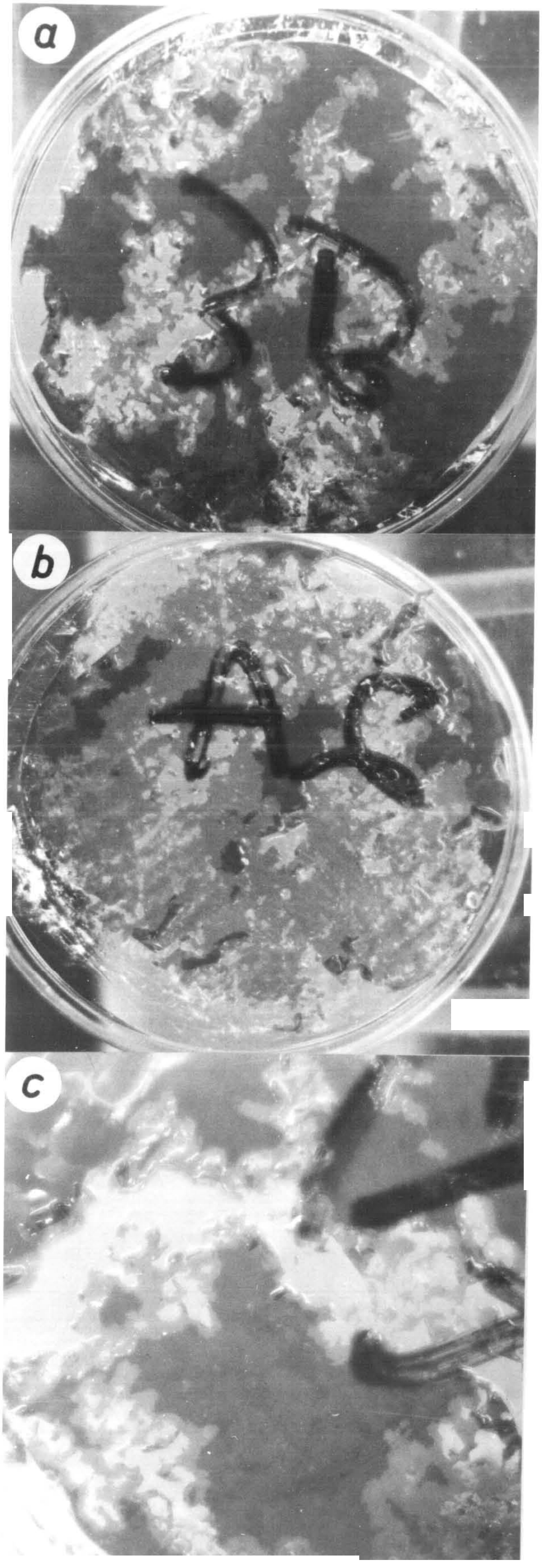
Tegula pulligo was observed to occur upon *Pterygophora californica* Ruprecht which was often situated near *M. integrifolia*. To test the feeding rate of *T. pulligo* on both species a laboratory experiment was performed in November, 1971. This experiment was conducted in a recycling seawater system using 5, 1 litre plastic beakers. These had holes covered with a plastic screening to allow for water circulation. *Tegula pulligo* collected from both algae were shipped in coolers to Vancouver. Groups of 10 snails ranging from 17 mm to 25 mm basal diameter were placed in each of 4 beakers and immersed in 10° C water, plant tissue alone in the fifth beaker was the control. Both species of algae were placed in equal weights in each

Figure 12 Petri dish lids (100 mm diamter) with *M. integrifolia* laminae glued to their surface

a. The result of 2 days of grazing by *T. pulligo*

b. The result of 3 days of grazing by *T. pulligo*

c. A 3X view of *T. pulligo* grazing damage


a
3B
b
A2
c

beaker. After two days without food, approximately 10 gm of P. californica and 10 gm of M. integrifolia were put into each beaker. The algal sections were weighed on a Mettler balance, Model 415 to 0.01 gm and at 0, 24 and 48 hours. Algal fragments less than 1 cm in any dimension were not recovered for weighing.

Diurnal Feeding Experiment

Tegula pulligo was observed on M. integrifolia during both day and night. A feeding experiment was designed to determine if light affected the feeding rate of T. pulligo.

An open seawater system at 8.5° C held 4, 1 litre beakers and 3, 4 litre aquaria. Tegula pulligo was collected in March from M. integrifolia at Wizard Islet, Scott's Bay and the Ross Islets. Fifteen animals in the 18 mm to 21 mm basal diameter size range from each location were placed in the beakers and aquaria. They were subjected to a 12/12 hour photoperiod for a week prior to the non-feeding period and through the experiment. After a 2 day non-feeding period, approximately 10 gm of M. integrifolia lamina was placed in each beaker and approximately 20 gm in each aquarium. At the end of each photoperiod, the algae were collected for weighing and the containers were cleaned once a day. The experiment continued for 4 days.

Long Term Feeding Experiment

The same snails used in the previous diurnal feeding experiment were used in a long term feeding experiment. The experiment followed the diurnal experiment procedure except the light period was 14/10 (day/night) and the weighings were made at 24 hour intervals for 8 days.

Consumption as a Function of Temperature

The procedure involving the gluing of lamina to plastic plates was used to determine the actual consumption of tissue and to compare feeding activity at different temperatures. The temperature was regulated with a refrigerated closed seawater module to within 1° C. All snails were collected at Wizard Islet in October, 1973. Forty-three individuals were placed in each of 4, 4 litre aquaria. The size range of the snails was 17.0 mm to 26.0 nn basal diamter in 3 aquaria and the fourth contained snails from 15.0 mm to 21.0 mm basal diameter. Each experiment began after a holding period of 3 days and a non-feeding period of 2 days and continued for 4 days. The temperatures selected (5°, 10°, 15° C) were within the temperature range in the field. The upper limit was 2° C below the summer maximum and the lower limit was at the extreme winter low (Fig. 13). At the completion of these experiments each group of *T. pulligo* was weighed to 0.5 gm. Algal plates were weighed to .01 gm before and after the 4 day feeding period.

Feeding Frequency

The feeding rates obtained in all grazing experiments were a mean of all the individual feeding rates in each container. However, it was not assumed that all snails were feeding at the same time. To obtain an indication of the number of potential feeding snails the number of

Figure 13 Monthly variation of temperature at one meter (---) and five meters (______) in Bamfield Inlet through 1969-70. (Provided in part by the Bamfield Marine Station). This figure reproduced with the permission of D. Pace

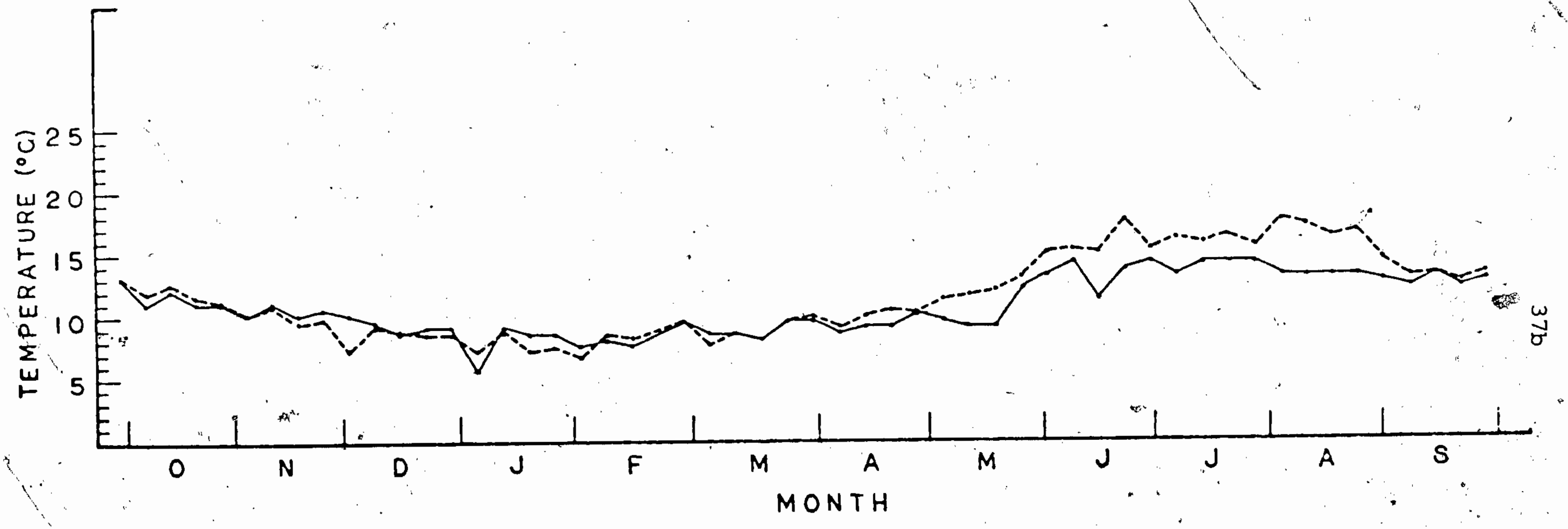

TEMPERATURE (°C)
25
20
15
10
5
O
N
D
J
F
M
A
M
J
J
A
S
MONTH

TABLE IV

Results of the General Survey of *T. pulligo* Distribution in Southeast Barkley Sound

Location	Depth m Below 0 Tide Level		Maximum Numbers/0.5m^2	
	Upper Limit	Lower Limit		
Fleming I.	2.6	7.3	3	*T. pulligo* found upon *Agarum cribrosum* Bory.
Scott's Bay	2.2	7.5	15	Highest density found on shell sand at 10 m.
Kelp Bay	1.4	6.0	1	*M. integrifolia* present to 2.5 m. *A cribrosum* to end of transect at 6 m. Few *T. pulligo* found on these plants.
Helby I.	.35	7.0	60	*T. pulligo* on *Laminaria* sp. Distribution continuous on rock and shell sand.
Swiss Boy I.	2.2	7.0	60	Highest densities on boulder area with encrusting reds.
Grappler Mouth	-	1.5	1	Found only among a narrow band of *M. integrifolia*.
Sanford I.	3.0	-	3	*T. pulligo* occurs after macrophyte cover ends.
Ross I.[a]	.2	-	4	Near transect found high densities (80/m^2) on drift alga.
Blue Stone Point[a]	-	-	5	Found on bedrock substrate with very few macrophytes.

a. Random quadrat survey

individuals upon the algal plates (the plates were 75% of total substrate) during the consumption experiments were counted periodically at 15° C.

RESULTS

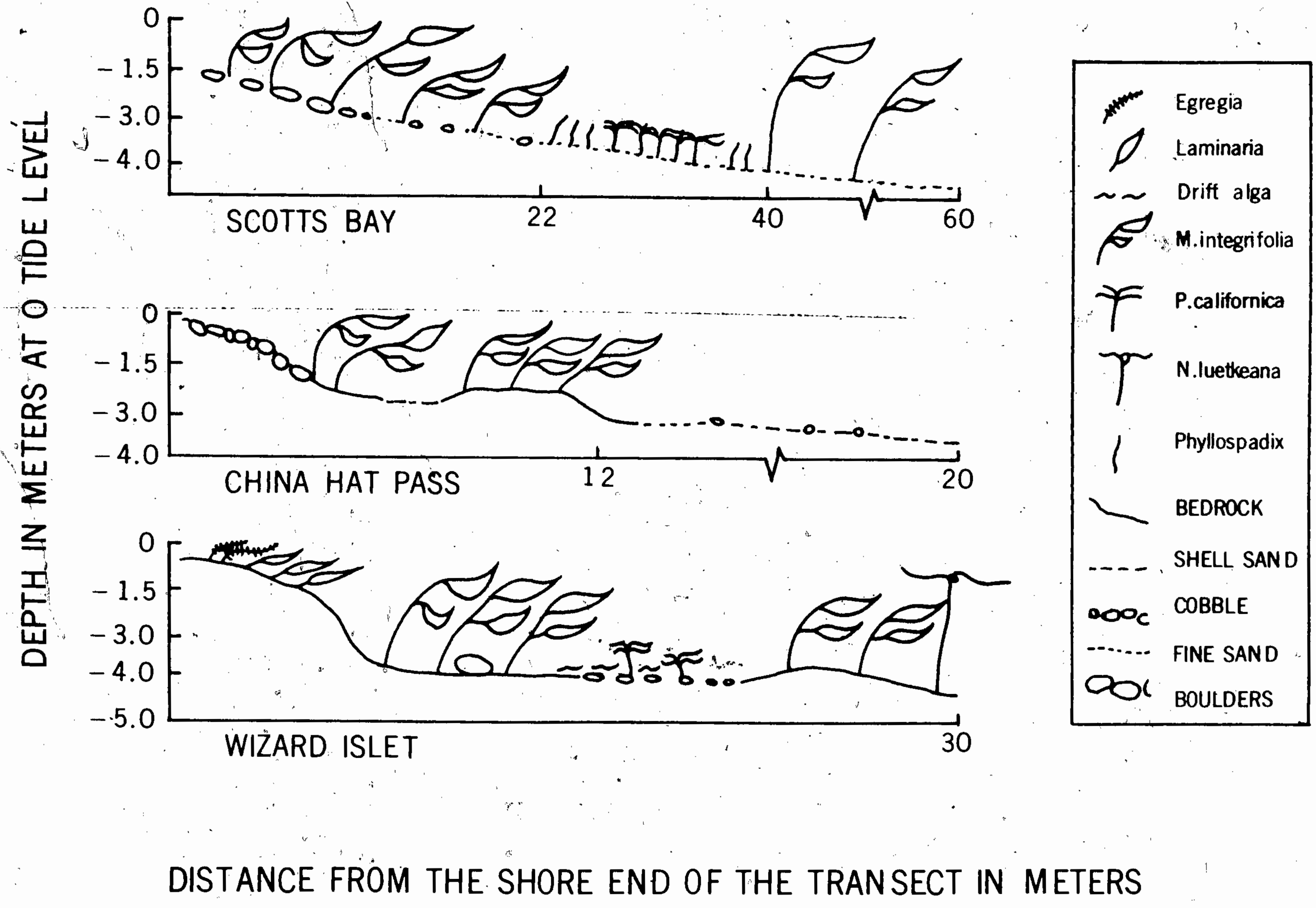
General Distribution of T. pulligo in Southeast Barkley Sound

Tegula pulligo was present at all of the nine survey sites. The exposure and the algal cover of the survey sites did not seem to affect the concentration or occurrence of T. pulligo (Table IV). Tegula pulligo was found on a wide range of substrates, the exceptions were fine sand and silt. The maximum depth of distribution was approximately 10 meters below 0 tide level.

I observed T. pulligo on all frond structures of M. integrifolia except the apical scimitar. The snails were widely distributed on the plant but were most concentrated on the basal laminae. Tegula pulligo was observed on the following macrophytes: Agarum cribosum Bory; Alaria marginata Postels & Ruprecht; Costaria costata (Turner) Saunders; Gigartina Stackhouse, 1890; Laminaria setchelli Silva; Laurencia Lamouroux, 1813; Leathesia diffoemia (Linneaus) Areschoug; Nereocystis luetkeana (Mertens) Postels and Ruprecht; Pterygophora californica Ruprecht; Ulva Linneaus, 1853. Tegula pulligo also tended to clump in areas of drift algae, a concentration of 206 in a 0.5 m^2 area of drift algae was recorded at Wizard Islet.

Figure 14 A schematic profile diagram of the Scott's Bay, China Hat Pass and Wizard Islet permanent transects showing the macrophyte canopy in the summer season

TRANSECT PROFILES MID SUMMER



Seasonal Distribution of T. pulligo and Other Herbivores

On all permanent transects T. pulligo consistently concentrated in one region. At Scott's Bay the area of concentration was on large solitary plants at the outer end of the transect (Fig. 14). A mixed canopy of P. californica and M. integrifolia over a cobble bottom held the highest concentrations of T. pulligo at the Wizard Islet transect (Fig. 14). The maximum concentration of T. pulligo at Kelp Bay was adjacent to the outer limit of M. integrifolia (Fig. 15). There was variation over the observation period at China Hat Pass but when M. integrifolia was present it supported the maximum concentration of T. pulligo (Fig. 14).

Seasonal distribution data was limited to Kelp Bay and China Hat Pass transects. At both sites there was a reduction in macrophyte cover during winter months as in Kelp Bay (Fig. 15). Between monthly surveys the total T. pulligo present in all the quadrats ranged from 36 to 255 at China Hat Pass (Fig. 17). Maximum numbers per square meter were recorded with the degradation of the China Hat Pass kelp bed in the winter (note numbers on M. integrifolia (Fig. 17). At Kelp Bay the band of high T. pulligo concentrations was widest in the fall and early winter months (Fig. 16).

Although the quadrat size used on the surveys of permanent transects was specifically chosen for T. pulligo some trends were observed in the counts of other herbivores.

