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The kelp forest ecosystem at Petticoe Wick Bay lat 55 55'N. Long 2 09'W: an ecological study

Whittock, Alan

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THE KELP FOREST ECOSYSTEM AT PETTICOE WICK BAY

LAT 55°55'N. LONG 2°09'W

AN ECOLOGICAL STUDY

by

ALAN WHITTICK

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University of Durham for
the Degree of Master of
Science.

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This thesis, which is entirely the
result of my own work, has not been
accepted for any degree and is not
being submitted concurrently in
candidature for anyother degree.

Alan Whitlick.

CONTENTS

ACKNOWLEDGEMENTS

ABSTRACT

The sublittoral vegetation at Petticoe Wick
Bay Lat 55°55'N. Long 2°09'W. is described using two
methods; a classificatory one (of the Zurich-Montpelier
School of Phytosociology) and an agglomerative one (the
Wisconsin Comparative Ordination Technique). Floristically
distinct groups are extracted and discussed.

Methods of measuring the net annual production
of the dominant kelp Laminaria hyperborea (Gunn)Foslie
and its associated epiphytes to assess their performance
in relation to depth of submersion are presented and the
results discussed. Data on the age structure of the
community and infestation levels of Patina pellucida L
is presented. The performance of L. hyperborea at three
other sites is studied and compared to the results from
Petticoe Wick.

CHAPTER 1

INTRODUCTION

The littoral zones of the world's oceans, especially those of north temperate regions, have been the subject of extensive ecological studies by numerous workers; Gislen (1930), Den Hartog (1959) and Lewis (1964) provide comprehensive reviews of much of this work.

Owing to its relative inaccessability, much less work has been carried out in the sublittoral. Early studies by means of grabs and dredges have provided descriptive data but in the main these have been confined to animal communities of soft substrates (Peterson 1911, 1913, 1915, 1918; Jones 1950).   "View boxes" allowing observation of the sublittoral (Chapman 1944, Walker 1947) have found only limited application.

The advent of diving techniques both of the traditional 'hard hat' surface air supply types and more recently, self contained underwater breathing apparatus, (S.C.U.B.A.), has made possible direct observation and sampling of sublittoral ecosystems.   The pioneer work of Gislen (1930) must be regarded as a classic of inshore marine biology;   he attempted a "blanket" survey in which sociological structure, biomass and seasonal aspects of

sublittoral communities were related to environmental factors. Many direct observations on the distribution of sublittoral algae followed, these range from simple species lists (Kain 1961, McAllister et al. 1967, Norton et al 1969) to more detailed studies of the distribution and ecology of various species (Kitching 1941, Forster 1958, Burrows 1958, Marshall, 1960, Kain 1962, 1963, 1966, 1967, Neushul 1967, Conway 1967, Norton 1968).

PRODUCTIVITY AND GROWTH STUDIES

"Long term (seasonal or yearly) production of organic matter has not been studied as thoroughly in littoral algae as in the algae of the open ocean".

This statement of Binks (1955) still holds true and is equally applicable to sublittoral ecosystems. Studies of the 'productivity' of sublittoral ecosystems around the British Isles have, in the past, been largely orientated to resource evaluation of commercially important species (Walker 1952, 1954a,b,c,d; 1955 ; 1958a,b; Walker and Richardson 1955, 1956, 1957a,b). They all involved the use of grabs and produced only very approximate measurements of biomass, which were at best rough estimates of cropping potential.

More detailed studies have been carried out on the growth rates of marine algae, various methods have been employed, the most common being the light and dark bottle method measuring assimilation over a short period of time by means of changes in oxygen concentration.

Gail (1918,1922), Erke (1929) and Printz (1939) used this technique with a variety of marine macrophytes and Levring (1947) made a comprehensive study using this method under varying conditions of depth, water turbulence and surface insolation. More recently short term assimilation in macrophytic marine algae has been measured using the $\left[C^{14}\right]$ method of Steeman Nielsen(1952), (Larkum et al 1967, Johnston and Cook 1968). Measurements of this type, while providing useful physiological data, have only limited relevance to long term growth studies for the following reasons:

(1) These measurements are rarely taken at more than one time and therefore only reflect the conditions at that time; conditions which are usually not measured.

(2) Tikhovskaya (1940) monitored photosynthesis and respiration of Laminaria saccharina (L.) Lamour and reported large seasonal fluctuations.

More direct studies of growth have been carried out. Measurements of changes in thallus length have been made, either directly (Rattray 1886, Fallis 1915, Klugh and Martin 1927, South and Burrows 1968), or by means of holes punched in the thallus (Parke 1948, Sundene 1962, Norton and Burrows 1969). Measurements based on biomass have also been made (Kirejava and Schapova 1938; Jones 1959; Kain 1963, 1967).

Sargent and Lantrip (1952) studied both assimilation (changes in oxygen concentration in light and dark bottles) and growth (increment cropping) in the giant kelp <u>Macroystis pyrifera</u> (Turn.)Ag. Other workers (Conover 1958, McFarland and Prescott 1959, North 1961, Neushull and Haxo 1963) have studied the metabolism and growth of whole ecosystems dominated by macrophytic marine algae.

Despite this previous work sublittoral production ecology is still at the stage of data collection and speculation. There are two outstanding questions yet to be answered:

(1) What range of production figures can be expected over wide geographic ranges?

(2) Is there sufficient variation between ecosystems, or is there too much variation within ecosystems, to make comparative studies worthwhile?

The data collected to date is stimulating but is insufficient to form a base on which to make generalisation What is needed is a rapid method which provides an integrated picture of primary production, a measure of the performance of a species and ecosystem in relation to the environment <u>in toto</u>.

AIMS OF THE STUDY

The study was designed:

(a) To test a rapid method for the measurement of the performance, measured as net primary production, of the <u>Laminaria hyperborea</u> (Gunn.)Foslie (Kelp) forest.

(b) To obtain data, relevant to question (2) above, by comparing the performance of the kelp forest in relation to depth at one site.

(c) To provide basic information regarding question (1), by comparison of similar data collected at three geographically distinct sites.

(d)   To describe the sublittoral vegetation of
the reference site, Petticoe Wick Bay (Grid Ref.
NU907692) using both classic (Zurich Montpelier)
and more modern (Wisconsin comparative ordination)
phytosociological techniques.   Petticoe Wick Bay
is being used as a non polluted reference site in
the study of marine pollution along the east coast
of Britain (Bellamy et al 1967a.)

Since the commencement of this study the methods
described here have been used with success in a number of
studies (Bellamy et al 1967b, 1968, Bellamy and Whittick
1968, John 1969).

THE TERM KELP

This term has passed into general usage to
describe members of the Laminariales although Chapman
(1944) has stated that this is incorrect and that the
term should be reserved for the ash produced by burning
marine algae.   In this thesis, 'kelp' is specifically
used to describe Laminaria hyperborea.

THE ECOSYSTEM

Laminaria hyperborea is the most important
sublittoral kelp in western Europe (Kain 1967).   The
southern limit of its distribution is on the coast of

Portugal, it has a somewhat disjunct localised distribution along the Atlantic coasts of France and Spain (Hamel 1931-1939; Miranda 1934; Ardre 1957, 1961; Seone-Camba 1960, 1966; Dixon 1961; deVirelle 1963). It is very common around most of the British coast but is rare on the East coast south of Yorkshire and in the Eastern basin of the English channel (Kain 1967). Although rarely found on the coasts of the Netherlands it is common in Heligoland (Den Hartog 1959). It occurs along the coast of Norway, north and at least as far as the U.S.S.R. border (Kain 1967) and is common in the Faeroe Islands and on the coast of Iceland (Borgesen, 1905; Borgesen and Johsson 1905).

Laminaria hyperborea is restricted to stable boulders and continuous rock surfaces (Kain 1962). The lower limit of its depth distribution varies greatly around the coasts of the British Isles. The plants grow densely in the immediate sublittoral forming a closed 'forest', the density tending to decrease with depth (Ernst, 1966) forming what has been described by Kitching (1941) as 'parkland'.

The typical kelp forest has a layered structure:

(1) Crustaceous lithophytes.

(2) A ground layer of micro and macrophytes.

(3) A canopy of the dominant.

A fourth structural unit, although not a layer in the strict sense of the word, must be recognised; that is the epiphytes growing on the stipes, haptera and also to a certain extent on the laminae of the dominant. The Laminaria hyperborea sporophyte is present both as canopy and understorey plant. The gametophyte generation is not obvious in the field but may be detected by microscopic examination of the substrate or by culturing samples of substrate in the laboratory.

This work is confined to a study of the sporophyte of L. hyperborea and to the macrophytic epiphyte flora of the stipes of this organism.

Areas Studied

Fig. 1 shows the areas visited during the course of this study.

FIGURE 1

The sites studied:

     (1)   Main study site - Petticoe Wick Bay.

     (2)   Flamborough Head

     (3)   Sennen Cove

     (4)   Dunmanus Bay.
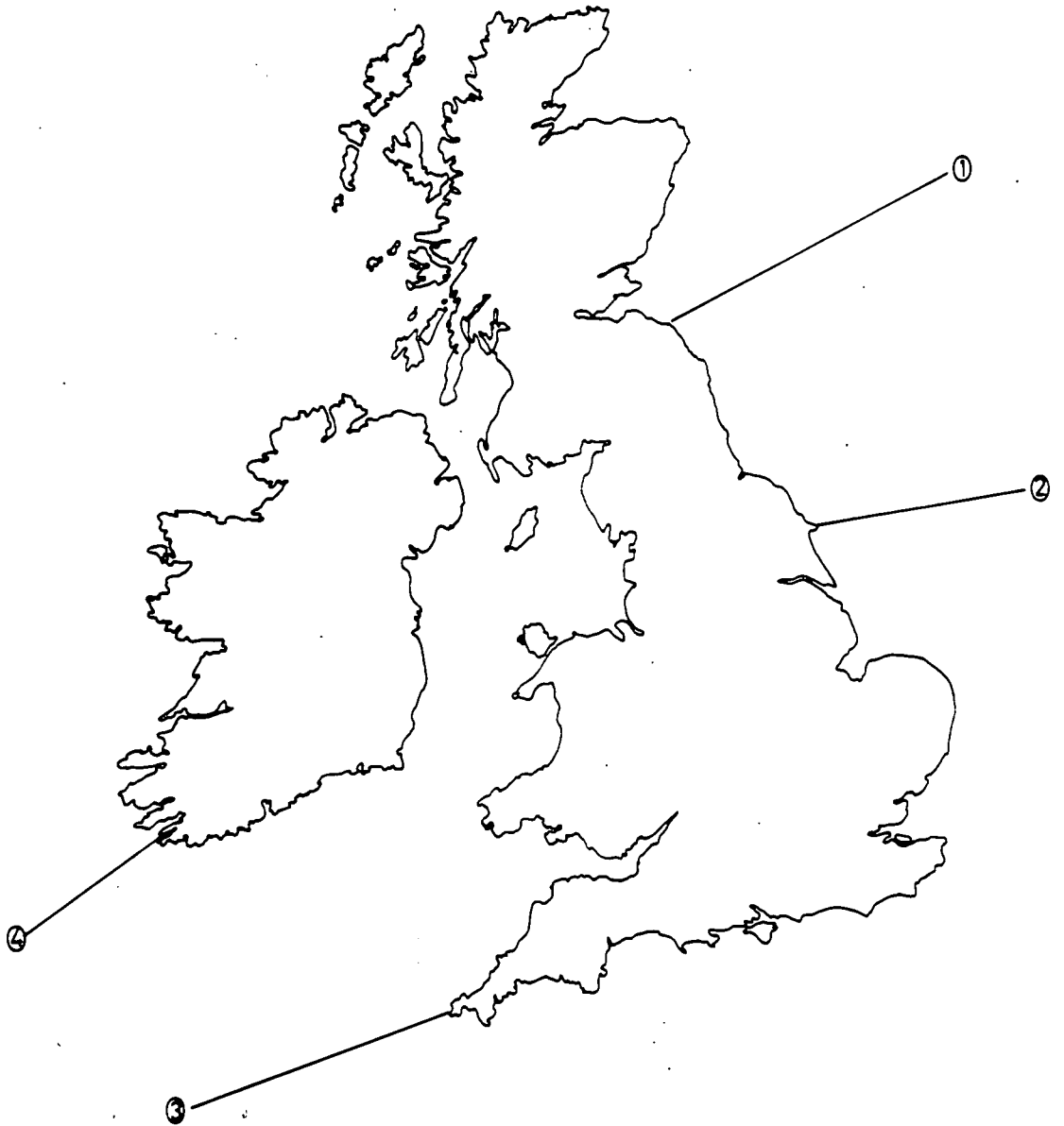
UNITS OF MEASUREMENT

All measurements, unless specifically stated, are as below:

(1) Length. All linear measurements are in centimetres (cm) except in the case of depths which are in metres (m) corrected to depths below mean low water spring tide levels.

(2) Measurements of biomass are in grammes (g) dry weight.

(3) Weight per unit length is measured in grammes per centimetre (g/cm).

(4) All results, where applicable, are given as a mean plus or minus the limit of confidence for the sample when $p = 0.05$ ($\bar{x} \pm 1$)

Algal taxonomic nomenclature follows that of Parke and Dixon (1968).

CHAPTER 2

SITE DESCRIPTION

SITE DESCRIPTION

The main study site is Petticoe Wick Bay, Fig.2 a small inlet situated North of St. Abbs Head on the Berwickshire coast Lat 55°55'N long 2°09'W. The primary reason for the selection of this site is the ease of access at all states of the tide and in all weather conditions. Preliminary investigations with an aqualung revealed an extensive sublittoral flora extending to depths of 13 m to 14 m. The substrate in the immediate sublittoral consists of large stable boulders which towards deeper water give way to gently sloping (< 10°) shelves of solid rock. At depths below 15 m this rock, is for the most part, covered by sand and coarse gravel, although extensive areas of bare rock can be found below this depth. Two areas in the bay form exceptions to this description. The centre of the bay at a depth range of 3 m to 10 m consists of small unstable boulders and the east face of the rock, Wick Gaut, in the centre of the bay is vertical from low water mark to a depth of 10 m.

The sublittoral vegetation can be divided on the dominant species of Phaeophyta into four groups:

FIGURE 2

Petticoe Wick Bay.

1. <u>Laminaria digitata</u>

2. <u>Laminaria hyperborea</u>

3. <u>Laminaria saccharina</u>

4. <u>Halidrys siliquosa</u>

Fig. 3 is a sketch map of the bay showing depth contours
and the approximate distribution of these groups.

FLORISTICS

Collection of Data

The initial selection of a suitable survey stand
for description was performed relatively quickly by diving
from the water surface and taking the stand of vegetation
immediately below. In this way, tendencies to choose
particular stands for description were minimised. No set
quadrat size was used for description, though in practice
areas described were approximately 3 x 3 metres dependent
of total stand size and visibility of the water at the
time. On occasions, a quadrat was used for the determination
of the minimal area for description.

The concept of minimal area is reviewed by
Hopkins (1957) and is based on a curve constructed by
plotting the number of species found against the size of
the area sampled. In this case, a quarter metre quadrat,
50 x 50 cms, was expanded by doubling up to 2 x 2 metres.

FIGURE 3

Sketch map of Petticoe Wick Bay showing sublittoral
depth contours and main dominant vegetation types.

    (1)   <u>Laminaria digitata</u>

    (2)   <u>Laminaria hyperborea</u>

    (3)   <u>Laminaria saccharina</u>

    (4)   <u>Halidrys siliquosa</u>

Scale 1:2000

PETTICOE WICK BAY

H.W.M.S.T.

L.W.M.S.T.

1 m

3 m

5 m

7 m

9 m

Wick
gaut

11 m

13 m

DEPTH (metres)

1

2

3

4
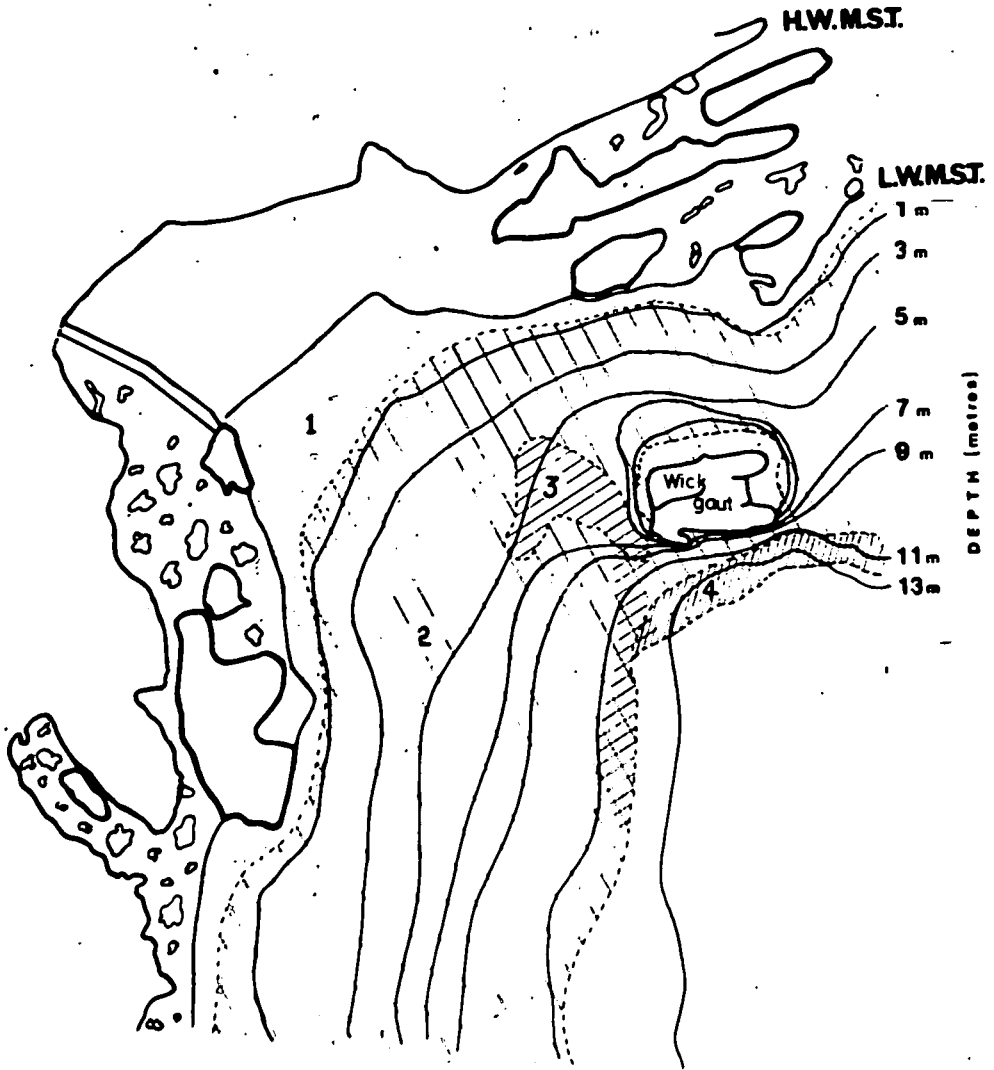
The results are shown in (Fig. 4).   The minimal area
is supposedly reached when the curve flattens out and no
further species are added with increase in quadrat size.
As pointed out by Hopkins (1957), this is an idealised
case and rarely occurs in practice and in the present
study it is seen that although the curve undergoes a
change in slope at the 1 sq. m level, species are still
added with further increase in quadrat size.   A subjective
judgement would be that the major change in slope of the
graph constitutes the point at which the minimal area is
reached.   This size of one square metre is in agreement
with the size for the marine communities studied by
Molinier and Picard (1952);   Den Hartog (1959) and
Kornas et al (1960).

The time for completion of a stand description
depended on a number of factors including density,
diversity, depth, water clarity, temperature and turbulence,
and could take up to 20 minutes of diving time.   29 survey
plots were described, selected to cover the entire depth
range of the sublittoral vegetation.   Species lists were
written in situ using a soft pencil on a roughened white
plastic sheet.   A typical description consisted of:

FIGURE 4

Minimal area curve for the sublittoral vegetation at
Petticoe Wick Bay.
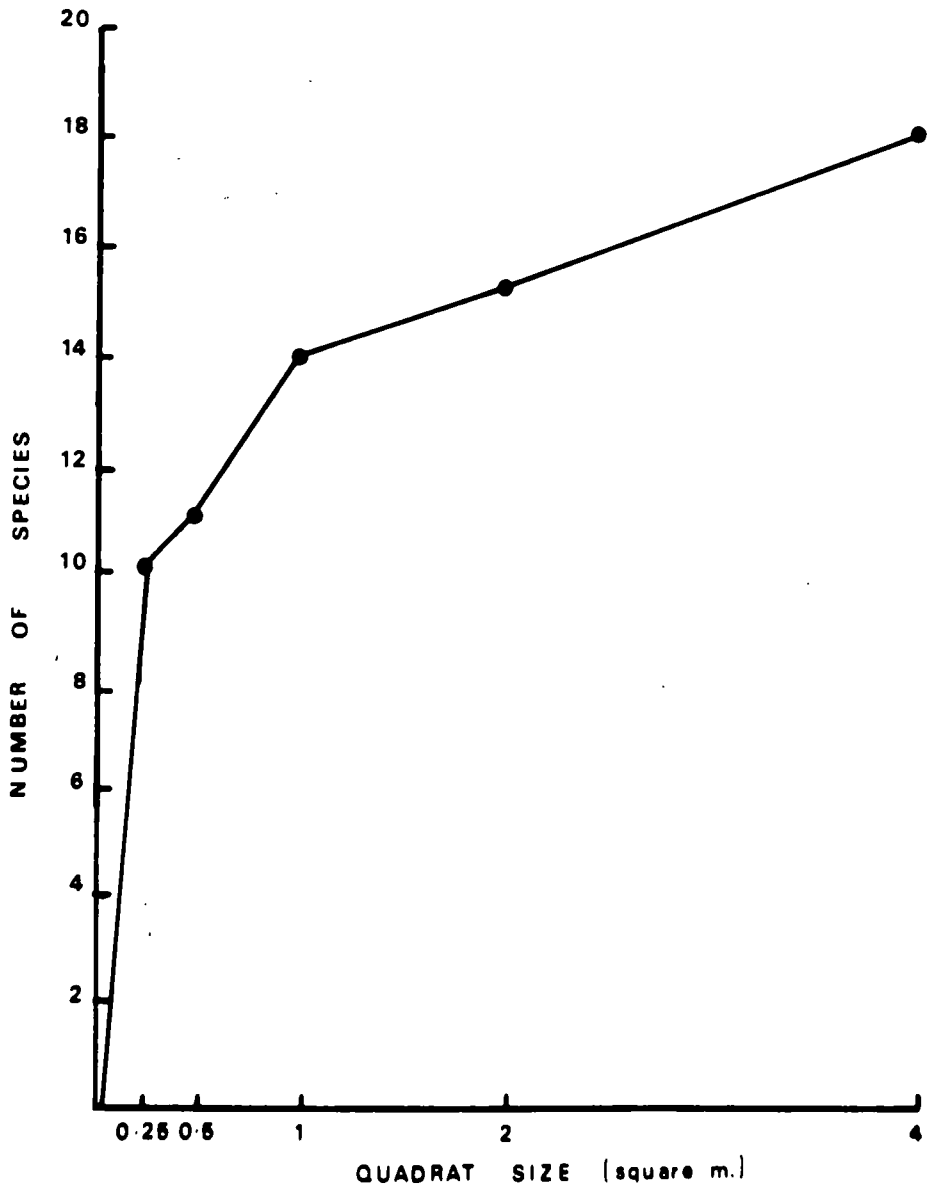
1. A full list of all the species in the survey plot; all those which could not be identified **in situ** were placed in numbered bags for subsequent determination in the laboratory.

2. Indices of cover abundance and sociability were noted for each species using the scales proposed by Braun Blanquet (1927,1951).

3. Various site data was also added - depth, type of substrate and total cover of vegetation.

In each survey plot, a number of individuals of the larger algae were collected and brought back to the laboratory where smaller epiphytic algae, which may have escaped detection in the field, were discovered and identified. It is realised that some of the smaller algae may have been overlooked and not included in the lists at the time of survey and this fact greatly influences the subsequent treatment of results.

TREATMENT OF DATA

The treatment of ecological data of a floristic descriptive nature, may be divided into two major types 'divisive' or 'agglomerative'. Divisive methods set up classifications of vegetation into groups which have been variously called associations, sociations, noda or communities. Divisive methods may be monothetic or

polythetic. Typical of monthetic methods are the
association analysis technique of Williams and Lambert
(1959) based on floristic homogeneity and the more
recent method of group analysis (Crawford and Wishart,
1968) wich is based on species gregariousness. Both
erect a classification based on the splitting of stand
groups at various levels on the presence and absence of
one species, hence the term monothetic. Polythetic
divisive systems again lead to a classification of
vegetation but the criterion here is not the presence or
absence of a single species but the total floristic
complement. This type of system reaches its greatest
refinement in the Zurich-Montpelier school of Phytosociology
of which detailed appraisal is given by Braun Blanquet
(1951), Westhoff (1951) and Becking (1957) and has
already been applied to marine vegetation by Kornas and
Medweka-Kornas (1948, 1949,1950); Waern(1952), Sundene (1953);
Molinier and Picard (1953) Den Hartog (1955, 1959) and Komas
et al (1960). The use of divisive methods in ecology
leads to a classification of vegetation and attempts to
erect natural groups.

Agglomerative techniques do not produce a classification into floristic groups but rather emphasise the concept of a continuum of vegetation. For a recent summary of these methods, see Whittaker (1967). Agglomerative methods range from simple applications of a coefficient of similarity (Kulchynski ., 1927, Sørensen 1948) through to methods such as that of Bray and Curtis (1957) with numerous modifications, for example, Austin and Orloci (1966); Orloci (1966), Bannister (1968) and to multivariate techniques based on factor analysis (Goodall, 1954; Dagnelie 1960). A variant of the latter technique 'cluster analysis' (Sokal and Sneath 1963) has been applied to sublittoral ecosystems in Western Washington (Neushull 1967). Because of the difficulties imposed by the environment and the problems of re-surveying the exact plots, it is possible that some small species of an ephemeral nature will be overlooked when carrying out stand descriptions. For this reasaon, monothetic divisive systems, where the presence or absence of one species may lead to the erection of spurious groupings, are rejected in the treatment of these results. It was decided to treat the data both from the divisive classificatory approach using the methods of the Zurich-Montpelier school of Phytosociology and the agglomerative using the Wisconsin comparative ordination technique based on the methods of Bray and Curtis (1957). The use of the

methods of the Zurich-Montpelier School of Phytosociology is limited purely to field work and to the principles of drawing up an association table.   No attempt is made to draw up a hierarchal classification of the vegetation units, nor are any stands rejected from the final table because of their non-homogeneous nature.   The results are presented as an association table (Table 1) and in Figs 5a and 5b as three dimensional ordinations.

Fig. 5a presents data worked on a species presence or absence basis and Fig. 5b where the data is loaded according to cover value.   The 'Mechanics' of obtaining the table and the ordinations are given in Appendices 1 and 2 respectively.   It has been stated earlier that the sublittoral vegetation at Petticoe Wick Bay can be divided on the dominant species into four main groups. From an examination of the association table this early division is largely upheld.   No strict delimitations of these communities' are seen, all stands overlap to a certain extent and extensive areas are present co-dominated by two or even three of these species.   It is thus suggested that the sublittoral vegetation here described can be treated as a continuum arranged along one or more environmental gradients but that for ease of discussion, stand groups are extracted.

Association Table of Sublittoral Vegetation from Petticoe Wick — Continued

Pseudolithoderma extensum	+ X	Lithophyllum haplidioides	+ N	Lomentaria articulata	+ N
Ulva lactuca	+ V + U	Ectocarpus fasciculatus	+ T + 3 Y	Spongonema tomentosum	+ N
Cystoclonium purpureum	+ V + N	Chondrus crispus	+ Q	Acrosiphonia arcta	+ L
Enteromorpha prolifera	+ L	Heterosiphonia plumosa	+20 +2N	Sphacelaria caespitula	+3M +3K
Erythrotrichia carnea	+ R	Enteromorpha compressa	+ N	Rhodophysema elegans	+3M +3L
Dictyota dichotoma	+ U + T	Polysiphonia nigrescens	+ N	Chaetomorpha melagonium	+ L
Ptilothamnion pluma	+2L	Achrochaetium daviesii	+ Y + K	Scytosiphon lomentarius	+ Y + K
Ectocarpus siliculosus	+ N	Rhodochorton floridulum	+3K	Giffordia granulosa	+3K

FIGURE 5

Three dimensional ordinations

      (a)   unloaded data

      (b)   loaded data
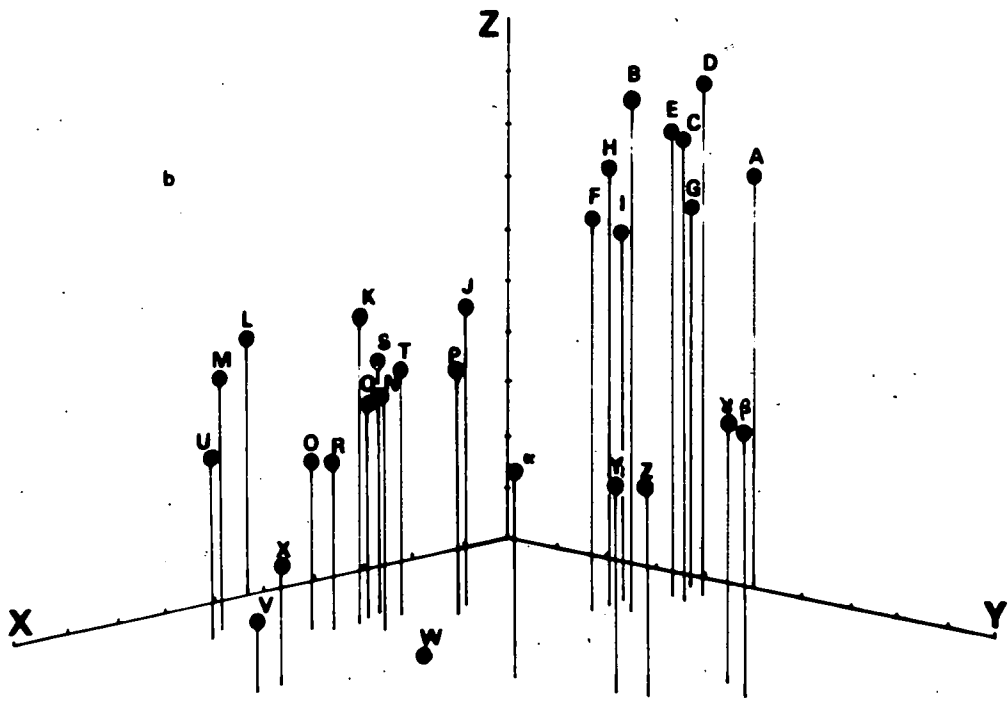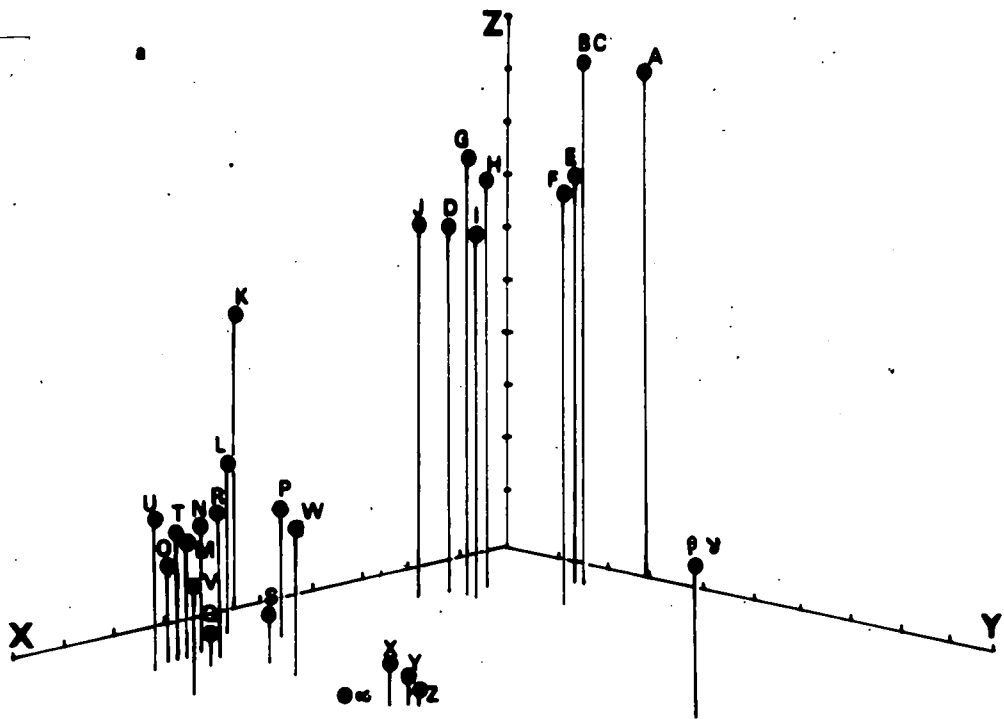
In terrestrial ecosystems, plant communities within one climatically uniform area are largely delimited by edaphic factors but in the marine environment with plants merely relying on the substrate to provide an anchorage, the effect of comparable factors will be slight. Various environmental factors operating within the subtidal are more readily likened to climatic changes between terrestrial communities. In the terrestrial environment under uniform edaphic conditions, two communities separated by climatic differences at their extremes will slowly merge into each other and no strict delimitation will be possible.