The combined means of shell diameter from shell sand and M. integrifolia collections of T. pulligo were not significantly different

Figure 15 A schematic profile diagram of the Kelp Bay permanent transect for early fall, winter and early summer showing the macrophyte cover and conspicuous members of the understory

PROFILE KELP BAY TRANSECT

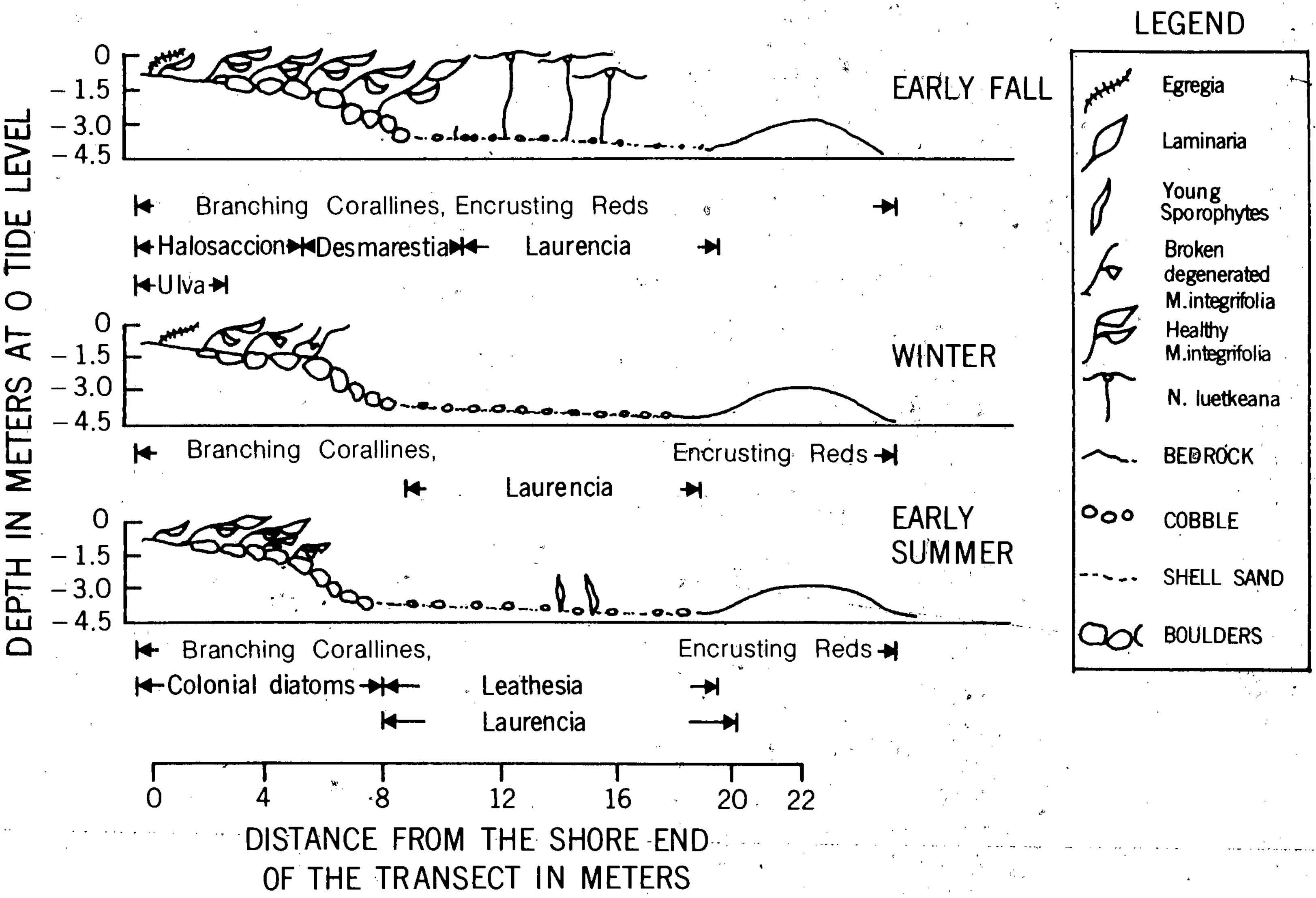


Figure 16 The distribution of T. pulligo on the Kelp Bay transect from September, 1972 to July, 1973

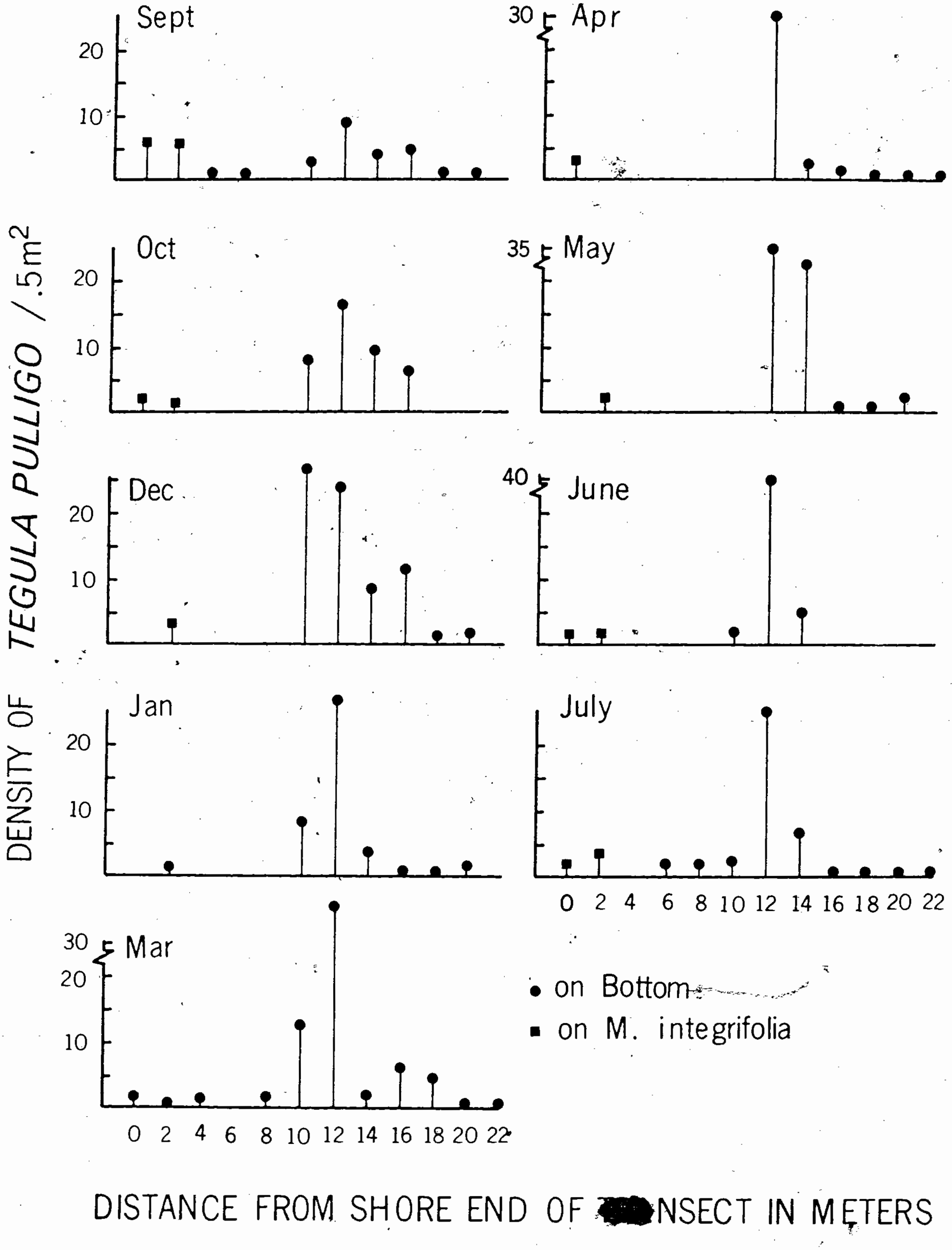

Sept
20
10
Apr
30
Oct
20
10
May
35
Dec
20
10
June
40
Jan
20
10
July
0 2 4 6 8 10 12 14 16 18 20 22
Mar
30
20
10
0 2 4 6 8 10 12 14 16 18 20 22
DENSITY OF TEGULA PULLIGO / .5m²
● on Bottom
■ on M. integrifolia
DISTANCE FROM SHORE END OF [illegible]NSECT IN METERS

Figure 17 The distribution of *T. pulligo* on the China Hat Pass transect from September, 1972 to July, 1973

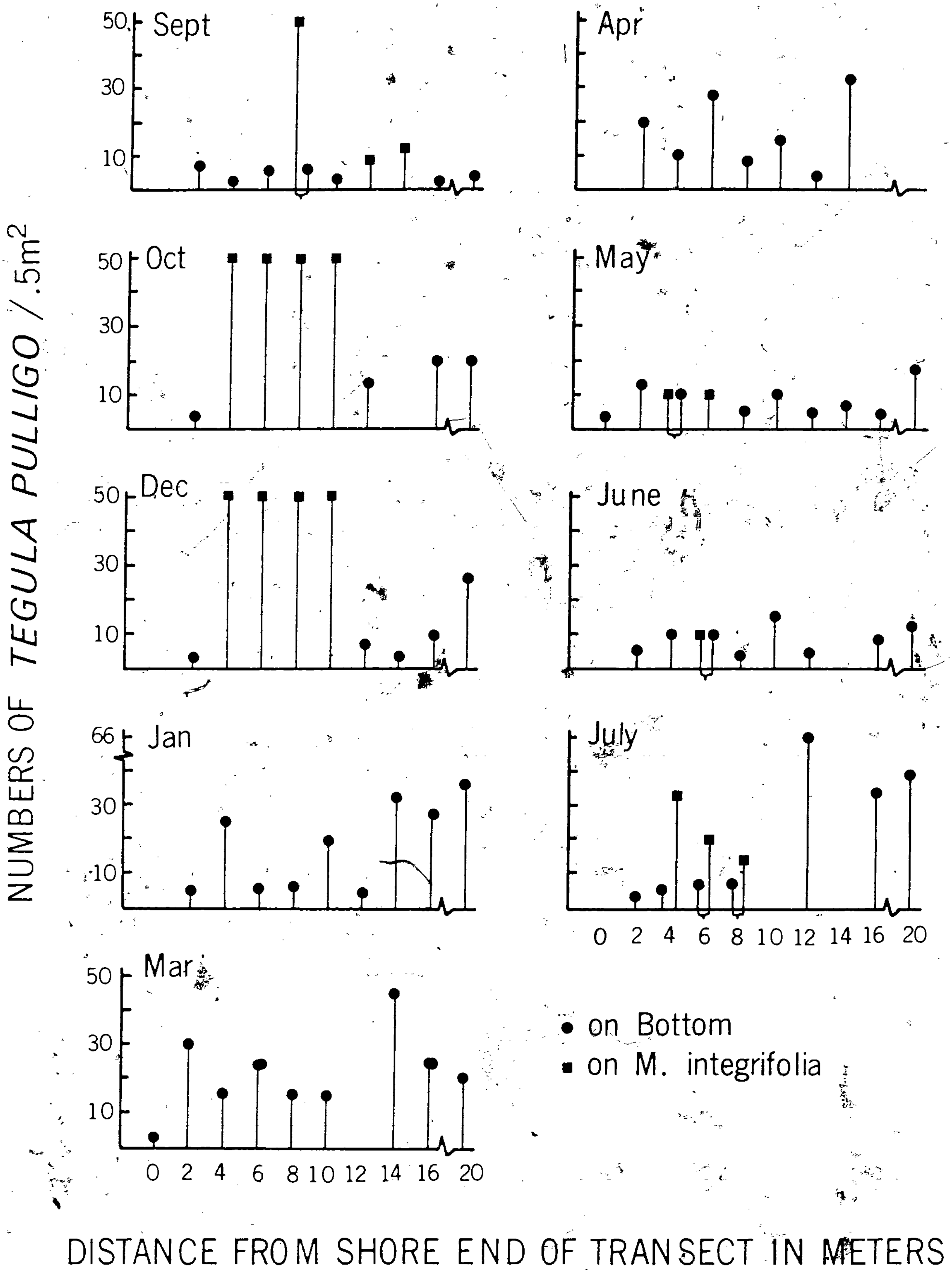
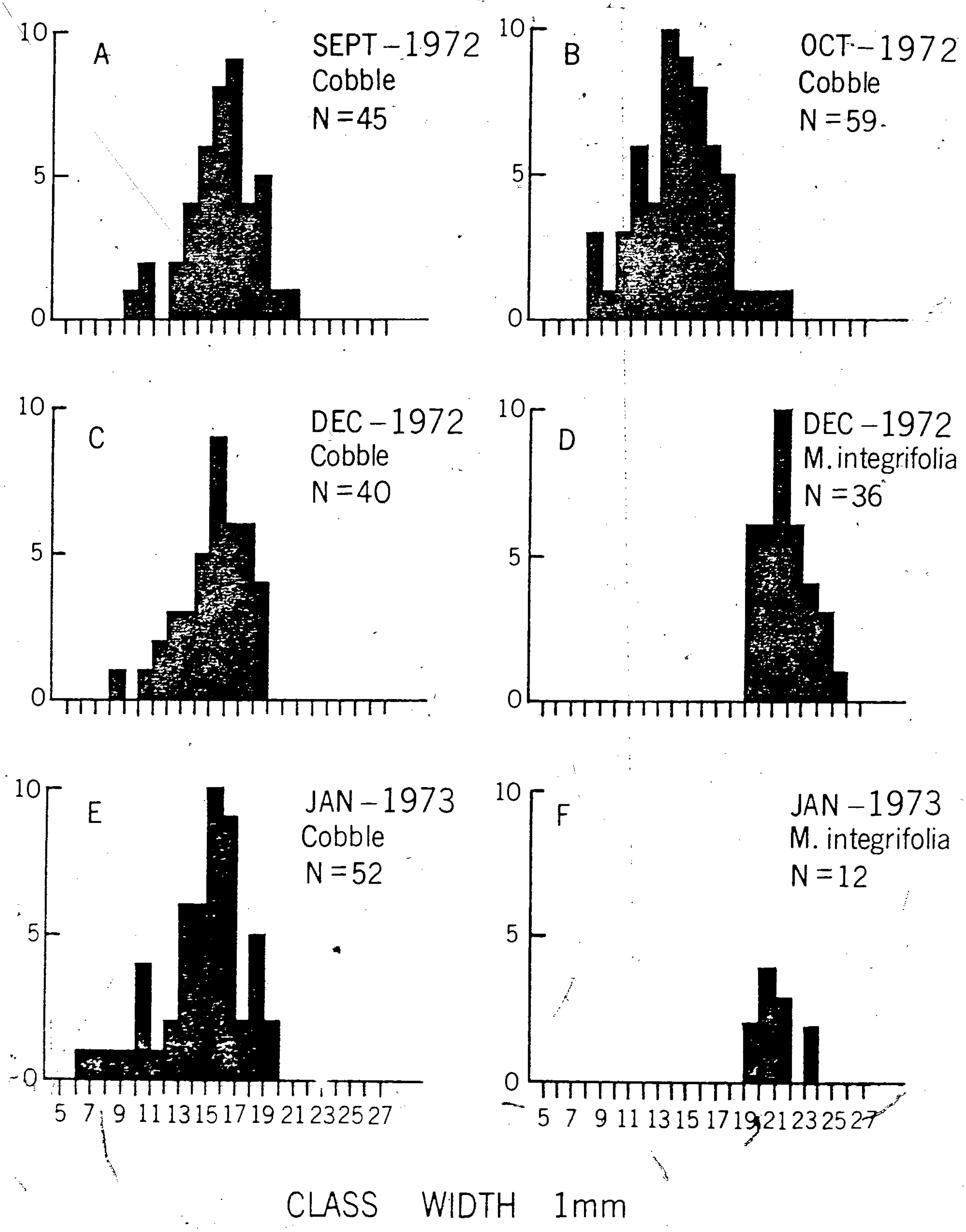

NUMBERS OF *TEGULA PULLIGO* / .5m²
Sept
Oct
Dec
Jan
Mar
Apr
May
June
July
50
30
10
66
0 2 4 6 8 10 12 14 16 20
● on Bottom
■ on M. integrifolia
DISTANCE FROM SHORE END OF TRANSECT IN METERS

Figure 18 A-L Histograms showing the size distribution of *T. pulligo* collected from a cobble substrate and from *M. integrifolia* during 1972 and 1973 at Kelp Bay


A
SEPT – 1972
Cobble
N = 45
B
OCT – 1972
Cobble
N = 59
C
DEC – 1972
Cobble
N = 40
D
DEC – 1972
M. integrifolia
N = 36
E
JAN – 1973
Cobble
N = 52
F
JAN – 1973
M. integrifolia
N = 12
0
5
10
5 7 9 11 13 15 17 19 21 23 25 27
CLASS WIDTH 1mm

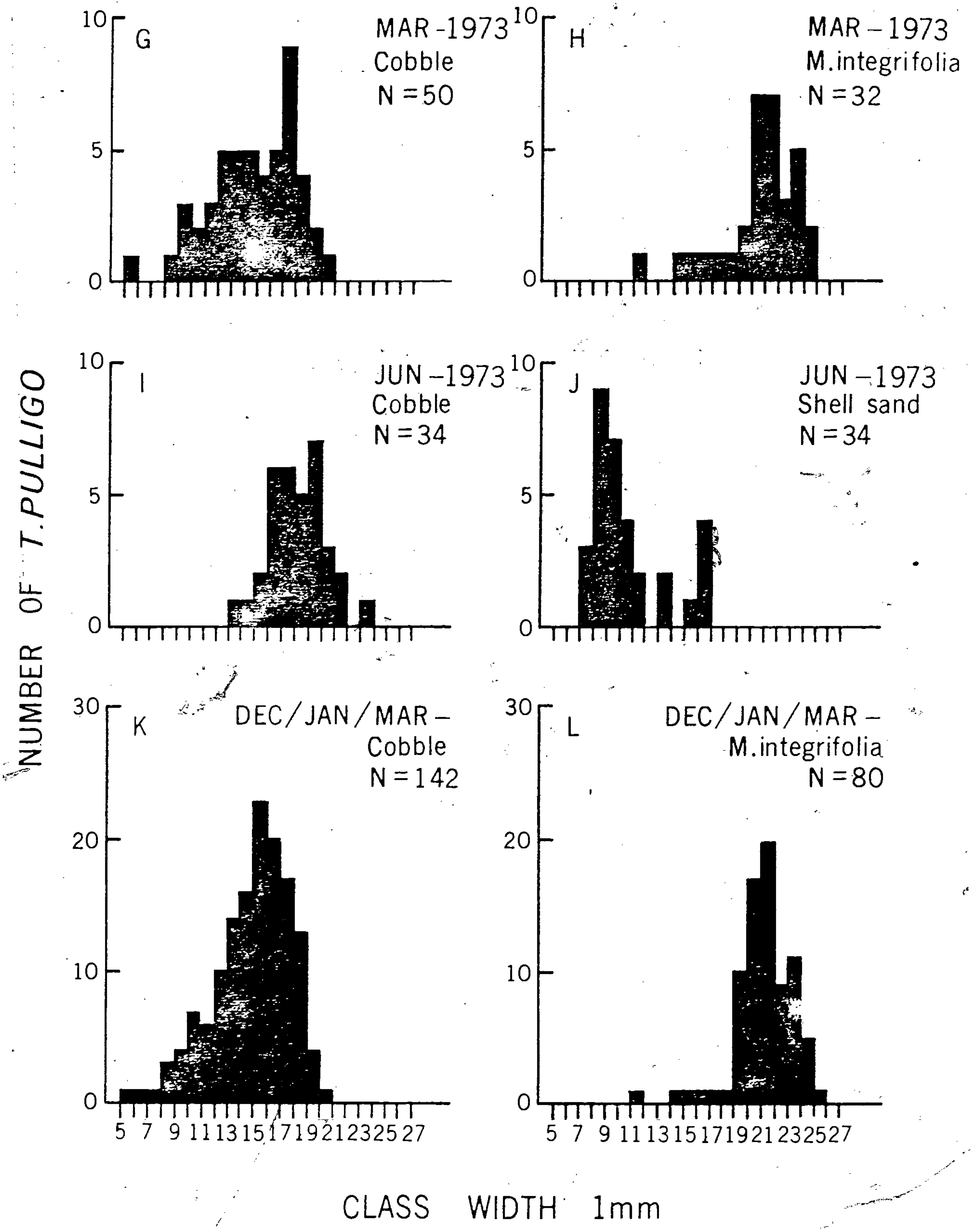
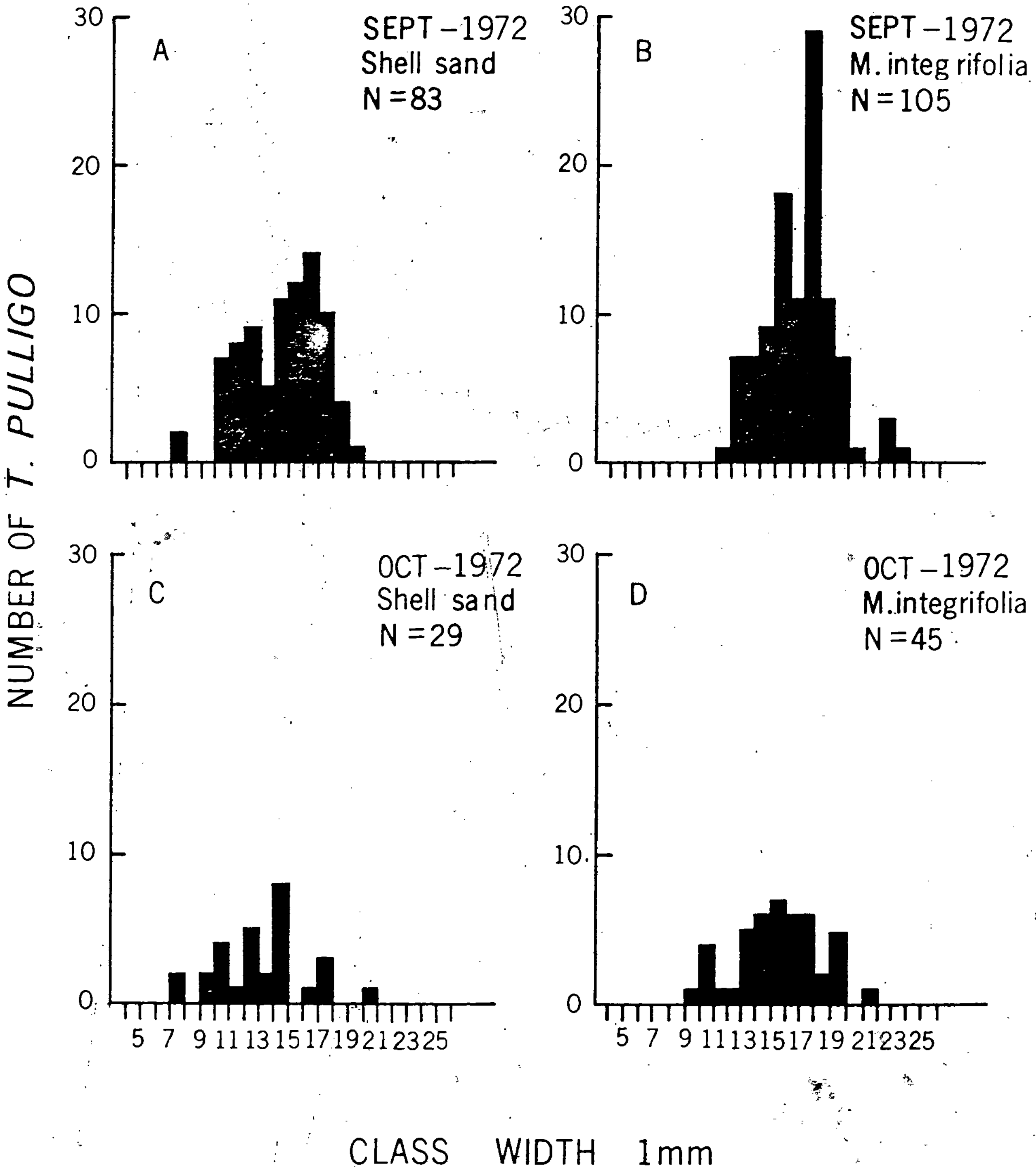
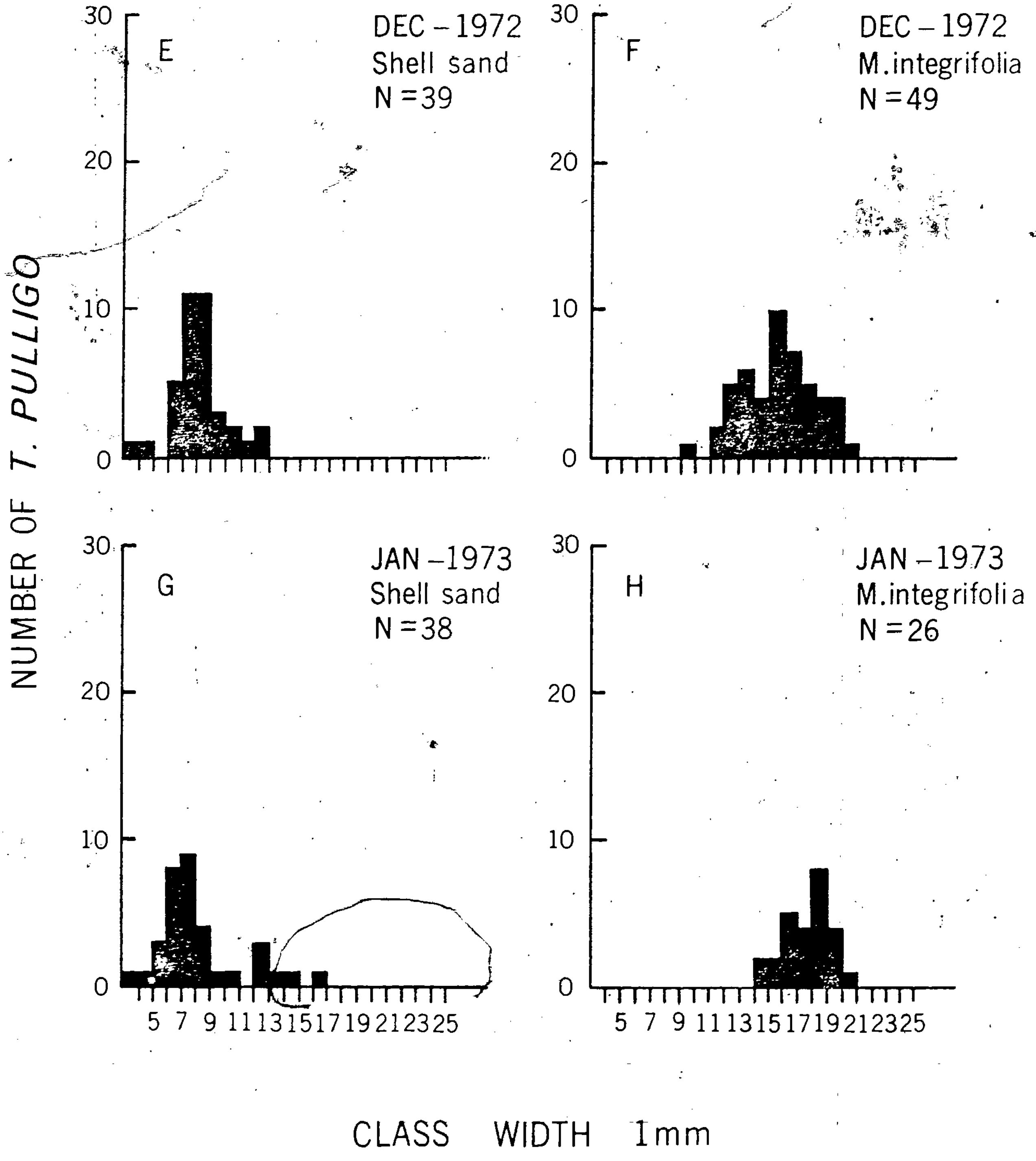
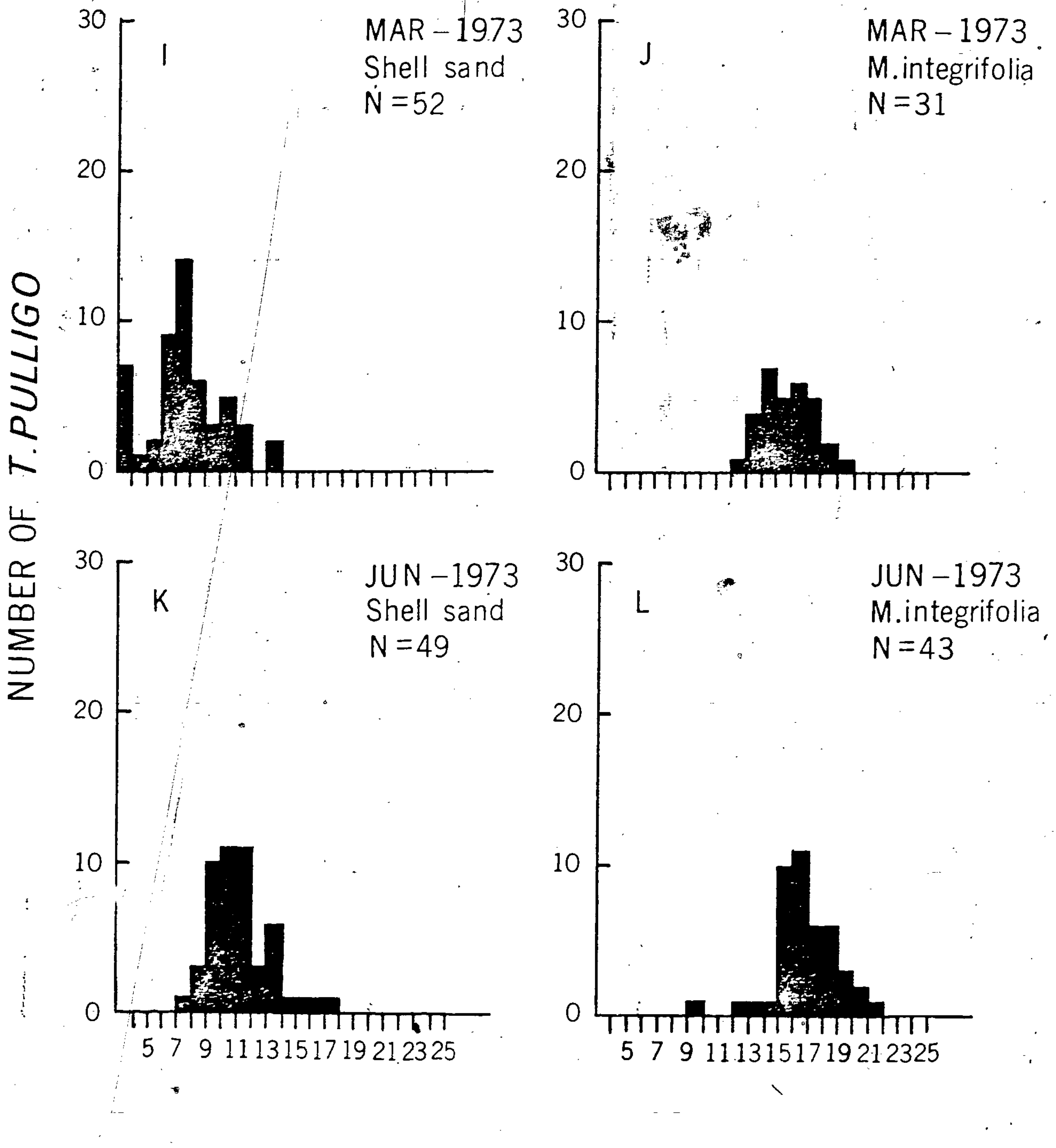

G
MAR -1973
Cobble
N =50
H
MAR – 1973
M.integrifolia
N =32
I
JUN –1973
Cobble
N =34
J
JUN –1973
Shell sand
N =34
K
DEC/JAN/MAR –
Cobble
N =142
L
DEC/JAN/MAR –
M.integrifolia
N =80
0
5
10
20
30
5 7 9 11 13 15 17 19 21 23 25 27
NUMBER OF T.PULLIGO
CLASS WIDTH 1mm

Figure 19 A-L Histograms showing the size distribution of _T. pulligo_ collected from a shell sand substrate and on _M. integrifolia_ during 1972 and 1973 at China Hat Pass


NUMBER OF T. PULLIGO
A
SEPT – 1972
Shell sand
N = 83
B
SEPT – 1972
M. integrifolia
N = 105
C
OCT – 1972
Shell sand
N = 29
D
OCT – 1972
M.integrifolia
N = 45
30
20
10
0
5 7 9 11 13 15 17 19 21 23 25
CLASS WIDTH 1mm


NUMBER OF T. PULLIGO
E
DEC – 1972
Shell sand
N = 39
F
DEC – 1972
M.integrifolia
N = 49
G
JAN – 1973
Shell sand
N = 38
H
JAN – 1973
M.integrifolia
N = 26
0
10
20
30
5 7 9 11 13 15 17 19 21 23 25
CLASS WIDTH 1mm


NUMBER OF T. PULLIGO
30
20
10
0
I
MAR – 1973
Shell sand
N = 52
J
MAR – 1973
M. integrifolia
N = 31
K
JUN – 1973
Shell sand
N = 49
L
JUN – 1973
M. integrifolia
N = 43
5 7 9 11 13 15 17 19 21 23 25
CLASS WIDTH 1mm

between January and June collections (Fig. 19; G & H, K & L).

Stronglylocentrotus franciscanus (A. Agassiz) moved up to the edge of the kelp bed in the early fall at China Hat Pass. Haliotis kamtschatkana Jonas was absent at China Hat Pass and abundant at Kelp Bay. A population of Pugettia gracilis Dana occurred on M. integrifolia at Scott's Bay and increased in mid-winter. Idotheid isopods reached high densities for short periods during the year.

T. pulligo Population Structure

I used only those samples collected by the same methods for statistical comparison. A compilation of sample means is presented in Table V).

The basal diameter of T. pulligo shells collected on the cobble substrate at Kelp Bay was significantly larger than from that of individuals collected on or beneath M. integrifolia (Fig. 18, A-L). From the single trial of separating adjacent shell sand and cobble collections the mean basal diameter of the shells were found to be significantly different (Fig. 18, I, J). To check for seasonal variation in the population structure the cobble sample of December was compared with the combined shell sand and cobble samples of June, the mean basal shell diameters were not significantly different (Fig. 18, C, I, J).

At China Hat Pass the numbers of T. pulligo less than 10 mm in basal diameter increased when the collecting method was modified to remove the upper 5 cm of the shell sand substrate in December (Fig. 19, E). Two population size modes were found at China Hat Pass, one of small snails

TABLE V

Basal Diameter of T. pulligo (mm) from collections

		On or beneath M. integrifolia			On cobble and shell sand			On shell sand		
Location	Month	n	mean	sd	n	mean	sd	n	mean	sd
Kelp Bay	Sept.				45	16.2	2.4			
" "	Oct.				59	14.6	2.7			
" "	Dec.	36	22.2	1.6	40	15.7	2.3			
" "	Jan.	12	21.9	1.6	52	14.9	3.2			
" "	Mar.	32	21.0	3.3	50	15.1	3.3			
" "	Apr.				37	16.2	4.3			
" "	Jun.				34[a]	18.6	2.1	34	11.2	2.6
China	Sept.	105	16.9	2.3				83	14.9	2.6
Hat	Oct.	45	15.9	2.7				29	13.5	3.1
Pass	Dec.	49	16.1	2.5				45[b]	8.8	2.3
"	Jan.	26	18.3	1.6				38[b]	8.4	3.6
"	Mar.	31	16.2	1.7				52[b]	8.0	2.4
"	Jun.	43	17.2	2.2				49[b]	11.7	3.2
Scott's	Sept.	33	25.7	2.9						
Bay	Oct.	25	27.5	4.1						
"	Jan.	35	25.7	4.0						
Wizard	Sept.	108	18.8	2.5	78	11.1	2.4			
Islet	Oct.	58	19.0	3.3	95	13.4	4.0			
	Feb.	18	18.9	3.7	20	10.8	2.4			

a cobble only

b substrate removal

upon the shell sand substrate and the other of large snails on M. integrifolia (Fig. 19).

Only one size mode was found in the collections from M. integrifolia at Scott's Bay and it was significantly larger in mean basal diameter from those on M. integrifolia at other sites (Table V). Wizard Islet followed the same pattern of size distribution as Kelp Bay in my samples (Table V).

Motility

Motility and Substrate Preference of Tagged T. pulligo

The movement of individuals after being placed on different substrates is expressed as a percentage of the totals recovered and tagged (Table VI). The total percentage of tagged T. pulligo recovered decreased with time. The distance of recovery from the deposit area increased with time (Table VI). The maximum recovery distance did not represent the total distance moved, as considerable multi-directional movement took place between surveys. One tagged individual moved a minimum distance of 1.75 m, although in the final 48 days survey it was 0.5 m from the deposit area (Fig. 20). A substrate preference would seem to be indicated by the movement of the tagged snails back to the area of their collection.

Motility of Tagged T. pulligo on M. integrifolia

There was a decrease in tagged snails and an increase in untagged snails

TABLE VI

Ross Islets Tagging Experiment

Distribution of Tagged Snails	Days from the Initial Deposit of Tagged *T. pulligo*			
	3	13	30	48
Percent recovered of total tagged	54	34	13	12
Percent of total recovered found within $.5\ m^2$ quadrat	45	61	50	18
Bedrock control group Percent remaining on bedrock from bedrock collection	96	93	84	42
Origin of other recovered snails	Shell Sand	Shell Sand	Shell Sand	Shell Sand and *M. intergrifolia*
M. integrifolia collection deposited on shell sand Percent remaining on shell sand	96	36	33	14
Origin of snails found but not deposited on shell sand	Shell Sand			
Shell sand collection deposited below *M. integrifolia* Percent remaining below or on *M. integrifolia*	100	54	14	25
Origin of snails found but not deposited below *M. integrifolia*	*M. integrifolia*			

Figure 20 Ross Islets tagging experiment search and deposit area for tagged T. *pulligo*

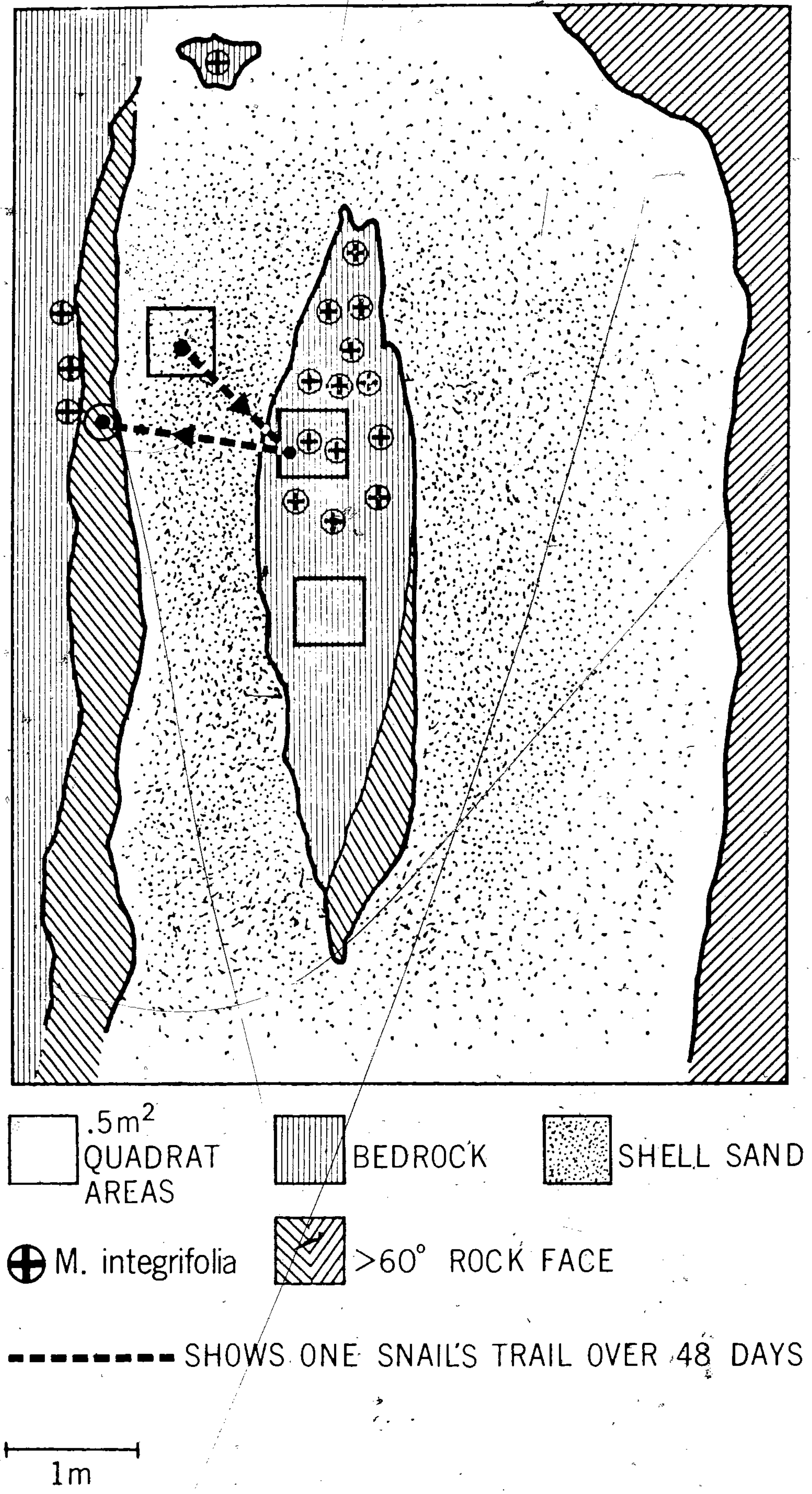

.5m² QUADRAT AREAS
BEDROCK
SHELL SAND
M. integrifolia
>60° ROCK FACE
SHOWS ONE SNAIL'S TRAIL OVER 48 DAYS
1m

TABLE VII

Scott's Bay Tagging Experiment

	Time from initial deposit (days)			
	5	10	15	88
Percent recovered of total tagged[a]	62	45	24	7
number recovered	18	13	7	2
number of untagged snails	58	30	13	20

[a] 29 *T. pulligo* were deposited at the base of the plant on 5/6/72

TABLE VIII

Kelp Bay Infestation Experiment

	Time Interval			
	2 days		4 days	
Transplant	Herbivores	Frond Condition	Herbivores	Frond Condition
A[a]	40 *T. pulligo*	Numerous spots of damage.	86 *T. pulligo*	Weighted to the bottom, heavy lamina damage.
B[b]	1 *T. pulligo* 2 *S. franciscanus*	Only stipe and one blade left.	6 *S. franciscanus*	Holdfast

a. This frond was 1.5 m long and was placed near the mid region of the Kelp Bay transect on a cobble bottom.

b. This frond was 1.5 m long and was placed beyond the end of the Kelp Bay transect on a shell sand bottom.

with time in this experiment (Table VII). Within 15 days a few individuals had reached the apical area of the plant a vertical distance of 6 m.