The main factors operating within the subtidal would appear to be:

1. Depth of immersion regulating the quantity and spectral quality of the light.

2. Degree of wave action - this is intimately linked with factor 1 as its effects would be expected to diminish with depth.

3. The Physical nature of the substrate i.e., solid or unstable - this factor must be linked with wave action as in conditions of strong water movement, unstable substrates would become inhospitable to algal growth.

Using data from association table and both ordinations,
it is possible to extract a number of floristically
similar stands.

Group   I   Stands A,B,C are characterised by dominance
               of _Laminaria digitata_ and absence of _Laminaria_
               hyperborea.   This group is shown clearly in
               Fig.5a but not in Fig. 5b.   It occurs in
               shallow water on stable boulders and is
               exposed to strong wave action.

Group   II   Stands D.E.F.G.H.I. form a transition zone,
               characterised by the presence of _Laminaria_
               hyperborea sometimes forming a pure stand
          and sometimes co-dominant with _Laminaria digitata_
               Species also present are _Fucus serratus_,
               Gigartina stellata, and _Cladophora rupestris_
               which are characteristic of the lower littoral.
               This group occurs in shallow water to a depth
               of 2 m on stable substrates.

Group   III Stands J and K both form another transition
               zone _Laminaria digitata_ is absent but _Gigartina_
               stellata, _Cladophora rupestris_ and _Rhodymenia_
               palmata are found together with other species
               such as _Delesseria sanguinea_, _Phycodrys rubens_

which are more characteristic of deeper water.

Group   IV   stands N.O.P.Q.R.S.T. These are representative
of the Laminaria hyperborea 'forest' proper.
This group is floristically rich and shows
preponderance of red algae, both as epiphytes
and as ground flora.   It extends between
depths of 2 m and 10 m. in depth on solid
substrate.

Group   V   Stands L.M.U.   This merely is a variant of
group IV.   Floristically, this is the richest
of all groups described both in terms of numbers
of species present and their high cover values.
It appears confined to the mid depth range of
L. hyperborea at 6m to 8 m.

Group   VI   Stands VWX.   This group is characterised by
the dominance of L. saccharina to the virtual
exclusion of L. hyperborea.   Desmarestia aculeata
is present in this group of stands in high
cover.   These two species Laminaria saccharina
and Desmarestia aculeata, show a high degree of
association.   This group occurs on unstable
substrate at depths between 6 and 12 m.

Group   VII   Stands α Y Z.   These stands are found on substrate
of boulders embedded in coarse gravel and are

characterised by the presence of <u>Laminaria</u>
<u>hyperborea</u> and <u>Halidrys siliquosa</u>, forming
an open community at depths of 10 - 12 m.

<u>Group VIII</u> <u>Stands β and γ</u>. This group is located on
coarse silt and small boulders at depths
between 11 and 13 m. It is dominated by <u>Halidrys</u>
<u>siliquosa</u> and at the time of description
July, 1968, the substrate was covered with
fine filaments of <u>Antithamnion spirographidis</u>.

Thus it would seem that the distribution of the
dominant is dependent mainly on depth of immersion and
on substrate type, <u>Laminaria digitata</u> and <u>L. hyperborea</u>
being confined to stable substrates. In unstable areas,
<u>L. hyperborea</u> is replaced by <u>L. saccharina</u> but only in
water deeper than 4 - 5 m. At depths above this, the
unstable substrate changes from coarse gravel and small
boulders to fine sand, devoid of all algal growth. This
distribution is in accordance with that reported by Kain
(1962) from the Isle of Man. At depths between 10 - 12 m,
a narrow zone of <u>Halidrys siliquosa</u> is found growing on
coarse gravel. This species does not grow in shallow water
but is quite common in sheltered littoral rock pools at
Petticoe wick and it is possible that wave action is an

important factor influencing the distribution of this species. The specimens growing between 10 and 12 m. are large plants growing up to 2 m in height.   Alaria esculenta is normally thought of as being indicative of exposed conditions (Ballantine 1962) where it replaces Laminaria digitata in the immediate sublittoral.   It occurs in a number of stands described but in only one, stand K, does it have any significant cover.   This stand is anomalous in that it occurs on a near vertical rock face on Wick Gaut in the centre of the bay;   here Laminaria hyperborea is co-dominant though the plants are all small, young individuals. In some cases (stands S and T) Laminaria saccharina is found as an understory plant, beneath L. hyperborea, on stable boulders.

In these descriptions the term 'Lithothamnia' embraces all calcareous encrusting algae and these are ubiquitous throughout the stands described.   In certain stands, and where these species occurred epiphytically, they were identified.   However, because of the difficulty experienced in removing these algae from the rock surface and subsequently identifying them, they are collectively refered to as Lithothamnia, and not used in the ordinations.

The techniques described, though developed for the study of terrestrial vegetation, are applicable in the

sublittoral and may be used to delimit vegetation groups.
The ordination techniques, whilst giving good pictoral
representation of interstand relationships, abscure a
great deal of detailed information.   Theirgreat value is
in comparing stands of vegetation from one area to pick
out environmental gradients.   In comparing loaded and
unloaded ordinations the latter more clearly delimits
vegetation groups of a radically different floristic nature
while the former, though perhaps less objective, gives a better
understanding of the relationships within a relatively
homogeneous community.   When the association table and
ordinations are used together, determination of vegetation
groups on floristic differences is greatly facilitated.

CHAPTER 3

PERFORMANCE STUDY METHODS

INTRODUCTION

The growth of a photosynthetic organism can be measured as net or gross production. Net production at anytime is the point of balance between the growth increment and loss due to damage, disease grazing, sporogenesis, extracellular products and respiration. The measurement of gross production requires a measure of the rate of photosynthesis of the organism as well as long term measurement of respiration and the monitoring of all the factors leading to breakdown. Estimates of net annual production can be obtained using simple techniques of peak or increment cropping as described by Penfound (1956) and Odum (1960).

Laminaria hyperborea appears to be ideal for this type of work and the epiphytes growing on its stipe are shown to be capable of treatment as annuals and amenable to increment cropping techniques. Estimates of the net annual production of the perennial parts of the plant (stipe and holdfast) can be obtained from a simple age-biomass relationship. The figues so obtained can be regarded as a measure of the performance of the species in relation to the environment over the life span of the sporophyte.

Similarly, net annual production of annual species or
annual parts of plants, in this case the lamina and
epiphyte flora, can be regarded as a measure of
performance in relation to the environment over the
current year.   It should therefore be possible to
obtain a meaningful comparison of the performance of
the kelp species and its dependant epiphytes in relation
to environmental factors, in particular, depth of
immersion below low water mark at one site and to obtain
comparative data from other sites.

One proviso to be considered in measuring the
performance of <u>Laminaria hyperborea</u> is the possibility
and accuracy of aging the organism.

Problems of Aging L. hyperborea

In all the perennial species of <u>Laminaria</u>,
there is a secondary meristem situated in the outer cortex
of the stipe.   This meristem increases the girth of the
stipe by producing radially arranged columns of cells.
The rate of division and growth is rapid at the beginning
of the year and the cortical cells produced are large
and translucent.   Later in the year when growth slows
down, small dense opaque cells are produced.   The

difference between the two types of cell is obvious,
even to the naked eye, when transverse or longitudinal
sections of the base of the stipe are examined with
background illumination.   Thus the aging of Laminaria
hyperborea is based on a ring count, analogous to aging
woody perennial terrestrial plants.

Le Jolis (1855) was one of the first workers
to suggest that the ennumeration of these contrasting
zones could be used to age individuals.   More recent
work on Laminaria saccharina (Parke, 1948), L. hyperborea
(Black et al., 1959) and L. ochroleuca (John, 1969) has
shown the validity of this method.   Kain (1963) summarised
some of the problems and precautions necessary when working
with Laminaria hyperborea.   These are:

(1)   Growth lines may be produced by disturbances
      in the growth rate, independent of seasonal
      effects.

(2)   Tissue may be removed from the base of the
      stipe by grazing organisms, in particular,
      Patina pellucida L. and this injury may
      stimulate the production of extra lines.

(3)   Favorable conditions for growth during normally

slow growth periods may result in no discernable

slow growth line being produced.

Black et al., (1959) recommended the counting of haptera

whorls as a rapid method of aging plants. The data they

presented however only applies to individuals of five years

and above. They give no data for one and two year old

plants and the results for three and four year old plants

are based on one and five individuals respectively.

Table 2 , shows the mean number of haptera whorls per hold-

fast in each age group determined by line counts. The

plants, used in this calculation, came from Petticoe Wick

Bay from all depths with approximately 25 plants in each

age class.

TABLE 2

Age determined by ring counts.

Age in Years	1	2	3	4	5	6	7
Mean No. of haptera whorls	2.6	2.6	1.4	1.1	1.1	0.9	0.9

It may be seen that there is no strict proportionality in the first three years but after that, the 1:1 ratio holds fairly true. The bad correlation in the earlier years can only be explained by the fact that more than one haptera whorl is produced and that these additional whorls disappear with time. This is confirmed by the observation that the small attenuated haptera, typical of one and two year old individuals, were not found in older plants.

The procedure finally adopted for aging the plants was the same as that described by Kain (1963). A longitudinal section was cut at the base of the stipe through the region where the haptera are produced. The dark lines were then followed to ascertain that they were associated with a haptera level. This prevented the boundary of the medulla being mistaken for a growth line and allowed for the recognition of interference lines. Where damage had occurred in the holdfast, either due to removal from the substrate or to the grazing activities of Patina pellucida, the number of growth lines present in a transverse section was taken as a measure of age.

COLLECTION OF MATERIAL

The 'kelp forest' at Petticoe Wick Bay extends from low water mark to a depth of 12-13 m.   Five sampling depths within this range were chosen.

Depth I at 1 m.   Laminaria hyperborea forms a
mixed community with L. digitata.

Depth II and III at 2 m and 6 m respectively.
A pure stand of Laminaria hyperborea forms
a dense canopy.

Depth IV at 10 m.   The kelp still forms a canopy
but this is very open and much less dense than
at 2 m. and 6 m.

Depth V at 12 m.   This is the lower limit of growth
and no canopy is formed.   The area corresponds
to the parkland described by Kitching (1941).

A cropping team dived within the study area using S.C.U.B.A., and within the depth range to be cropped, subjectively selected a uniform stand of Laminaria hyperborea for study.   The depths were measured using capillary depth gauges, all measurements being taken at substrate level.   The time and the state of the tide were noted and the appropriate correction was calculated using

Admiralty Tide Tables (1967, 1968, 1969).   The site at
Petticoe Wick Bay was visited at various times throughout
the years of 1967, 1968 and 1969.

Two methods of cropping were employed:

(1) Random cropping of approximately fifty individuals
ranging from sporelings to canopy plants from within
the limits of the stand chosen.   In returning to
the site for increment croppings, no attempt was
made to return to exactly the same plot.

(2) Cropping all individuals from within a series
of metre square quadrats (constructed from light
alloy dexion) placed well within the chosen stand.

The former method was used most frequently as it was more
easily carried out with less help from other divers.
Under certain weather conditions, in particular in rough
seas, in shallow water and in conditions of high turbidity
(causing a reduction in underwater visibility), the latter
method proved unsuitable.

The plants were removed intact from the subtrate by
inserting a strong knife between the rock race and the base
of the holdfast and applying twisting motions which usually
resulted in the removal of the plant with little damage

to the haptera.   The crops were then packed into linen
bags or wire baskets which were labelled before being
brought to the surface.   When possible, the crops were
brought directly to the laboratory for further study.
Storage, when necessary, was at 5°C.

LABORATORY TREATMENT OF MATERIAL

(1) Laminaria hyperborea

On return to the laboratory, each individual
kelp plant was treated as follows:

(a) The species of epiphyte on the stipe were noted
and the position of the major species components
present was measured, to give an upper and lower
limit of distribution of each on the stipe.   The
epiphytes were then removed by gently "shaving" the
stipe with a sharp knife.   They were then placed in
polythene bags and stored at -10°C.

(b) The condition of each kelp plant was recorded,
infestation by Patina pellucida, breakdown of the
lamina, the presence of the previous years lamina
and any other unusual features were noted.

(c) The length of the stipe from the upper limit of

the haptera whorls to the point of expansion of the lamina was measured.

(d) The plant was divided into three parts, lamina, stipe and holdfast.   In cases where the previous year's lamina was present, this was also cut off and treated separately. The point of division of the stipe and hold fast was taken to be immediately above the level of the top whorl of haptera.

Stipe and haptera were dealt with separately for the following reasons.   It was realized that serious error might arise when dealing with the holdfast due to damage in removal from the substrate or due to infestation by _Patina pellucida_.   There is also a large amount of animal encrusting matter and detritus which is very difficult to clear from the haptera. Obviously, damaged individuals were always rejected and undamaged ones washed in seawater to remove extraneous material.   The stipe is rarely damaged and is easily cleared of adherent material.

(e) A longitudinal section of the base of the stipe was cut and the number of growth lines counted.

(f) The various parts of the plants were placed in separate labelled paper bags and dried to constant weight in an air circulating oven at 100°C.

(g) When dry, the component parts of the plant were weighed.

(h) Sub samples of material from various age classes were removed and ground in a laboratory mill to pass ɾ ɔ a fine mesh. These were then ashed to constant weight in a muffle furnace at 440°C.

It was realized that differential losses (due to disease, damage or grazing) between different crops could obscure any real differences in results. To help overcome this, data from any obviously damaged individuals was rejected. In an organism with the relatively simple morphology of Laminaria hyperborea, this is a perfectly objective approach. It is realised that because of the method of separating the stipes and holdfasts that all the measured attributes of these organs (stipe length, stipe biomass, holdfast biomass) only have meaning within the context of the methods of study employed. It is suggested because of the difficulty in assessing damage to the lamina, that measurements performed on the stipes will give the most accurate data for

comparative study.

(2) The Epiphyte Component

The epiphytes which were removed from the stipes
were stored at -10°C in polythene bags labelled with the
date and depth of cropping and the age of the 'host' plant.
The material was thawed quickly by immersing the bags in
hot water.   The epiphytes were then sorted into their
component species, weighed wet and sub samples taken for
drying to constant weight.   It was observed that in the
vast majority of samples, only four species of epiphyte were
present.   These were Rhodymenia palmata, Ptilotia plumosa,
Membranoptera alata and Phycodrys rubens. Other species,
when present, were in amounts comprising of less than one
per cent of the total epiphyte biomass.   For purposes of
further quantitative study, these other species were ignored.

At certain times of the year, from depths of 2 m
and 10 m, the upper and lower limits of the kelp forest
canopy, individual weights of epiphytes were obtained. This
was accomplished by shaving an area of stipe and sorting the
epiphytes which were then weighed individually.   This
procedure was adopted rather than picking out plants from
previously sorted epiphytes to eliminate the errors which
may arise due to the unconscious selection of large

individuals. The individual weighings were obtained with wet plants and sub samples taken to enable calculation of a drying coefficient to reduce the data to dry weights. Dry sub samples were retained and ashed as for <u>Laminaria</u> <u>hyperborea</u>.

CHAPTER 4

PERFORMANCE RESULTS FROM PETTICOE WICK

(1) <u>Laminaria hyperborea</u> *

  The graphs of the mean values of stipe length, stipe biomass and hapteron biomass against age are plotted using the dry weight data from undamaged individuals. This allows the calculation of the following growth increments either directly from the results or from the slopes of the appropriate portions of the graphs.

  Net annual stipe biomass increment.

  Annual stipe length increment.

  Net annual holdfast biomass increment.

The lamina biomass for each age class at each depth is plotted against time of cropping. This allows the calculation of peak lamina biomass.

  Increment growth of the lamina throughout its life. Graphs of stipe weight per unit length are also plotted and allow a comparison of stipe morphology in relation to depth. The figures obtained for net annual stipe and holdfast production can be added to the figure for peak lamina biomass to produce the mean net annual individual production in a particular age class in the year of study.

* As few plants older than 7 years were encountered during the study, it was decided to present data, only from plants of 1-7 years of age.

In some cases it is possible to arrive at a figure for net annual plot production (g/sq m/yr) by multiplying the net annual individual production for each age class by the number of individuals of these age classes present in a known area. This figure is only valid for the specific areas cropped. The great variation in density and age structure of a population present in one area would appear to make comparisons of plot production between sites of doubtful validity.

The composite mean cropping data is given in Tables 15-19 Appendix 3, along with confidence limits (p = 0.05) where applicable. The data is presented as follows in graphic form to highlight significant trends, for the sake of clarity no confidence limits are presented on the graphs. Fig. 6 shows respectively the mean increment cropping results for laminae in each age class found at two depths 2 m and 10 m over the life of the lamina in 1967-1968.

Fig. 7 shows the mean increment cropping data for the laminae in 1968-1969 at five depths sampled.

Fig. 8 shows the growth of new laminae in the early months of 1969.

Fig.9 shows peak lamina size in each age class plotted against depth.

FIGURE 6

Seasonal variation in lamina biomass at two depths at
Petticoe Wick in 1967-1968.

Age in years

7 ▲————▲

6 ●－－－－●

.5 ·+········+

4 ○————○

3 ●————●

2 ●————●

Time of cropping (months of 1967/1968)
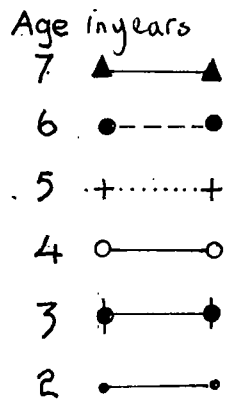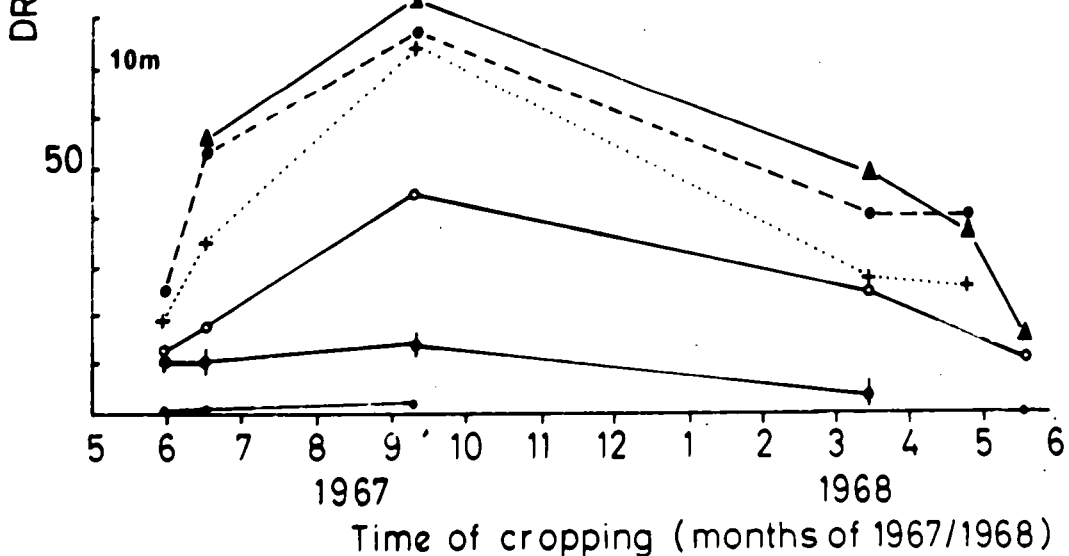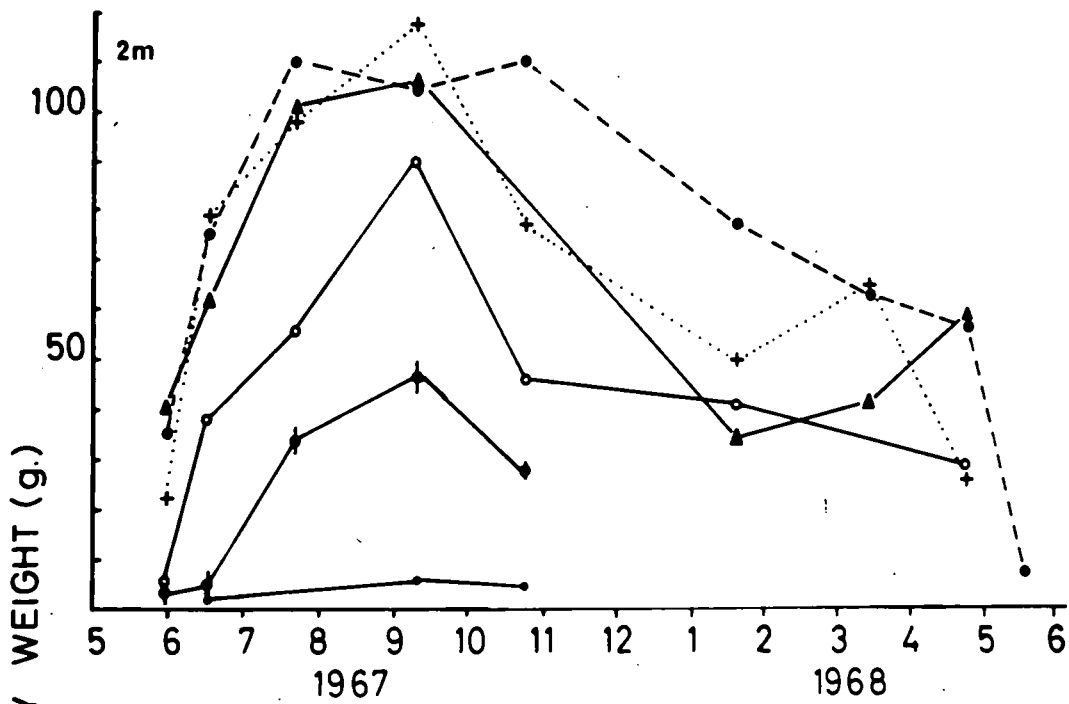
FIGURE 7

Seasonal variation in lamina biomass for the five

depths sampled at Petticoe Wick Bay.

Age 7   ▲————▲
in
years 6   ●– – – –●

5   +·······+

4   ○————○

3   ◆————◆

2   •————•
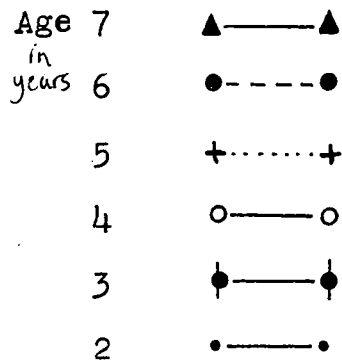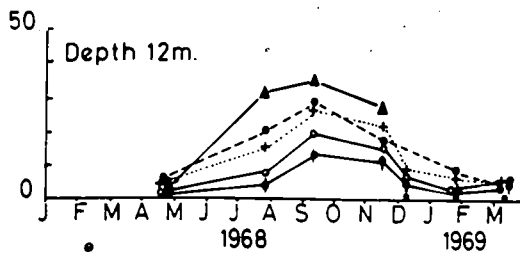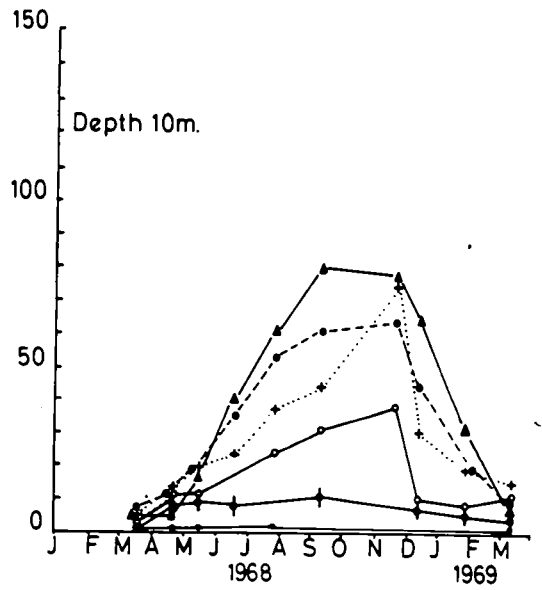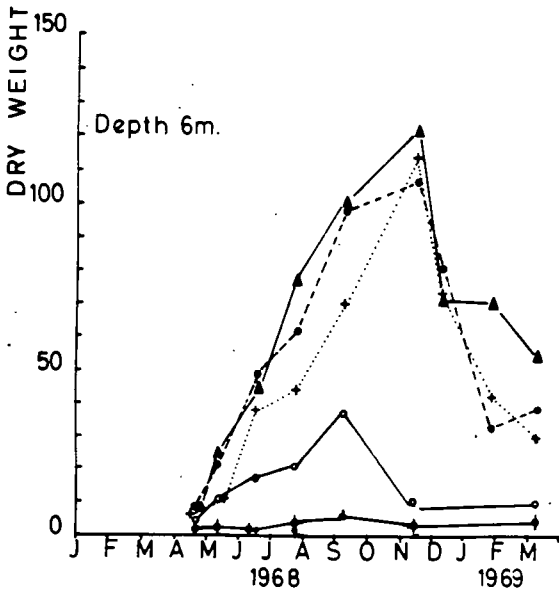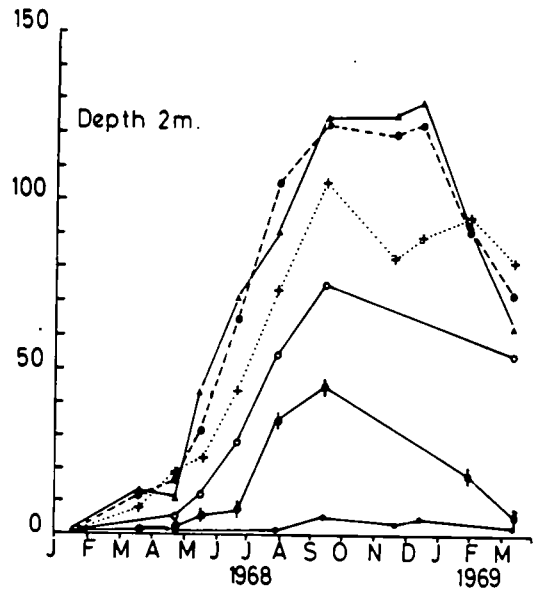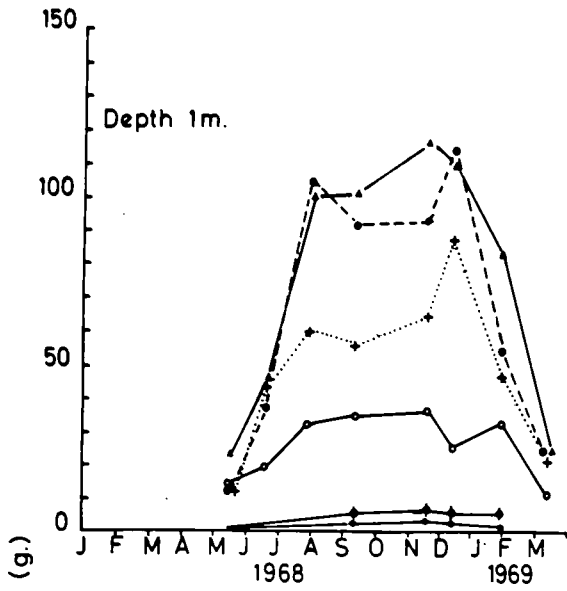
Time of cropping (Months of 1968/1969)

FIGURE 8

Increase in lamina biomass in early months of 1969
at the five depths studied at Petticoe Wick Bay.
Age in years is given with each graph.

LAMINA BIOMASS (g.)

1m   2m   6m   10m   12m

MONTHS OF 1969
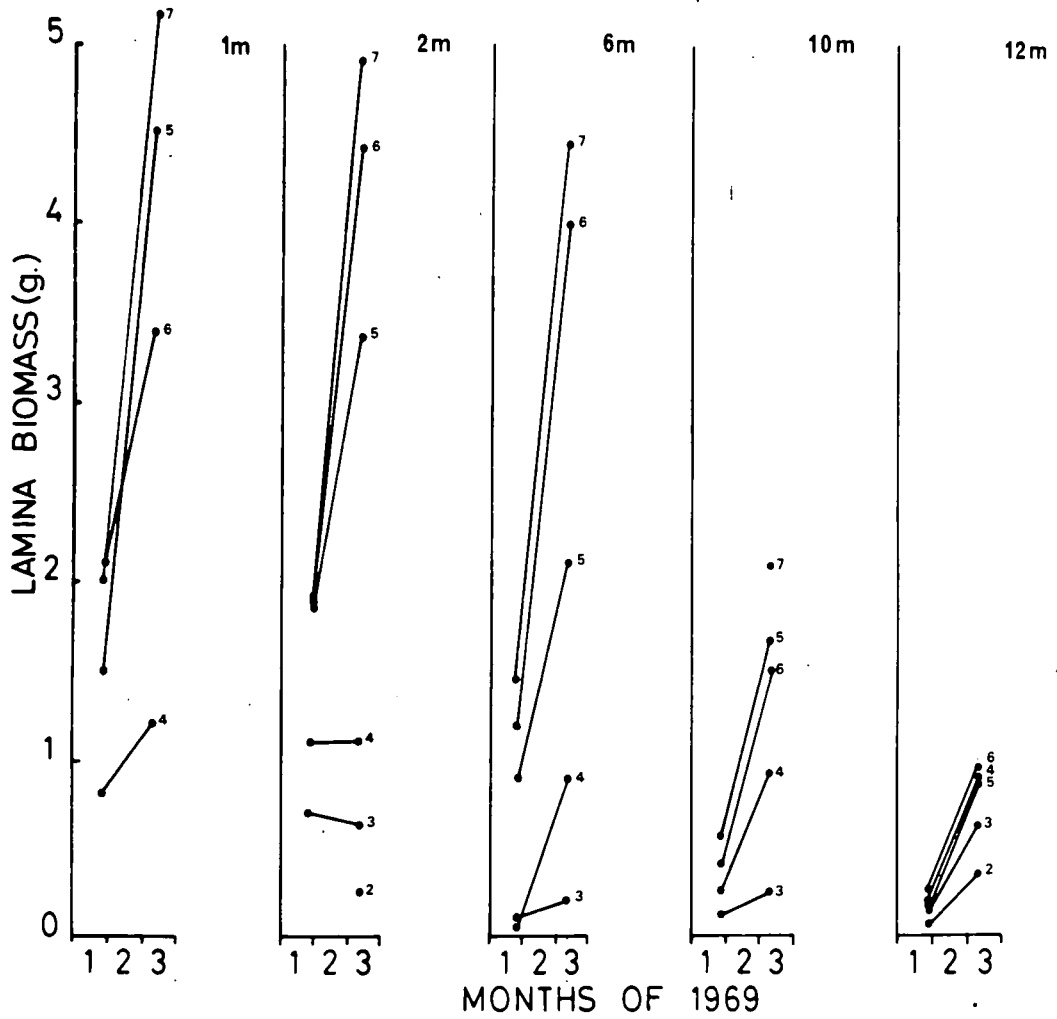
FIGURE 9

Peak lamina biomass (1968) at the five depths sampled
at Petticoe Wick Bay.
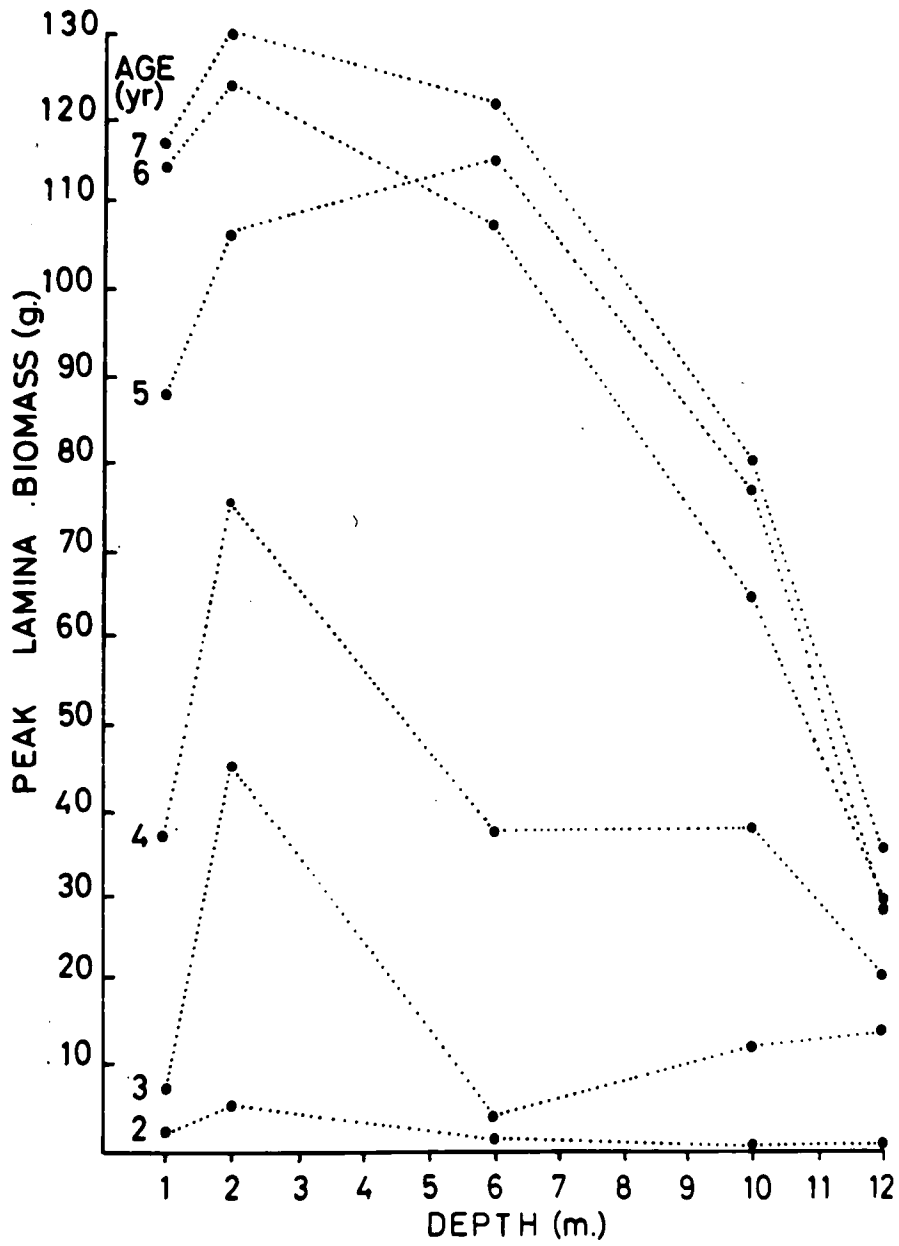
Fig. 10 a and b show respectively mean stipe biomass and
mean holdfast biomass against age for all depths studied.
Fig.11 shows stipe length against age and Fig.12 weight
per unit length plotted against age for each depth sampled.

Stipe biomass

Stipe biomass shows a progressive increase with
age from all depths.   There is an initial "lag period"
followed by a period of rapid growth in three, four and
five year old plants and a progressive tailing off in
growth with further increases in age.   This holds for all
depths sampled except at 12 m where biomass progressively
increases with age throughout the life of the plant but
shows no period of abrupt rapid growth.

From the depths studied, maximum stipe biomass
in the upper age classes is at 6 m.   Plants from the lower
age classes at 6 m however show a marked reduction in stipe
biomass when compared with individuals in the same age classes
at 1 m, 2 m and 10 m.   In the plants from 12 m, stipe
biomass is very much less in all age classes than from all
the other depths studied.   Individuals from 1 m depth
show a marked reduction in stipe biomass when compared with
individuals from 2 m, being more comparable in size to
plants from 10 m.

FIGURE 10

Biomass of (a) stipe (b) holdfast at the five depths
sampled at Petticoe Wick Bay.

Depth (m)

1 ●————●

2 ▲—·—·—▲

6 ○————○

10 +———+

12 ●·······●

STIPE BIOMASS (g.)

AGE (years)

a.

HOLDFAST BIOMASS (g.)

AGE (years)

b.
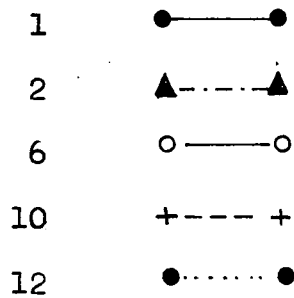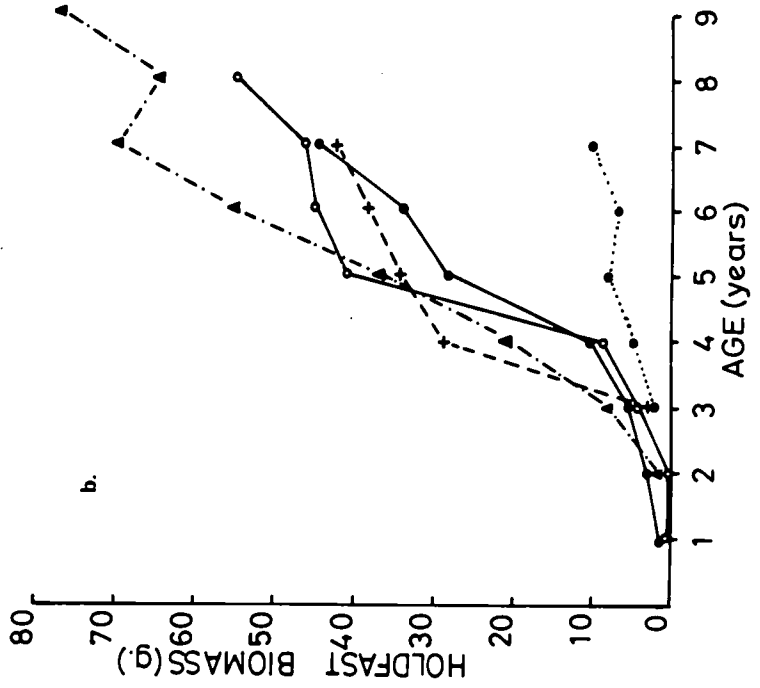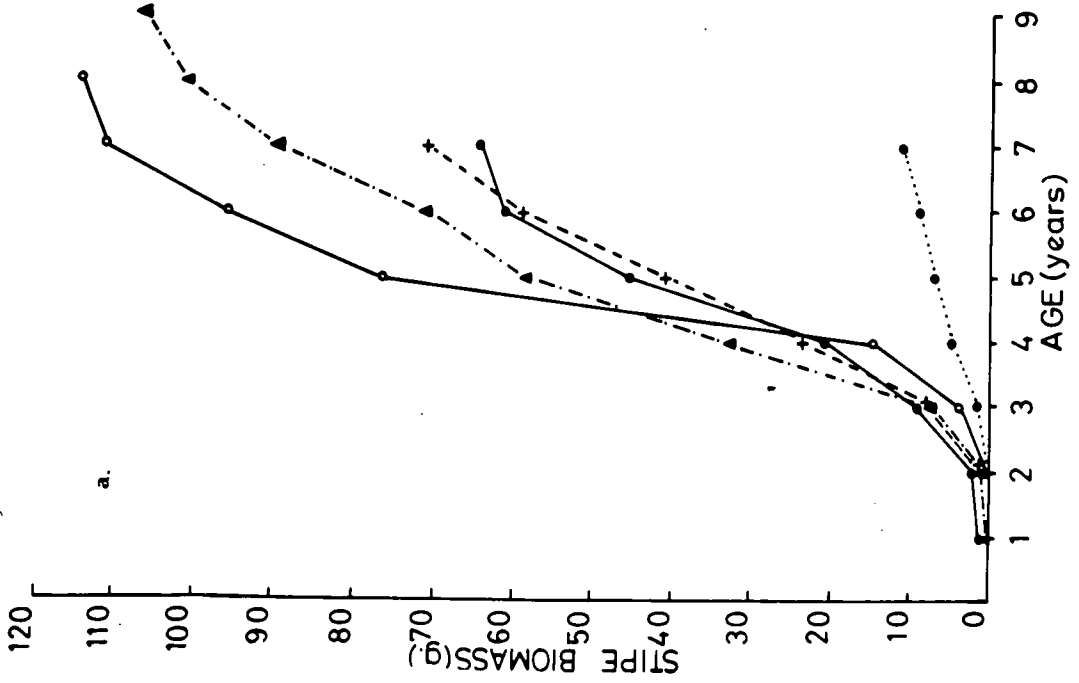
FIGURE 11

Stipe length at five depths sampled at Petticoe Wick Bay.

Depth (m)

1 ●———●

2 ▲-·—·-▲

6 ○———○

10 +－－－+

12 ●······●
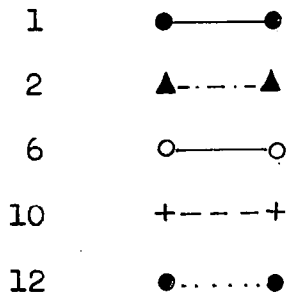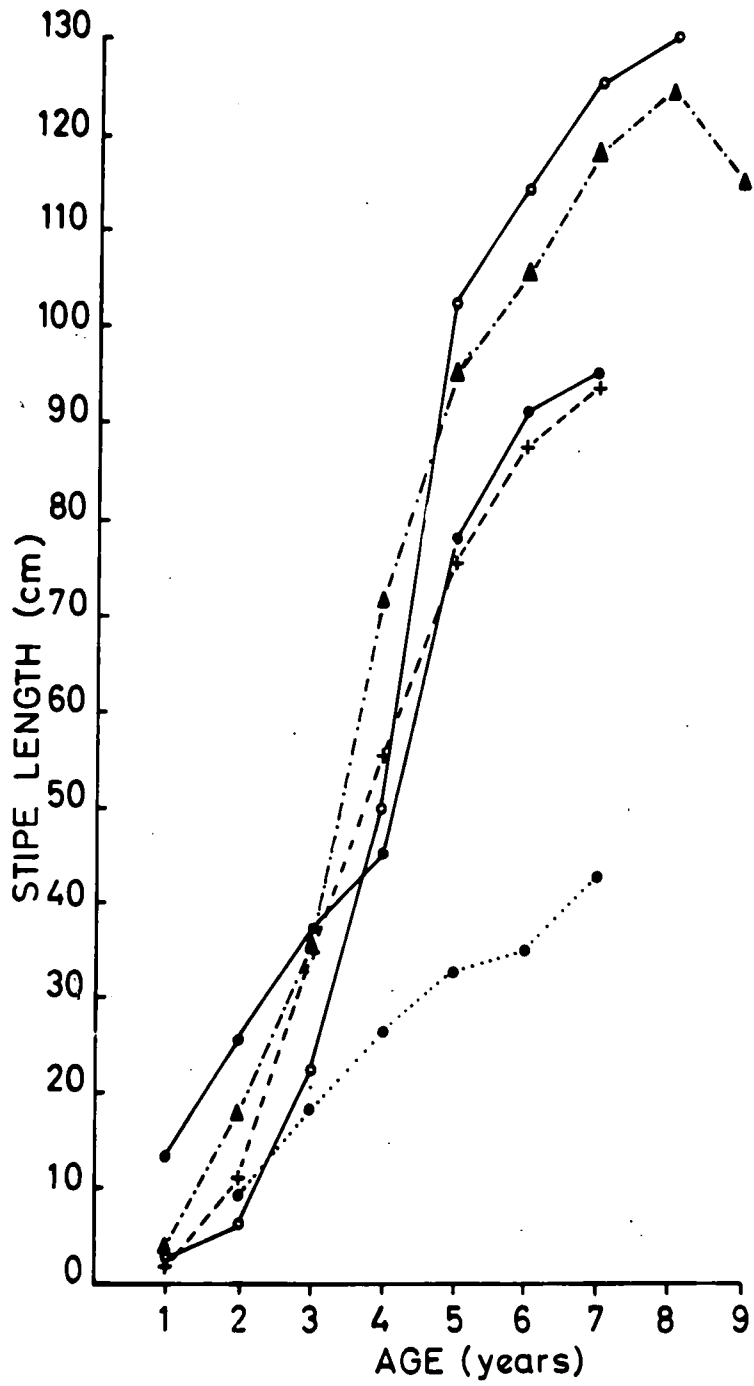
FIGURE 12

Weight per unit length at five depths sampled at Petticoe Wick Bay.

Depth (m)

1	●———●
2	▲—·—·▲
6	○———○
10	+———+
12	●·····●
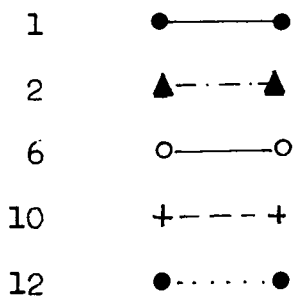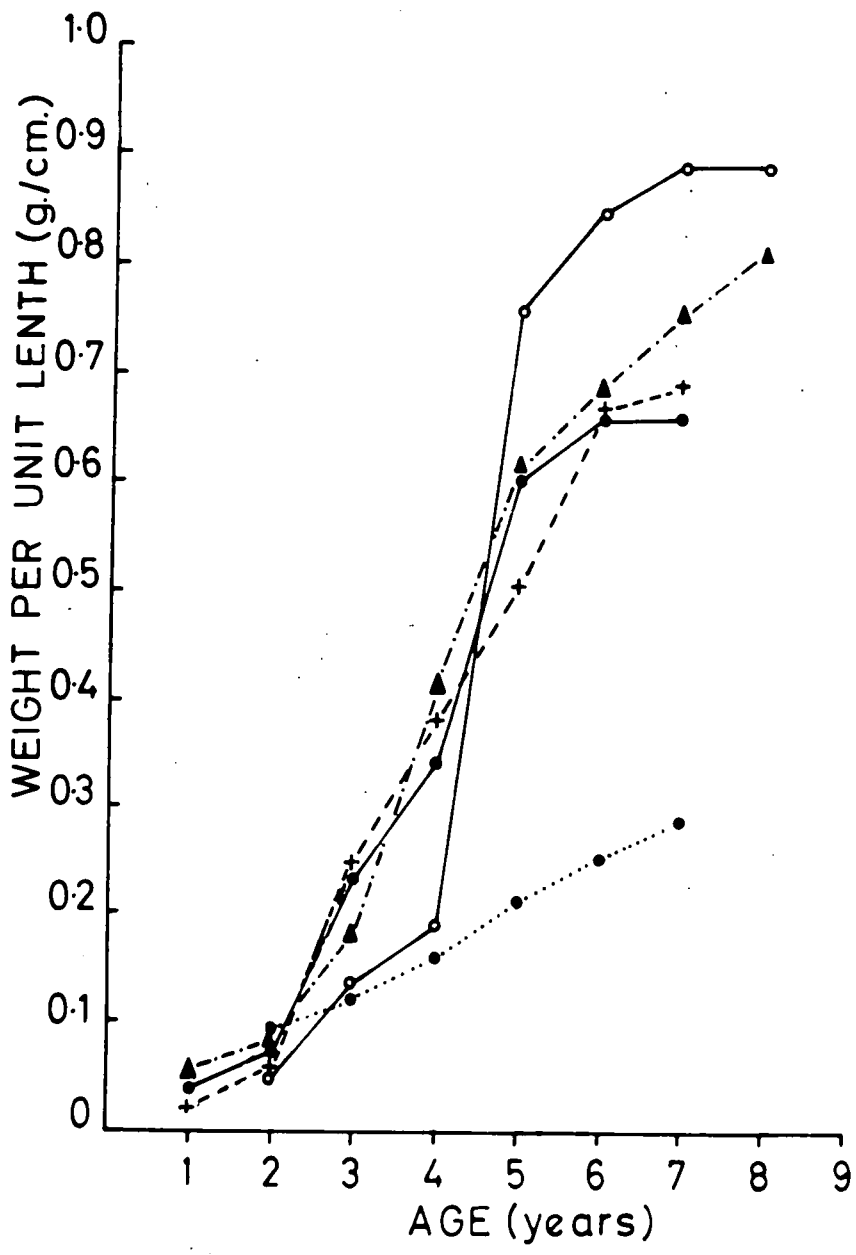
Holdfast biomass

The results for holdfast biomass mirror to a large extent the results for the stipe , except that, in this case, holdfasts from 2 m are the largest.

Stipe length

Stipe lengths follow the same general trends as stipe biomasses except that in the lower age classes from 1 m depth, they are significantly longer than from other depths.

Stipe weight per unit length

This can be roughly equated with stipe circumference, or 'girth', and as such will be indicative of stipe morphology. After an initial lag period in the first two years of growth, there is a rapid increase in weight per unit length concomitant with increase in stipe length and biomass. Stipes from 6 m in age classes three and four have a lower weight per unit length than stipes in the same age classes from all other depths sampled except 12 m.

Lamina biomass

The laminae commence growth at all depths in January and after an initial period of slow growth begin rapid growth in April - May. They reach a peak size in

September at all depths except the shallowest where a peak
is reached in July and from 6 m where a peak appears to be
reached, at least in the upper age classes, in November.
Plants in the upper age classes from 1 m and 2 m, maintain
their maximum lamina biomass until the commencement of
growth of the new lamina when a progressive decline occurs,
the old lamina being finally lost between late April and
early May. In plants from 6 m and deeper the peak lamina
biomass once reached rapidly declines, commencing in
November-December at 6 m and earlier with increase in depth.

Peak lamina biomass appears to be dependent on
the age of the plant, at least in the lower age classes
up to the age of five years. After the age of five, lamina
biomass does not significantly increase with increase in
age. In plants from 6 m, the peak lamina biomass in age
classes three and four are significantly less than those
from plants in the same age classes from 2 m depth. Plants
in age class three have a much reduced lamina biomass than
similar plants from 10 m. The greatest lamina biomass in
the upper age classes is reached in individuals at 2 m
and 6 m depth, thereafter a decline occurs with increasing
depth. Individuals from 1 m depth show slightly reduced
lamina sizes from those at 2 m and 6 m but in many cases
these difference are not significant.

The graphs presented for seasonal changes
in lamina biomass for the years 1967-1968 from 2 m and
10 m show comparable growth patterns and the regular,
seasonal, nature of lamina growth.

Whole Plants

From the results given, it is possible to
construct an 'average' plant in each age class for the
depths studied by addition of the mean value for stipe
hapteron and lamina biomass.   These results together
with the net annual individual production are given in
Appendix 3, tables 19.   All plants increase in
total biomass with age.   In plants from 12 m the net
annual production appears to increase with age but in
plants from all the other depths studied maximum net
production is reached at five years and thereafter a
decline occurs.   The largest of all individuals are
found in age classes six and seven at depths of 2 m and
6 m. The differences in total biomass between plants
at 10 m and 12 m are particularly striking in age classes
six and seven, as plants from 12 m have biomasses of
less than half those from 10 m.

(2) Epiphytes

Epiphytism in seaweeds is in certain cases a
fixed characteristic of a species but in others merely
an occasional phenomenon occurring only by chance
(Tokida 1960).   At Petticoe Wick the epiphytes occurring
on the stipes of Laminaria hyperborea fall into this
latter category as nearly all of them were also found
growing on the surrounding rock substrate.

Tobler (1908) provides what is probably the
first comprehensive work on the epiphytes of L. hyperborea
and Newton (1931) notes that the stipes of L. hyperborea
are covered with epiphytic algae in summer and that the
epiphytes show a distinct zonation upon the stipes.
Tokida (1960) lists 126 genera and 285 species of algae
reported to be epiphytic on members of the Laminariales
of these L. hyperborea supports 50 genera and 66 species.
Marshall (1960) lists algae epiphytic on the stipes of
Laminaria hyperborea at Petticoe Wick and comments on their
distribution in relation to depth.

A full list of the macro algae found growing
epiphytically on the stipes of L. hyperborea at Petticoe
Wick during the course of this study is given in Table 3
It has already been stated that four species, Rhodymenia

TABLE 3

MACRO-EPIPHYTIC SPECIES - PETTICOE WICK

	Depth (m)				
	1	2	6	10	12
Rhodymenia palmata	+	+			
Ptilotia plumosa	+	+	+	+	
Membranoptera alata	+	+	+	+	+
Phycodrys rubens	+	+	+	+	+
Giffordia granulosa		+			
Ectocarpus fasciculatus		+		+	
Gigartina stellata		+			
Phyllophora membranifolia		+	+	+	
Plocamium cartilagineum		+	+	+	
Lithophyllum crouanii		+	+	+	
Polysiphonia urceolata		+	+	+	
Polysiphonia brodiaei		+	+	+	
Ptilothamnion pluma		+	+		
Achrochaetium daviesii		+		+	
Sphacelaria caespitula			+		
Rhodophysema elegans			+		
Delesseria sanguinea			+		
Crytopleura ramosa			+	+	+
Callophyllis lacinata			+	+	+
Ceramium rubrum		+	+	+	
Lomentaria clavellosa		+	+		
Lomentaria articulata		+			
Lithophyllum haplidioides			+		
Erythrotrichia carnea			+		
Enteromorpha compressa			+		

palmata, Membranoptera alata, Ptilotia plumosa and
Phycodrys rubens make up over 99 per cent of the total
epiphyte biomass and two of these Membranoptera alata
and Phycodrys rubens are present as epiphytes throughout
the depth range of Laminaria hyperborea. It was
decided therefore to concentrate on these four species.
The distribution of these epiphytes is given in Fig. 13
the shaded areas on the generalised stipes represent
the distances between the mean upper and lower limits
found on the stipes examined from plants aged five years
and above. In order to compare distributions along stipes
of different length, all stipe lengths were reduced to one
metre and distributions correspondingly adjusted. It is
emphasized that the results in these diagrams are a
composite mean and a number of plants were found not
corresponding to this presented scheme.

Rhodymenia palmata occurs only on stipes from
the depths studied at 1 m and 2 m. At 1 m, it appears
on the upper half of the stipe and at 2 m, the mean lower
limit of its occurrence is raised so that it covers only
the top third of the stipe. All the stipes examined had
epiphytes confined to the lower rugose part and the area
of new stipe growth immediately below the lamina was
always free from epiphytic growth.

FIGURE 13

Distribution of epiphytes on the stipes of _Laminaria_
hyperborea at Petticoe Wick Bay.

The black area represents the distance between
the mean upper and lower limits of distribution; all
stipe lengths are adjusted to one metre.

Depth m.

STIPE LENGTH (cm)

Rhodvmenia palmata

Ptilotia plumosa

Membranoptera alata

Phvcodrvs rubens
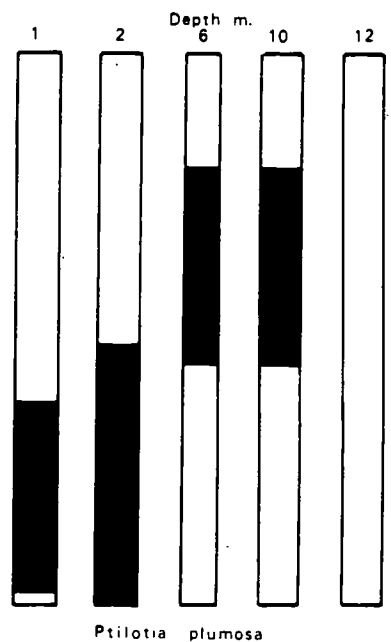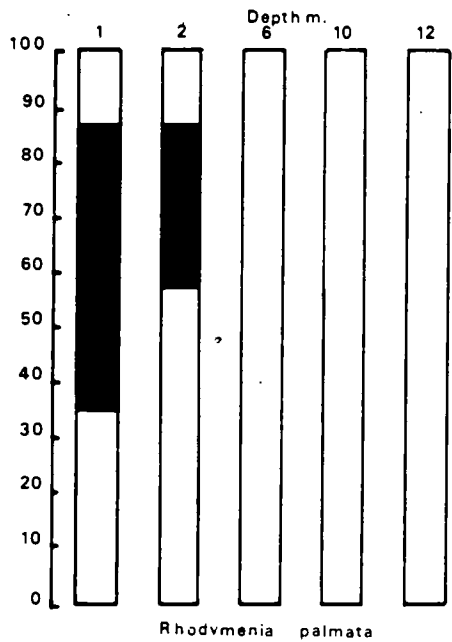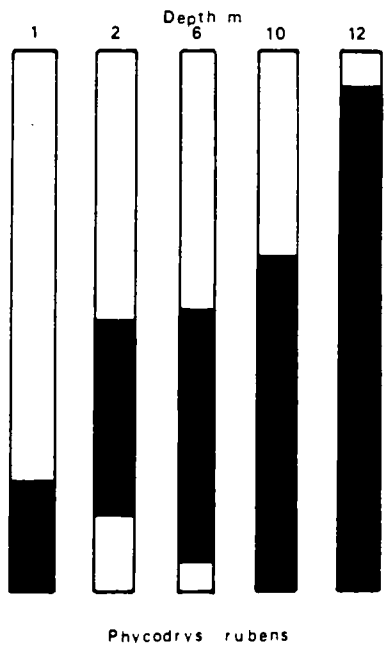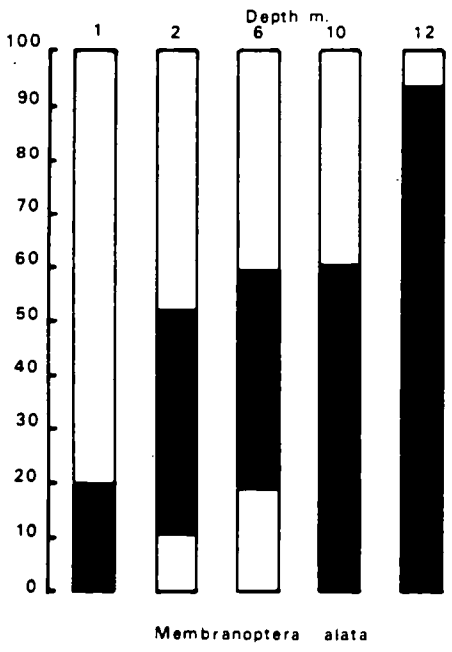
Rhodymenia palmata was absent from stipes obtained from 6 m and 10 m and its position at these depths was taken by Ptilotia plumosa. Membranoptera alata and Phycodrys rubens always appear to occupy the bottom portions of the stipes except at 12 m where Ptilotia plumosa is absent, and they occupy all the available stipe length.

The mean biomass of epiphytes present on the stipes in September-November at 2 m and November at 10 m, are related to the age of the 'host' plants. The results are given in Table 23, Appendix 3 and summarised in Fig. 14. The epiphytes are absent from the younger plants and have small biomass on plants aged three to four years; in the older plants, five to seven years, there is no significant increase in epiphyte biomass with increase in age. For this reason all canopy plants five years old and above are treated together and all further results are from these age groups. Fig. 15 summarises the results given in Table 24 Appendix 3 of the change in mean epiphyte biomass per stipe at the various times of cropping in 1968-69, from all depths studied. Fig. 16 shows the percentage of the total biomass that each component epiphyte species

FIGURE 14

Epiphyte biomass per stipe in each age class at 2 m
(September and November) and 10 m (November) with
limits p = 0.05.
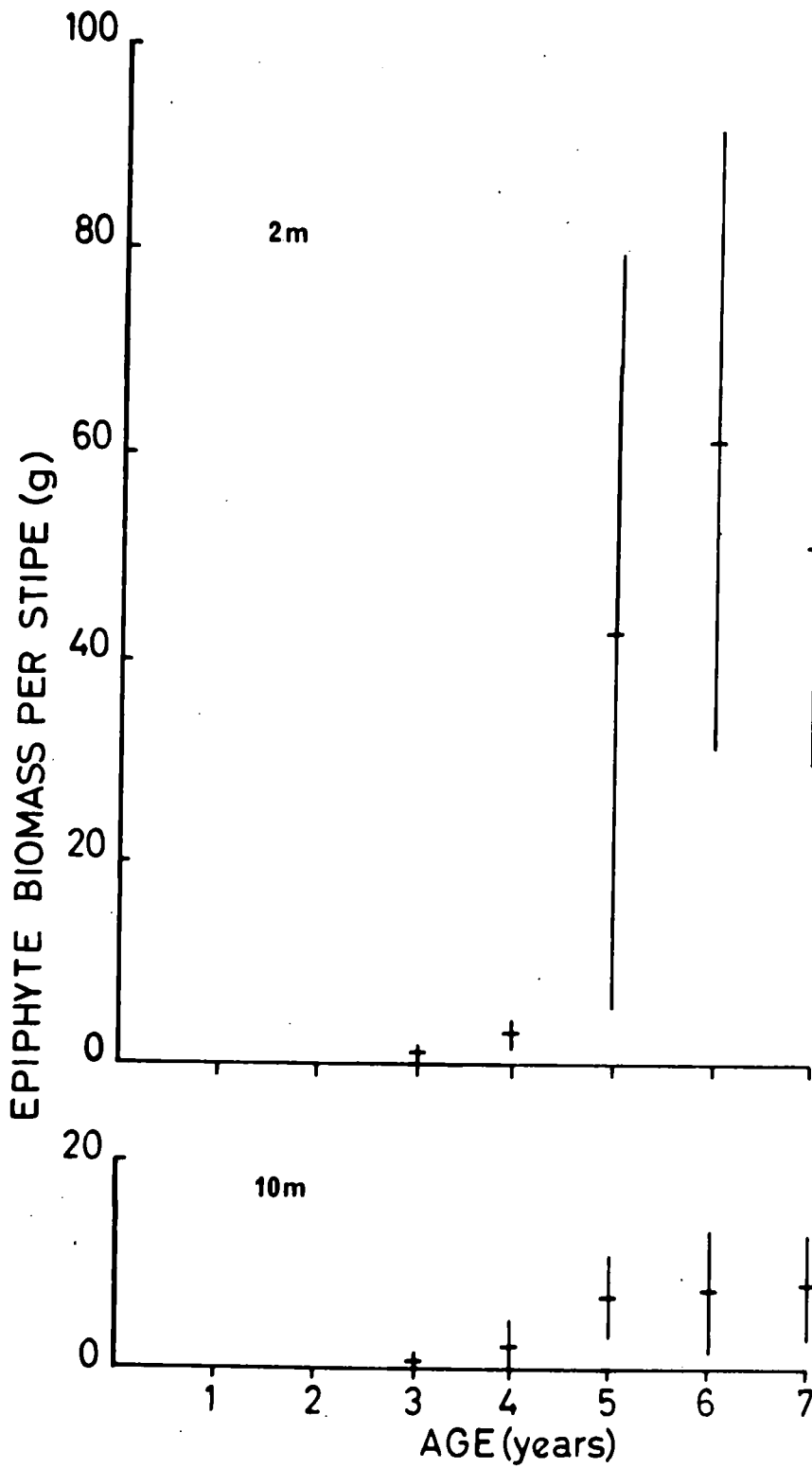
FIGURE 15

Seasonal changes in epiphyte biomass per stipe at
four depths at Petticoe Wick Bay.

Total epiphytes	●——●
<u>Rhodymenia palmata</u>	○————○
<u>Ptilotia plumosa</u>	+········+
<u>Phycodrys rubens</u>	+—·—··+
<u>Membranoptera alata</u>	○————○

Depth 1 m

Depth 2 m

Depth 6 m

Depth 10 m

R. palmata
Other epiphytes

DRY WEIGHT (g.)