Kelp Bay Infestation Experiment

The importance of spatial separation of herbivores was illustrated by this experiment. The horizontal distance separating the two plants was approximately 15 m and there was a 2 m differential in depth. However, S. franciscanus at the deeper transplant did not move shoreward to feed on transplant A after consuming the transplant B (Table VIII). The concentration of T. pulligo on the single 1.5 m frond was exceeded only by the counts of T. pulligo on drift alga.

Motility as Related to Water Movement

During a period of maximum tidal flow (.5 knots), T. pulligo was observed on M. integrifolia in concentrations exceeding 30 per plant. At this time the plants were displaced up to 50 degrees from the vertical. At Kelp Bay a one meter (wave height) chop causing violent plant motion did not dislodge T. pulligo.

Feeding Behaviour

All results were expressed in fresh blotted weight of plant in grams per gram fresh blotted body weight of T. pulligo (including shell) per 24 hours grazing. The controls did not show any significant net change in weight in any of the feeding experiments.

TABLE IX

Feeding Rate Experiment on Two Species of Algae

		M. integrifolia		*P. californica*	
Day	Group	gm/snail	gm/gm/24[a]	gm/snail	gm/gm/24
1	1	.16	.07	.07	.03
1	2	.05	.02	.00	.00
1	3	.07	.03	.01	.00
1	4	.04	.03	.00	.00
2	1	.03	.02	.01	.01
2	2	.11	.05	.00	.00
2	3	.10	.04	.01	.00
2	4	.08	.05	.00	.00
Total for 48 hours		$\bar{x}$ = .04	sd = ± .02	$\bar{x}$ = .01	sd = ± .01

[a] grams of plant lamina fresh weight per gram of blotted body weight of *T. pulligo*

TABLE X

Diurnal Feeding Experiment

Containers	Areas of Collection	Group	Grams of *M. integrifolia* per gram *T. pulligo* per 24 hrs					
			Day 1	Day 2	Day 3	Night 1	Night 2	Night 3
Beakers								
1 liter	Wizard Islet	1	.02	.00	.00	.01	.03	.02
1 liter	Scott's Bay	2	.05	.04	.00	.00	.05	.00
1 liter	Ross Islets	3	.11	.01	.11	.00	.04	.02
Aquaria								
4 liter	Wizard Islet	4	.10	.08	.02	.00	.03	.04
4 liter	Scott's Bay	5	.01	.03	.03	.02	.00	.03
4 liter	Ross Islets	6	.04	.00	.02	.01	.06	.07

Day: $\bar{x} = .03$ sd = $\pm .03$

Night: $\bar{x} = .03$ sd = $\pm .02$

Feeding Experiment to Test Feeding Rates on Two Algae

The mean feeding rate of T. pulligo on P. californica was four times less than that for M. integrifolia. This was a significant difference although the experiment was terminated after only 2 days (Table IX).

Diurnal Feeding Experiment

There was no significant difference in the mean feeding rate of T. pulligo on M. integrifolia during the day and night feeding periods. Extreme values for feeding occurred during both day and night feeding periods (Table X).

Long Term Feeding Experiment

An elevated feeding rate was observed for T. pulligo during the first three days of this experiment (Fig. 21). A complete factorial Anova was applied to the results using the place of origin and the days as two factors. The major component of feeding rate variation was in the days of the experiment. The variation between the places of origin was significant but not as great as between the days (Table XI).

Consumption as a Function of Temperature

The grand means calculated for each experiment excluded the first day's results. There was a significant difference in the feeding rates at 5° C and 15° C. Feeding rates at 10° C were not significantly different than 5° C. Feeding ceased when the temperature reached 18° C (when cooling unit malfunctioned) (Table XII).

Figure 21 Variation in the feeding rates of _T. pulligo_ with time at 10° C. ---- grand mean of days 2 to 8

vertical lines	range in	gm/gm/24 hr
horizontal lines	mean	gm/gm/24 hr
vertical axis rectangle	SD	gm/gm/24 hr

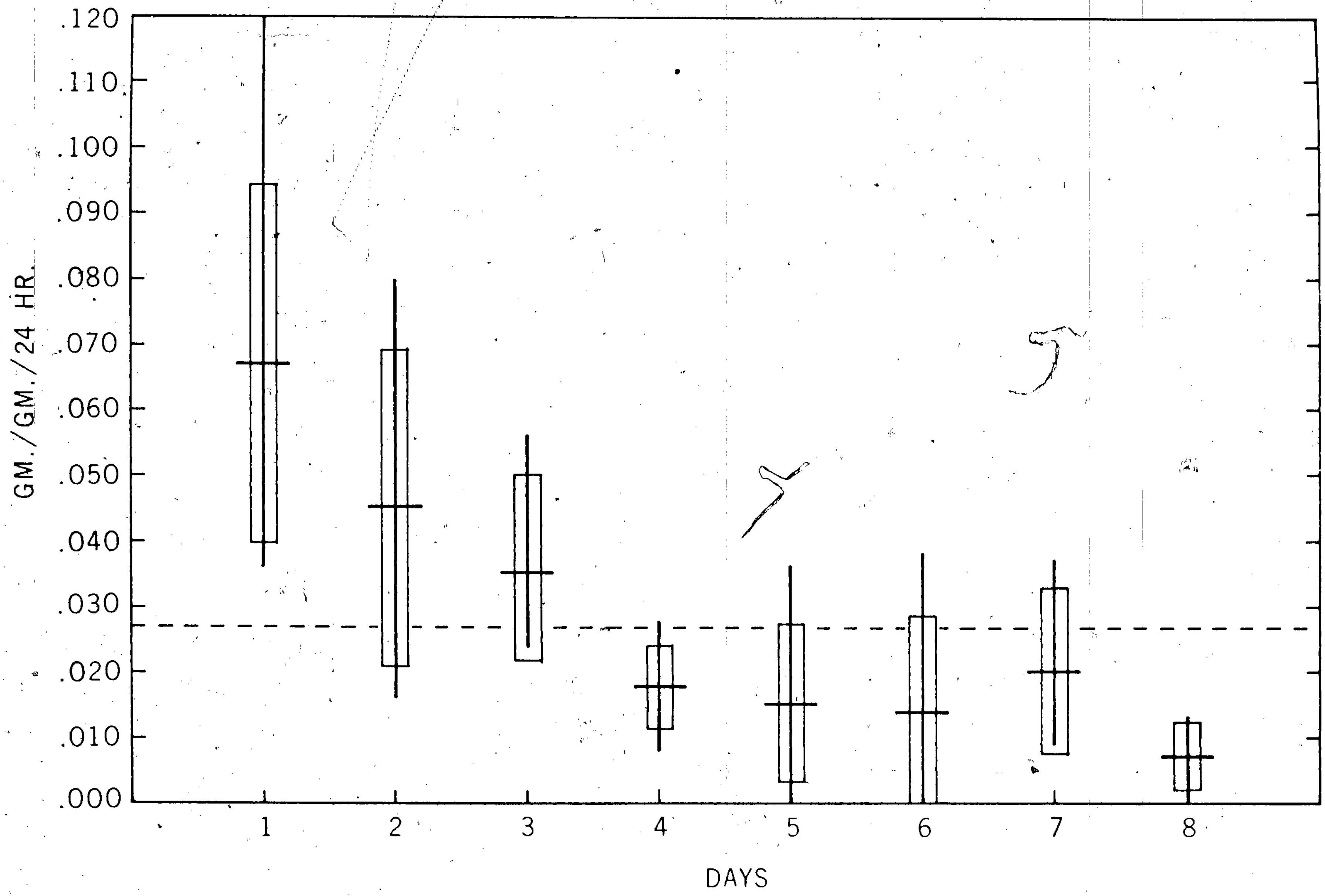

GM./GM./24 HR.
.120
.110
.100
.090
.080
.070
.060
.050
.040
.030
.020
.010
.000
1
2
3
4
5
6
7
8
DAYS

TABLE XI

Complete Factorial Anova of the Results of the Long-Term Feeding Rate Experiment

Factors	df	F	P	Percent of Variance
Place of Origin	5	3.6	.009	15.1
Days	7	9.6	.000	55.7

TABLE XII

Consumption Rate Experiments at 3 Temperatures

°C	Group	Day 1	Day 2	Day 3	Day 4
			gm/gm/24[a]		
5°	1	.003	.003	.005	.002
	2	.006	.005	.004	.000
	3	.005	.005	.001	.002
	4	.006	.004	.003	.000
		$\bar{x}$ = .003[b]	sd = ± .002		
10°	1	.007	.004	.006	.002
	2	.009	.009	.009	.007
	3	.015	.009	.010	.009
	4	.18	.012	.013	.008
		$\bar{x}$ = .011[b]	sd = ± .003		
15°	1	.012	.012	.008	.015
	2	.013	.010	.006	.011
	3	.011	.010	.010	.012
	4	.022	.017	.027	.019
		$\bar{x}$ = .013[b]	sd = ± .006		

a. grams of plant lamina per gram of blotted body weight, *T. pulligo*

b. excluding one day

Feeding Frequency

The percent of individuals on algal plates in the feeding tanks of the 15° C consumption experiment ranged from 40 to 0 percent of the tank population. The mean for 40 observations was 12.5 SD ± 6 percent. It was not possible to distinguish feeding individuals from non-feeding individuals on the plates.

DISCUSSION

Food resources may be an underlying factor in the distributional pattern of *T. pulligo*. Algal cover decreases with depth and fine sand and silt rarely support multicellular algae. The range of macrophytes inhabited by *T. pulligo* suggests feeding preference was not an important factor in the distribution of populations. Despite the differences in the feeding rates on *P. californica* and on *M. integrifolia*; *T. pulligo* inhabited both species.

The bimodal distribution of *T. pulligo* requires an explanation. The lack of small individuals on the kelp suggests a steady immigration is required to maintain this population. This size factor may be related to the feeding mechanism of the snail and selective predation on the snail.

Visual sensing of prey plays a part in the capture of food by fishes and *T. pulligo* forms a portion of the diet of *Hexagrammus decagrammus* (Pallus, 1810), (Leaman, pers. comm.). Therefore, camouflaging of organisms would be important in their survival on a given substrate.

Young snails living in a shell sand substrate blend into the background because of their brown and white colouration. This colouration changes as they grow due to increasing encrustration by the red alga <u>Peysonnelia</u> <u>pacifica</u> (Kylin). Young individuals therefore would be more visible than older snails on a brown macrophyte background subjecting them to greater predation.

The substrate may be very important in the ability of <u>T</u>. <u>pulligo</u> to feed efficiently. The feeding action of <u>T</u>. <u>pulligo</u> is similar to other herbivorous prosobranch gastropods which requires the radula to be flattened over a bending plane as it is applied to the food substrate (Purchon, 1968). The extremely rough texture and small size of shell sand fragments require a very small radula to harvest the micro-algal cover. Since the radular size increases with the growth of the snail then the efficiency of feeding will decrease on the shell sand substrate. The increase in radular size and change in colouration with age may then contribute to the biomodal population distribution.

<u>Tegula</u> in central California kelp beds are described as highly motile (Pearse, pers. comm.). <u>Tegula</u> <u>funebralis</u> with a similar foot structure to <u>T</u>. <u>pulligo</u> has the potential to move 10 m per hour on a smooth surface (Miller, 1974). Further, the rate of recapture in tagging experiments suggest rapid dispersion. However, the problems with tag loss, selective predation due to tag visibility, the high relief of the substrate and the limitations of underwater searches all contributed to a low recovery rate.

The lack of unidirectional movement by tagged snails and the seasonal stability of the population structure indicate that a mass movement in and out of the kelp bed is unlikely.

In the spectrum of factors affecting the feeding rates of herbivores I have only studied a few for T. pulligo. The difference in feeding rates of T. pulligo for M. integrifolia and P. californica was not clearly exhibited in the field distribution. The greater surface area provided by M. integrifolia could account for any larger numbers per plant in the field. The strong afinity shown by intertidal T. funebralis for M. integrifolia (Best, 1964) when it has only indirect access to the plant suggests preference must be related more directly to the field situation.

The use of a non-feeding period in these experiments did cause an accelerated grazing rate for the first few days of the experiment. However, the mean values important to this study were calculated by deleting the first day's results to partially compensate for this factor. There is an evident need for long term feeding experiments in the laboratory and in the field to detect any seasonal or cyclic feeding variation. Feeding rates at various temperatures partially fills this gap and indicate mid winter feeding rates are less than summer and fall feeding rates.

In terms of body weight and feeding rate T. pulligo would appear to be an unimportant herbivore. However, let us consider the relative feeding rates of a number of herbivores.

The feeding rates of a variety of herbivores have been obtained using the algal weight or area loss method by several workers (Best, 1964; Jones, 1971; Leighton, 1971). I have converted their values to a standard, grams of plant tissue per gram blotted body weight of herbivore per 24 hours feeding; to compare the feeding potentials of herbivores (Table XIII).

TABLE XIII

Selected Herbivore Feeding Rates

Herbivore	gm alga/ individual	Mean weight individual	Mean* gm/gm/24	Investigator
Astraea undosa	2.50	187	.013[a]	Leighton, 1971
Haliotis corrugata	8.50	578	.015	Leighton, 1971
Pugettia producta	2.00	54	.037	Leighton, 1971
Strongylocentrotus franciscanus	5.70	235	.024	Leighton, 1971
Tegula funebralis	.80	6.0	.013[b]	Best, 1964
Idotea resecata	.09	.08	1.12[c]	Jones, 1971
Tegula pulligo	.70	2.3	.03[d]	Sharp. 1973

* Wet weight of animals, with exoskeleton.

a. One of two individuals per experiment at 12.8° C - 13.9° C. For six periods of six days each. Four phaeophyte species offered as food.

b. Sixteen individuals for 3 1/2 days at 14° C - food - *M. pyrifera*.

c. Mean ten individuals calculated from initial weight at 13.9° C - 17.2° C - food - *M. pyrifera*.

d. Mean for ninety individuals for eight days at 10° C - food - *M. integrifolia*.

In terms of consumption per individual the herbivores with the greatest feeding potentials per individual organism are the abalone and the sea urchins, the largest herbivores. However, the high feeding rate per unit weight of Idothea means that large numbers of this isopod can cause significant grazing damage. A large migration of Idothea destroyed the canopy of a M. pyrifera bed in California (Jones, 1971). Size therefore is not always a good criterion; motility and numbers may be more important.

From conducting feeding experiments with T. pulligo, I realized incidental tissue loss is also an important factor in grazing potential. An extreme case of incidental tissue loss is exemplified by S. franciscanus which can sever the stipe of a frond while only consuming a few grams of tissue (Leighton et al., 1966). My feeding experiments have shown T. pulligo does cause incidental tissue loss even in laboratory experiments under quiescent conditions. At the same temperature (10° C) there was a 3 fold difference between the algal plate and free algal section experiments, due to loss of non-weighable fragments in the latter experiment.

The previous discussion of comparative feeding potentials relates directly to the question what is the relative importance of T. pulligo in the kelp bed. There are herbivores feeding upon M. integrifolia tissue with a greater biomass per individual than T. pulligo thus a greater feeding potential per individual. Astrea gibberosa and H. kamtschatkana are two such large herbivores with a greater feeding potential than T. pulligo but they feed only indirectly on M. integrifolia in drift material. Stronglyocentratus franciscanus is another obvious large herbivore and its ability to decimate large kelp beds has been well documented (North, 1960-1974). In the Barkley Sound area S. franciscanus is only a periodic inhabitant of the kelp bed and is also limited in its shoreward incursions into the kelp bed (Pace, pers. comm.). The kelp crab was not evident in the kelp bed except during the final degradation of the kelp bed.

It appears there is no continuous grazing pressure from any of the large herbivores present in the kelp bed.

Small herbivores with a high feeding rate per unit weight such as isopods were always present in the kelp bed but only when the population peaked for short periods was consequential impact possible.

Tegula pulligo, although intermediate in both size and feeding rate of all kelp bed herbivores was the single herbivore present feeding on M. integrifolia in high concentration throughout the plant's growth and degradation. Furthermore, a percentage of the T. pulligo population was feeding 24 hours a day on M. integrifolia. This herbivore also remains in the area of the bed throughout the year and is present upon the earliest young sporophytes.

The incidental tissue loss due to T. pulligo grazing is a significant addition to the actual consumption of M. integrifolia tissue.

I conclude T. pulligo exerts the greatest continuous grazing pressure in M. integrifolia in Barkley Sound kelp beds.

PLANT-HERBIVORE INTERACTION

METHODS

Grazing Damage

To characterize the grazing damage caused by T. pulligo, I observed damage caused in feeding experiments and with high concentrations of the snails on M. integrifolia in the field. This damage was recorded with photographs and drawings.