A M J J A S O N D J F M

A M J J A S O N D J F M
1968   1969

A M J J A S O N D J F M
1968   1969
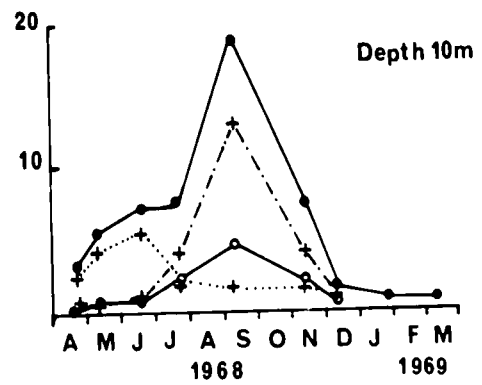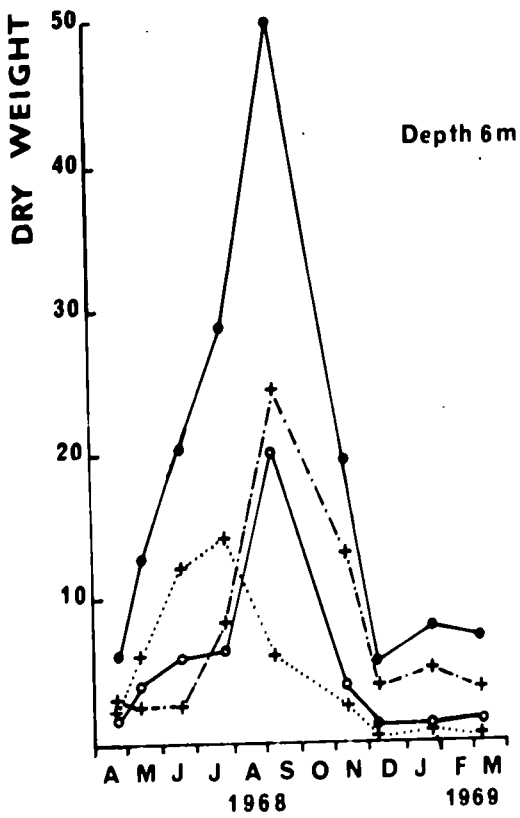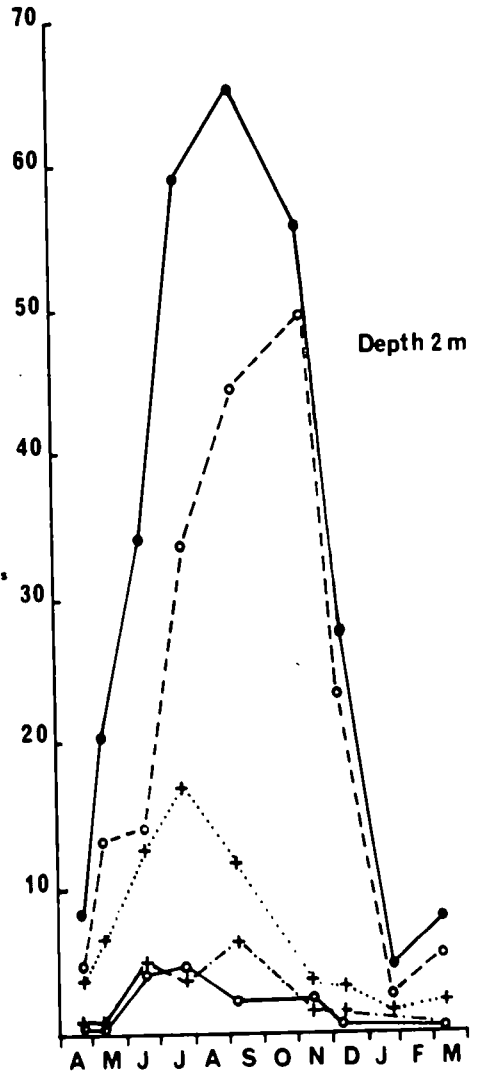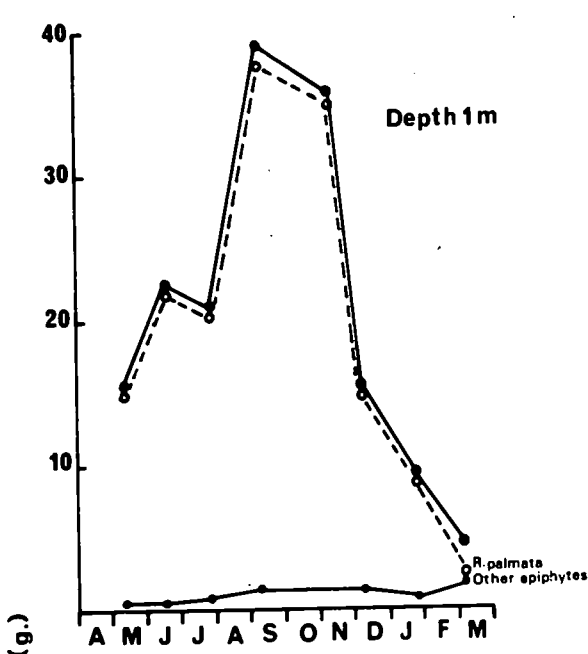
Time of cropping (months of 1968/1969)

FIGURE 16

Percentage of total epiphyte biomass at the five
depths sampled at Petticoe Wick Bay.

<u>Rhodymenia palmata</u>   o-----o

<u>Ptilotia plumosa</u>   +········+

<u>Membranoptera alata</u>   o———o

<u>Phycodrys rubens</u>   +—·—·—+
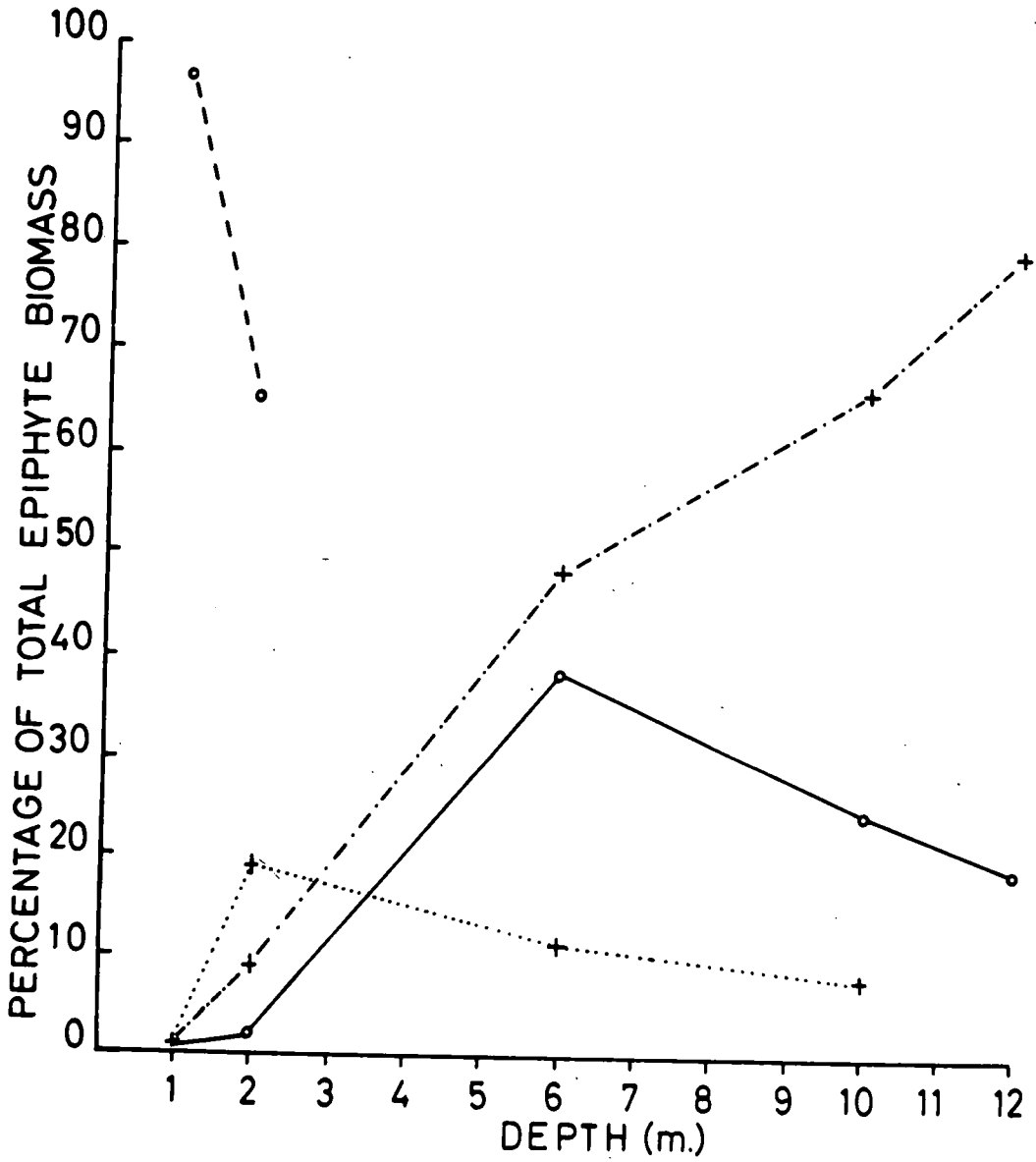
comprises at time of peak standing crop in relation to depth. The mean individual plant weights of each epiphyte species from depths 2 m and 10 m for various times of cropping throughout the year are given in Table 25 Appendix 3.

The epiphyte flora of _Laminaria hyperborea_ at Petticoe Wick shows marked seasonal changes in biomass. At no time of the year are the stipes completely free of epiphytes but a minimum biomass is present in January and the maximum is reached in September. In plants from 6 m, the mean minimum is reached in December but this result is not significantly different from the mean result for January.

In plants from 1 m and 2 m there is a gradual decrease in epiphyte biomass during the autumn and a sudden drop occurs in December. In deeper water maximum epiphyte biomass is still reached in September but the decline comes sooner and is faster. _Ptilotia plumosa_ grows at a much more rapid rate early in the growing season than the other component epiphytes and reaches a maximum biomass in June-July.

The seasonal variation in mean individual biomass of the epiphyte plants is given in Table 25 Appendix 3.

The trends do not exactly follow the pattern of the mean
epiphyte biomass per stipe.   At 2 m depth minimum
individual weight occurs in July and maximum in November
for all species except Ptilotia plumosa which reaches its
maximum mean individual biomass in September.   At 10 m
mean minimum biomass is reached in March-May and maximum
in September except in the case of Ptilotia plumosa,
which reaches a mean maximum in November, but this is not
significantly different from the mean biomass figure for
September.

In terms of percentage of peak standing crop,
Rhodymenia palmata makes up 97 per cent of epiphyte biomass
at 1 m depth and 67 per cent at 2 m, it is not found in any
quantity below this depth.   At 6 m it is completely absent.
Ptilotia plumosa reaches its maximum as a percentage of
total epiphytes at 2 m at 19 per cent and declines steadily
to 10 m where it comprises 8 per cent of total epiphyte
biomass.   Phycodrys rubens and Membranoptera alata are
present in small amounts at 1 m and rapidly increase in
proportion with increase in depth;   at 6 m they comprise
40 per cent and 48 per cent of total epiphyte biomass
respectively.   Below 6 m Membranoptera alata declines
in percentage to 12 m where it makes up 19 per cent of the

epiphyte biomass and <u>Phycodrys rubens</u> makes up the remainder.
Epiphytes reach their maximum standing crop per stipe at
2 m and this decreases with depth.

SUMMARY

(1) Stipe biomass increases with age, there is an initial "lag period" in the early years of growth followed by a rapid growth period in age classes three and four with a reduction in growth in the later years.

(2) Stipe biomass in the upper age classes increases with depth to 6 m, below this depth a reduction occurs.

(3) Increase in length of the stipe occurs concomittantly with increase in length and biomass.

(4) The lamina commences growth in January; the old laminae are completely lost by May and at this time the lamina commences rapid growth to reach a peak biomass in September at all depths except 1 m where it is reached in July.

(5) Peak lamina biomass increases with the age of the plant up to five years.

(6) Lamina biomass is greatest at 2 m and decreases with depth.

(7) The breakdown of the lamina occurs faster in deeper water than in the immediate sublittoral.

(8) The understorey plants from 6 m have greatly reduced stipe and lamina biomasses in comparison to plants from 2 m and 10 m.

(9) Four species, <u>Rhodymenia palmata</u>, <u>Ptilotia plumosa</u>, <u>Membranoptera alata</u> and <u>Phycodrys rubens</u>; make up nearly all the total epiphyte biomass.

(10) The epiphytes show a zonation on the stipes with depth of submersion with <u>Rhodymenia palmata</u> at the top followed by <u>Ptilotia plumosa</u> and with <u>Phycodrys</u> rubens and <u>Membranoptera alata</u> at the base.

(11) Epiphyte biomass per stipe increases with the age of the stipe up to five years, no significant increase occurs after this time.

(12) Epiphyte biomass shows a seasonal variation with a minimum in late winter and spring and a maximum in early autumn.

(13) <u>Ptilotia plumosa</u> reaches its maximum biomass earlier than the other species.

(14) Epiphyte biomass is greatest at 2 m and decreases with depth.

(15) <u>Rhodymenia palmata</u> makes up nearly all the epiphyte biomass at 1 m but decreases rapidly with depth and is absent at 6 m. <u>Ptilotia plumosa</u> occurs down to 10 m depth and has its maximum biomass at 2 m; at 10 m and below <u>Phycodrys rubens</u> is the dominant epiphyte.

CHAPTER 5

PLOT DENSITY

The density of _Laminaria hyperborea_ has been reported by various workers. Walker (1952, 1954a,b,c,d; 1955, 1956a,b, 1958a,b) and Walker and Richardson (1955, 1956, 1957a,b). sampled areas around the coast of Scotland using a grab and gave densities expressed both as wet weight and numbers per square yard. Ernst (1966) reported on the density from the shores of Brittany using S.C.U.B.A. and expressed his results as the number of individuals per square metre in relation to depth. Kain (1963) sampled populations on the Isle of Man and related density to height and age classes.

It is obvious when swimming over the kelp forest canopy at Petticoe Wick that a mosaic of plant density is present. The forest was sampled by cropping a series of one metre square areas. The metre quadrat was placed over a selected stand and all the plants whose holdfasts fell within this were removed and placed in a labelled bag. On return to the laboratory the plants were removed from the bag and aged using the method described in Chapter 3.

Plants of one year of age and less were discarded as cropping was carried out at different times over a period of two years and owing to the extended reproductive season of _Laminaria hyperborea_ comparisons of the density of these

"sporlings" would be meaningless.   The results are shown
in the form of histograms in Fig. 17 .   Five columns of
histograms are shown, each column representing one depth
range as indicated.   Each histogram represents the
number of individuals in each age class.   The figure
on the right of each histogram is the number of canopy
plants in the quadrat;   plants in age classes five and
above are considered to make up the canopy.

The quadrats from 1 m. in depth were taken
from areas co-dominated with Laminaria digitata and show
low density.   In the kelp forest at 2 m. and below the
canopy density, of the densest areas cropped, declines
with increase in depth and is significantly less dense,
at 10 m depth.   Below this depth a very open community
exists to depths of 12 - 13 m;   the maximum depth at which
Laminaria hyperborea occurs at this site.

In these deep water areas plants of older age
classes (six and seven) are comparatively rare whereas in
shallower water crops plants are commonly found to seven
years old.   In the general sampling for production data
few plants were found older than seven years;   though on
occasions plants aged up to nine and ten years were found.
The older plants are confined to areas between 2 m and 6 m

FIGURE 17

Number of individuals in each age class per metre
square at the five depths sampled at Petticoe Wick
Bay.   The number by each histogram is the number
of canopy plants.

Depth 1m. 2m. 6m. 10m. 12m.

NUMBER OF PLANTS
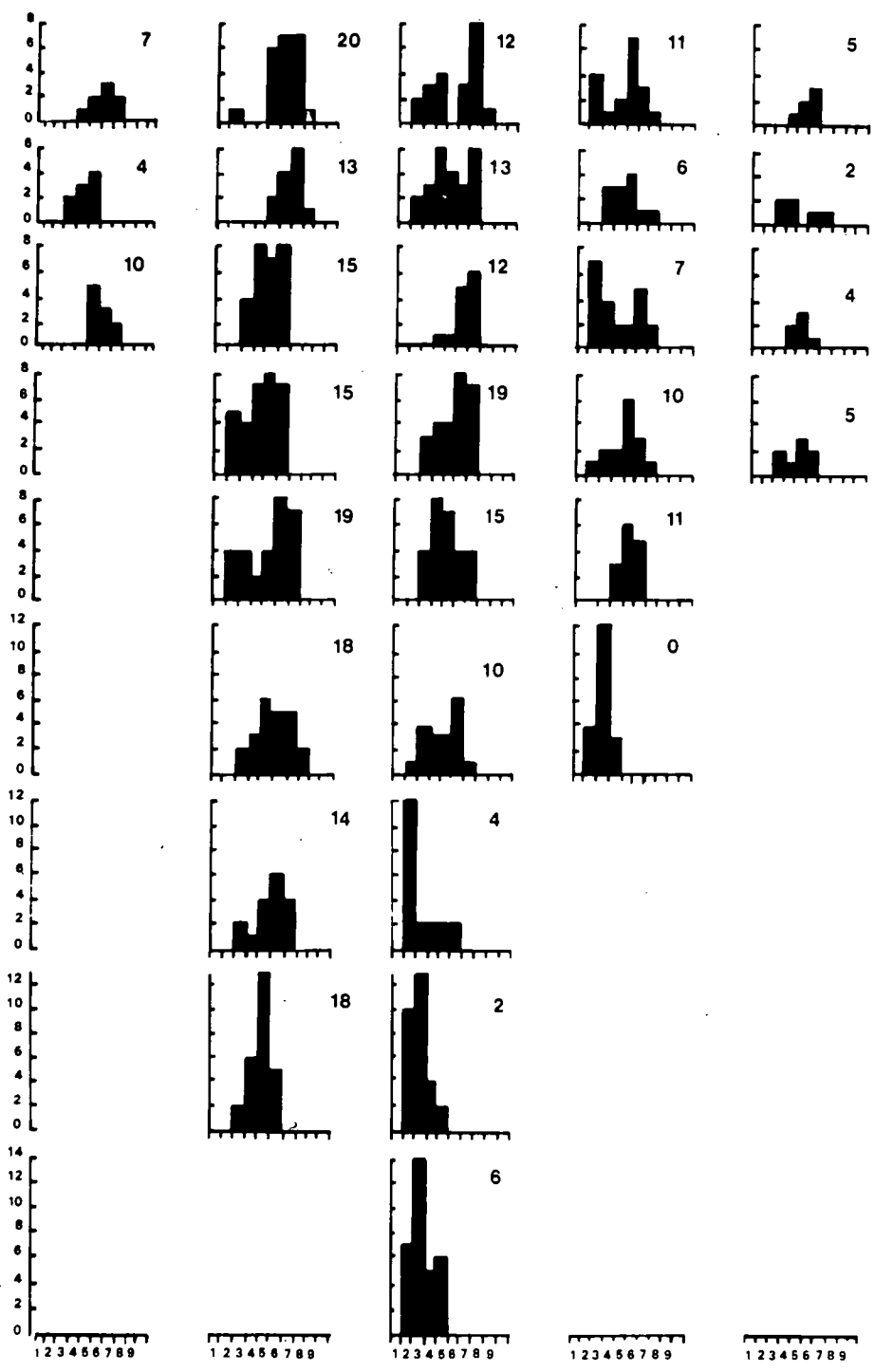
AGE (years)

in depth. One pattern that emerges from Fig. 17 is that
in the quadrats cropped which include a large number of
older canopy plants the number of younger plants is
reduced in comparison with quadrats containing fewer old
plants.

Patina pellucida L. has been reported as a
grazer on Laminaria hyperborea both of lamina and holdfast
(Graham and Fretter, 1947). Kain (1963) suggests that this
organism could have a profound effect on the density of
Laminaria hyperborea populations studied on the Isle of Man.

Patina pellucida can affect Laminaria hyperborea in
two ways. Firstly, by entering and living within the base
of the stipe where it eats out a cavity; (Graham and Fretter
1947), this can bring about a marked weakening of the holdfast
region and may well cause the loss of the individual during
rough sea conditions. The weakening effect of such grazing
on the holdfast may be partly counteracted by the production
of secondary haptera, which seems to take place in response
to damage by P. pellucida. Secondly, the infestation of the
lamina may cause losses of the photosynthetic area due to
grazing. The level of infestation of L. hyperborea by
P. pellucida is given in each age class Fig. 18, as a
histogram of percentage infestation, the figures above each

column indicate the number of plants sampled. The data

is taken from all depths down to six metres. In croppings

from ten and twelve metres little sign of infestation

by P. pellucida is found. In recording the level of

infestation any individual with one or more cavities in the

base of the stipe, whether occupied or not, was counted

as infested. The results show that the level of

infestation is low and is confined mainly to the upper

age classes. The level of infestation is less than that

found by Kain (1963) in the Isle of Man which was as high

as 40 - 50%.

FIGURE 18

by Patinapellucida

Percentage infestation ∧ of individuals of <u>Laminaria</u>

<u>hyperborea</u> in each age class.   The figure above

each column indicates the number of individuals

sampled in that age class.
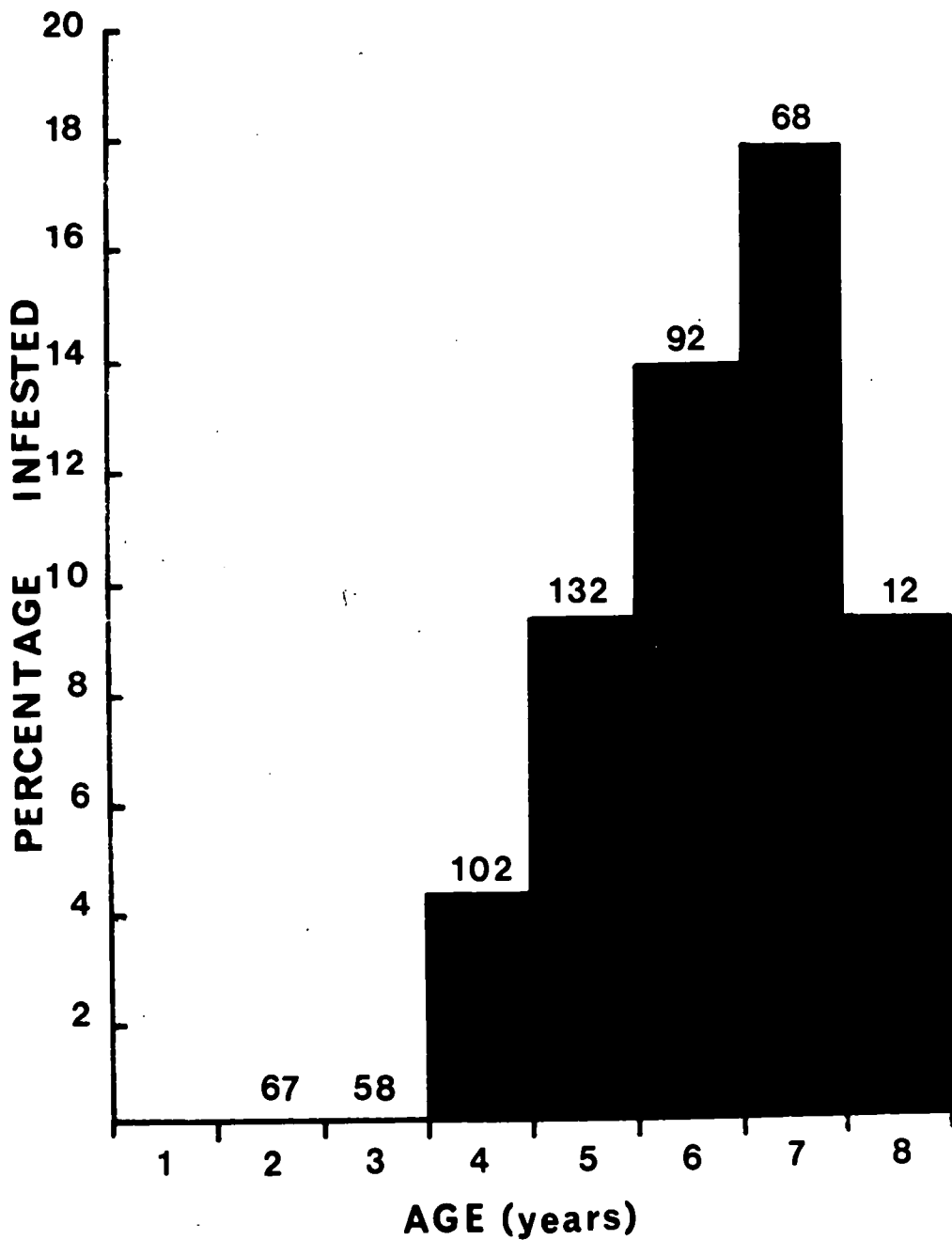
SUMMARY

(1) Canopy density decreases with depth, below 10 m the canopy opens up and scattered individuals occur to 13 m.

(2) The canopy seems to have a regulating effect on the
number of ~~plants of~~ understorey plants; ~~in~~ stands containing
plants of L. hyperborea in the
a large number of canopy plants the numbers of understorey individuals are reduced.

(3) Infestation levels of the holdfasts of <u>Laminaria hyperborea</u> by <u>Patina pellucida</u> increase with age of the host at least up to seven years. The levels even in the upper age classes are lower than those reported by Kain (1963) from the Isle of Man.
NB. Generalisations refer to the site under investigation

CHAPTER 6

PERFORMANCE RESULTS FROM COMPARATIVE SITES

The main study site at Petticoe Wick has been visited on a number of occasions during the years 1967, 1968 and 1969, and data on the performance of the dominant _Laminaria hyperborea_ and its associated epiphytes obtained. In order to further test the techniques outlined in Chapter 2, and to obtain comparative performance data three other geographically distinct sites have been visited. These sites were visited in the late summer and early autumn and in the absence of increment cropping data it could only be assumed that the laminae had reached peak biomass. The location of these three sites is shown on the map in Chapter 1.

The sites are:

(1) North Landing, Flamborough, Yorkshire
Lat 54°8'N Long 0°5'W   Date of Visit 17.9.68

(2) Dunmanus Bay, Co. Cork, Eire
Lat 51°35'N Long 9°45'W   Date of Visit 28.9.68

(3) Sennen Cove, Cornwall
Lat 50°5'N Long 5°25'W   Date of Visit 26.8.67

The methods used in these areas both for the cropping of _Laminaria hyperborea_ and its subsequent treatment were the same as for the main study site, with the exceptions noted below:

1. Collected material was wet weighed; subsamples
    were air dried before being transported back to
    the Laboratory for final drying and analysis.

2. No attempt was made to sort epiphytes into
    component species.

3. Because only one visit was made to these sites,
    no increment cropping data is presented for
    lamina biomass.

Site 1: North Landing Flamborough

This is an exposed site characterised by the
presence of a large amount of suspended material in the
water and a fine layer of sediment covering the substrate.
Laminaria hyperborea is found from low water mark to a depth
of 8 m. It was sampled at three depths, 1.5 m, 5 m and 8 m.
Graphs of the mean stipe and mean peak lamina biomass for
each age class at the depths sampled are given in Fig. 19
and Fig. 20 respectively and stipe length and weight per
unit length in Fig. 21 a and b.   The full cropping data
is presented in Table 20   Appendix 3.

The laminae show a regular increase in biomass
with age at all depths and a decrease in biomass with
increasing depth.   In all age classes and at all depths,
they are significantly smaller than the equivalent laminae at

FIGURE 19

Stipe biomass at three depths sampled at Flamborough

Depth (m)

1.5 ●——————●

5 ○—·—·—○

8 ▲— — —▲
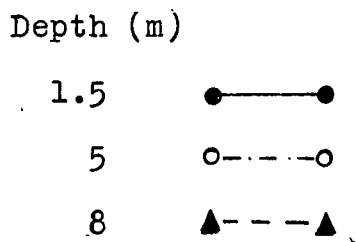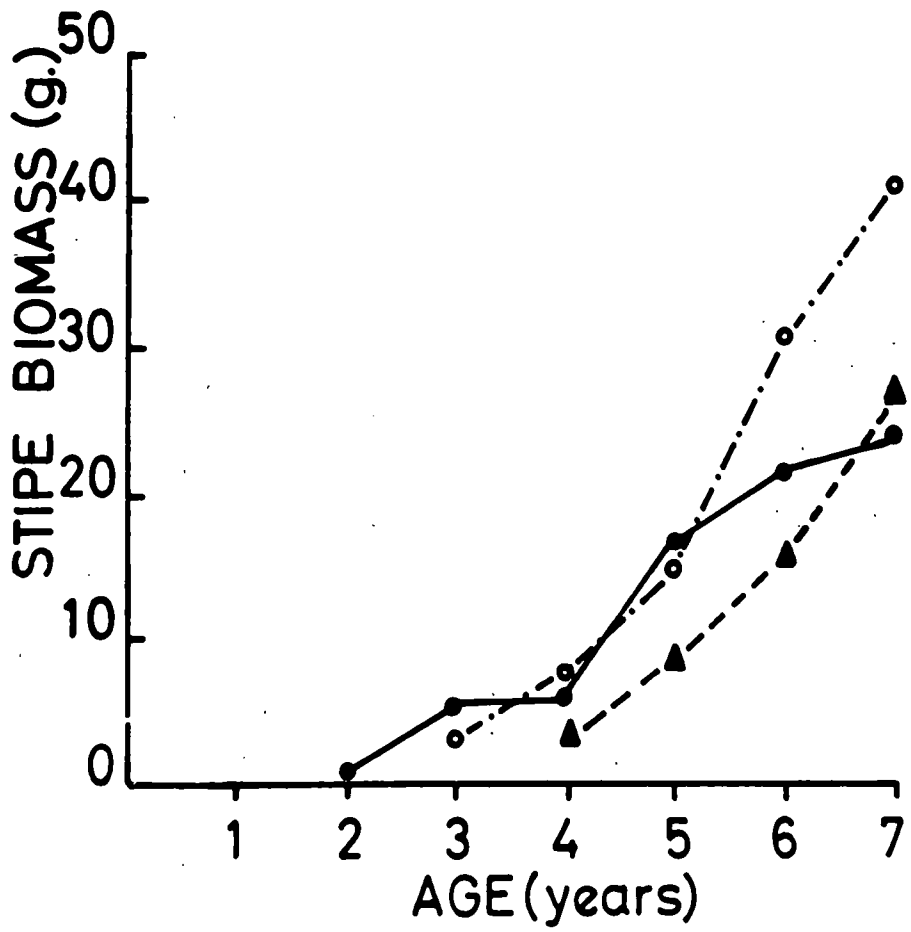
FIGURE 20

Lamina biomass at three depths sampled at Flamborough.
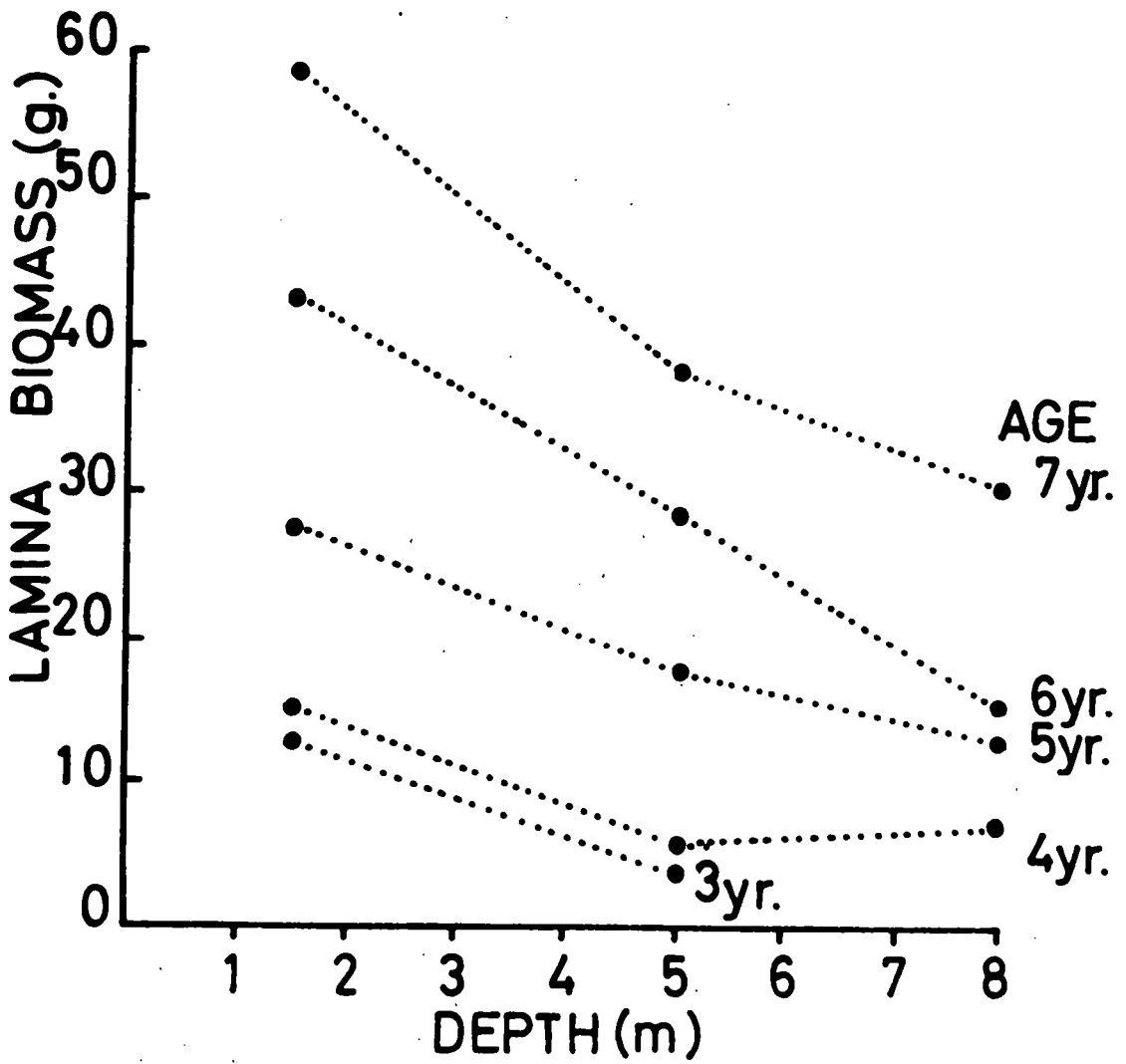
FIGURE 21

Stipe length at three depths sampled at Flamborough

Depth (m)

1.5   ●————●

5   O—·—··—O

8   ▲— — — —▲
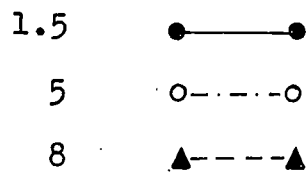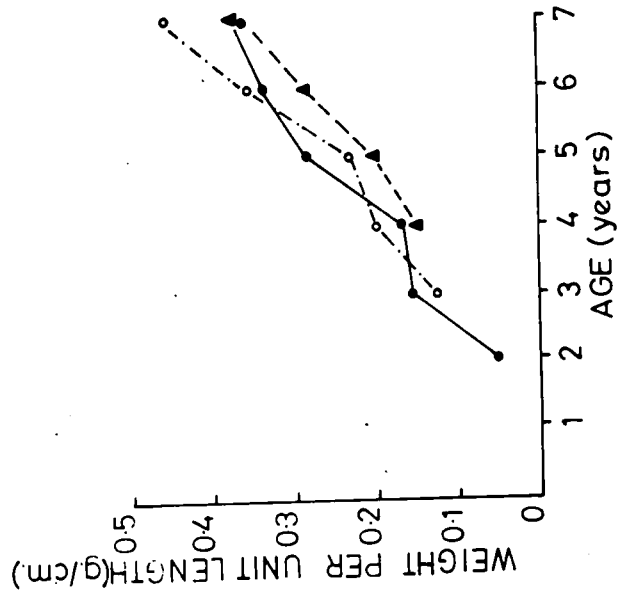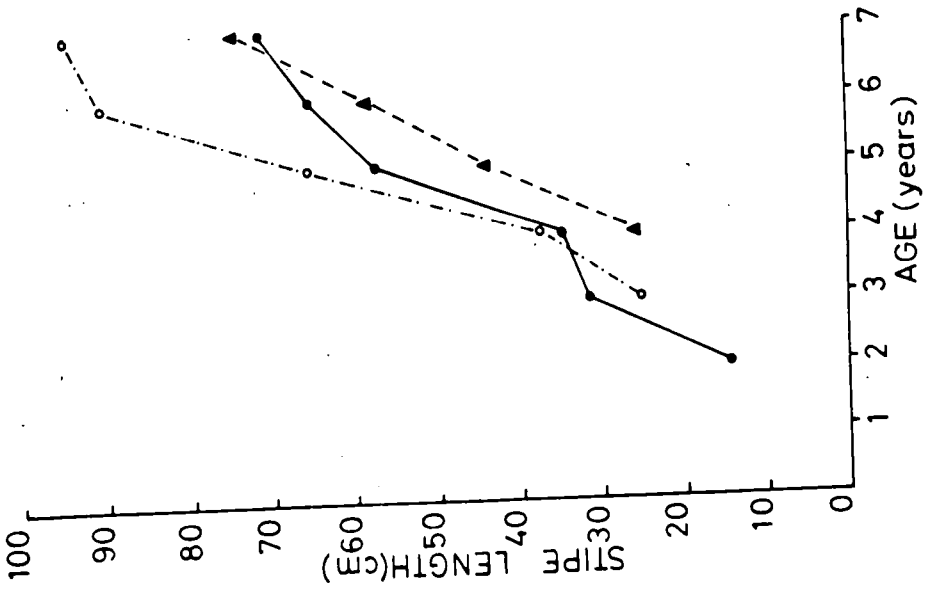
Petticoe Wick.   Stipe biomasses in the younger age classes
(one to five years) from 1.5 m and 5 m show no significant
differences but in six and seven year old plants, the
biomass is greatest at 5 m.   The mean of the stipe
biomass in plants from 8 m is less in all ages than from
those at either 1.5 m or 5 m depth though from the numbers
of samples taken this difference is not significant.