To access grazing damage and erosion in the field, a total of 107 fronds were collected during the spring and summer of 1973 from 5 kelp beds. Fifty-five of these fronds were collected from Wizard Islet, Ross Islets and Scott's Bay within one week in June, 1973. Observations were made of stipe length, blade number, an estimate of lamina tissue loss, the nature of the damage and region of damage. The estimation of lamina tissue loss was based on a comparison with whole lamina on the same frond. The regions of damage were characterized as peripheral, central, distal and proximal. The nature of the damage was characterized by shape and colour, such as hole, slit, indentation and discolouration. The initial cause of the damage was rarely decipherable, because growth, decay and erosion obscured the original grazing damage.

Frond degradation, grazing and erosion

In the field, grazing and erosion act together in the degradation of algae. The following experiments were designed to quantify the relationship between the combined effects of erosion and grazing on M. integrifolia tissue loss in the field. These experiments also provided a comparison of laboratory feeding rates with field interaction of grazing and erosion. A preliminary experiment was used to determine the experimental period and overall experimental design. The results are presented here to explain the reasons for final experimental design.

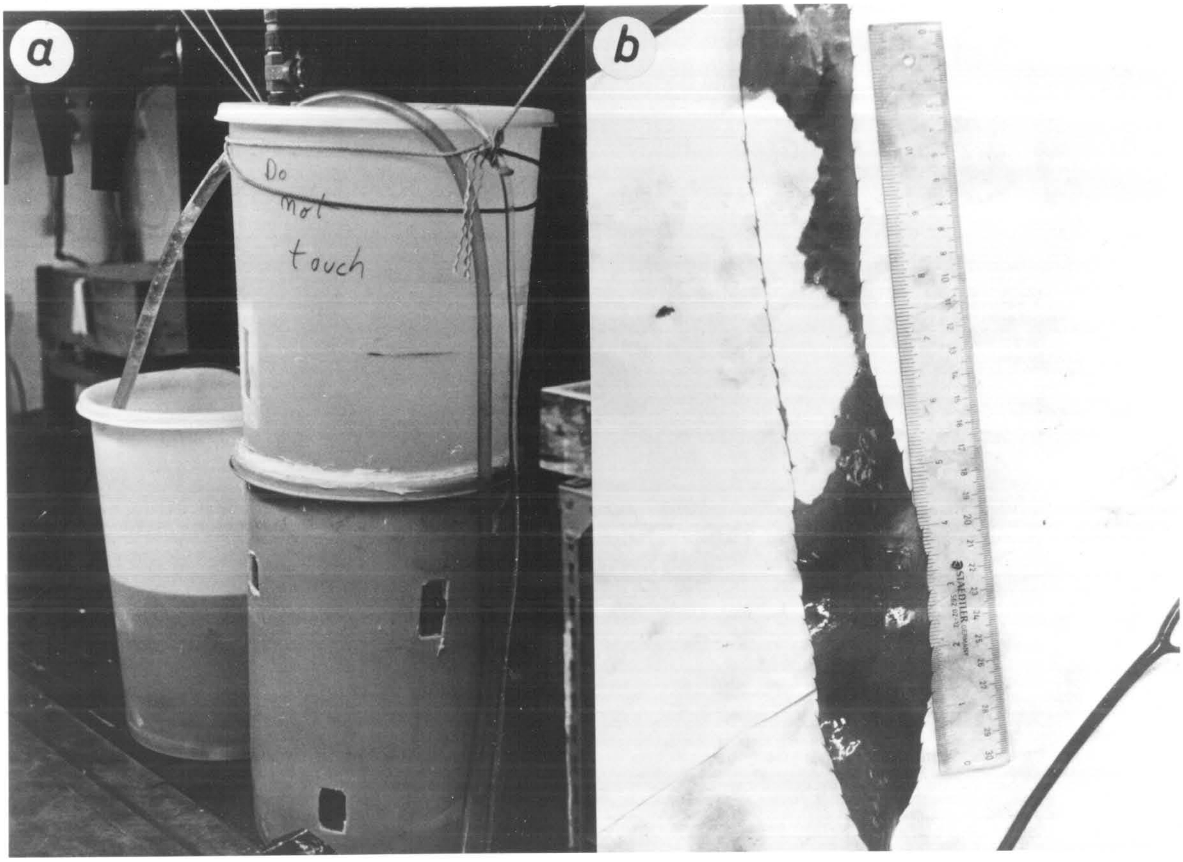
Fronds were collected from an islolated kelp bed subject to strong tidal currents in Bamfield inlet. The fronds collected had only traces of damage on their laminae since few grazers were present in this kelp bed. The fronds were separated into 3 groups of 2 fronds each; independent laminae were truncated by cutting off the uneven tips; then, marked with tape and measured for length. Stones were tied to the holdfast of each frond to permit free floation of the upper frond. One group was deposited in a concentration of T. pulligo at Wizard Islet. A second group was placed in a cylindrical tank, 2.5 x 0.5 m with 100 T. pulligo collected from M. integrifolia at Wizard Islet. An adjacent 1.0 x 0.5 m tank held the third, a control group with no snails (Fig. 22a). The fronds were left under these conditions for 5 days.

To give these fronds field exposure after removal of T. pulligo, a moderately wave-exposed site was chosen at Scott's Bay at a depth of 2 m, with a fine sand substrate devoid of plants and herbivores (Fig. 23). Eight large (10 - 15 kg) boulders were wrapped with rubber bands and deposited at the experimental site. After 5 days each lamina from the three groups was remeasured and the fronds were transferred to the boulders at the Scott's Bay field site. The fronds were retrieved after 21 days in

Figure 22 . Grazing and erosion interaction experiment

a. The feeding (tall) and control (short) tanks connected to an open seawater system

b. An extreme case of lamina damage following a 7 day feeding period in the feeding tank


a
Do not touch
b
STAEDTLER GERMANY

the field. Only the control showed net laminae growth (Table XIV). Since the experimental plants grew and lost tissue during this period it was difficult to obtain a true value for the interaction of eriosion and grazing with this exposure period. No quantitative relationship could be established between tissue loss and field grazing when the number of potential herbivores were unknown.

Two full scale experiments followed the above method described for the trial experiment except the exposure period was shortened and all experimental fronds were grazed on in the laboratory tank by a known population size of T. pulligo.

Four fronds were used per group in both experiments. The two experimental periods were 3 days feeding and 7 days field exposure; 7 days feeding and 4 days field exposure respectively. The wind velocities and directions plus sea conditions were obtained from 3 daily readings at the Cape Beale lighthouse for the experimental period. This information allowed comparison of the different exposure periods in terms of tissue loss.

Drift Algal Collection

Numerous observations of drift algal accumulations were made during survey dives. The origin, character and amount of this material was investigated in this study to provide information on the nature of tissue loss by erosion and grazing.

To collect this drifting material, one gallon buckets were covered with heavy plastic except for a 15 cm diameter hole. The numbered buckets

Figure 23

The grazing and erosion experimental site located in Scott's Bay with a detailed analysis of its open angle and fetch. The range of fetch in km is listed for each subdivision of the open angle

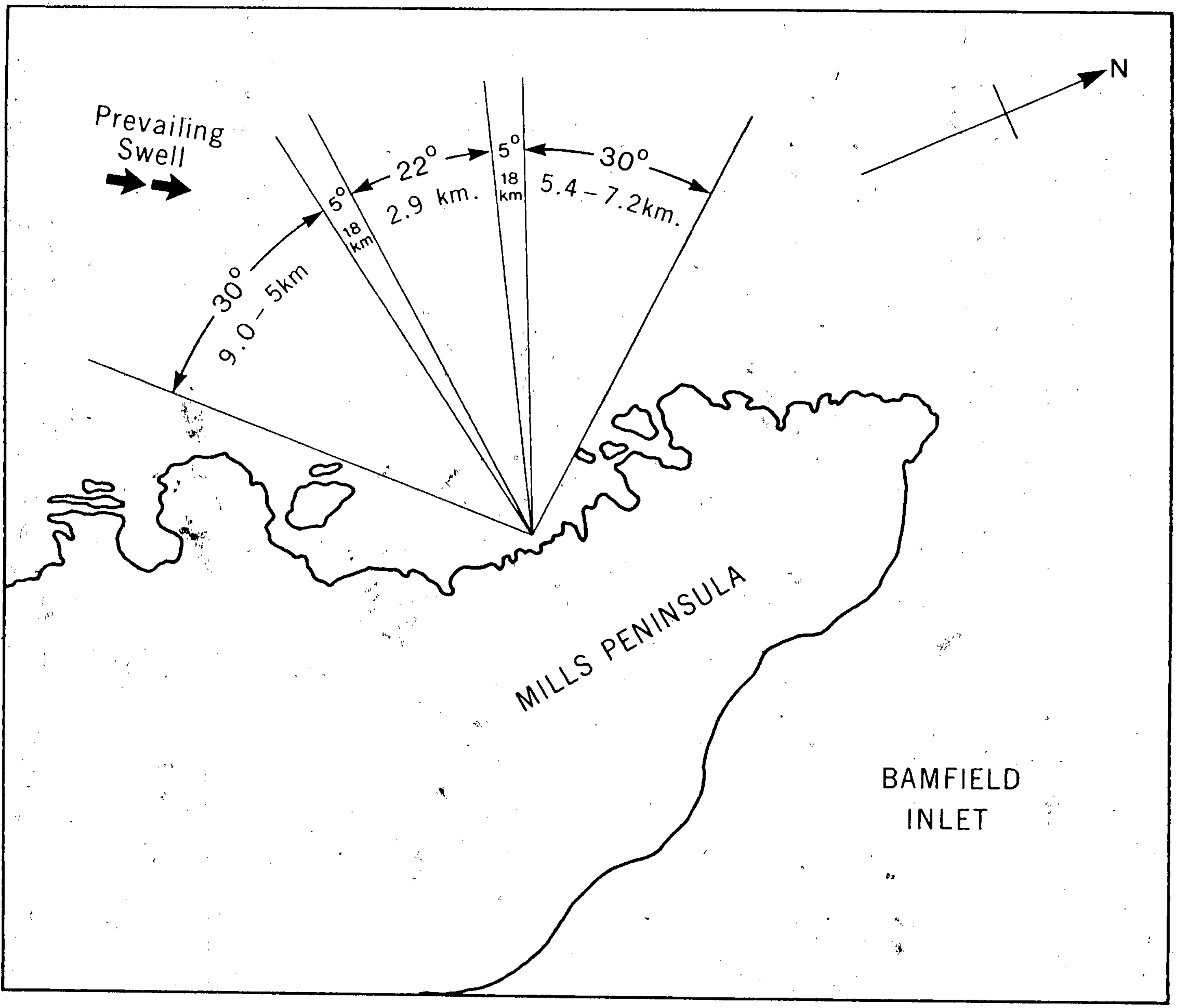

N
Prevailing
Swell
30°
9.0 – 5km
5°
18 km
22°
2.9 km.
5°
18 km
30°
5.4 – 7.2km.
MILLS PENINSULA
BAMFIELD
INLET

TABLE XIV

Grazing and Erosion Preliminary Experiment
Number 1

Frond Group	Length Change (cm) of each Laminae Basal to Apical Position							Total Laminae Net Δ Length	Per Lamina Length Δ	Per Lamina Standard Deviation
Control[a]	+40	+10	-10	-20	-10			+10	+ 2	±24
21 day [c]										
field exposure	+ 3	0	0	+20				+23	+ 6	±10
Tank[b]	+ 3	-10	0	+50	+ 5	+ 5		-47	- 8	±21
21 day[c]										
field exposure	+10	+10	-20	- 5	0	0	+7	- 3	- 1	±10
Wizard[d]	+ 8	+ 6	0	- 2	-30	0		-18	- 3	±14
21 day[c]										
field exposure	-35	-65	-29	-50	- 3	0		-209	-35	±26

[a] In laboratory, five day no feeding period

[b] In laboratory, five day feeding period

[c] 10/2/73 to 10/23/73

[d] Five day feeding period at Wizard Islet

were buried in pairs up to 5 cm from their lips. Five sites were chosen in the Ross Islets Plateau kelp bed. Three sites were within the bed in shell sand and cobble channels; one site was at the outer edge of the kelp bed and the fifth site was at the bottom of a rock cliff on a sediment plain.

The algae were collected from the buckets 24, 31 and 46 days after October 4, 1973. The largest fragments were picked up by hand and the rest were removed by a slurp gun and exhausted into a muslin bag. In the laboratory the recognizable fragments were separated, blotted and weighed on a triple beam balance to 0.1 gm.

RESULTS

Grazing Damage

Tegula pulligo grazing damage was very distinct; its radula removed tissue layer by layer (Fig. 24). The meristoderm and part of the cortical tissue were frequently removed and if the snail remained in one place it created a hole. *Tegula pulligo* were most common on the laminae of the fronds and grazing damage was widely distributed on the lamina.

It was found in the general grazing damage and erosion survey that mature and well differentiated sporophylls received less damage than the nearest basal blades (Fig. 25). The more basal was the lamina the greater was the damage found on it. Grazing damage was not restricted to any portion of the lamina; although peripheral damage was most common. The apical scimitar was rarely damaged by herbivores and the pneumatocysts were only damaged on old fronds after the loss of laminae.

The fronds collected from the Ross Islets, Wizard Islet and Scott's Bay were grouped into 5 size classes. The percentage of blades on the fronds in each size class which had less than 10 percent of their original tissue (less than 5 cm in length, degenerate laminae) increased with the length of the frond (Fig. 26).

Frond Degradation, Erosion and Grazing

For both full scale experiments (Numbers 2 and 3) exposure periods were comparable since the wind velocities and directions recorded at Cape Beale indicated a strong southeast wind, causing a moderate swell at the Scott's Bay site during both experimental periods (Table XV).

A total of 305 cm of lamina (length) was lost in experiment 2 with 7 days field exposure, and the control showed no net change in this exposure period (Table XVI). When the field exposure time was shortened but feeding exposure lengthened in experiment 3, loss of laminae length was one third of plants with 7 days exposure (Table XVII).

It was evident from the grazing damage that lamina area would have been a better indicator of tissue loss (Fig. 22b). Apical scimitars were not tagged or measured but they did not sustain grazing damage.

The calculation of a rate of tissue loss combining the effects of erosion and grazing damage was based on experiment 2. The experimental laminae had an average width of 10 cm and a weight .03 gm/cm^2 of tissue loss. The result of 3 days feeding and 7 days exposure was a grazing erosion rate of 0.3 gm of M. integrifolia lamina lost per gram body weight of snail per 24 hours grazing ± .2 gm.

Figure 24 Characteristic grazing damage of isolated _T. pulligo_ on a _M. integrifolia_ lamina

75b

Figure 25 M. integrifolia in various states of degradation collected in May

a. A healthy young frond all laminae complete

b. A young frond missing 4 laminae but with sporophylls (arrow) only partially damaged

c-d. Fronds which survived the winter and show new growth but are missing most of the previous years laminae

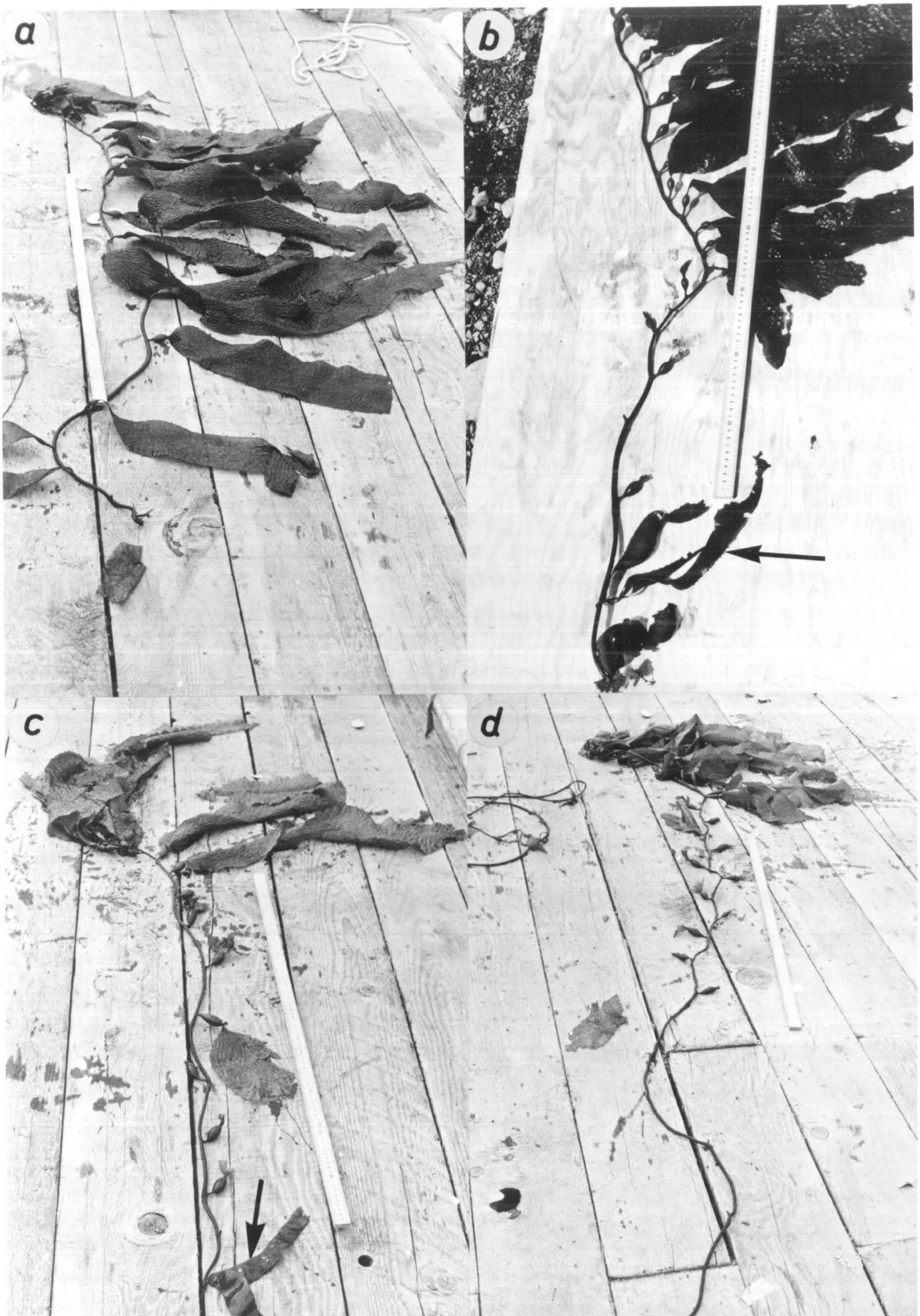
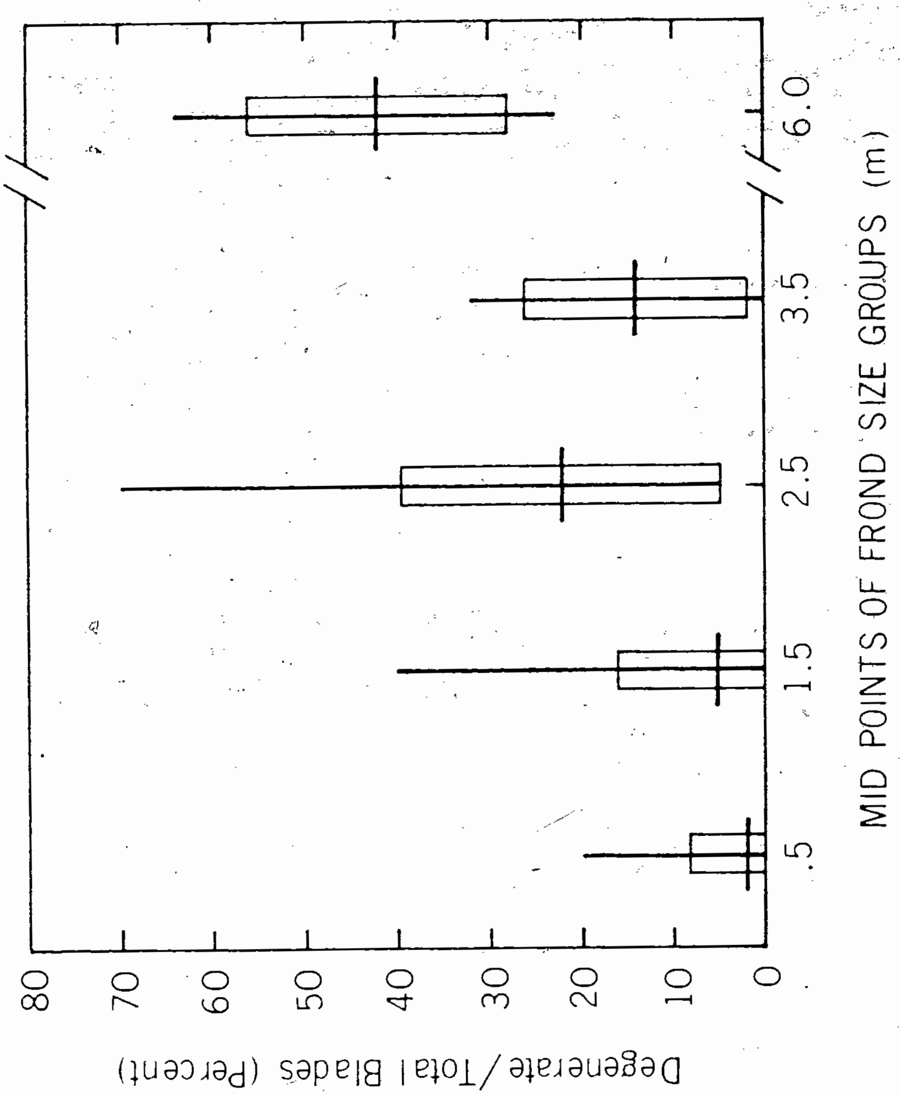

a
b
c
d

Figure 26 Variation in the percentage of total blades missing more than 80 percent of their tissue (degenerate laminae) with the length of frond

Frond size classes (m)	mid point	N
0 - 1	.5	17
1 - 2	1.5	13
2 - 3	2.5	11
3 - 4	3.5	6
4	6.0	8


Degenerate/Total Blades (Percent)
0
10
20
30
40
50
60
70
80
MID POINTS OF FROND SIZE GROUPS (m)
.5
1.5
2.5
3.5
6.0

Drift Algal Collection

The collection period was a time of accelerated degradation in the Ross Islets kelp beds. The kelp bed at the collection site was open to a north-west chop which was common during the late fall. Maximum accumulation of algal fragments occurred in the buckets within and at the edge of the kelp bed (Table XVIII). *Macrocystis integrifolia* was the main constituent of all collections and far exceeded the quantities of *Ulva*, *Fucus* Linneaus 1753 and *Ptilota* C.A. Agardh, 1857 (Fig. 27; Table XVIII). No analysis of fragment size was attempted but the bulk of the material exceeded 5 cm in one dimension and 20 cm pieces of lamina was not uncommon (Fig. 27a). Lamina tissue was the main frond structure represented; pneumatocysts and stipe fragments were rare (Fig. 27c).

Herbivores were found in some buckets and they probably reduced the total tissue recovered. The limited holding capacity of the buckets (approximately 160 gm) caused the loss of some material.

DISCUSSION

In general the results of the grazing damage survey showed that the longer tissue is exposed to grazing the greater is the tissue damage and loss. The cumulative effect of damage on the frond also explains the lack of damage on the apical scimitar. The tissue of the apical scimitar has been in existence for the least amount of time of any structure on the frond. By the time the herbivore moves up from feeding on lower laminae there is a new set of laminae and a new apical scimitar.

The survival of the stipe, pneumatocysts and sporophylls long after

TABLE XV

Wind Velocity and Direction at Cape Beale
During Erosion and Grazing Experiments

	Experiment 2	Experiment 3
Direction	23/11/73 - 30/11/73[a]	30/11/73 - 4/12/73[a]
	Velocity Kn./Hr[b].	Velocity Kn./Hr[b].
N	5	
NE	8 8 5 12 10 10 6	8 6
E	12	5
SE	35 20 25 25 25	28 15 35
S		
SW	4 7 18 18 15	25
W	15 15 10	15
NW	6	20 12

[a] swell Low to Moderate - surface Light Choppy to Choppy

[b] three readings per day

TABLE XVI

Grazing and Erosion Experiment Number 2

Frond Group	Frond	Length Change (cm) of each Laminae						Total Laminae	Per Lamina	
		Basal to Apical Position						Net Length	Length	Standard Deviation
Tank A fronds after 3 days feeding	A	0	-13	- 3				-16	- 5.3	± 6.8
	B	-12	-15	- 4	0	0	0	-31	- 5.2	± 7.0
	C	-12	-11	- 1	-10	-1		-35	- 7.0	± 5.5
	D	- 6	- 4	- 1				-11	- 3.7	± 2.5
Tank A fronds after 7 days field exposure	A	-40	-20	+ 1				-59	-19.7	±20.5
	B	- 6	-22	-20	-32	-8	-1	-89		
	C	- 9	- 7	-22	-11	0		-49		
	D	-12	- 3	0				-15		
Control fronds after 7 days^{a} field exposure	E	- 7	0	+ 1	- 1	0		- 7	- 1.4	± 3.2
	F	0	+ 2	0				+ 2	+ 0.6	± 1.1
	G	- 4	- 1	- 1	- 2	-1		- 9	- 1.8	± 1.3
	H	- 1	- 3	+ 8	+ 1			+ 5	+ 1.2	± 5.0

a. 23/1/73 to 30/11/73.

TABLE XVII

Grazing and Erosion Experiment Number 3

Frond Group	Frond	Length Change (cm) of each Laminae Basal to Apical Position					Total Laminae Net Length	Per Lamina Length	Standard Deviation
Tank A fronds after 7 days feeding	A	-15	-23	-14	-5	0	-57	+11.4	+ 9.01
	B	- 6	+ 1	0	+1		- 4	- 1.0	± 3.37
	C	-30	- 5	- 2	0		-37	- 9.2	±13.98
	D	0	0	- 1	+1	+4	+ 4	- 0.8	± 1.93
Tank A fronds after 4 days field exposure	A	- 1	0	- 2	-1	-1	- 3	0.6	± .71
	B	- 4	- 1	0	-1		- 6	- 1.5	± 1.7
	C	- 1	- 1	- 1	-4		- 7	- 1.6	± 1.3
	D	+ 1	0	- 2	-2	-2	- 5	- 1.0	± 1.4
Control[a] fronds after 4 days field exposure	E	- 5	- 1	- 1	-1	0	- 9	- 1.6	± 1.9
	F	0	0	- 1	0	0	- 1	- 0.2	± .5
	G	0	- 2	0	0	0	- 2	- 0.4	± 1.0
	H	0	0	0	0	+2	+ 2	+ 0.4	± 1.0

a. 30/11/73 to 4/12/73

other frond structures are lost may be due to the mechanical resistance to herbivore mouth parts.

The principle: "Where there is an abundance of feed, the grazing animal can express its preferences freely. As the feed supply decreases the animal must eat less acceptable plant material or starve" (Arnold, 1964) would explain the ultimate feeding upon stipes, pneumatocysts and sporophylls.

The frond degradation, erosion and grazing experiments relate directly to the consistent pattern of growth and degradation of kelp beds at my study sites in Barkley Sound. The growth of new fronds and the settlement of new plants occurred during the spring and summer. The kelp bed reached maximum density of fronds by late summer to early fall. Urchins began to move up into the kelp bed at this time whereas T. pulligo had been active throughout the summer. Up to October growth of the plants exceeded grazing and erosion tissue loss. The plants ceased growing in late October to early November (Lobban, pers. comm.). By this time the urchins reached maximum penetration in the kelp bed (Pace, pers. comm.). The plants remaining above the urchin line had lost most of their blades by the end of December.

Corresponding to this time of kelp bed degradation there is a steady increase in the mean wind velocity and winds from a northerly direction (Table XIX). The prevailing wind direction changed the exposure index for many kelp beds, including the Ross Islet Plateau kelp bed (Fig. 33).

This pattern of tissue loss when wave-exposure is increased and grazing pressure is constant was reflected in the grazing and erosion

Figure 27 Fragments of drift algae removed from catch buckets at the Ross Islets Plateau kelp bed in October to November, 1973

a. The entire contents of a bucket - note some fragments are almost complete laminae (arrow)

b. Fucus and Ulva found in one collection (arrow)

c. Average size algal fragments


c
b
a

TABLE XVIII

Drift Alga Collections (Beginning October 1, 1973)

Site	Bucket	Total[a] Wt. gm	Gm/ Day	Percentage *M. integrifolia*
		1st Interval 24 days		
1	A	169.1	7.0	86
	B	164.4	6.8	69
2	C	64.6	2.7	68
3	D	172.2	7.2	71
4	E	--------	N I L	-----------
	F	--------	N I L	-----------
		2nd Interval 24 days		
1	A	21.8	3.1	91
	B	70.8	10.1	91
2	C	3.5	.5	86
3	D	75.0	10.7	83
4	E	-------	N I L	-----------
	F	-------	N I L	-----------
		3rd Interval 15 days		
1	A	-	-	-
	B	28.1	1.9	100
2	C	-	-	-
3	D	10.7	2.0	100
4	E	-------	N I L	-----------
	F	-------	N I L	-----------

[a] fresh blotted weight

experiments. The grazing-erosion experiments have shown an increase in wave-exposure period will increase the loss of tissue damaged by previous grazing. If we remove the grazers as in the controls of these experiments, the tissue loss is minimal until winter storms destroy the plant.

The elimination of the major herbivore S. franciscanus from a M. pyrifera bed resulted in the degradation of the bed being delayed from mid winter to mid spring (North, 1958). Therefore, it is evident that grazing and erosion are not acting separately in the field, since grazing facilitates the final degradation of the kelp bed.

The value of .3 gram of M. integrifolia tissue lost per gram body weight of snail per 24 hours grazing calculated for the interaction of grazing and erosion on tissue loss is an approximate value. The conditions of exposure and wave action change with time and place and can change within the area of the kelp bed. This value is conservative since it is baded on linear tissue loss and not a true area measurement (this excludes holes). The plants used were of the wave-exposed type described by Pace (1972). This type has stronger wave modified laminae than the sheltered lamina since these plants can vary their morphology. This would add another conservative factor to the calculation. However, the conditions prevailing at the time of the field experiments represented a moderate active water action and erosion period, creating a higher than average erosion factor.

The discussion of drift material is intimately connected with the previous subsection on grazing and erosion. Grazing and erosion rates

TABLE XIX

Cape Beale Light, British Columbia

Percentage Frequency Wind Direction (and Calms)[a] and Mean Speed by Months

	J	F	M	A	M	J	J	A	S	O	N	D
N	2	6	3	2	3	2	2	4	5	6	4	6
NE	35	23	16	10	8	2	3	4	11	13	18	32
E	6	10	5	6	4	2	3	3	5	8	9	10
SE	24	34	37	34	32	35	32	37	40	43	40	26
S	4	6	6	8	6	8	9	8	10	6	5	4
SW	7	8	8	11	7	7	8	5	5	4	6	5
W	11	8	17	21	28	31	29	24	15	12	10	9
NW	11	6	8	8	11	12	13	13	7	7	8	8
CALM	0	0	0	0	1	1	1	2	2	1	0	0
MEAN SPEED (kn/hr)	13.5	11.3	12.6	13.5	10.0	9.5	8.7	8.2	8.9	10.4	12.1	12.5

[a] of total readings per month over 10 years to June, 1973

determine the amount of drift material present as well as its character.

The large size of algal fragments suggests that erosion and grazing are acting together as grazing damage would tend to weaken lamina tissue allowing large healthy pieces to break off. If erosion was acting alone at the tips of the laminae then small fragments would be lost as in Laminaria, (Mann, 1972).

Drift algal collections made during the fall in a M. pyrifera kelp bed ranged from 6 to 78 gm/m^2 (Lowery and Pearse, 1973). Extrapolation from the accumulations in my catch buckets results in values from 100 to 500 gm/m^2. However, the buckets acted like crevices and accumulated the drift material at a higher concentration than the surrounding area. The work of Lowery and Pearse involved collections from substrate surface only.

The drift material in my study consisted almost entirely of M. integrifolia. This fact, plus the absence of drift material in the buckets outside the kelp bed, suggests that the algal fragments are not carried far from the kelp bed. However, more extensive studies are required to prove this statement.

DETAILED STUDY OF A KELP BED

METHODS

A 100 m quadrat was chosen within the Ross Islets Plateau kelp bed for a comprehensive study of plant and herbivore distribution. Initial insitu counts of the organisms were made and after 2 months all M. integrifolia and herbivores were removed from the plot.

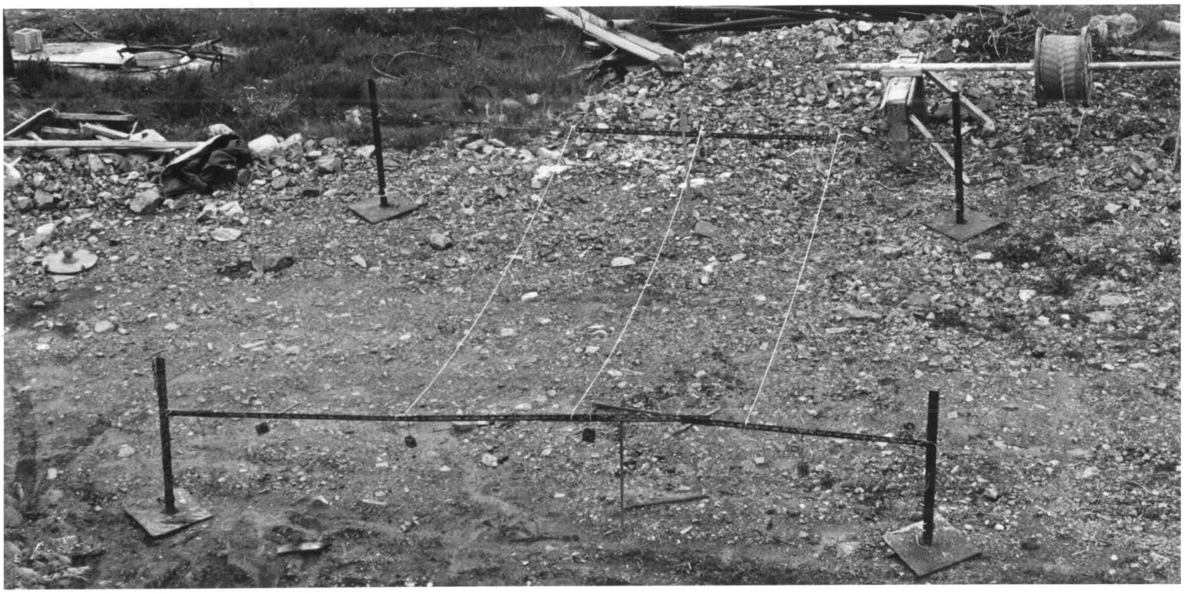
An initial survey of the study area over a two week period beginning June 18, 1973 was completed without disrupting the plant or animal populations. The area was divided up into 4, 5m x 5m sectors with lines and pins. These lines served as a guide for the placement of a moveable grid system to divide each section into 25 quadrats. This grid was held approximately 1 m above the substrate and levelled prior to my making observations (Fig. 28).

Standard symbols defined substrate, animals and plants. Divers carried writing slates which were grided into 5 cm sections. The relative position of plants and animals in each quadrat was recorded as a sketch on one slate. Herbivores upon plants were recorded as number per plant.

Following the complete removal of all plants in a sector the herbivores on the bottom were collected by hand. In the case of the shell sand substrate a 1 m quadrat of substrate was removed to a depth of 5 cm for laboratory examination. The basal diameter of all T. pulligo was measured with vernier calipers to 0.1 mm.

The wind velocity and direction for the past 10 years were obtained from the records of the Cape Beale lighthouse. Periodic salinity and

Figure 28 The moveable grid system used at the Ross Islets detailed study site to subdivide 5 x 5 m sectors into 1 m quadrats. This reconstruction of the grid does not include all the meter lines used to join the parallel lengths of angle iron or the one meter steel rods used to complete each quadrat



temperature readings were made with a Beckman insitu Salinometer Model RS 503 (Beckman Instruments Inc., Cedar Grove, N.J., U.S.A.) to a depth of 6 m during the study period.

RESULTS

There were two main types of substrate in the survey site and these are depicted in Fig. 29. The chart drawn from the initial survey does not show the exact details of topography but gives the major topographical features of the site (Fig. 30).

The understory of the site was not included in the final pictorial presentation (Fig. 31). In general this cover was sparse except for encrusting reds and corallines. Ptilota and articulate corallines were present as scattered tufts and Ulva occurred in a few areas.

The canopy was dominated by M. integrifolia except at the shallow area of the site where Laminaria groenlandica and Alaria marginata were dominant (Fig. 32). During the survey it was not possible to determine the exact boundaries of each M. integrifolia plant due to the overlap of plant holdfasts. Tegula pulligo was the numerically dominant large herbivore on the macrophytes (Table XX).

The position of the herbivores on the bottom as shown in Fig. 33 represents the general distribution of individuals rather than their exact spacial separation. The herbivores on the shell sand portion of the site were those visible to the diver, since the substrate was not disturbed in the initial survey.