All stipe biomasses show considerable reduction
when compared to plants of the same age from similar depths
at Petticoe Wick.

Stipe length is greatest in plants from age
classes six and seven at 5 m, though in other age classes,
there are no significant differences between individuals
from 1.5 m and 5 m.   The mean stipe length of individuals
from 8 m depth is not significantly different from those
at 1 m but is significantly less than those from 5 m in
age classes, five, six and seven.   There is no significant
difference in stipe weight per unit length between plants
in the same age class at the depths studied.

The epiphytes found on the stipes at the depths
studied are presented in Table 4 .   There is a distinct
reduction in the number of species present when compared to
Petticoe Wick.   The most noticeable is the total absence

TABLE 4

MACRO-EPIPHYTIC SPECIES - FLAMBOROUGH

	Depth (m)		
	1.5	5	8
Membranoptera alata	+	+	+
Phycodrys rubens	+	+	+
Sphacelaria plumigera	+		
Ulva lactuca	+		
Ectocarpus fasciculatus	+		
Rhodymenia palmata	+		
Ceramium rubrum	+	+	
Plocamium cartilagineum	+	+	
Lithophyllum Sp.	+	+	
Polysiphonia brodeaei	+	+	
Polysiphonia urceolata	+	+	
Plumaria elegans	+	+	
Hypoglossum woodwardii		+	+
Peyssonelia atropurpurea		+	+
Cryptopleura ramosa		+	+

of <u>Ptilotia plumosa</u> and the extension of the depth range
of <u>Rhodymenia palmata</u> to 5 m.

The biomass per stipe of the main component
epiphytes occurring at the depths sampled is given in
Fig. 22 and the results on a percentage basis in Fig. 23
At 8 m, <u>Cryptopleura ramosa</u> forms a significant proportion
of the total epiphytes. The total biomass of epiphytes is
much reduced in comparison with the epiphytes from
Petticoe Wick. There is a gradual decrease in epiphyte
biomass with increase in depth. <u>Phycodrys rubens</u> and
<u>Membranoptera alata</u> reach their greatest biomass on the
stipes from 5 and 8 m depth.

Site 2: Dunmanus Bay

At this site <u>Laminaria hyperborea</u> was found to
depth of 18 m; below this depth in the area studied the
rock gave way to a sandy substrate and it is possible that
this limitted the vertical distribution of <u>L.hyperborea</u>
Graphs of stipe biomass, stipe length, peak lamina biomass
and stipe weight per unit length are presented as before
(Figs. 24 - 27 respectively). Composite data is given
in Table 21   Appendix 3.

FIGURE 22

Epiphyte biomass per stipe at the three depths
sampled at Flamborough

Total epiphyte biomass	●———●
<u>Rhodymenia palmata</u>	○– – – –○
<u>Phycodrys rubens</u>	+—·—·–+
<u>Membranoptera alata</u>	○———○
<u>Cryptopleura ramosa</u>	▲
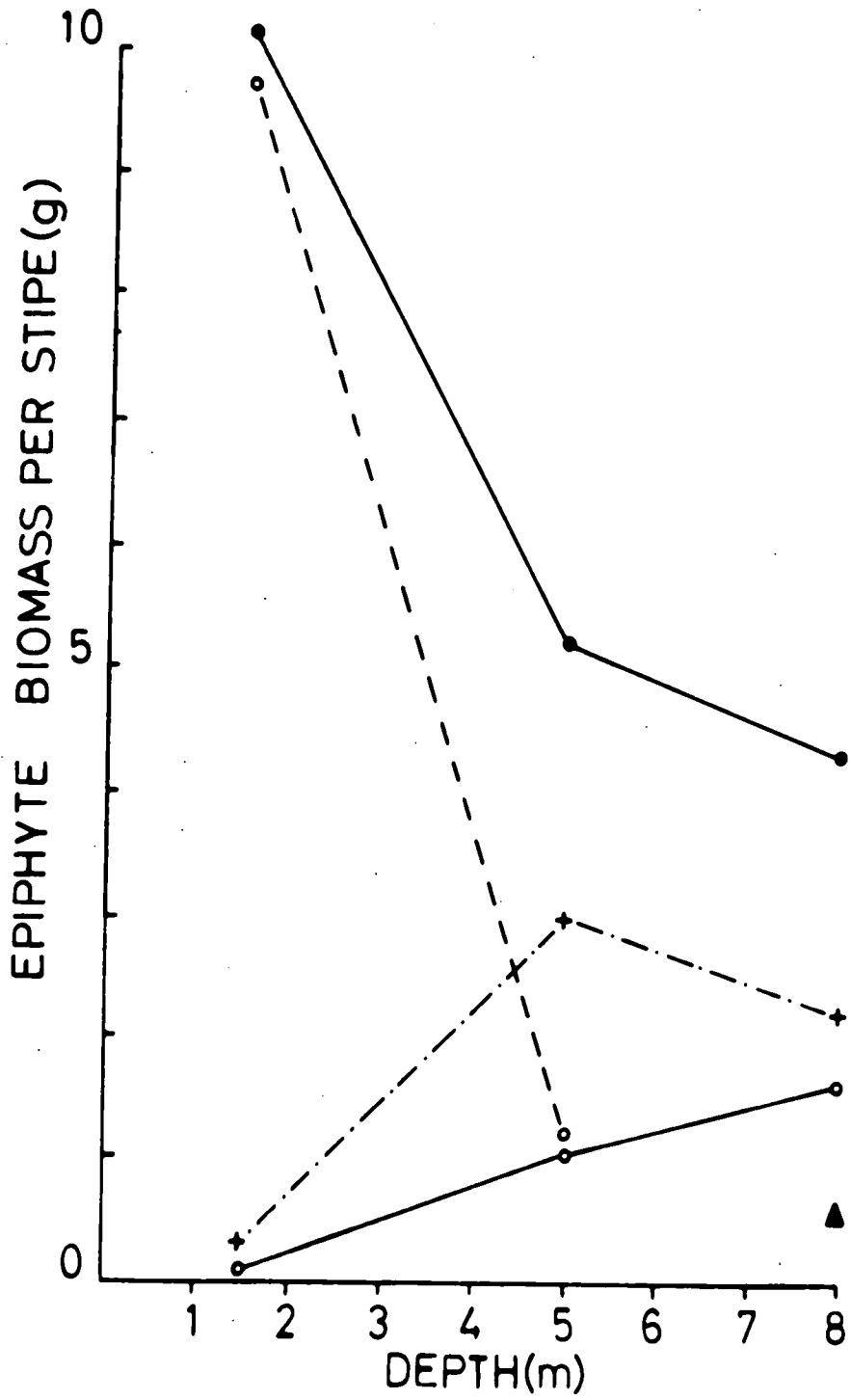
FIGURE 23

Percentage of total epiphyte biomass at the three

depths sampled at Flamborough

<u>Rhodymenia palmata</u>   o— — — —o

<u>Phycodrys rubens</u>   +— · — · —+

<u>Membranoptera alata</u>   o————o
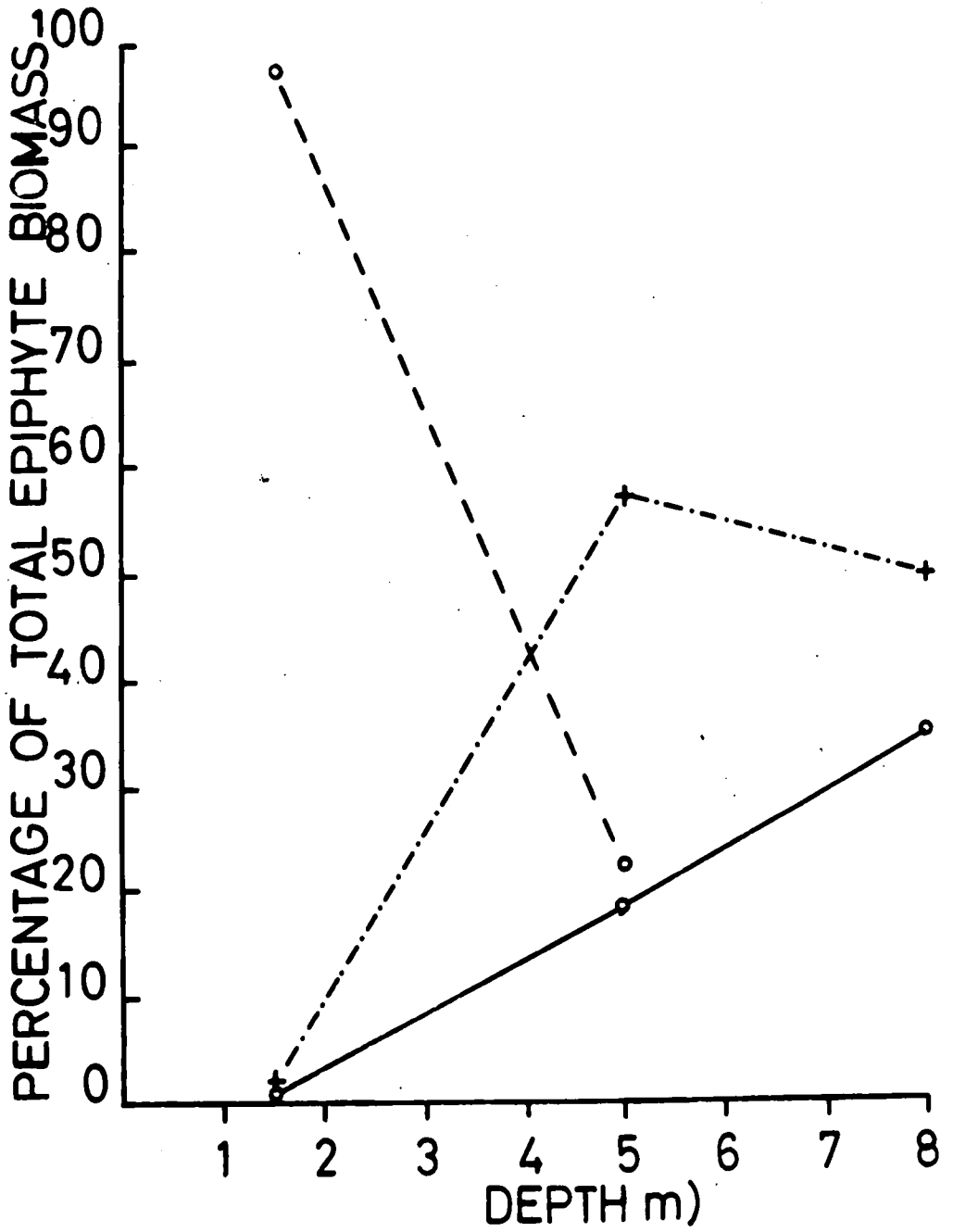
FIGURE 24

Stipe biomass at four depths sampled at Dunmanus Bay

Depth (m)

2	●————●
5	▲————▲
12	○—·—·—○
18	●········●
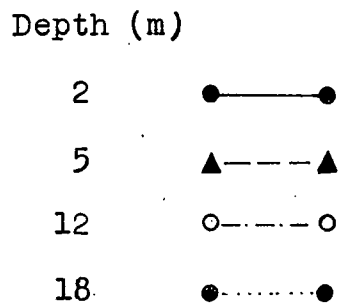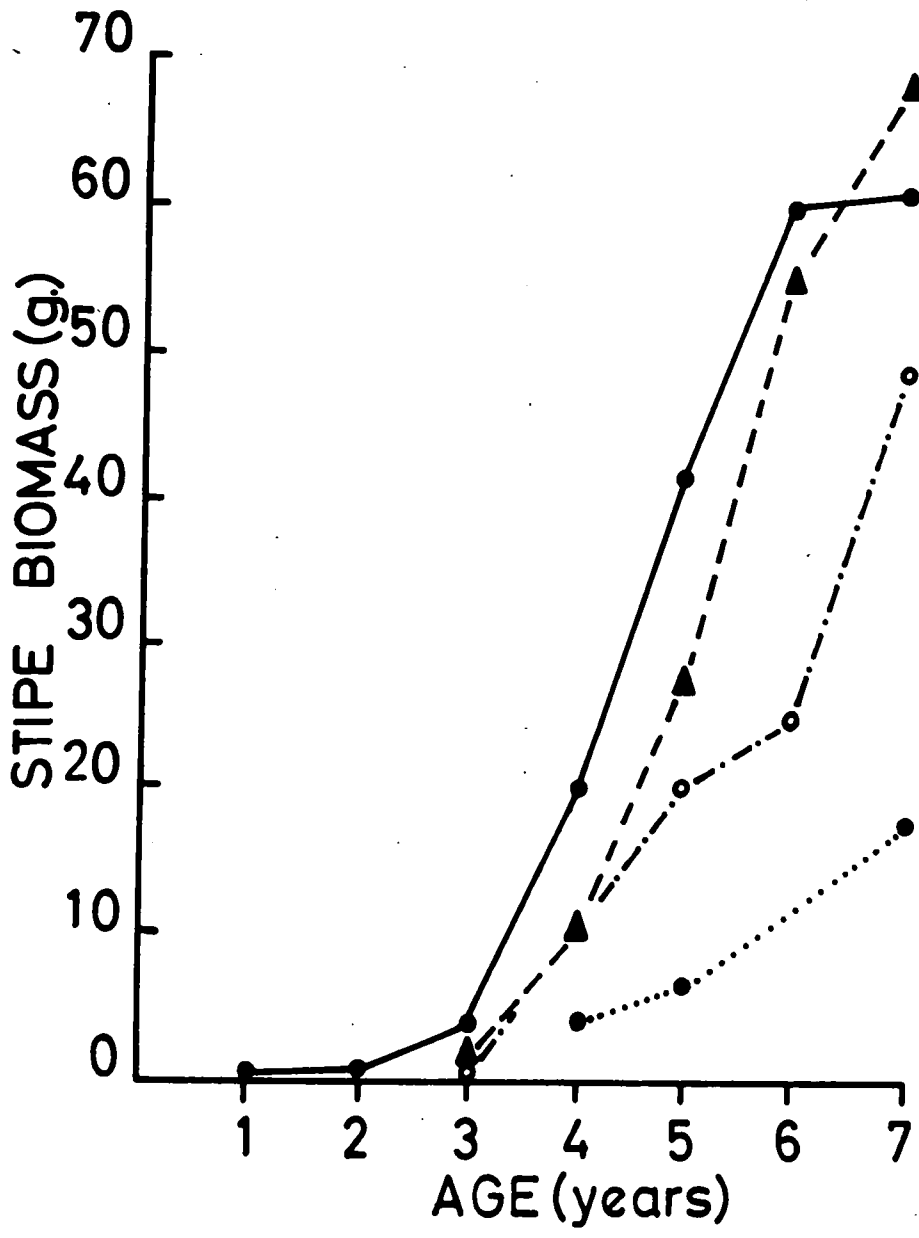
FIGURE 25

Stipe length at four depths sampled at Dunmanus Bay.

Depth (m)

2   ●————●

5   ▲ — — —▲

12   ○—.—.—○

18   ●·······●
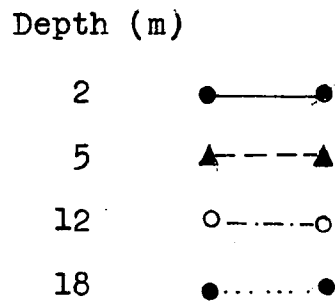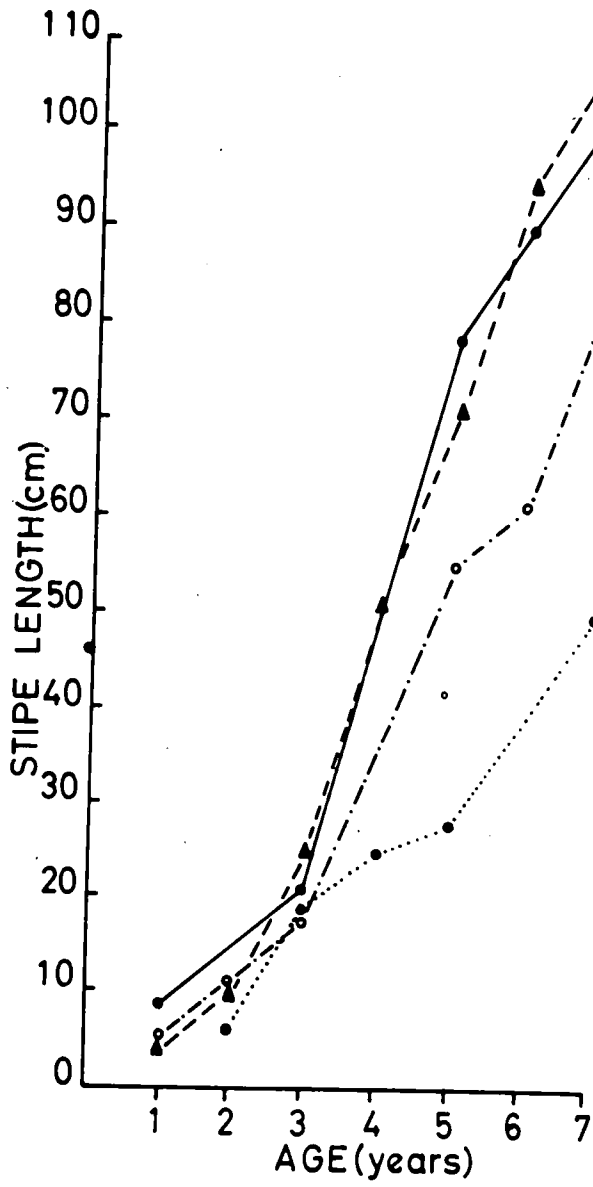
FIGURE 26

Lamina biomass at the four depth sampled at Dunmanus Bay.
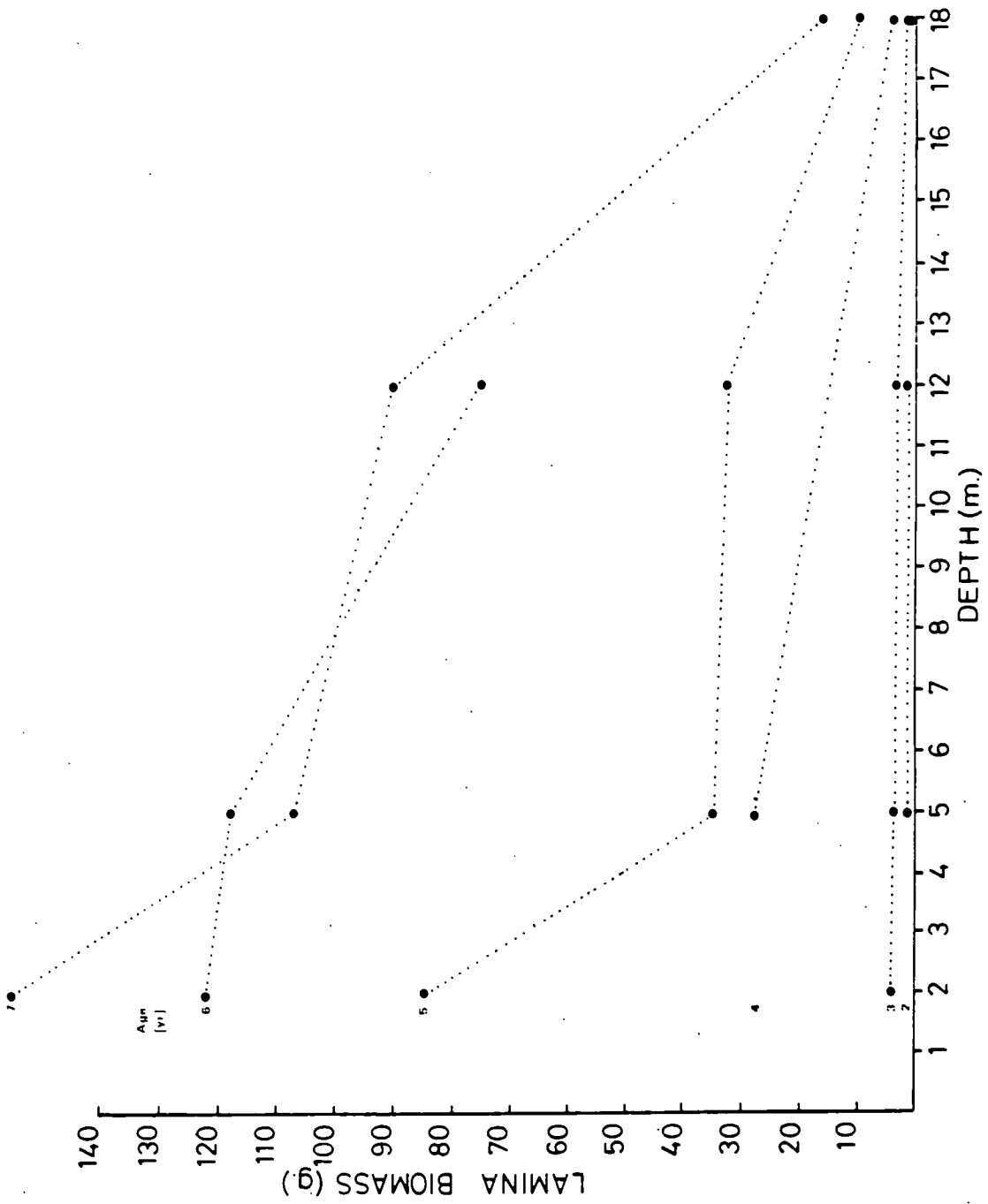
FIGURE 27

Weight per unit length of stipe at four depths sampled
at Dunmanus Bay.

Depth (m)

2   ●————●

5   ▲----▲

12   o--·--·--o

18   ●······●
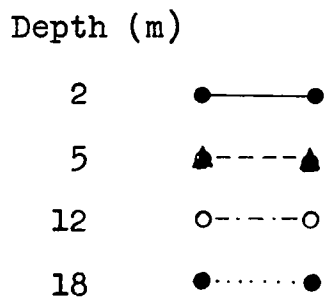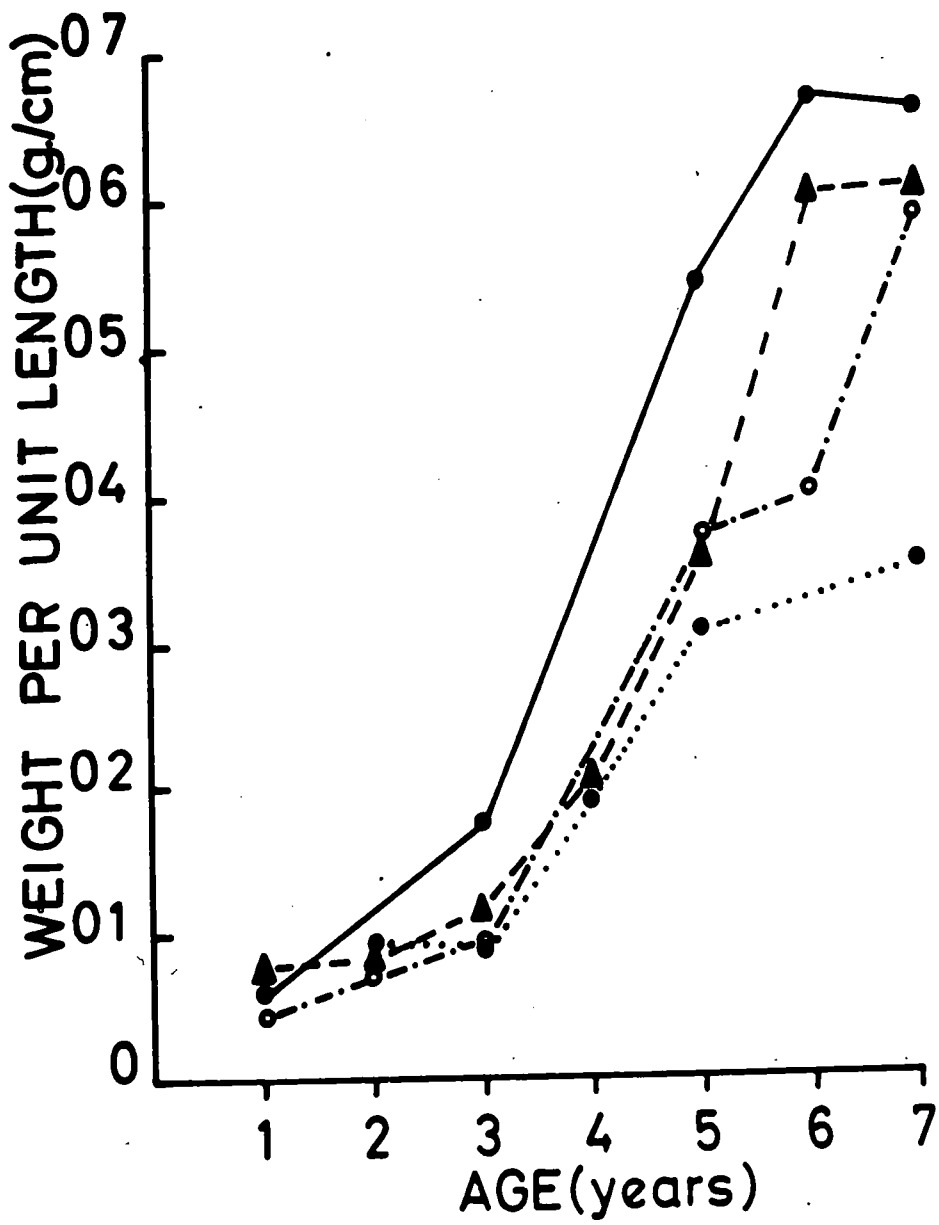
Lamina biomass increases with age up to age classes six and seven but laminae from age class five show significantly lower biomasses. The general overall trend in lamina biomass in relation to depth follows the trends shown over the equivalent depth ranges at Petticoe Wick. The mean stipe biomass shows a decrease with depth. In the lower age classes from depths 2 m, 5 m and 12 m, stipe biomass is not significantly different with change in depth. In the upper age classes, stipe biomass at 12 m is significantly smaller than those from 2 or 5 m. Stipe biomass from 18 m is much less than from other depths in all age classes. In the upper age classes stipe biomass is significantly less than that of the same age plants from equivalent depths at Petticoe Wick.

Stipe length follows the same overall pattern as stipe biomass, there being no significant differences between individuals in the same age class with depths up to three years of age. Individuals from 2 m and 6 m show no significant difference in length throughout the life of the plant but a reduction in length in the upper age class individuals with increase in depth is evident below the 6 m mark.

Weight per unit length of stipe increases progressively with age. There is a tendency for a decrease in weight per unit length with increase in depth. Plants in the upper age classes from 18 m depth have significantly reduced weights per unit length than those from other depths.

Table 5 gives a list of the epiphytes found at Dunmanus Bay. Greatest epiphyte diversity occurs within the depth range 6 m to 10 m. Rhodymenia palmata is found to a depth of 10 m. Fig. 28 shows mean epiphyte biomass per stipe in relation to depth. This shows a correlation of decrease in biomass with increase in depth.