Tegula pulligo was twice as numerous on the macrophytes than on the

Figure 29 The two major substrate types found at the Ross Islets detailed study site

a. High relief bedrock substrate

A. gibberosa (arrow)

b. Shell sand substrate with half shells of dead bivalves


a

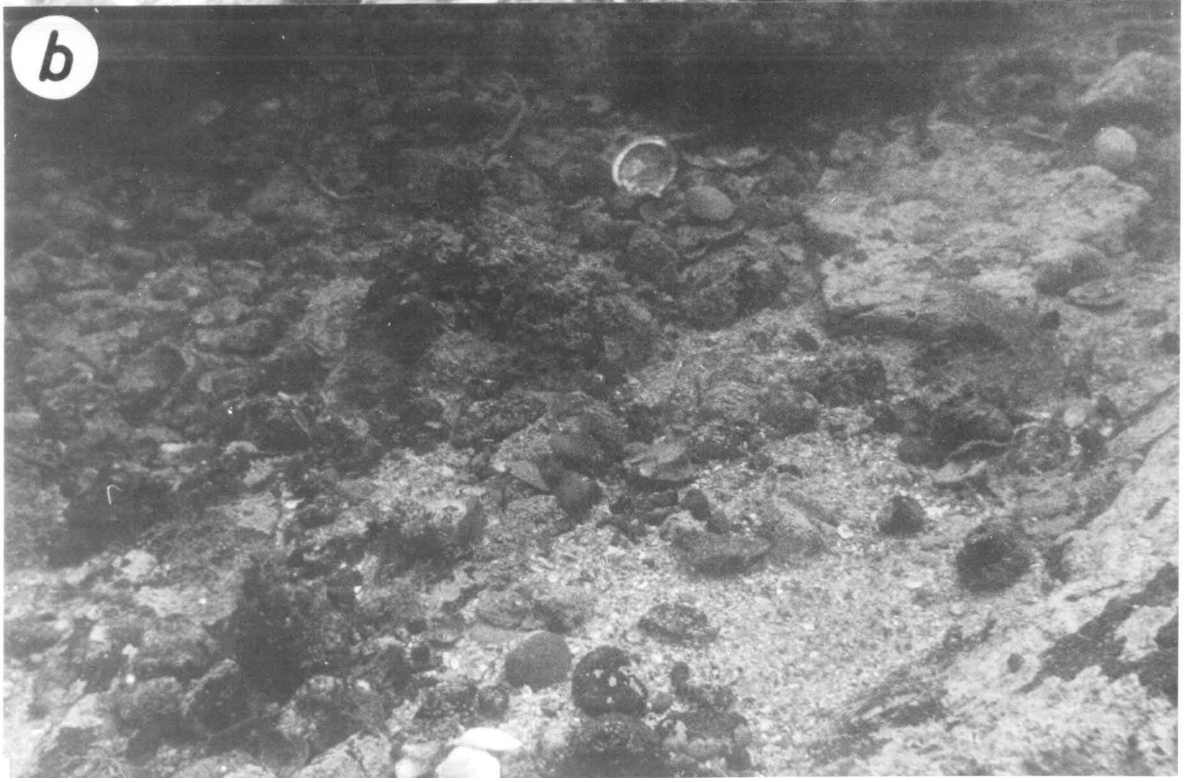

b

Figure 30 The topography of the Ross Islets Plateau Kelp bed study site

sector	position
1	NE
2	SE
3	SW
4	NW

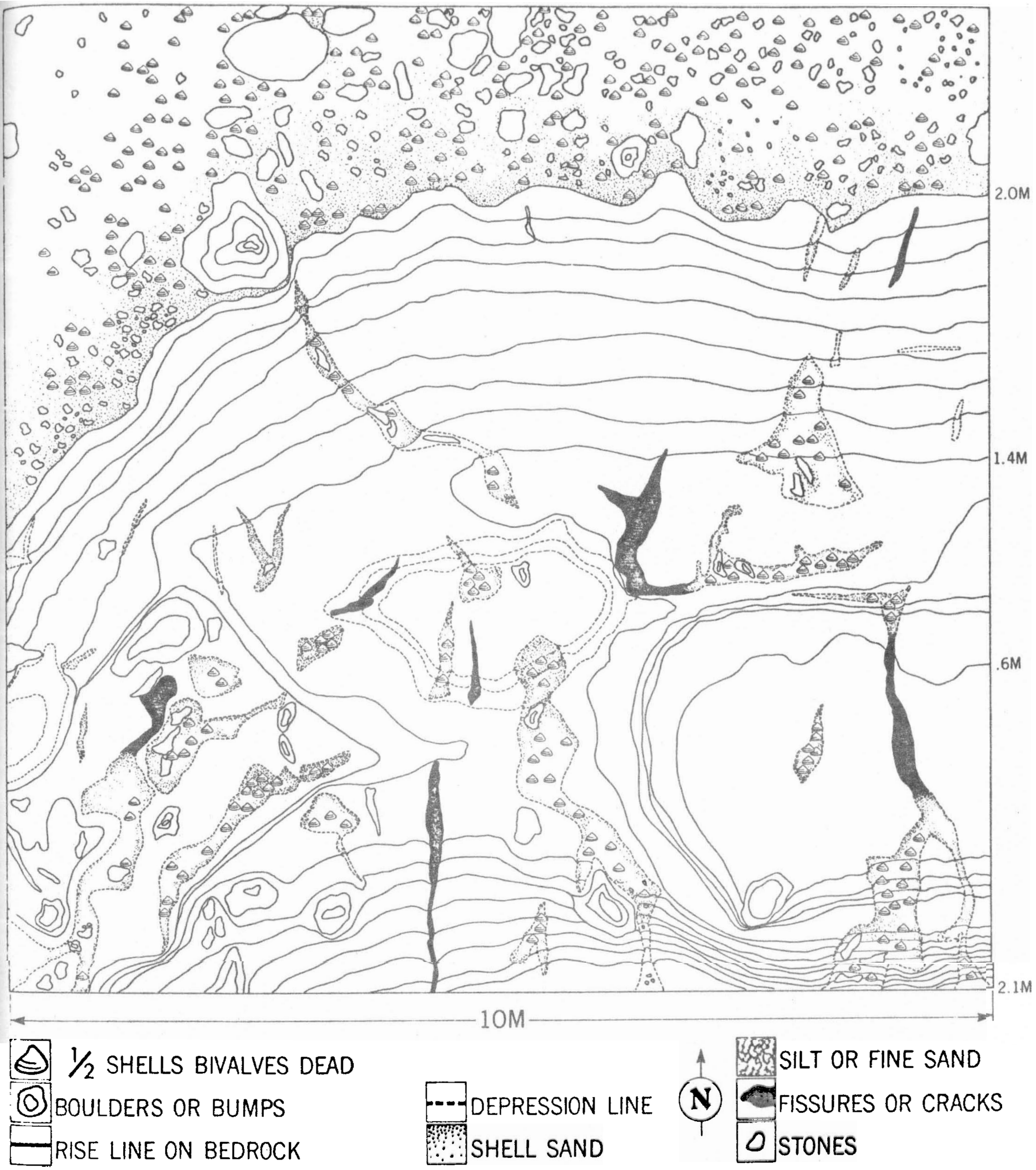

2.0M
1.4M
.6M
2.1M
10M
½ SHELLS BIVALVES DEAD
BOULDERS OR BUMPS
RISE LINE ON BEDROCK
DEPRESSION LINE
SHELL SAND
N
SILT OR FINE SAND
FISSURES OR CRACKS
STONES

Figure 31 Symbols used to represent plants and herbivores in figures 32 and 33

PLANTS

- □ Alaria
- △ Laminaria
- ⬡ P. californica
- ○ M. integrifolia
- ⊗ young M. integrifolia
- ◌ dead holdfast

ANIMALS

- ☆ A. gibberosa
- ○ H. kamtschatkana
- ▲ P. gracilis
- ● S. drobachiensis
- ■ T. pulligo

Figure 32 The macrophyte canopy at the Ross Islets Plateau kelp bed study site including large herbivores on each plant in June, 1973

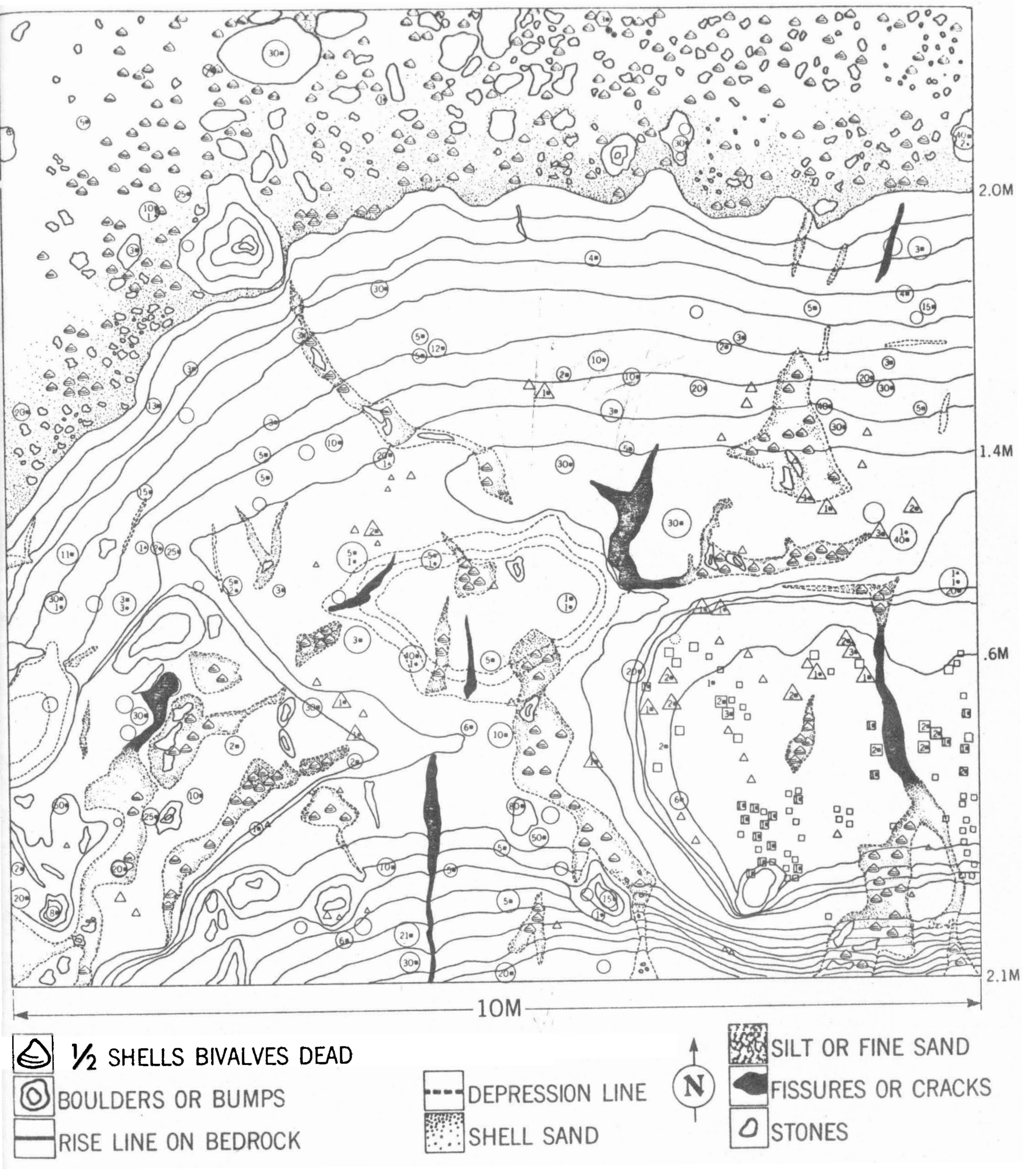
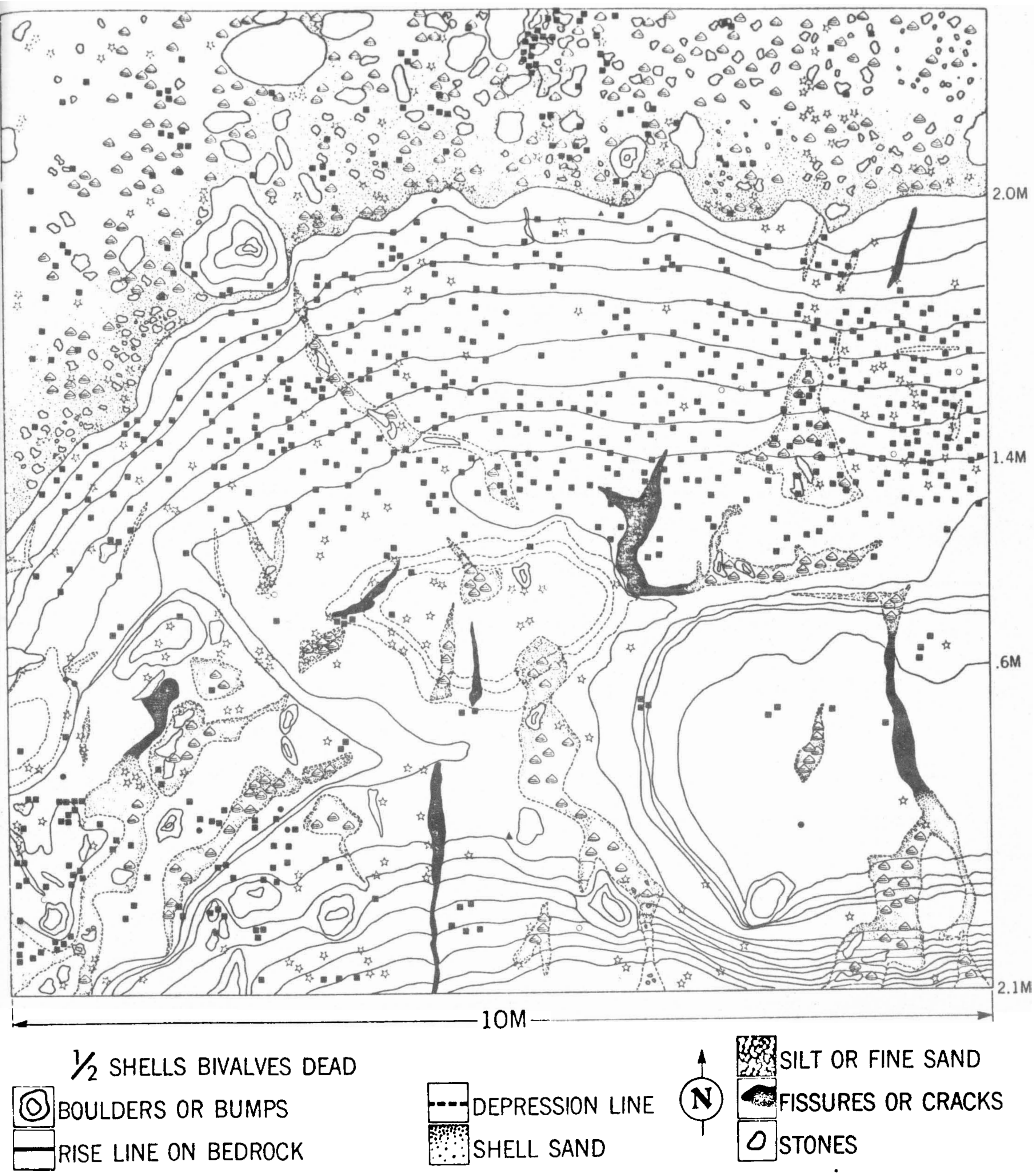

2.0M
1.4M
.6M
2.1M
10M
½ SHELLS BIVALVES DEAD
BOULDERS OR BUMPS
RISE LINE ON BEDROCK
DEPRESSION LINE
SHELL SAND
N
SILT OR FINE SAND
FISSURES OR CRACKS
STONES

Figure 33 The distribution of large herbivores on the bottom at the Ross Islets Plateau kelp bed June, 1973


2.0M
1.4M
.6M
2.1M
10M
½ SHELLS BIVALVES DEAD
BOULDERS OR BUMPS
RISE LINE ON BEDROCK
DEPRESSION LINE
SHELL SAND
N
SILT OR FINE SAND
FISSURES OR CRACKS
STONES

bottom (Table XX). Further *T. pulligo* were larger but fewer on the bedrock than on shell sand surface. *Strongylocentrotus droebachiensis* was the second most abundant large herbivore on *M. integrifolia*. *Astraea gibberosa* was evenly distributed in the survey site except clumping occurred ~~in~~ the crevices (Fig. 33, Table XX).

The following harvesting results include population structure and distribution data. Degenerate (greater than 80% of laminae missing) and healthy fronds were considered productive parts of the population and were grouped together. Broken frond pieces were considered to be drift material and were eliminated from the results. Modes of frond size distribution were less than 100 cm and the mean length was less than 200 cm indicating a very young and productive kelp bed (Fig. 34 A). The majority of degenerate fronds were in the 225 - 250 cm class (Fig. 34 B) and their mean was 365 cm and 80 percent of all fronds in the 450 to 500 cm class were degenerate (Fig. 34 C).

A total of 404 kg wet weight of *M. integrifolia* tissue was harvested from the 100 m quadrat. Twenty-nine kg of the total weight was holdfast tissue. It was not possible to remove all the holdfast tissue, approximately 50 percent of this tissue remained on the substrate.

The *T. pulligo* population as harvested was within 25 percent of the initial visual survey estimate (Table XX). *Tegula pulligo* harvested from the shell sand area were considered separately from the individuals on bedrock because the total for the area was the result of extrapolation from a single 1 m quadrat sample. The mean basal diameter of this population significantly less than for the bedrock population, 8.8 mm vs 21.2 mm

TABLE XX

Herbivore Survey[a] and Harvest Results[b] Ross Islet's Study Area

Sector	Position	Species T.pulligo		A.gibberosa		S.drobachiensis		P.gracilis		P.producta		H.kamtschatkana	
		a	b	a	b	a	b	a	b	a	b	a	b
1	Substrate	227	69 + 690[c]	71	47	3	1	-	-	-	-	-	-
	Alga	219	455	-	-	-	4	1	27	1	1	1	-
2	Substrate	104	92	95	69	7	2	-	-	-	-	4	3
	Alga	398	510	-	-	10	7	1	10	-	-	-	-
3	Substrate	34	53	26	74	3	6	1	-	-	-	-	2
	Alga	385	466	-	-	6	12	-	23	-	1	-	-
4	Substrate	319	77 + 828[c]	72	69	6	3	-	-	-	-	-	2
	Alga	321	281	-	-	-	7	2	20	-	1	-	-
Totals	Substrate	684	281 + 1518[c]	264	259	19	12	1	-	-	-	5	7
	Alga	1323	1712	-	-	16	30	4	80	1	3	-	-

[a] visual counts from June 15, 1973 to July 1, 1973

[b] collections from August 20, 1973 to August 23, 1973

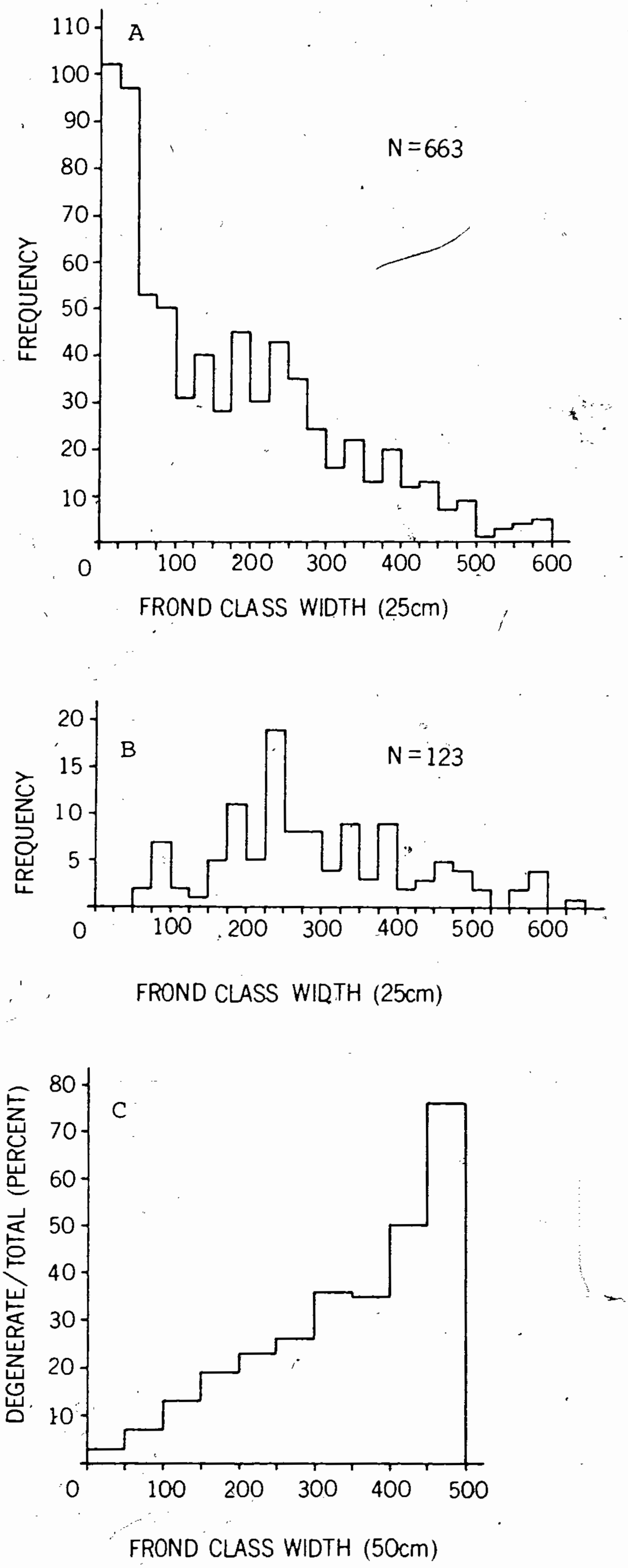
[c] extrapolated from a 1 m^2 substrate collection

Figure 34 Population structure of M. integrifolia fronds collected at the Ross Islets study site from August 20 to 23, 1973

a. Histogram of the size (length) distribution of degenerate and healthy fronds (Class width 25 cm)

b. Histogram of the size distribution of degenerate fronds (Class width 25 cm)

c. The percentage of degenerate fronds in each size class of total fronds (Class with 25 cm)


A
N=663
FREQUENCY
110
100
90
80
70
60
50
40
30
20
10
0
100
200
300
400
500
600
FROND CLASS WIDTH (25cm)
B
N=123
FREQUENCY
20
15
10
5
0
100
200
300
400
500
600
FROND CLASS WIDTH (25cm)
C
DEGENERATE/TOTAL (PERCENT)
80
70
60
50
40
30
20
10
0
100
200
300
400
500
FROND CLASS WIDTH (50cm)

(Fig. 35). The mean basal diameter of *T. pulligo* collected from *M. integrifolia* was 20.1 mm (Fig. 36).

The total population of *A. gibberosa* at the site did not change between the surveys (Table XX). The kelp crab *P. gracilis* was the second most abundant large herbivore on *M. integrifolia* (Table XX). There was no large change in the total numbers of the green sea urchin, S. droebachiensis population (Table XX).

During and prior to the study period the wind velocity was low and not from the exposed northerly direction of the study site. Therefore erosion was not yet accelerated in this bed. The temperature at 4 meters ranged from 13.1 to 16.1° C in 8 readings during July 24 to September 28, 1973.

The results of this detailed study were in agreement with my previous seasonal studied of *T. pulligo* and *M. integrifolia*.

Tegula pulligo was the numerically dominant herbivore in the Ross Islet kelp bed. The majority were potential *M. integrifolia* grazers, being found on the plants. General distribution and bimodal population structure were the same as found in seasonal transect surveys and monthly samples (Fig. 35, 36).

The kelp bed was in a stage of rapid growth with the majority of fronds less than 100 cm and healthy. This was the condition of all surveyed beds during mid to late summer.

The following sub-section calculating *T. pulligo* grazing impact is based upon the plant and herbivore populations of the study area.

Figure 35 Histogram of the size distribution (basal diameter) of *T. pulligo* collected from substrate in the Ross Islets study site

main figure	*T. pulligo* collected from bedrock substrate
insert	*T. pulligo* collected from a 1 m quadrat sample of shell sand substrate

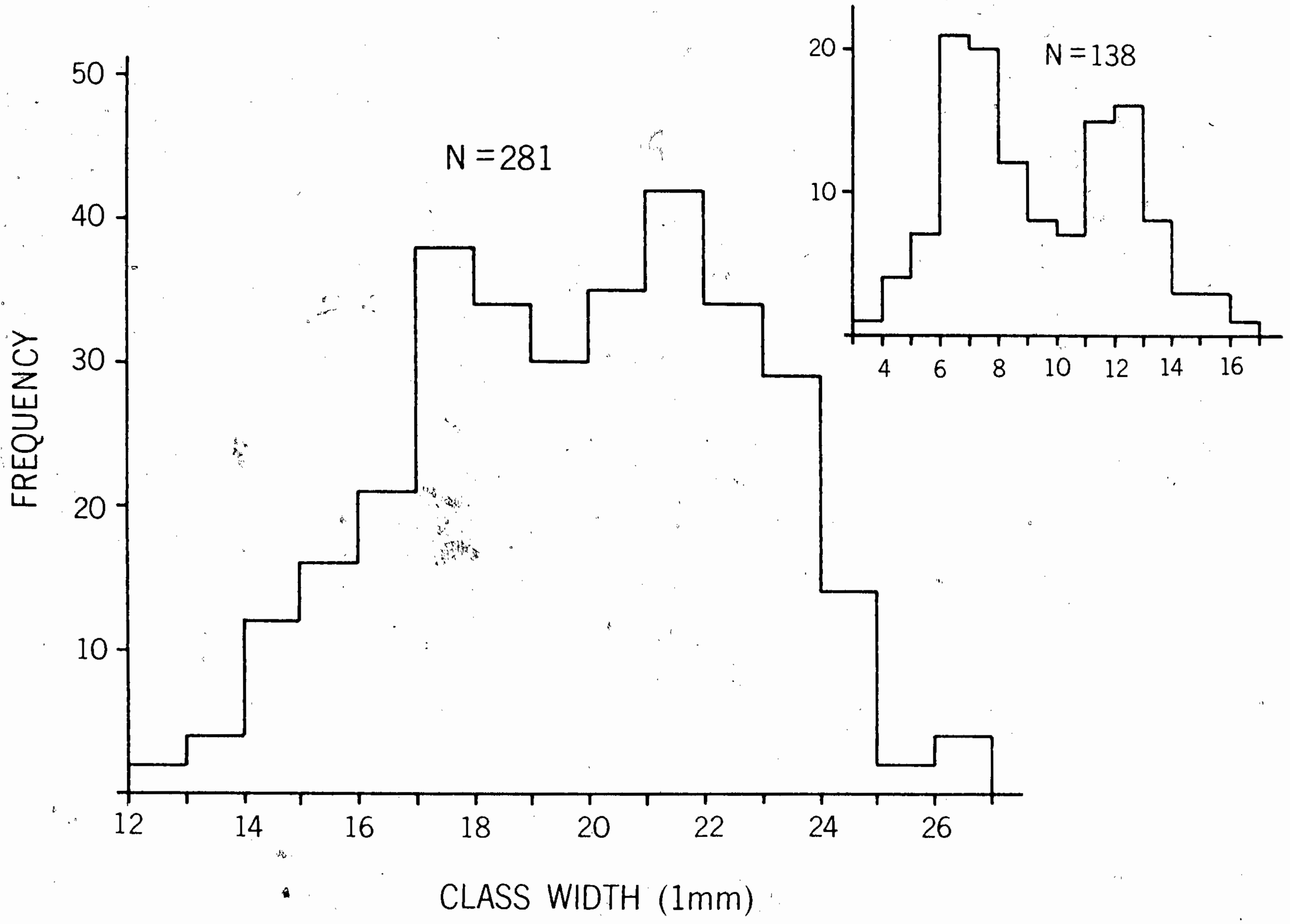
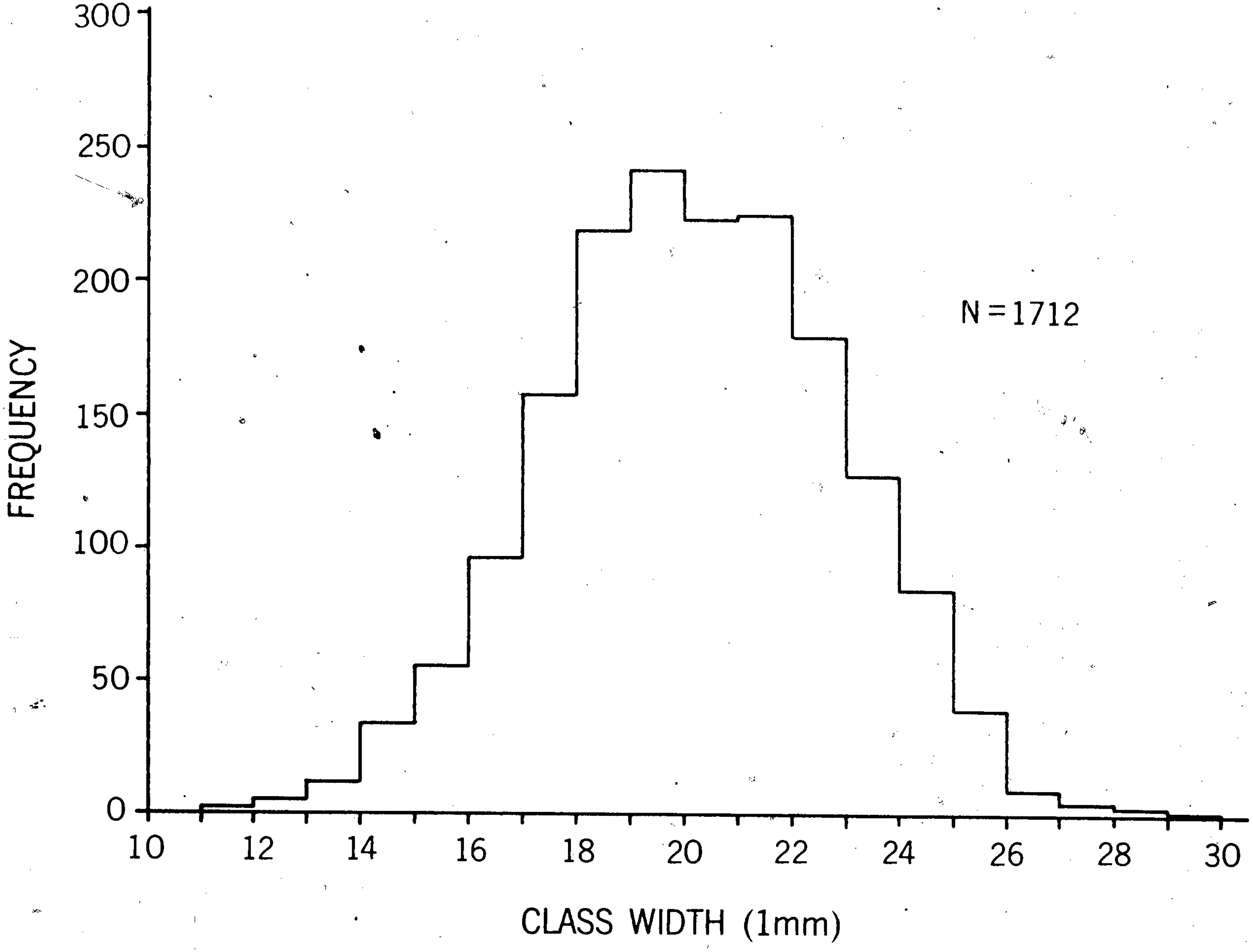

N = 281
FREQUENCY
10
20
30
40
50
12
14
16
18
20
22
24
26
CLASS WIDTH (1mm)
N = 138
10
20
4
6
8
10
12
14
16

Figure 36 Histogram of the size distribution (basal diameter) of T. pulligo collected on M. integrifolia harvested at the Ross Islets study site


FREQUENCY
300
250
200
150
100
50
0
N = 1712
10
12
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CLASS WIDTH (1mm)

Calculation of T. pulligo Grazing Impact at the Study Site

The calculation of a value to reflect the impact of T. pulligo on the net production of M. integrifolia was based on the application of general conclusions and constants drawn from my plant and animal studies to the specific situation encountered at the Ross Islets Plateau kelp bed.

The net production of the kelp bed was calculated using the most important structure for net production, the lamina. The tissue loss due to T. pulligo grazing was calculated from the actual tissue consumed in laboratory grazing experiments and the tissue loss due to grazing damage and erosion as determined in laboratory and field studies. The period chosen for the calculation was from August 18, 1973 to September 18, 1973.

The basic assumptions made in the calculation were considered in previous discussions;

a) The lamina was the most important structure in the continued life and production of the frond.

b) The population structure and concentration of T. pulligo in the study area were constant for the calculation period.

c) There were no changes in physical parameters which would have changed the feeding rate of T. pulligo or the growth rate of M. integrifolia appreciably during the calculation period.

The constants used in the calculation were mean values obtained from previous sections of this thesis appropriate to the prevailing physical and biological conditions and are as follows:

a) One lamina was formed every 2.5 SD ± 0.5 days.

b) A lamina grew in area for 22 days after splitting from the apical scimitar.

c) The lamina grew at the rate of 0.4 SD ± 0.30 cm per day in width and 1.9 SD ± 0.9 cm per day in length for a total area increment of 364 SD ± 167 cm^2 over 22 days.

d) The first 9 SD ± 2 independent laminae were actively growing on all fronds.

e) The fresh weight of lamina tissue excluding sporophylls was 0.033 SD ± 0.007 gm/cm^2.

f) The consumption rate of T. pulligo feeding on M. integrifolia was at 0.013 SD ± 0.006 grams per gram of body weight per 24 hours at 15°C.

g) Grazing damage and erosion caused by T. pulligo were equivalent to a tissue loss rate of 0.3 grams per gram of body weight per 24 hours ± 70%.

h) Tegula pulligo on a shell sand substrate were not potential grazers of M. integrifolia.

i) A total of 663 fronds with a mean length of 200 cm were active at the beginning of the calculation period.

j) On a mean frond for the study site there were 20 independent laminae and 13 terminal slits for a total blade number of 33.

k) The area of an independent lamina is 660 SD ± 116 cm^2.

l) The temperature at 3 m below the surface between August 18 and September 18, 1973, was 13.1°C to 14.6°C. This temperature range was comparable to the 15°C consumption rate experiment but 5C° higher than the erosion-grazing experiment.

m) One-thousand nine-hundred and ninety-three T. pulligo with a mean basal diameter of 20.1 and a mean weight of 3.0 gm were actively feeding on

M. integrifolia during the calculation period.

From my growth studies the equation (1) for total area increment of a frond's laminae can be applied to the study site. An average frond from this study site growing during a 30 day period would have a total lamina area increment of 4020 cm^2 ± 60%. Since there were 663 actively growing fronds in the study site, there was a total of 2.7 million cm^2 ± 60% increment in lamina surface area for the study site over 30 days. At .033 SD ± .007 gm/cm^2, this surface area was equivalent to a total fresh weight biomass of 102 kgm ± 70%.

A total of 1993 *T. pulligo* with a total weight of 5,980 gm consuming .013 SD ± .007 gm/gm/24 hr of *M. integrifolia* laminae will consume 78 SD ± 42 gm in 24 hours and 2.3 SD ± 1.2 kgm for the 30 day calculation period. However, using the grazing-erosion constant of 0.3 gm/gm/24 hr *M. integrifolia* tissue loss, there is a total of 55 SD ± kgm lost over 30 days ± 70%. Using the minimum and maximum values for consumption, grazing and erosion, and production, I obtained a range of values expressed as a percentage of total lamina production. *Tegula pulligo* consumed 2.3% of the total lamina biomass production ± 1.6%, but its impact (grazing-erosion) was 55% of the total lamina biomass production ± 38.5%.

GENERAL DISCUSSION

The four sections of this thesis can be treated as independent units. However, each section has contributed specific information to answer the question "What is the impact of T. pulligo on tissue loss in M. integrifolia kelp beds".

Plant growth studies have been approached by the suggestion:

> "Sometimes it may be convenient to refer the standing crop to the feeding activities of a particular herbivore rather than to a human harvesting technique . . . . " (Westlake, 1963).

The lamina was chosen for both its importance in plant productivity and as sites of herbivore grazing damage. The general morphology of M. pyrifera is similar to that of M. integrifolia and M. pyrifera laminae are the sites of 88 percent of the frond photosynthetic capacity (Sargent and Lantrip, 1952). In terms of standing crop the laminae of M. integrifolia represent two thirds of the total dry plant weight (Scagel, 1947).

The surveys of T. pulligo and M. integrifolia distribution have shown T. pulligo to be the only large herbivore present on the plant during its entire development and degradation.

Feeding experiments have shown T. pulligo can feed continuously (as a total population) on M. integrifolia during the plant's entire life history. This grazing was also recognized as being composed of tissue consumption and incidental tissue loss.

Erosion and grazing damage studies required that a field assessment of grazing impact must be combined with the physical erosion forces for the period under study.

Finally, a very close study of one small part of a kelp bed over a one month period has provided a model situation. Using a known population of plants and herbivores plus assumptions and constants derived from previous studies, an actual figure was calculated for the grazing impact of T. pulligo.

The calculation of a value which reflects the importance of a herbivore in a community has generally been based on the consumption rate of the herbivore and the total production of tissue in the plant (Teal, 1962). And if one considers only consumption, it may be true that:

> "In almost every case it appears that macrophytes yield only a small fraction of their production to grazing food chains" (Mann, 1972).

However, this statement is very misleading when one considers the total loss of tissue due to the activities of T. pulligo in the Macrocystis beds of the Northeast Pacific Coast.

Using the food chain method of calculating herbivore importance in the community I found T. pulligo was consuming only 2.3 percent of lamina production during the late summer at the Ross Islets Plateau kelp bed. However, the actual impact of the snail on tissue loss is probably much closer to the figure of 55 percent of lamina production based on grazing-erosion experiments.

To clarify the point, let us consider the fate of one lamina on a M. integrifolia frond as exemplified by my studies. After a lamina is free from the apical scimitar it grows vigorously for the first 5 to 10 days.

Then its overall growth rate slows and ceases after 22 to 24 days. During this period it may be subject to light grazing pressure but generally the herbivores are active on lower laminae.

As the grazing pressure is increased when the lamina becomes more basal relative to the apical scimitar, and the lamina is no longer adding tissue the balance is changed to net tissue loss. This results from consumption, weakening of tissue due to consumption and perhaps microbial degradation. Large pieces of tissue are lost because the grazing damage has weakened the lamina and wave action places stress on the damaged area.

The large fragments become drift material which can be utilized by lower level herbivores such as A. gibberosa. Such secondary grazing increases the reduction of particle size. Paine (1971) suggests a portion of this drift material is utilized by intertidal herbivores. Other fragments may be more slowly broken down by bacterial degradation. The fate of these small particles and fragments was beyond the scope of this study, but it is reasonable to assume the utilization of this material by detritus feeding invertebrates and at least some conversion into dissolved organic matter (Khailow & Burlakova, 1969; Mann, 1972). Even if the tissue loss from the incidental effects of T. pulligo grazing on M. integrifolia does not enter a herbivore food chain, it is still lost to the plant.

In conclusion, my study has pointed out the need to distinguish between the consumption of plant tissue by a herbivore and the actual impact of the herbivore upon the loss of plant tissue in the field. These two approaches were seen to differ over 20 fold in my study.

The ranges of M. integrifolia and T. pulligo overlap in the Northern Pacific. If their local distribution and association in Barkley Sound is typical, T. pulligo has an important part in the turnover of organical material in these kelp bed communities.

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