Site 3: Sennan Cove

This is a very exposed site. In shallow water, Laminaria digitata is replaced by Alaria esculenta and Laminaria hyperborea is not found until a depth of 3 m is reached, where it forms a mixed community with Saccorhiza polyschides. At this site, Laminaria hyperborea extends as a close canopy to a depth of 16 m and scattered individual plants are found to a depth of 37 m. Croppings were taken at the following depths: 3 m, 7 m, 10 m, 13 m, 23 m, 30 m and 37 m depth. The results for stipe weight, stipe length, weight per unit length and lamina biomass are shown in Figs. 29 - 32 respectively. The composite

TABLE 5

MACRO-EPIPHYTIC SPECIES - IRELAND DUNMANUS BAY

	Depth (m)			
	2	6	12	18
Rhodymenia palmata	+	+	+	
Callithamnion tetragonium	+			
Erythroglossum sandrianum	+	+		
Polysiphonia urceolata	+			
Ceramium rubrum	+		+	
Ceramium shuttleworthianum		+		
Cryptopleura ramosa		+	+	
Lithophyllum crouanii		+	+	
Lomentaria articulata		+	+	
Plocamium cartilagineum		+	+	
Chaetomorpha linum		+		
Antithamnion spirographidis		+	+	
Membranoptera alata			+	
Erythrotrichia carnea			+	
Antithamnion cruciatum			+	
Phycodrys rubens		+	+	+
Ptilothamnion pluma		+	+	+

FIGURE 28

Epiphyte biomass per stipe at the four depths sampled
at Dunmanus Bay.
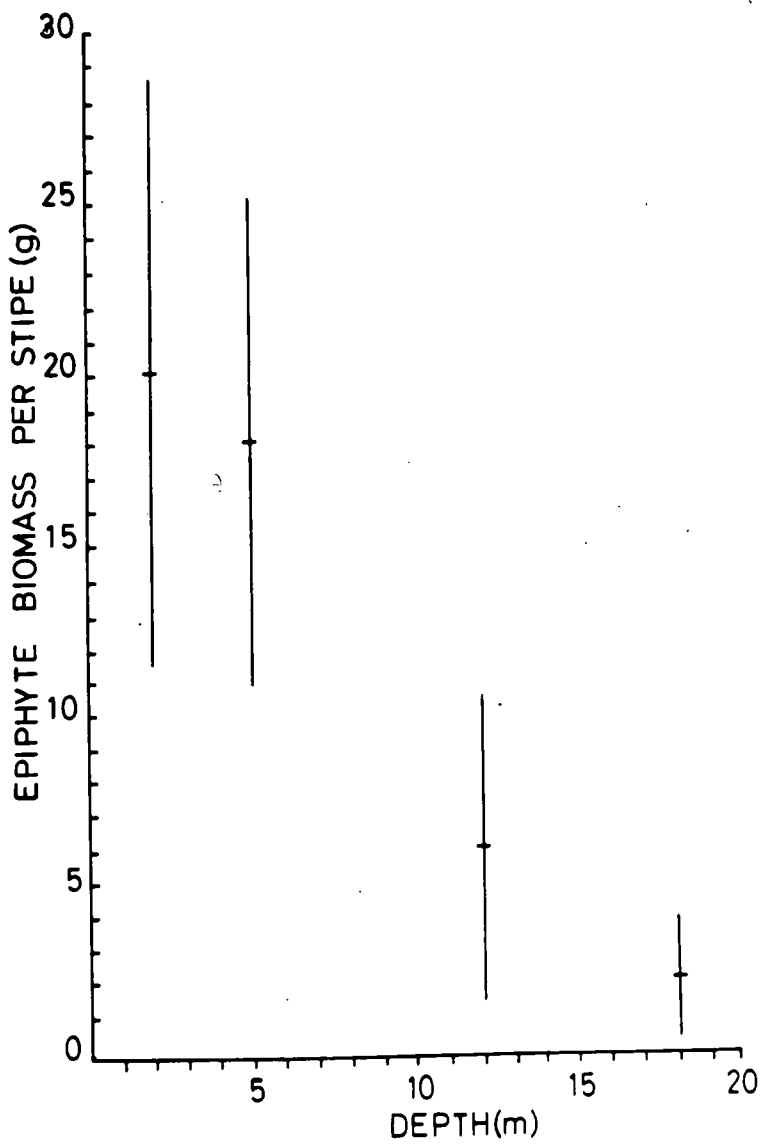
FIGURE 29

Stipe biomass in each age class at the seven depths
sampled at Sennen Cove.

Depth (m)

3	●——●
7	o– – –o
10	▲–·–·–▲
13	●·········●
23	o———o
30	+———+
37	●– – –●
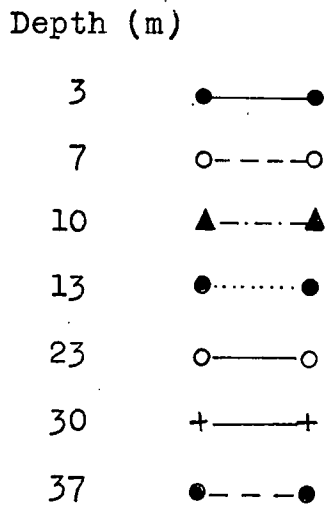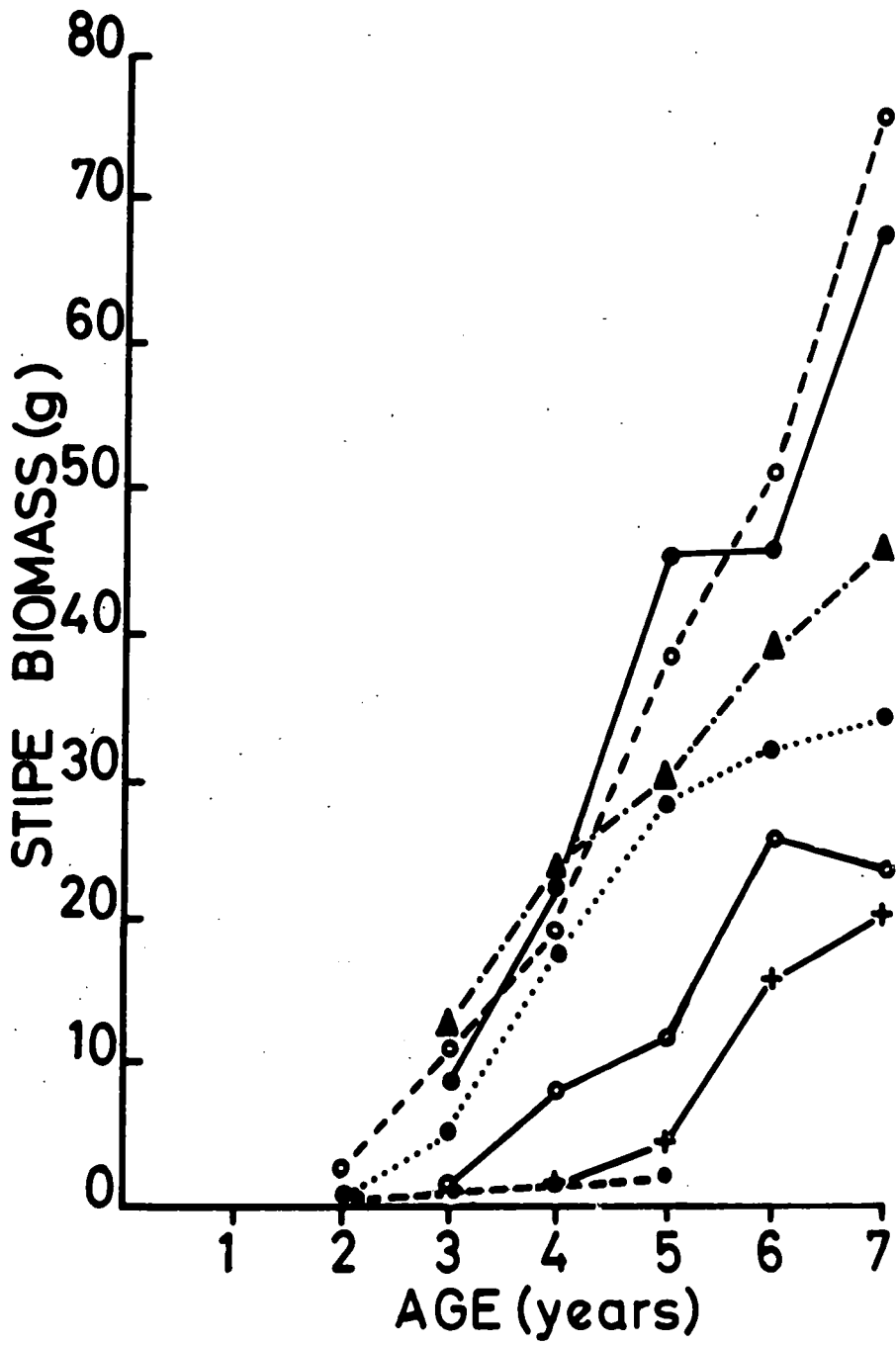
FIGURE 30

Stipe length in each age class at the seven depths
sampled at Sennen Cove.
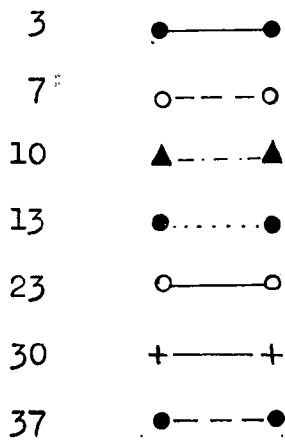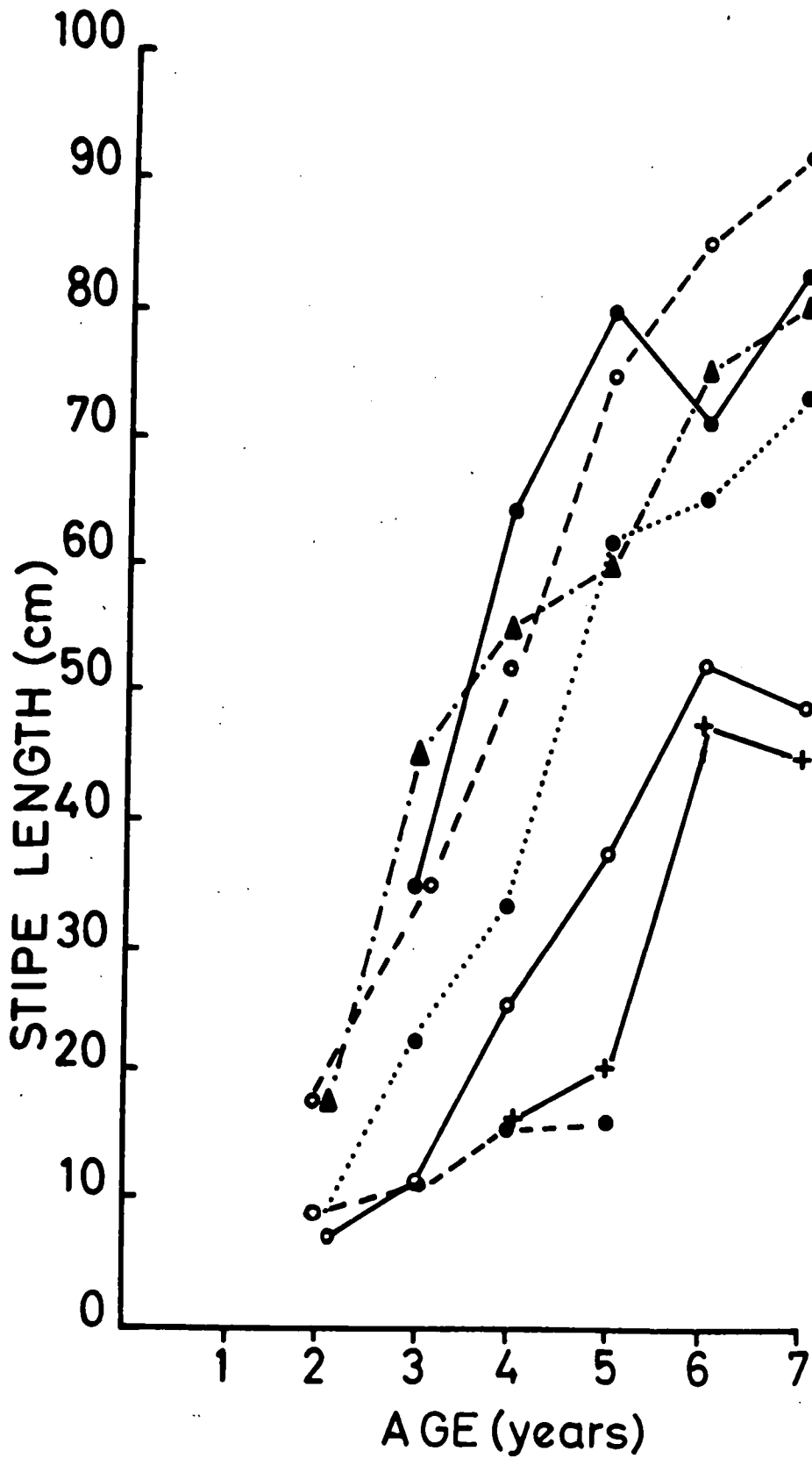
Depth (m)

FIGURE 31

Weight per unit length of stipes in each age class for the seven depths studied at Sennen Cove.

Depth (m)

3	•———•
7	o----o
10	▲—·—·—▲
13	•·······•
23	o———o
30	+———+
37	•---•
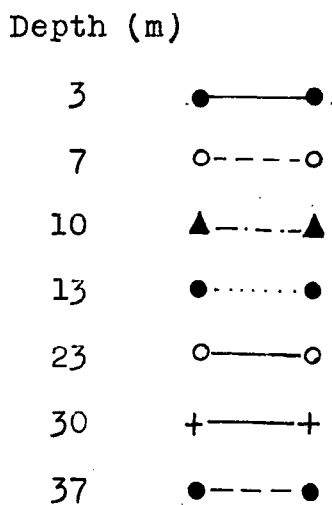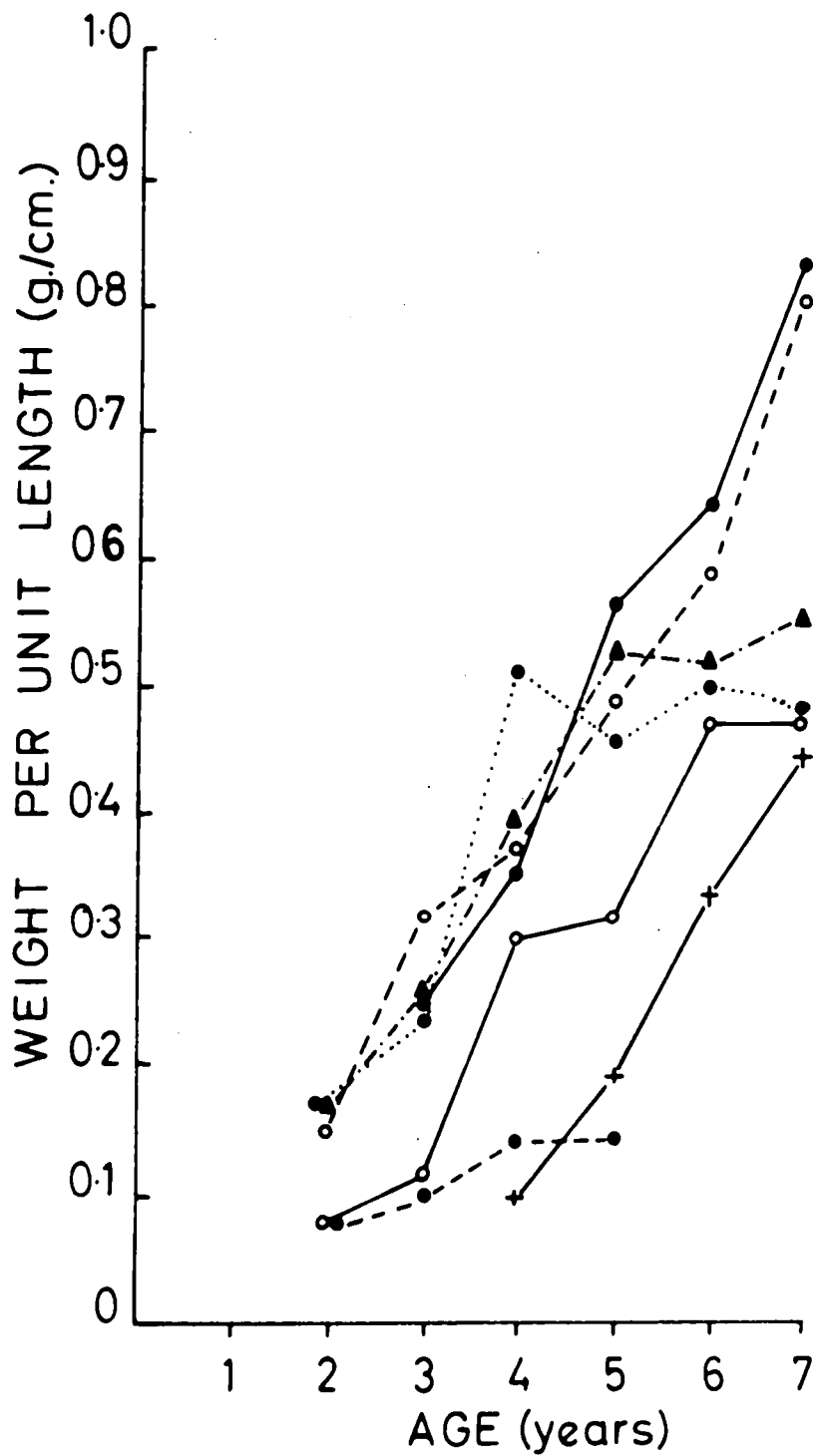
FIGURE 32

Lamina biomass at the seven depths sampled at Sennen
Cove.
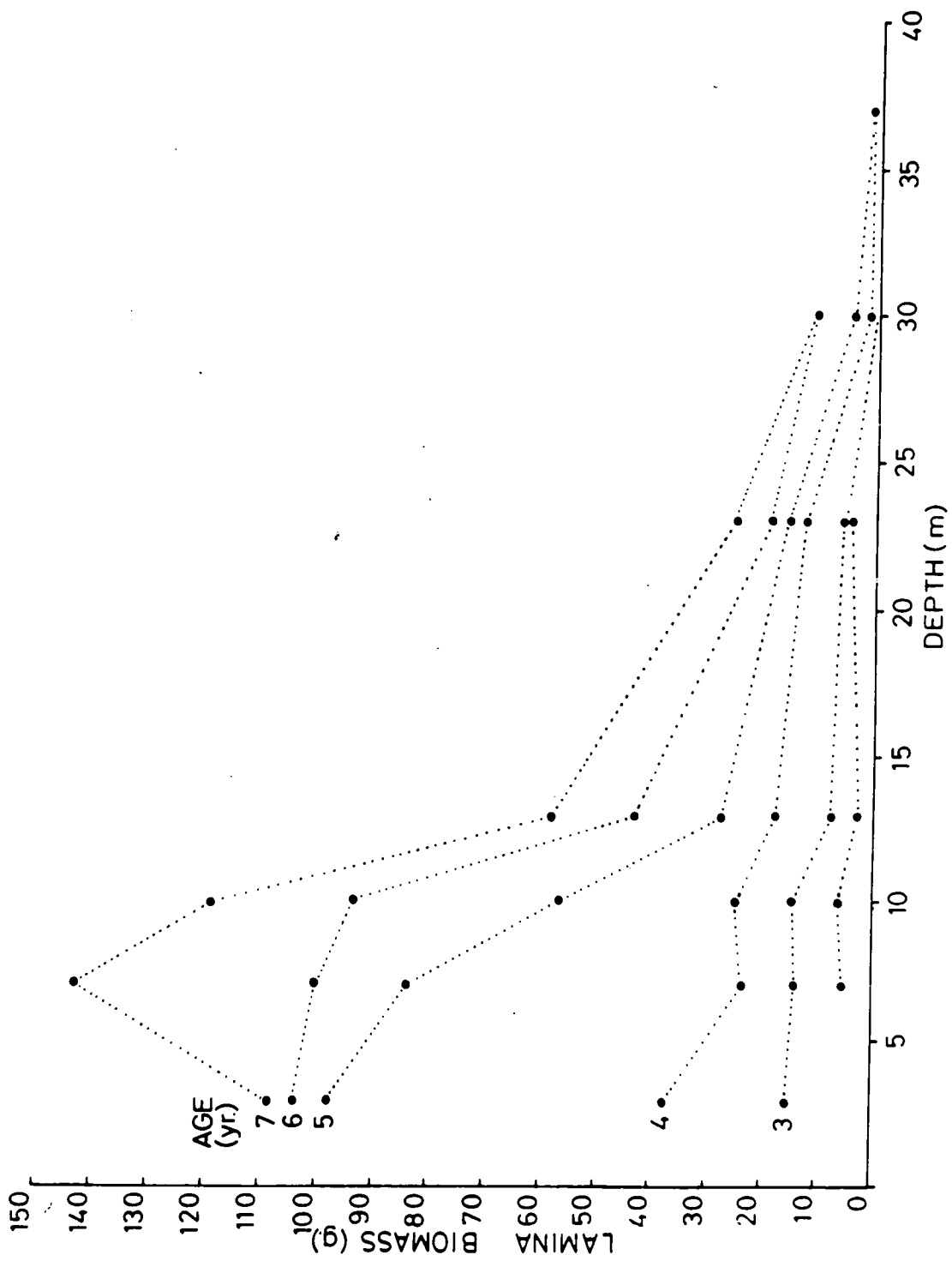
data from this site is given in Table 22 Appendix 3.

The mean stipe weights from the lower age classes (one to four years), from depths 3 m to 10 m do not show any significant differences within each age class. There is no significant difference in stipe biomass between individuals from 3 m and 7 m in the same age class. Below 13 m there is a gradual decrease in stipe biomass with increase in depth in all age classes.

In the upper age classes (five to seven years) stipe biomass shows a marked reduction when compared to individuals in the same age classes, from equivalent depths, at Petticoe Wick. There are no significant differences shown by the lower age classes to a depth of 10 m. At 13 m plants in the lower age classes have greater stipe biomasses than those from 12 m at Petticoe Wick.

The increase of lamina biomass can be correlated with increase in age but in the upper age classes (five to seven years) this difference is not significant. Generally lamina biomasses decrease with depth but in the shallower depths 3 m to 10 m this difference is not significant. Lamina biomasses at Sennen Cove are similar to those from equivalent plants at Petticoe Wick.

Stipe lengths reflect the results for stipe biomasses and in the upper age classes are significantly shorter than equivalent plants at Petticoe Wick.

The mean weights per unit length show an upward trend with age at all depths studied up to the age of four years. At depths 3 and 7 m this occurs throughout the life of the plant but at other depths 10 m, 13 m, 23 m, weight per unit length does not significantly increase after ages four or five years. The weight per unit length of stipe is approximately the same as that from Petticoe Wick over equivalent depths.

Table 6 lists the algae found epiphytic on the stipes of Laminaria hyperborea at Sennen Cove; no epiphytes are found below 23 m; greatest floristic diversity occurs at a depth of 13 m. Rhodymenia palmata is found at all depths where epiphytes occur. Figure 33 shows the change in epiphyte biomass with increasing depth. Greatest biomass is found at 7 to 10 m. Epiphyte biomass at 3 m is less than that at 10 m.

The results for stipe and lamina biomass for these three sites along with peak results from Petticoe Wick are summarised in Table 7. The figures are obtained by taking the area under the curve for the graphs of stipe biomass against age and peak lamina biomass against age, up to the age of seven years.

TABLE 6

MACRO-EPIPHYTIC SPECIES - SENNEN COVE

	Depth (m)				
	3	7	10	13	23
Rhodymenia palmata	+	+	+	+	+
Membranoptera alata		+	+	+	+
Callophyllis lacinata	+	+	+	+	+
Crytopleura ramosa	+	+	+	+	+
Lomentaria articulata	+	+	+	+	+
Hypoglossum woodwardii		+		+	
Phycodrys rubens		+	+	+	+
Ptilothamnion pluma		+	+	+	+
Plocamium cartilagineum				+	
Ceramium rubrum				+	
Polyneura hilliae				+	
Erythroglossum sandrianum				+	
Phyllophora crispa					+
Polysiphonia urceolata					+
Phyllophora brodiaei		+	+	+	
Plumaria elegans				+	
Ectocarpus fasciculatus	+	+		+	
Radicilingua thysanorhizans				+	
Chondrus crispus				+	
Cladostephus verticilatus				+	
Sphacelaria caespitula	+			+	
Sphacelaria cirrosa				+	
Nitophyllum punctatum		+			
Rhodochorton purpureum		+			
Callithamnion granulatum		+			

FIGURE 33

Epiphyte biomass per stipe at five depths at Sennen
Cove.

TABLE 7

INTEGRATED PERFORMANCE FIGURES

Depth (m)	Location							
	Petticoe Wick		Flamborough		Dunmanus Bay		Sennen Cove	
	Stipe	Lam	Stipe	Lam	Stipe	Lam	Stipe	Lam
1	160	270						
1.5			61	122				
2	190	430			144	317		
3							152	305
5			77	66	131	232		
6	225	262						
7							157	284
8			47	57				
10	163	230					119	222
12	30	112			90	180		
13							98	118
18					30	41		
23							55	68
30							35	25
37							8	10
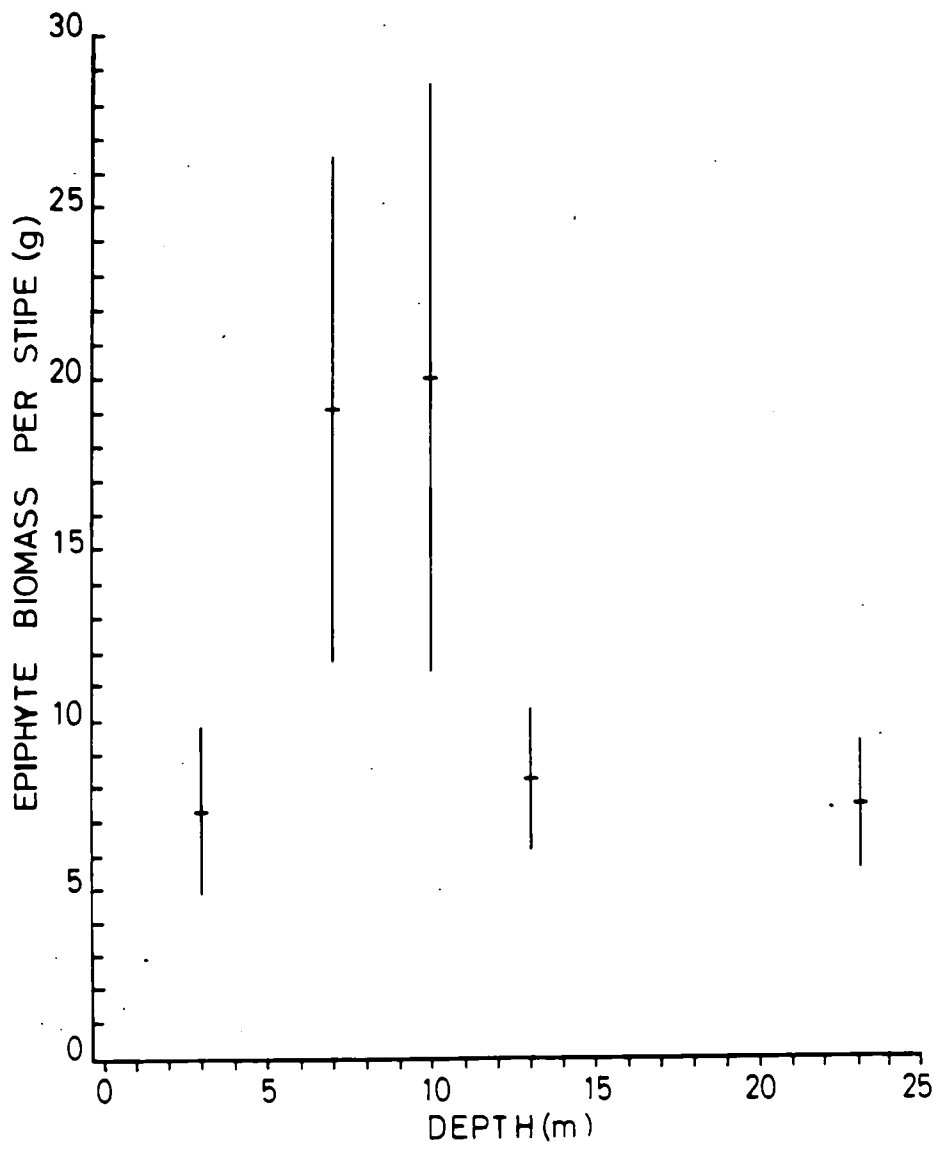
Thus the figures are:

$$\int_{o}^{7} w \, dt$$

where w is the biomass.

Although the different depths studied at the separate sites do not allow direct comparison the following trends emerge.

(1) The overall stipe performance at Petticoe Wick is greater than at the other sites.

(2) Stipe performance remains constant or increases from low water mark to depths of 5 to 6 m.

(3) Below 2 m depth lamina performance decreases with depth.

(4) The ratio of the integrated performance figures for stipe and lamina are similar for equivalent depths at all the sites studied.

(5) Flamborough is an anomalous site in that figures are very much less than those from other sites.

SUMMARY

FLAMBOROUGH

(1) An exposed site with a large amount of suspended material causing turbidity.

(2) The depth range of Laminaria hyperborea is reduced to 8 m.

(3) Both lamina and stipe biomasses are much less than those from equivalent plants at Petticoe Wick.

(4) Ptilotia plumosa is absent as an epiphytic species and Rhodymenia palmata extends to 5 m depth.

SENNEN COVE

(1) A very exposed site.

(2) Laminaria hyperborea is not present in the immediate sublittoral, it occurs at 3 m and extends to 37 m in depth.

(3) Stipe biomass is less than that from equivalent plants at Petticoe Wick; lamina biomass is much the same for plants of similar age and depth.

(4) Epiphytes extend to 23 m and have their greatest biomass at 10 m.

DUNMANUS BAY

(1) Exposure to wave action is much less than at Sennen.

(2) <u>Laminaria hyperborea</u> extends from low water mark to 18 m in depth where it is limited by a sandy substrate.

(3) Stipe biomass is less than that for equivalent plants at Petticoe Wick; lamina biomass is much the same for plants of similar age and depth.

(4) Greatest lamina biomass occurs at 2 m and this decreases with increase in depth.

(5) Epiphytes occur throughout the depth range and have their greatest biomass at 2 m; <u>Rhodymenia palmata</u> is found to 12 m.

CHAPTER 7

ASH CONTENT

Significant seasonal changes in the ash content of various species of kelp have been reported by a number of workers including Lapique (1919), Lunde (1937), Trofimov (1938), Black (1948a,b, 1950a,b, 1954), Haugh and Jensen (1954), Jensen and Haugh (1956).

METHOD

Dried sub-samples of the plants were ground in a laboratory mill to pass a sieve of fine mesh; (3,600 holes per square inch) they were then dried to constant weight at $100^{\circ}C$. This ground dried material was then ashed to constant weight at $440^{\circ}C$ in a muffle furnace.

RESULTS

Table 8 shows the results for stipes and laminae in each age class from material cropped in May, 1968 from one depth 2 m. Three samples were taken in each case and the mean and standard error are presented.

TABLE 8

	Age (yrs.)					
	2	3	4	5	6	7
Stipe	35±2.3	36±3.6	34±1.2	35±2.4	34.6±3.4	35±2
New Lamina	28±2	28±2.3	28.6±0.67	30±2	29 ±3.2	26±3
Old Lamina	28±4.6	27±4.5	33±4.4	34±3.2	28±6	30.3±1.5

There appears to be no significant differences between plants of different ages.

Table 9 shows the mean percentage of ash obtained from plants cropped over a depth range at Petticoe Wick in September, 1968.

TABLE 9

	Depth (m)				
	1 m	2 m	6 m	10 m	12 m
Stipe	34±4.8	36.6±4.3	33.3±2.6	35.6±3.7	34.3±6.9
Lamina	17.3±2.1	21.3±4.8	19±2.6	20.6±4.1	18.6±1.8

There are no significant differences in ash content at one time between the depths studied.

The results for seasonal variation in ash content
of the laminae and stipes are presented in Table 27 Appendix
3 (mean ± limit) and summarised in Fig. 34 a and b respectively.

In the developing lamina, maximum ash content is
reached in March-April and minimum in September thereafter
ash content rises until the lamina is lost the following
spring.   These results are as found by Black (1950).
The mean values for the ash content of the stipe reach a
maximum in summer. at 38.6 and a minimum in winter of 32%,
however these differences are barely significant.
Black (1950) found similar seasonal changes in ash content
but later (Black et al 1959) stated that these changes were
not significant.

Table 10 shows percentage ash contents for
Laminaria hyperborea from the other sites sampled (mean ±
standard error).

TABLE 10

	Lamina	Stipe
Sennen Cove	18.6 ± 3.6	35.4 ± 2.6
Flamborough	17.3 ± 4.3	37.4 ± 4.8
Dunmanus Bay	20.4 ± 2.2	36.6 ± 3.7

FIGURE 34

Seasonal variation in ash content of <u>Laminaria hyperborea</u>

    A. Lamina ⎫
                ⎬ AT PETTICOE WICK
    B. Stipe ⎭
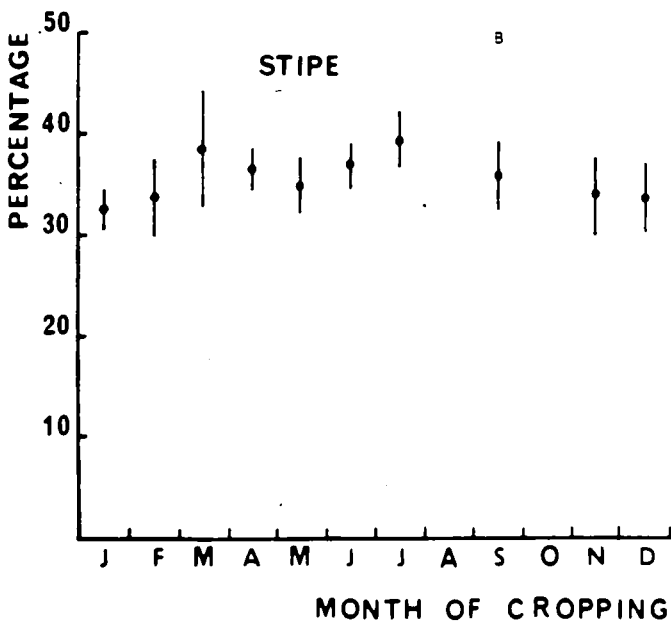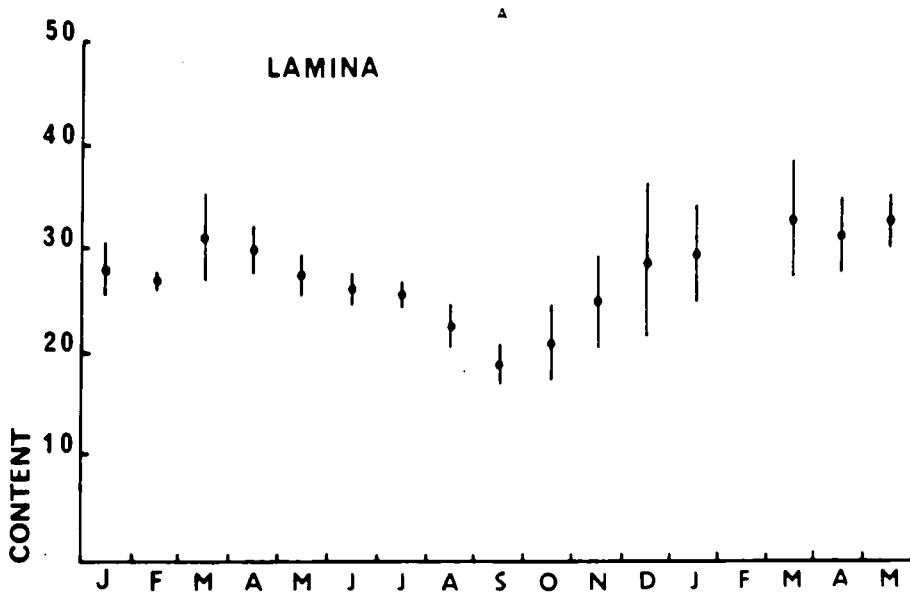
The ash contents of the plants sampled from the comparative sites show no significant differences with plants from the main site at Petticoe Wick.

Ash Content of the Epiphytes

All epiphytes came from depths of 2 m and 6 m. The treatment of these was the same as the treatment of <u>Laminaria hyperborea</u>. Table 11 shows percentage ash content of the epiphytes at five times throughout the years 1968 and 1969, (mean $\pm$ standard error).

TABLE 11

| | Month | | | | |
	April	July	Sept.	Nov.	Jan.
<u>Rhodymenia palmata</u>	27±2.6	31±1.8	32±2.4	25.8	26±3.8
<u>Membranoptera alata</u>	37±4.2	35.9±5.7		45±3.6	34.8±1.5
<u>Ptilotia plumosa</u>	35.9±3.6	35±2	33±7.1	41±6	30±7
<u>Phycodrys rubens</u>	35±2.2	41±3	45.6±6	43±4	35±3

There are no significant seasonal changes in percentage ash content of the major epiphytes at Petticoe Wick.

SUMMARY

(1)   There are no significant differences in ash content
of the stipe of lamina of <u>Laminaria hyperborea</u> with
either age or depth.

(2)   There is a marked seasonal change in ash content of
the lamina with a maximum in March and a minimum in
September after which an increase occurs to reach a
steady maximum in the following year.

(3)   Ash content of the stipe shows some seasonal change
with a maximum in the summer months and a minimum in
winter.   Though in many cases these differences are
not significant.

(4)   The ash content of <u>Laminaria hyperborea</u> from the
comparative sites is not significantly different than
that of plants from the main study site.

(5)   The epiphyte species studied do not show any significant
seasonal variation in ash content.

CHAPTER 8

GENERAL DISCUSSION

METHODS

        In this study assessment of the performance of
the kelp forests is based on the measurement of net
annual production obtained by peak and increment cropping.
The biomass of the perennial parts of the plants plotted
against age gives a good approximation to a sigmoid curve
in the majority of cases.   In some cases the differences
in biomass between adjacent age classes, especially in the
upper and lower range, are not significant.   However the
growth curves obtained indicate the validity of the method,
allowing the calculation of net annual growth increments.
Stipe growth is a seasonal phenomenon (Kain, 1963) with a
slow growth period in the latter part of the year and a fast
growth period in the spring.   The variation shown in stipe
biomass at any one time, coupled with the extensive period
of settlement and development of the young sporophyte is
sufficient to obscure any significant seasonal differences
in stipe biomass from one age class.   The perennial parts of
the plants were therefore placed together in age classes
irrespective of the time of cropping.   Lamina biomass is
also related to age but as lamina growth is a seasonal
phenomenon starting at one time, increment cropping
throughout the year can be used to produce a growth curve
allowing the recognition of peak biomass.   This peak biomass
figure is taken as the net annual lamina production for the

year. The lamina biomass at any one time is the point of balance between growth and loss of material, thus before peak biomass is reached, growth exceeds loss and after peak biomass loss is greater than growth.

The assessment of performance of Laminaria hyperborea throughout its life, from one location, can be expressed as a single figure for comparative purposes. This figure is obtained by taking the graphs of biomass against age for the perennial parts of the plants and peak lamina biomass against age over the life span of the plant, and measuring the area under the curve in each case. This method however obscures details of growth and the same results could be obtained from two curves as shown in Fig.35 which have different shapes. Fig.35a shows the growth curve of a plant which has a fast growth rate in its initial stages followed by a slow growth rate in its later years, the other plant (Fig.35b) shows the converse; both have the same integrated performance Figure. In the perennial parts of the plant the integrated figure allows comparison of biomass rather than production; however as the form of the age:biomass graph is the same in the majority of cases (sigmoid) this integrated figure for biomass allows indirect comparisons of performance. Peak lamina biomass can be treated in a similar manner but as the lamina biomass is produced each

FIGURE 35.

Two graphs of stipe biomass against age having identical
areas under the curve.
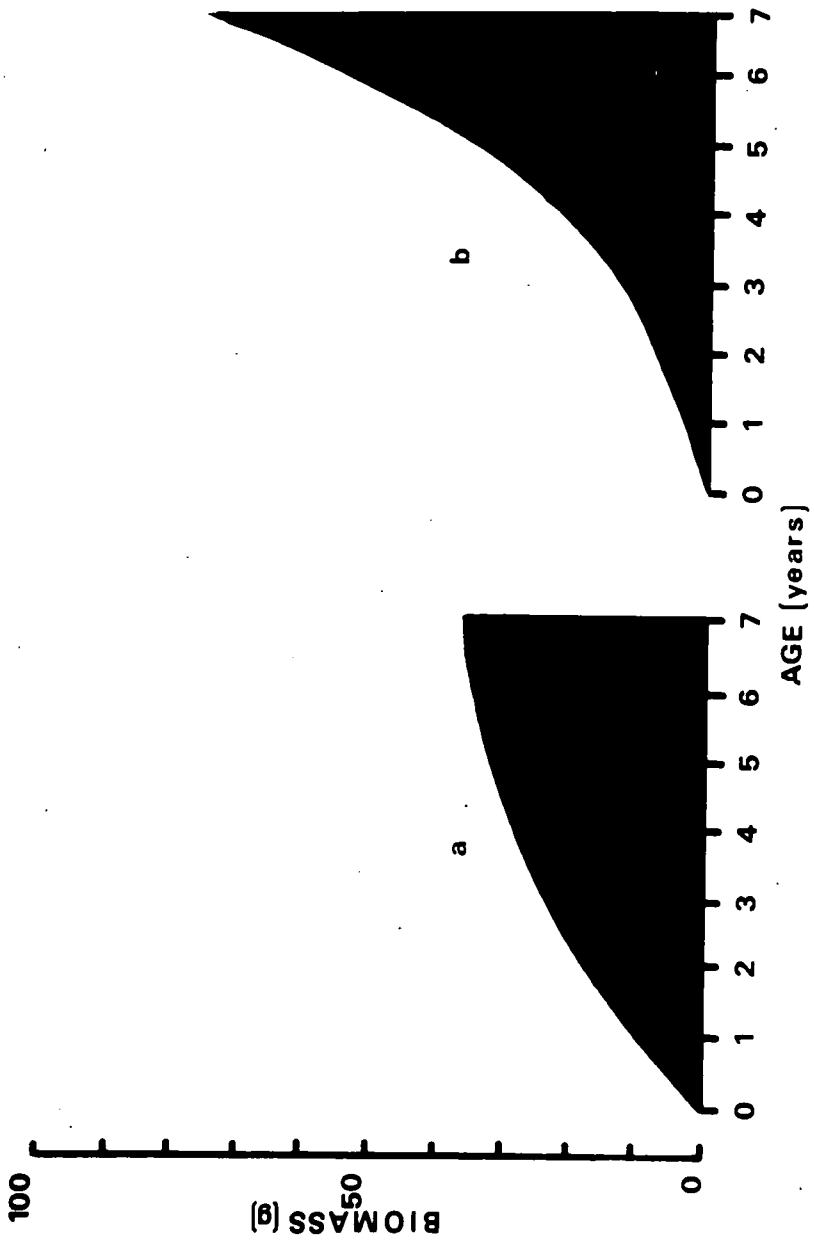
year the integrated figure obtained allows direct comparison of performance measured as net production. The figures for net production include both organic and inorganic material and a better measure of performance would be net organic production, this would be more directly comparable to results from assimalation measurements. Measurement of percentage ash content allows the calculation of net organic production. The seasonal variation in percentage ash content shown, particularly, in the lamina of <u>Laminaria hyperborea</u> could obscure differences in net production, between plants from different sites, if this change varied from site to site. The results in Tables 9, and 10 , show there are no significant differences in percentage ash content at the same time of the year between plants from all depths and sites studied.

The epiphytes occurring on the stipes of <u>Laminaria hyperborea</u> at Petticoe Wick Bay show marked seasonal variations in biomass. Many plants persist from one year to the next but their winter biomass is very small and they can be treated <u>in toto</u> as annuals, and as such are amenable to increment cropping techniques. The differences in biomass between minimum and maximum standing crop over one year will give a figure for net annual production.

THE ENVIRONMENT

The results of the phytosociological study at Petticoe Wick Bay allow a number of floristically distinct types to be recognised. The origin and maintenance of these distinct vegetation types must be, at least in part, due to environmental differences between them. The main environmental gradients shown by the ordinations (Fig. 5 Chapter 2) are depth of submersion and substrate stability. As the kelp Laminaria hyperborea occurs in the majority of the vegetation stands described, the environmental differences between them would be expected to affect its performance.

The monitoring of environmental factors in the sublittoral is particularly difficult. Many spot measurements have been made but these can only provide limited comparative data at one instant of time. The development of data logging equipment, capable of providing a long term integrated measure of environmental parameters, is highly desirable. However where such devices are available, cost often precludes their adoption on a wide scale. This study attempts to measure the net production of the dominant kelp, Laminaria hyperborea, in relation to the environmental conditions operating within the areas sampled. One of the major factors operating in the sublittoral would appear to be light and its progressive fall off in intensity and spectral range with depth

(Jerlov, 1951; Holmes, 1954). The amount of light falling
on the benthos has been shown to vary greatly with the degree
of wave action, geographic location and the amount of
suspended material in the water. (Sverdrup et al 1942,
Fritz, in Malone 1951; Jerlov, 1951).

Any particulate matter present in suspension,
be it natural or man made, must finally settle out and the
sediment so formed can affect the ecosystem in a number of
ways.

(1) Sediment settling on the surface of photosynthetic
organs will cause a reduction in the amount of
available light and hence reduce the rate of
photosynthesis, bringing about a corresponding
reduction in the growth rate (Gislen, 1930).

(2) The settlement and establishment of many marine
algae is dependent on the availability of suitable
substrate; deposition of sediment could have a
profound effect on the type of substrate and limit
the extent of ecosystem development.

(3) The rate of deposition of sediment will be greatest
at depth and in sheltered waters.

Water movement both due to direct wave action and to tidal surges, such as the Lough Ine rapids (Kitching et al 1952) will have a pronounced effect on the environment. The effects of wave action on the littoral zones of rocky shores have already been the subject of extensive studies (Ballantine, 1962; Lewis, 1964). Whilst it is unlikely that the effects in sublittoral will be as marked, water movement must still play an important role. In shallow water, wave action can cause removal of whole plants reducing plot density and can also damage photosynthetic organs, causing a reduction in growth. However, a certain amount of water movement may be advantageous for the following reasons:

(1) Prevention of temperature and salinity stratification.

(2) Increase in nutrients available to plants in unit period of time (Odum and Hodkin, 1958).

(3) Prevention of fouling of individuals by particulate matter and may, in the same way, influence the settlement and growth of certain organisms, such as Hydroids and Polyzoa on the laminas of the macrophytes.

(4) Increase in the amount of light available to understorey plants by causing movement in the canopy plants sheltering them (Jones, 1959).

Strong water currents have been shown to have a profound effect on the physiology of certain algae. Whitford and Schumacher (1961) observed a manyfold increase in the rate of respiration of the fresh water alga Oedogonium kurzii Zeller., under conditions of water movement. It seems possible that currents could increase metabolism by steepening the diffusion gradient over the surface of the plant and thus enhancing gaseous and mineral exchange. Water movement influences the morphology of certain marine algae (Sundene, 1962; Norton and Burrows, 1969), and in the present study the laminae of Laminaria hyperborea were observed to be more digitate in exposed situations than under sheltered ones.

INDIVIDUAL PERFORMANCE

At Petticoe Wick, Laminaria hyperborea, over its entire depth range, commences production of its new lamina in January. The new lamina appears to undergo a "lag phase" in growth and then enters a period of rapid growth in April-May. The commencement of lamina growth in L. hyperborea has been shown (Luning, 1969) to be capable of taking place in total darkness. It would therefore seem likely that at least part of this early growth takes place at the expense of material stored in the old lamina (Kylin, 1916; Luning, 1969). Sargent and Lantrip (1952) have shown that in Macrocystis pyrifera the growth of new

blades is aided by substances synthesised in the old blades.
Black (1950) found that in the lamina of _Laminaria hyperborea_
a peak concentration of laminarin and mannitol in the lamina
was reached in the autumn, with a decrease occurring over
the winter months to reach a minimum concentration the
following spring.   The rise in percentage ash content of
the old lamina (Fig.34 Chapter 7) indicates a corresponding
decrease in organic material and whilst it is possible that thi
is lost by leaching or sporogenesis;   it would seem possible
that some of this material is translocated back into the new
lamina.   Commencement of rapid growth in the new lamina
takes place in late April and this coupled with the loss of
the old lamina would indicate that from this time, further
growth of the lamina is mainly dependent on its own
assimalation.   From the results of this study it would
seem that lamina biomass is largely dependent on the age
of the plant.   This could be due, in the earlier stages of
lamina development, to the larger amounts of material available
stored in the old lamina and in the later stages to competition
for light, with the older canopy individuals shading the
younger understorey plants.   At Petticoe Wick plants in the
upper age classes (five six and seven) show no significant
differences in peak lamina biomasses at all depths.
Svendsen (1968) is quoted by Luning (1969) as stating that
the maximum biomass of the lamina of _Laminaria hyperborea_ is

reached after four years. The maximum size of the lamina can be explained by the fact that lamina biomass at any one time represents the point of balance between growth and loss, whether due to grazing or to wave action. The larger the lamina the more likely it is to suffer this kind of damage. Initially, the younger plants have a smaller lamina and will be protected to some extent by the shelter afforded by the older canopy plants. However this shelter will also reduce the amount of light available for photosynthesis.

The co-importance of available light and water temperature has been emphasised by several workers (Sundene, 1962, 1964) has shown that the decrease in growth rate of _Laminaria digitata_ towards autumn is related to the increase in water temperature. High summer temperature has been found to bring about the cessation of growth in _Laminaria japonica_ Aresch. (Tseng _et al_, 1957) and in _L. angustata_ Kjllm. (Hasegawa, 1962). Tseng _et al_ (1957) found that this cessation could be partially counteracted by the addition of phosphates and nitrates to the surrounding sea. It is therefore possible that nutrient levels may play some part in controlling the growth of kelps. The fact that the ratio of assimalation to respiration is high at low temperatures and decreases rapidly with increase in temperature has been demonstrated under field conditions by

Tikhovskaya (1940)for _Laminaria saccharina_ where the ratio was at a maximum from February to May. As water temperature rises, this ratio is lowered until it reaches unity precluding further growth. A point must be reached where the rate of loss exceeds the rate of growth and the lamina biomass will gradually diminish. This is seen to occur at Petticoe Wick where in the shallower water lamina biomass is maintained in the canopy plants until the new lamina commences growth. This will produce larger amounts of assimalates available for sporogenesis as well as for growth of the new lamina and stipe. With increase in depth of submersion the time of commencement of lamina breakdown becomes earlier and this is also shown by the understorey plants from the shallower waters. It would seem therefore, that in the immediate sublittoral the amount of light available for continued assimulation is at least sufficient to balance the rate of breakdown and the increased respiratory load brought about by the rise in water temperature. In an area such as Petticoe Wick, where the algae reach only modest depths it would seem unlikely that there is any significant difference in water temperature over the depth range concerned; measurements taken during the course of this study bear this out. However, over this same depth range there is a vast reduction in the amount of light available for photosynthesis (Levring, 1947; Jerlov, 1951). The

amount of light is still further reduced in autumn, by the onset of winter storms causing an increase in water turbidity and the lower angle of solar insolation causing a greater amount of light to be reflected from the surface of the sea. These facts can account for the early breakdown of the lamina in deeper water where there is insufficient light to maintain the system above the compensation point. These findings are at variance with the normal supposition that the main factor causing breakdown of the lamina is wave action, which must be more effective in the shallower water.

Whilst the growth of the lamina reflects environmental changes over its limited life span, the perennial part of the plant will give a long term measure over a number of years. In addition, the damage to perennial parts is more easily assessed than damage to the lamina. At all depths the plants show a period of slow growth until they are approximately three years old, when a period of rapid growth commences. At the age of five to six years this growth rate decreases. Stipe biomass can be correlated with lamina biomass (Kain, 1963); the stipe with its dense covering of epiphytes, must be mainly dependent on assimalates translocated from the lamina and a limit must eventually be reached when stipe biomass cannot increase without an equivalent increase in lamina biomass or

photosynthetic efficiency. Lamina biomass does not
significantly increase after the plant reaches the age of
five years and this could account for the reduction in
stipe production in the upper age classes. At the 12 m
depth the total biomass of the plants is much less than
those from the other depths studied and stipe biomass
increases progressively with age; this rate of increase
is not significantly reduced in the upper age classes.
In the upper age classes the biomass of the stipes increases
from low water mark to a depth of 6 m; below this depth
a reduction occurs. This correlates well with lamina
biomass and although there is a considerable reduction in
available light over this depth range, water movement is
also decreased presumably reducing the amount of physical
damage to the laminae. At the 10 m level the understorey
plants, especially in age class three and four, have
considerably larger stipe biomasses than plants in the same
age classes at 6 m. This seemingly contradictory
phenomenon can be explained by the shading affect of the
canopy coupled with the decrease in light with depth.
Canopy density changes little from the immediate sublittoral
to a depth of 6 m (Fig.17 Chapter 5) but at 10 m density
is much reduced allowing proportionally more available light
to reach the understorey plants. The possible role of
the canopy, preventing or retarding growth of the understorey

component, has been discussed by Kain (1963, 1966). The
suggestion by Kain (1963) that young plants are retarded
by the forest canopy and then only grow rapidly to fill in
gaps, when these occur, is only partially true. If this
hypothesis is correct a layered structure should be evident
of canopy and understorey plants independent of ages of the
individuals present. Understorey plants found during the
course of this study were predominantly young individuals,
no retarded plants of five years of age or older were found.
It would seem that any retardation effect is confined to
the younger age classes and that available canopy gaps are
only filled by three to four year old individuals, which
have reached a point at which they are capable of rapid
growth if the stimulus of a gap in the canopy occurs.
Plants in these age groups were found both as understorey
plants and as part of the canopy. The failure to find
any significant numbers of older individuals in the
understory layers would point to the conclusion that plants,
having attained a certain age and not being presented
with the opportunity for rapid growth, do not survive.
The reasons for this could be the increased respiration
due to greater biomass and the inadequate light available
in the understorey to support this increased load.

In very shallow waters (1 m) a mixed community of Laminaria hyperborea and L. digitata occurs.   Laminaria hyperborea shows a significant reduction in stipe biomass and length compared with equivalent plants from 2 m; there is also a reduction in lamina size.   At the 1 m depth the laminae are exposed at low water and this, coupled with the increased exposure to water movement, could account for the reduction in performance.

Stipe length in most cases follows the same trends as stipe biomass.   The ratio of weight per unit length of stipe gives some indication of overall stipe morphology and can be equated to stipe girth.   During the period of rapid growth, in age classes three and four, this ratio increases rapidly showing that growth in length is not at the expense of growth in girth and that the two take place concomittantly.   The stipes of the understorey plants from 6 m, in age classes three and four, are however considerably 'thinner' than equivalent plants from all depths except 12 m;   this can be explained by the effect of canopy density cutting down the available light and producing a phenomenon analogous to etioclation in terrestrial plants.

EPIPHYTE PERFORMANCE

The epiphyte flora of _Laminaria hyperborea_ at Petticoe Wick Bay reaches its greatest biomass on plants in the upper age classes which make up the forest canopy. A number of explanations can be put forward to account for this:

(1) The stipes in the upper age classes are larger and more rugose and hence provide a greater surface area available for colonisation.

(2) The effect of shading due to the density of the forest canopy reduces the opportunity for rapid epiphytic growth on the stipes of young understorey individuals. The epiphytes, when present on the understorey individuals, show similarity to the epiphytes on the canopy plants from deeper water, both in the species present and in the percentage of the total epiphyte biomass that these species constitute.

In the more open community at 10 m the differences in epiphyte biomass per stipe are not so great between the upper and lower age classes.

(3) The epiphyte species are not truly annual and some plants over-winter to contribute to the next seasons biomass.

The epiphyte flora at Petticoe Wick shows marked seasonal changes in biomass. This is caused not only by the numbers of individuals present on the stipes but also by their growth pattern. In the early part of the year the mean individual epiphyte biomass falls while the mean biomass per stipe increases. This is due to the development of a large number of new individuals. During the latter part of the year both biomass per stipe and individual biomass decrease until only a few individual plants remain to overwinter.

The maximum epiphyte biomass per stipe is reached in the early autumn and the subsequent pattern of decline follows to a large extent that shown by the lamina of <u>Laminaria hyperborea</u>, with a more rapid decline occurring in deeper water. Not all the component species grow at the same rate; it is very noticeable that <u>Ptilotia plumosa</u> grows at a more rapid rate earlier in the season and reaches its peak in July some two months earlier than the other component species. This is interesting because <u>Ptilotia plumosa</u> has a more northern distribution than the other epiphyte species on the east coast of Britain and reaches its southern limit, as an important species, on the coast of Co. Durham. Plants of this species have been found at Robin Hoods Bay and at Flamborough but in none of these areas is it present in any quantity.

The marked seasonal changes in biomass of the epiphyte component of the kelp forest allow it to be treated as an annual and be subjected to increment cropping techniques. The epiphyte flora shows a distinct zonation with depth, _Rhodymenia palmata_ dominates the immediate sublittoral and_Phycodrys rubens_ dominates at the lower limits of the kelp forest. _Ptilotia plumosa_ and _Membranoptera alata_ reach their maximum between these limits. This overall picture is reflected by the zonation on the stipes and is in agreement with the observations of Marshall (1960). At Petticoe Wick Bay, _Rhodymenia palmata, Ptilotia plumosa_ and _Membranoptera alata_ occur on the littoral whereas _Phycodrys rubens_ is confined to the sublittoral,

PLOT PERFORMANCE

The pattern of plot density, at one depth, in a topographically uniform area, where the differences in environmental factors at different points would appear to be minimal, is likely to be a temporal one, _sensu_ Watt (1947). In the metre square croppings taken in this study (Fig. 17 Chapter 5) a pattern emerges where the number of older individuals appears to have a strong affect on the density of the younger individuals beneath them. In an area where a large number of upper age class plants are present the numbers of understorey plants are correspondingly reduced; the converse also appears to hold true. It appears that

with the exception of the shallowest areas, where a mixed community of <u>Laminaria hyperborea</u> and <u>L. digitata</u> occurs, there is a slight decrease in canopy density with increasing depth. Below 10 m there is a much more rapid fall off in density and the lower level of the kelp is reached at 12-13 m where only scattered individuals occur. The factors controlling plant density must be many, apart from competition within the canopy for light and the effects of senscence causing the removal of indifiduals. At the upper limit of growth in the immediate sublittoral competition for space with <u>Laminaria digitata</u> and the increased effects of water movement will have a pronounced effect. The effect of grazing has been stressed by Kain (1963) and Jones and Kain (1967) as a controlling influence on the density of the kelp forest. Two main grazers appear to be present, <u>Patina pellucida</u> and <u>Echinus esculentus L</u>. Kain (1963) reported infestation levels of the holdfasts of <u>Laminaria hyperborea</u> from populations in the Isle of Man to be as high as 40% At Petticoe Wick Bay levels are much lower than this, approaching 20% in seven year old plants and much less still in plants from the lower age classes. Kain (1967) has reported a complete lack of <u>Patina</u> infesting the holdfasts of <u>Laminaria hyperborea</u> on the coasts of Norway. The variation shown in levels of infestation between the Isle of Man, Petticoe Wick and the Norwegian coast make it tempting to speculate that these are part of a

progressive decline brought about by some geographic factor.
In the absence of information from many more sites any such
suggestions remain conjecture.   Jones and Kain (1967) have
suggested that especially at the lower limits of its depth
range the density of Laminaria hyperborea is controlled by
the grazing of young individuals by Echinus esculentus.
Throughout this study Echinus was found at the lower depth
limits of L. hyperborea in considerable numbers (up to
20-30 per square m).   Fig. 36 (included by kind permission
of Mr. D.J.Jones) shows a three year old plant which when
found, at 12 m depth at Petticoe Wick had five individuals
of Echinus esculentus grazing on its lamina.   On many
occasions Echinus was found browsing the epiphytes on the
stipes of L. hyperborea but rarely was found on the laminae
of canopy plants.   It would seem a reasonable supposition
that Echinus is one controlling factor at the lower depth
limits of Laminaria hyperborea.

THE COMPARATIVE SITES

These sites were visted only once in the course
of this study and the data obtained is therefore limited.

Flamborough Head

Laminaria hyperborea which is limited by its need of
attachment to solid rock or stable boulders, (Kain 1962)
approaches its southern limit on the East coast of England

FIGURE 36

The effect of grazing by <u>Echinus esculentus</u> on the
lamina of <u>Laminaria hyperborea</u>.
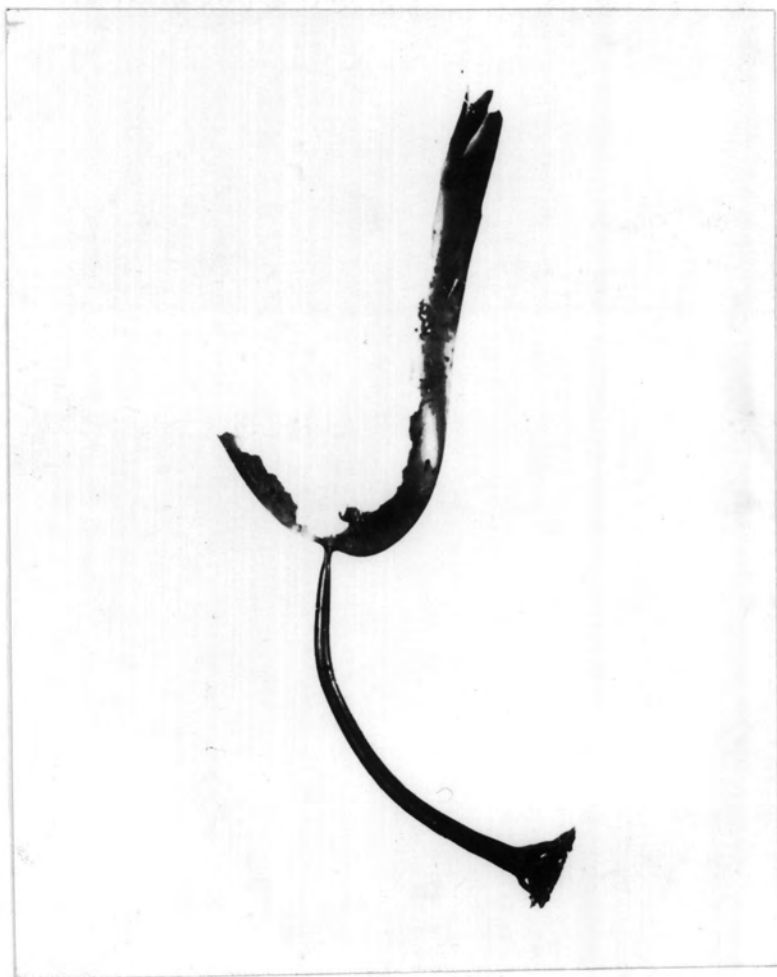
at Flamborough Head;   further south isolated outcrops may

occur but nowhere is a large stable forest community found.

The stipes of plants at this site are much reduced in biomass

when compared to plants in the same age classes from

equivalent depths at Petticoe Wick.   The degree of reduction

of stipe length is not as great and hence the stipes tend

to be 'thinner'.   The laminae show a corresponding reduction

in overall biomass.   Both stipe and lamina biomasses increase

progressively with age and show no tendencies to a reduction

in the rate of growth in the upper age classes.   The physical

environment at this site is one of high exposure (subjectively

assessed) coupled with a large amount of natural suspended

material from the chalk cliffs.   This leads to a high

level of turbidity and a corresponding decrease in the amount

of light available in the sublittoral.

Laminaria hyperborea only extends to a depth of 8 m

and the forest throughout its depth range is very open in

character.   It would appear, that in this situation, the

reduction in the amount of light in the sublittoral, due

to the increased turbidity, is equivalent in its affects on

the kelp plants to an increase in depth of submersion.

Plants from this site from the immediate sublittoral to the

maximum depth at 8 m closely resemble, both in productivity

and morphology, plants from 10 m and below at Petticoe Wick.

The situation at this site is further complicated by the high

degree of exposure to wave action and this probably contributes directly to the low productivity of the immediate sublittoral.

At Flamborough Head, Rhodymenia palmata occurs as an epiphyte to a depth of 5 m; this would seem to be at variance with the observation that in the clearer waters of Petticoe Wick it is only found at 1 and 2 m in depth. One other major difference between the epiphyte components at Flamborough and Petticoe Wick is the absence of Ptilotia plumosa. This, coupled with the overall reduction in epiphyte biomass, could account for the ability of Rhodymenia palmata to extend its depth range. Thus it would appear that a factor influencing the depth range of Rhodymenia palmata, as an epiphyte, is competition for space with other epiphytes on the stipes of the "host" plants.

The two other comparative study sites, Sennen Cove and Dunmanus Bay, are from a different geographical region, not only are they further South but they are also much more Westerly stations. The many environmental differences over a relatively short stretch of coast, between the eastern and western basins of the English Channel, have been pointed out by Crisp and Southward (1958) and are summarised by John (1969). It would seem likely that many comparable differences would exist between the geographic areas of the North East and the South West visited in the course of this study.

Sennen Cove

One of the most noticeable differences between this site and the sites on the East coast of Britain is the depth to which <u>Laminaria hyperborea</u> extends and its greater density in shallower waters. This site is exposed to the main force of Atlantic waves and this presumably precludes the growth of the kelp in the immediate sublittoral. Plants were found growing to a depth of 37 m and the forest extended as a dense canopy to 16 m. The clarity of the water at this site (assessed subjectively) was much greater than that found on the East coast sites.

The overall individual biomasses of the stipes are less than those from Petticoe Wick over the same depth range, especially in the upper age classes and hence performance is reduced. Understorey plants in shallower waters, although growing under a denser canopy than that found at Petticoe Wick at 6 m, do not show the same proportional reduction in performance when compared to the canopy plants. Among the factors which could account for this are the reduced turbidity of the water and the increased exposure causing greater movement in the canopy plants; both could increase the amount of light available in the understorey. The lamina biomasses are much the same as those from equivalent depths at Petticoe Wick, though in the upper age classes (six and seven) they are

greater at 10 m. Thus at this site it seems likely that the increased available light, due to latitude and water clarity, is offset by the increased exposure in the shallower waters. The ratio of stipe biomass to lamina biomass (crudely photosynthetic to non-photosynthetic biomass) in the upper age classes in shallow water is greater than that found at Petticoe Wick. The mean sea temperature in this area will be higher (no reliable long term measurements could be found) than that from the East coast of Britain. The increase in the ratio of photosynthetic tissue to non-photosynthetic tissue, would help overcome increased loss due to respiration at these higher temperatures. This phenomenon has been shown, much more strikingly by John (1969) in populations of Laminaria ochroleuca from Spain and South West England.

At Sennen Cove a great reduction in canopy density occurs between 13 m and 23 m, this is analogous to the reduction occurring below 10 m at Petticoe Wick. The epiphytes found at Sennen Cove have a much reduced biomass when compared to epiphytes from equivalent depths at Petticoe Wick and this, in part, may be due to the increased canopy density. At this site Rhodymenia palmata reaches a depth of 23 m.

Dunmanus Bay

In a number of respects this site is similar to Sennen Cove. The situation however is not so exposed and Laminaria hyperborea extends to a depth of 18 m. This lower extent is however limited by substrate; the rocks give way to a sandy bottom and it is possible that this is not the true lower limit. However the closed canopy of the forest extends to a depth of 14 m and below this only isolated plants are found. Thus at this site also, there is a point in depth at which a sudden reduction in canopy density occurs.

The overall individual biomasses and net production follow those from Sennen Cove, over equivalent depth ranges, and in the shallower waters stipe performance is less than that from Petticoe Wick. At this site epiphyte biomasses are reduced in comparison to Petticoe Wick. In the immediate sublittoral they are much greater than those from Sennen Cove and this is possibly due to the reduced exposure of the site. Rhodymenia palmata at this site extends to a depth of 12 m.

One point emerging from this study is that at three of the sites studied (Flamborough, because of its turbidity, must be regarded as anomalous) at a distinct depth there is a sudden reduction in canopy density. A number of factors may combine to bring about this change.

The most obvious explanation is that at this depth the
respiration:photosynthesis balance becomes limiting,
however the occurrence of plants to much greater depths
makes this explanation seam unlikely.   The density of the
canopy is shown to exert a large affect on both the numbers
and the performance of understorey individuals.   With
increasing depth the competition for light within the canopy
will reduce the numbers of understorey individuals and hence
eventually limit the density of the canopy.// This study
was undertaken to test the methods described in an attempt
to measure the net annual production and growth parameters
of ecosytems dominated by _Laminaria hyperborea_ and to use such
results as a measure of the environmental variables acting
upon these ecosystems.   The relatively simple measurements,
based on peak and increment cropping, are shown capable of
assessing the net annual production of the kelp.   The
increment cropping technique provides more data and a reliable
method of determining the time when peak lamina biomass occurs.
The time of peak crop from other sites, not visited throughout
the year, must be subjectively assessed.   It is seen from
the results of the main study area that peak lamina biomass
once reached, persists for a number of months;   hence it
would seem justifiable to compare sites at this time of year.
The variation in biomass between individuals in the same age
class from similar locations is not sufficiently great to
preclude meaniful comparisons with individuals from other

locations, providing adequate samples are taken. It is possible by using individual production figures for each age class coupled with measurements of density and age structure of known areas to calculate figures for net annual production on an area basis. The figures ($3280-3499g/m^2/yr$) for the two stands of greatest density sampled from 2 m at Petticoe Wick show that in these areas the kelp forest is highly productive and can be compared with figures of $3500g/m^2/yr$ given by Westlake (1963) for crops under intensive cultivation. More work is needed on the density and age structure of kelp forests as well as more detailed work on the affects of density on individual production before reliable figures for net annual production can be given on an area basis. Further quantitiative studies need also to be carried out on the amount of material, from previous years growth, translocated back into the new lamina to assess the importance that this plays in the growth of the organism. The data presented allows some qualitative speculation about the effects of the environment. However before any ridgid conclusions can be drawn plants from many more localities should be studied, preferably together with direct measurement of environmental parameters.

APPENDIX 1

(1)   ZURICH-MONTPELIER METHODOLOGY

The previous applications of the Z.M. School
of phytosociology to marine vegetation have been noted
in Part 2. The procedures used in this study are an
adaptation of some of these methods. This adaptation
is confined to the use of the field methods of the school
and in the manner of drawing up the 'association table'.
No attempt has been made to construct hierarchal scheme
for the classification of the vegetational units delimited,
even if it is accepted that this would be valid or
desirable, there is no justification for this from results
based on stands of vegetation described from one area
alone.

The scales of cover abundance and sociability
of the school are given in Table 12.

The raw floristic data obtained by methods
described in Chapter 2 was tabulated. Such a Table
was laid out with all the species listed along the left
hand side, arranged in rows and all the stands listed
vertically (columns) together with the various physical
stand data. The raw table laid out in this manner
permitted the easy checking of species for penence or
absence in all stands simultaneously. The table was

TABLE 12

SCALES OF COVER-ABUNDANCE AND SOCIABILITY

Cover-Abundance

+ Occasional and less than 5% total plot area.

1. Abundant but insignificant in cover, less than 5%.

2. Very Abundant, 5 - 25% of total plot area.

3. 25 - 50% Cover of total plot area irrespective of number of species.

4. 50 - 75% Cover of total plot area irrespective of number of species.

5. 75 -100% Cover of total plot area irrespective of number of species.

Sociability

1. Growing singly.

2. Growing in small groups of a few individuals.

3. Large groups of many individuals, small scattered patches.

4. Patches or a broken mat.

5. Extensive mat almost, or completely, covering the whole plot area.

Where a species has a cover of + and a

Sociability of 1. it is recorded simply as +.

edited many times with the grouping of stands by vertical

rearrangement and the grouping of species by horizontal

rearrangement.   The final Table is shown inChapter 2

Table 1 , which has been arranged, as far as possible,

to show grouped blocks of mutually exclusive species in

various stands.

APPENDIX 2

BRAY AND CURTIS ORDINATION

The so called ordination methods of describing vegetation do not presuppose the existence of plant communities or extract these from collected data. They represent the stands of vegetation described as geometric models with the distances between the stands, within these generated models, representing the degree of similarity of the floristics of the actual stands. In this way stands from relatively homogeneous vegetation will be clumped together within the model and stands of wide floristic difference will be set at a distance. It is hoped that the ordering of the stands within the model will point to environmental gradients within the population sampled. The method of Bray and Curtis (1957) is perhaps the simplest method to operate and the picture it presents of the vegetation stands described has been shown to be reasonably accurate.

The method depends basically on the calculation of a coefficient of similarity between all the stands described. Numerous methods of calculating these coefficients have been suggested and these are reviewed by Sokal and Sneath (1963). Two forms of ordination are attempted in this work, a loaded and an unloaded form. In the former the data is loaded on cover value,

percentage covers being substituted for Z.M cover values as in Table 13.

TABLE 13

Z.M.Cover Value	Percentage equivalent
+	1
1	2.5
2	10
3	37.5
4	62.5
5	87.5

In the unloaded form the data is used simply on a presence or absence basis and a relatively simple coefficient of similarity, (Dice 1945, Sørensen 1948) is used.

$$\text{Coefficient of similarity (c)} = \frac{2\ w}{a + b}$$

where w = number of species common to both stands

a = the number of species in one stand

b = the number of species in the other stand.

The coefficient always lies between zero, when no species are found in common between two compared stands, and one in identical stands. The ordination technique however depends on maximum spacial separation between dissimilar stands, hence an inverted coefficient of similarity is calculated. This is simply accomplished by subtracting the calculated coefficient of similarity from unity and multiplying the result by one hundred to obtain it on a percentage basis. Thus a value of 100 denotes no similarity between stands, and zero identical stands. This inverted coefficient of similarity (I.C.S.) is calculated for every stand pair and the results expressed as a matrix (Fig.37).

The technique depends on the selection of a pair of reference stands for the determination of stand positions along the first (x) axis of ordination. The choice of reference stands for the construction of the $\underline{x}$ axis is analogous to choosing two points to form the ends of a base line in plane table surveying. The greater the distance between the reference stands, the more accurate is the fixation of other positions. Referring to Fig.37 it is seen that a number of reference stands, having no degree of association, can be chosen. Whittaker (1967) suggests that this problem can be overcome by adding the I.C.S.

FIGURE 37

Matrix of inverted coefficients of similarity
for unloaded data.

Unloaded Data

```
A    0
B    25 0
C    25 0 0
D    33 33 38 0
E    60 20 20 14 0
F    33 33 33 54 9  0
G    25 25 25 38 20 33 0
H    33 33 33 38 9  20 33 0
I    50 50 50 33 20 11 50 11 0
J    60 60 60 47 41 38 60 50 46 0
K    75 75 75 57 61 84 75 60 66 55 0
L    92 92 92 65 78 77 84 71 84 50 46 0
M    100 100 100 85 92 92 91 92 91 60 64 35 0
N    100 100 100 79 89 88 92 92 84 68 61 52 45 0
O    100 100 100 85 92 91 91 91 91 79 63 42 40 33 0
P    83 100 100 50 71 69 83 60 66 68 64 65 78 65 62 0
Q    100 100 100 78 88 87 86 87 86 71 73 48 59 54 36 66 0
R    100 100 100 90 89 89 88 89 88 66 70 53 56 48 38 62 48 0
S    100 100 100 75 86 85 83 85 83 79 79 55 56 72 46 63 33 71 0
T    100 100 100 91 90 89 88 89 88 83 65 60 45 71 53 63 50 63 36 0
U    100 100 100 79 92 92 92 92 92 80 65 51 28 66 37 64 40 52 42 24 0
V    100 90 90 76 82 81 92 82 81 86 68 68 55 63 49 60 48 60 44 45 35 0
W    100 100 100 88 100 100 100 100 100 90 86 80 64 80 55 53 68 64 53 74 52 61 0
X    100 100 100 86 100 100 100 100 100 100 93 86 77 86 68 87 65 60 46 72 63 50 37 0
Y    100 100 100 75 85 85 83 85 83 89 86 72 70 72 61 75 55 62 50 63 57 52 65 46 0
Z    100 100 100 76 87 86 85 86 85 90 86 73 71 73 63 76 47 64 53 65 59 53 67 50 0 6 0
α    100 100 100 71 83 82 80 82 80 88 82 70 68 70 58 71 37 60 43 70 62 47 60 38 14 20 0
β    100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 89 100 50 60 64 75 0
γ    100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 89 100 78 81 64 75 0 0
```

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z α β γ

values for each stand and taking the stand with the maximum value obtained as one reference point and the stand showing the maximum dissimilarity to the stand as the other point. It is seen from Fig. 37 that the maximum value is obtained in stands β and γ which are identical. However, the choice of the second stand is difficult as both stands, β and γ, show no degree of association with twenty-two of the twenty-nine stands described. For this reason, this modification of Whittaker's is rejected.

Bray and Curtis (1957) suggest that a pair of reference stands with no coefficient of community (I.C.S. = 100) be chosen only if each member of the pair shows an I.C.S. value of less than one hundred with all other stands. Stand V shows no similarity with stand A but some degree of similarity with all other stands. These two stands were taken as the extreme ends of the first axis ($\underline{x}$). It must be emphasised that the choice of reference stands for construction of the ordination axis only affects the absolute positions of the stands and in no way affects their relative spacial location. The relative locations are determined by the calculated coefficient of similarity and the ordination is merely a geometric representation of their locations.

Having decided on stand A and V as the reference stands at either end of the x axis, the location of the other stands on the axis is arrived at by constructing arcs of radius equal to the I.C.S. values of the stand from the reference stands. The inter- section of these arcs is then projected at right angles and the point of intersection is the x co-ordinate. x co-ordinates for all stands are found in this way. The stands, which have x co-ordinates close together but which show the maximum separation on the I.6.S. matrix, are chosen as reference stands for the Y axis. The chosen stands are K and β, which have x co-ordinates of 55 and 60.3 respectively and I.C.S. value of 100. The Y co-ordinates of the other stands were then found along the axis using the method described for the x axis, (Austin and Orloci 1966). The co-ordinates were examined as before, and end points for a third Z axis extracted. These are given by stands B and α. Calculation for further axes by this method is possible. However, it is impossible to represent more than three axes diagrammatically at one time.

The co-ordinates of the stands along axes X, Y and Z are shown in Table 14, these are plotted in the form of a three dimensional graph, shown in Figure 5a, Chapter 2.

TABLE 14

	'Loaded' Co-Ordinates			'Unloaded' Co-Ordinates		
	X	Y	Z	X	Y	Z
A	0	50	79.5	0	28.5	97
B	24.4	49.2	100	12.6	28.5	100
C	12.7	49.2	89.4	12.6	28.5	100
D	18.1	47.2	98.1	26;5	16.2	70
E	12.9	46.8	90.8	34.8	19.0	82.5
F	25.8	43.6	75.5	22.6	35.5	78
G	3.8	44.4	72.6	12.6	28.5	78.5
H	22.1	43.6	84.9	21.8	18.1	78
I	21.3	43.6	76.6	29.6	22.0	69
J	42.2	33.3	59.7	31	15.0	71
K	57.1	26.7	60.7	55	0	55.5
L	52.8	0	49.6	69.2	11.1	32
M	73.1	14.2	48	84.8	20.5	23
N	60	34.2	45.7	80.1	19.0	24.5
O	63	22.9	32.2	87.9	20	17
P	47.6	36.7	49.4	66	20.5	25
Q	56.7	26.4	41.4	88	27	7
R	63.7	27.6	32	82	42.5	28
S	53.4	27.1	48.5	80.3	31	9.5
T	53.5	31.0	48.7	89.8	21.5	24.5
U	82	20.8	35.4	93.8	21.5	29
V	100	48.2	14.3	100	38.1	21
W	64.6	48.7	0	31.3	40	28
X	94.1	47.7	23.6	87.5	63.9	8
Y	64.3	87.9	41.4	86.4	69	1
Z	63.7	92.3	41.4	85.9	66.2	2
α	62.1	64.4	41.4	88.9	55.1	0
β	50	100	50	60.3	100	28
γ	50	95.5	50	60.3	100	28

The distance in a three dimensional space between any two
represented stands (which can be calculated from the formula

$$d = \sqrt{(x - x^1)^2 + (y - y^1)^2 + (z - z^1)^2}$$

where x, y, z, and x^1, y^1 and z^1; are the co-ordinates
of the two stands, it has been shown to be a highly
significant measure of the degree of floristic difference
between the two stands (Bray and Curtis, 1957).

The loaded data was treated in an identical
manner to the unloaded data, except in the initial
calculation of coefficients of similarity.   The percentage
cover values are converted in a simple two step proccess
(Bray and Curtis 1957, Whittaker 1967).

1. In each horizontal row (species) all values are
    converted to percentages of the maximum value in
    that row.

2. These values are then converted to percentages
    of the sum of the values of the column (stand)
    in which they occur.

Columns are then directly compared with
percentage coefficients of similarity computed by summing the
lesser of the two compared percentages for each species.

These values are then inverted by subtraction from one
hundred and the data presented in the form of a matrix
Fig. 38 .   The data is treated in exactly the same
manner as the unloaded data.   Co-ordinates are given in
Table 14 and plotted as a three dimensional graph in
Fig. 5b Chapter 2.

FIGURE 38

Matrix of inverted coefficients of similarity for loaded data.

Loaded Data

```
A   0
B   64 0
C   42 46 0
D   39 28 39 0
E   42 43 0.9 35 0
F   66 70 45 46 46 0
G   25 34 49 71 54 79 0
H   60 55 55 54 80 54 67 0
I   70 74 49 51 50 4 79 53 0
J   83 88 83 83 90 76 85 87 76 0
K   98 87 83 80 86 80 81 81 79 74 0
L   100 99 99 97 97 93 94 93 98 82 73 0
M   100 100 100 99 98 94 89 92 94 83 88 53 0
N   100 100 100 99 99 99 99 99 99 92 93 83 79 0
O   99 99 99 89 98 93 94 93 93 83 90 68 65 69 0
P   98 100 100 96 99 92 88 90 92 96 89 86 88 97 80 0
Q   100 100 100 99 97 94 76 92 94 83 92 73 64 84 61 85 0
R   100 100 100 99 96 94 87 92 94 93 92 73 73 8 72 69 62 3 0
S   100 100 100 99 98 94 81 92 94 87 92 73 75 96 78 85 51 82 0
T   100 100 100 99 98 99 99 99 99 67 81 78 75 95 85 98 77 84 77 0
U   100 100 100 99 99 94 94 94 94 89 87 64 36 79 65 91 67 73 78 62 0
V   100 96 96 96 98 96 99 96 95 91 90 97 73 89 85 79 93 85 96 96 60 0
W   100 100 100 99 95 100 100 100 100 98 98 98 87 95 78 55 92 79 99 98 84 46 0
X   100 100 100 99 100 100 100 100 100 100 99 99 99 96 89 99 87 94 97 88 94 83 69 0
Y   100 100 100 99 98 92 97 95 97 99 97 95 94 94 86 97 83 85 94 98 84 93 91 75 0
Z   100 100 100 99 99 99 99 99 99 99 99 98 60 94 88 98 85 86 99 91 85 92 91 75 2 0
α   100 100 100 99 99 99 91 99 99 99 98 96 96 94 87 98 84 92 94 97 87 93 91 75 64 52 0
β   100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 99 100 95 38 35 80 0
γ   100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 99 100 95 44 35 50 30
```

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z α β

APPENDIX 3

PERFORMANCE DATA

TABLE 15

PETTICOE WICK   SEASONAL CHANGES IN LAMINA BIOMASS 1967-1968

Depth	Age	30.5.67	16.6.67	26.7.67	7.9.67	26.10.67	19.1.68	9.3.68	24.4.68	15.5.68
2 m	1		0.2		0.8±0.78	0.59±0.51				
	2		2.1±1.2		6.6±4.8	4.5 ±2.5				
	3	3.0	5.7±5.4	34	47±3.8	27 ±7.9			29.2	
	4	5.3±2.8	39±17.2	57±10.8	90±16.7	46.1 ±20.8	41±54		28.4±20.4	
	5	22.1±5.3	79.2±15.8	98±15.1	117±13.8	77.5 ±11.4	50±22.8	65±14.4	56 ±18.3	
	6	36.3±3.3	76.2±25	110±11	104±16.3	110 ±19.3	76±19.3	63±21.9	56.5±38	
	7	41.3±14.4	62 ±17.2	102±13.1	106±21.7		36±31	42.2±27.2		7.6±14
10 m	1			0.45±0.2						0.3±0.2
	2		1.6±2.8	2.2 ±1.3				2.2±2.0		
	3	0.8±0.4	10.5±10.2	14.7±2.3				4 ±10		12.1±10
	4	10.8±2.3	18.3± 5.8	46 ±6.2				26.5±6.3	26±4.6	
	5	12.8±5.3	35.5± 6.1	75.8 ±7.9				28 ±20.2	41±18.7	
	6	19.9±10.2	54.4±17.2	78.8 ±22				41 ±8.6	38±12.5	
	7	25.4±9.4	56.6± 7.7	84 ±25				50	15 ±12	

TABLE 16

PETTICOE WICK BAY   SEASONAL CHANGES IN LAMINA BIOMASS 1968-1969

Depth	Age	Date of Cropping										
		19.1.68	9.3.68	24.4.68	15.5.68	19.6.68	30.7.68	11.9.68	17.11.68	9.12.68	29.1.69	11.3.69
1 m	1							0.12±0.023	0.45	0.7	0.6	
	2				0.2			2.3 ±0.28	3	2.7±0.28	1	
	3				1.8			6.0±0.4	7.3±1.6	6.8±0.97	5.0	
	4				13±4	20 ± 0	32±15	35 ± 15	37 ±10	26.3±2.1	33	11.2
	5				12±2	44 ±4.6	60±9.7	56 ±13.8	64 ±8.2	88 ±10	47.3±5.9	21.9
	6				12±0.5	37 ±3.5	105±9.4	91 ±31	93.8±9	114 ±21	54.6±12	25.1
	7				23±12	46 ±6.7	100±10	102 ±12	117 ± 6	110 ±	83.7±14.2	24.3
2 m	1		0.16			0.8		0.75±0.6				
	2	0.99	0.83	1.1			1.5±1.2	6±0.9		4.3±0.75		1.3±0.68
	3	0.14		2.8	6.4		35±4.5	45±5	3.7		19.6±3.7	6.7±0.26
	4	0.8±0.14		5.4±1.2	12.3±6	29±3.2	56±3.7	76±6			55±5.5	
	5	1.1±0.57	8.6	18±4	23 ±3	44±8	74.8±4.5	106±11.2	84±4	90±5.8	82±21	
	6	1.1±0.14	11.6±4	17±2.8	31 ±4	65±6.3	106.5±5	123±9.8	120±8.6	123±25	91±11	72.6±41
	7	0.7±0.14	12.4±3.8	12±8	44 ±3	72±10	92.4±105	124±8.5	126±16	130±16.9	92.7±16.4	63±21

TABLE 17

PETTICOE WICK BAY   SEASONAL CHANGES IN LAMINA BIOMASS

Depth	Age	9.3.68	24.4.68	15.5.68	19.6.68	30.7.68	11.9.68	17.11.68	9.12.68	29.1.69	11.3.69
						Date of Cropping					
6 m	1		0.2±0.2	0.2±0.54		0.5±0.2					
	2		2.5±1.3	1.8±0.5	1.6	2.1±0.8		0.75±			0.66
	3		2±1.8	1.3±0.8	1.6	3.9±2.1	4.2	3±1.1			4±0.92
	4		4.5±2	12±6.8	18±7.6	21±5.7	38±4.8	9.6			10.8±6.5
	5		7±1.6	12±5.7	38±10.1	45±17	70±8.6	115 ±8	71.7±19.2	43.4±12.2	30.8±10.2
	6		9±3.6	22±8.7	50±6.2	63±4.7	99±16.7	108 ±18	80.4±16.2	33.7±16	39±10.6
	7		9±4.7	25±12	48±8	78±14	102±18	122 ±15	71.5±20	70.5±14.6	57.3±22
10 m	1										0.2
	2		0.61±0.15	0.75±0.2		0.2±0.06					1.3
	3	0.5±0.2	9.9 ±0.61	10±3	9.5±46	1.2±0.15	12		7.5	6	5
	4	4.8±1.2	11.9 ±1.0	11±1	23.6±6	25±1.5	31±10	38.5±10	11.7±0.35	9.7	11±3.4
	5	5.5±0.8	14.7± 0.8	20±1.5	36±4.7	37±3.9	44±12	77±11	31.2	20±2.7	16±2.7
	6	8.5±3.3	11.5±0.8	20±1.5	40±10.2	54±9.8	61	64±5.3	45.2±14	20±3.5	10±2.9
	7	5.2±2.5	6.9±1	18±4		60±8	80	78±10.2	64.7±1.4	32±12	8±3
12 m	1										
	2		0.35±								
	3		0.35			4.1±1.27	13.6±4.2	13±1.5		1.05±0.4	1.3±0.6
	4		1.5±0.42			9.4±22	20±7	16±2.5	1.4±0.8	3.4 ±0.8	3.9±1.2
	5		4.1±2.7			15.6±3.4	28±6.3	22±4.4	6.6±2.7	3.4±0.78	7.6±1.3
	6		5.4±0.46			21.0±5.1	29±4.8	17±5	7.2±3	7.0±1.1	7.4±2.8
	7		4.4±0.45			32±3.2	36±3	28±8	8±4.2	9.1±1.0	5±2

TABLE 18

PETTICOE WICK   GROWTH OF NEW LAMINA 1969

Date	Age	1 m	2 m	Depths 6 m	10 m	12 m
29.1.69	1					
	2					0.05±0.016
	3		0.69±0.49	0.095±0.075	0.11	0.143±0.1
	4	0.8±0.4	1.1 ±1.0	0.055±0.35	0.26±0.14	0.155±0.036
	5	1.5±0.7	1.85±0.32	0.9 ±0.41	0.57±0.22	0.172±0.14
	6	2.1±0.69	1.9 ±1.3	1.2 ±0.9	0.4	0.25 ±0.12
	7	2.0±0.8	1.9± 1.1	1.47 ±0.22		
9.3.69	1					
	2		0.25±0.11	0.12±0.016	0.16	0.34
	3		0.61±0.15	0.19±0.09	0.24	0.61±0.38
	4	1.2±0.8	1.2 ±0.8	0.89±0.69	0.94±0.49	0.89±0.34
	5	4.5±0.92	3.5 ±1.5	2.1 ±1.1	1.7 ±0.36	0.87±0.46
	6	3.4±2.3	4.4 ±1.4	4.0 ±1.3	1.5 ±0.69	0.97±0.73
	7	5.16±0.71	4.9 ±1.4	4.5 ±0.87	2.1 ±0.57	

PETTICOE WICK   MEAN CROPPING DATA AND PRODUCTION FIGURES

Depth	Age	Holdfast Biomass	Holdfast Annual Increment	Stipe Biomass	Stipe Annual Increment	Length	Annual Increment	Biomass /Unit Length	Peak Lamina Biomass 1967	Peak Lamina Biomass 1968	Total Biomass 1967	Total Biomass 1968	Net Annual Production 1967	Net Annual Production 1968
1 m	1	0.12±0.1	0.12	0.5±0.2	0.05	13.5±6.7	13.5	0.037±0.017		0.7		0.87		0.87
	2	2.8±1.2	2.68	2±0.4	1.95	26±8	12.5	0.075±0.014		3		7.8		7.6
	3	6.2±2	3.4	8.9±2.6	6.9	37.5±2.6	11.5	0.23±0.06		7.3±1.6		22.4		17.6
	4	10.3±3.6	4.1	21±5.8	12.1	45.6±16	8.1	0.34±0.12		37±10		68.3		53.2
	5	29±4.2	18.7	45±5	24	78±5.2	32	0.6±0.2		88±10		162		137
	6	33±10	4	61±6.2	16	91±7	13	0.66±0.04		114±21		208		134
	7	45±13.6	12	63.8±6	2.8	94.5±18	3.5	0.66±0.04		117±6		225		131
2 m	1	0.43±0.23	0.43	0.25±0.02	0.25	2.5±1.6	2.5	0.1±0.007	0.78	0.8	1.35	1.25	0.89	0.84
	2	1.4±1.3	0.97	1.9±0.8	1.87	18±6	15.5	0.08±0.02	6.6±4.8	6±0.9	9.6	8.3	9.4	8.8
	3	8.4±3.4	7	7.5±2.8	5.6	37±6	19	0.18±0.02	47±13.8	45±5	63	61	59.6	57.6
	4	22±8.5	13.6	31.7±4.6	24	74±7	37	0.41±0.04	90±26	76±6	143.7	129.7	127.6	113.6
	5	37±7.7	15	59±4.4	27.3	95±4	21	0.61±0.06	117±23	106±11.2	215	204	159	148.3
	6	54±16	17	71.6±4.2	12.6	105±4	10	0.68±0.03	110±21.3	123±9.8	235	248.6	139	152
	7	71±22	17	89.6±6.0	18	118±6	13	0.76±0.09	106±16.2	130±9,5	266.6	290	141	165
	8	66±14.5		101±18.5	11.4	124±8.6	6	0.81						
	9	78±20		105±40	4	113±49								
6 m	1	0.08±0.07	0.08	0.125±0.03	0.125	2.4±0.7	2.4	0.053±0.05		0.5		0.705		0.705
	2	0.68±0.6	0.06	0.35±0.12	0.22	6.9±0.8	4.5	0.05±0.08		2.1		3.13		2.4
	3	4.6±2.1	3.92	2.8±0.53	2.2	22±3.4	15.1	0.126±0.15		4.2		11.6		10.3
	4	9.7±4.5	5.1	14.9±4.5	12.1	50±10.6	28	0.19±0.22		38		62.6		55.2
	5	41.6±21	31.9	77±10.4	62	102±8.2	52	0.75±0.04		115		233.0		208.9
	6	46±7.9	4.4	96.3±10.3	19.3	114±6.9	12	0.84±0.06		108		250		131.7
	7	47±7.2	1.0	111±11.2	14.7	125±9.4	11	0.88±0.06		122		280		137.7
	8	55.6±8.4		114±19.6		130±22								
10 m	1	0.06±0.03	0.06	0.022±0.03	0.022	1.62±0.18	1.62	0.014±0.03	0.45	0.2±0.6		0.282		0.28
	2	0.74±0.3	0.68	0.62±0.3	0.6	10.6±1.9	8.98	0.05±0.02	2.2	1.3	3.53	2.66	3.45	2.58
	3	3.6±0.8	2.86	8.8±2.2	8.1	34.7±6.3	24.1	0.24±0.04	14.7±2.3	12	24.1	24.4	22.66	22.9
	4	28.5±4.2	24.9	22.9±2.8	14.1	55±4	20.3	0.38±0.04	46±6.2	38.5±10	97.4	99.9	85.0	77.5
	5	35±12.2	6.5	41±4	18.1	76.8±4	21.8	0.51±0.3	76±7.9	77±11	152.	153.	100.6	101.6
	6	39±10	4	60±6.7	19	88±6	11.2	0.67±0.04	79±22	64±5.3	178	163	102	87
	7	43±20	4	71±6.0	11	94±12.6	6	0.69±0.1	84±25	80	159	194	99	95
12 m	1	0.8±0.8		0.07±0.42		10±1.04		0.08±0.017		1.4±0.8		2.97		
	2	2.4±1.1	1.6	2.2±0.43	1.33	18.5±2.2	8.5	0.116±0.016		13.6±4.2	18.2	18.2		16.5
	3	5.1±2.4	2.7	4.6±0.49	2.4	27±2.8	8.5	0.17±0.018		20±7		29.7		25
	4	7.3±3	2.2	6.9±1.05	2.3	32.6±4	5.6	0.21±0.018		28±6.3		42.2		
	5													

TABLE 20

MEAN CROPPING DATA AND PRODUCTION FIGURES

FLAMBOROUGH

Depth	Age	Holdfast Biomass	Holdfast Annual Increment	Stipe Biomass	Stipe Annual Increment	Stipe Length	Stipe Annual Increment	Stipe Biomass/Unit Length	Lamina Biomass	Net Annual Prod.	Total Biomass	No. Plants per sq. m
1.5 m	1											
	2			0.75		14		0.053	3.1			1
	3			5.1±0.6	4.35	32±2.1	18	0.153	13±3.7			2
	4	4.8±1.2		5.7±1.3	0.6	34±4.6	2	0.167	15.3±4.5		22.9	3
	5	5.1±1.8	0.6	16.4±6.0	10.7	57±10.1	23	0.29	27±8.2	16.5	26.4	5
	6	5.6±4.5	0.2	22±3.4	-3.8	65±6.0	8	0.33	43±8.3	37.9	49	2
	7	13.8±1.8	8.2	25.6±4.2	3.6	71±3.5	6	0.36	58.4±4.7	55	78.8	3
5 m	1											
	2											
	3			3±1.3		25±5.3		0.12	4.2±1.1		20.5	3
	4			7.5±2	4.5	36±4.7	11	0.2	6.3±2.4			2
	5	6.7		15	7.5	65±7	29	0.23	17			1
	6	13.5		31.5	16.5	89	24	0.35	28		73	1
	7	24.5±3	11	42.3±7.6	10.8	94±10.7	5	0.45	36.8±7.9	58.6	103.6	3
8 m	1											
	2											
	3											
	4	6.4		4.2±2		26±5		0.16	8.0±3.7			1
	5	15	8.6	9.0±2.9	4.8	43±3.5	17	0.2	13.8±4.7	27.2	37.8	2
	6	15±3.3	0	16.4±6.3	7.4	57±17	14	0.28	15±11	22.4	46.4	1
	7	17.5	2.5	26.6±7.8	10.2	73±6.3	16	0.36	31±8	43.7	75.1	1

TABLE 21

DUNMANUS BAY — MEAN CROPPING AND PRODUCTION FIGURES

Depth	Age	Holdfast Biomass	Holdfast Annual Increment	Stipe Biomass	Stipe Annual Increment	Stipe Length	Stipe Annual Increment	Stipe Biomass/Unit Length	Lamina Biomass	Net Annual Production	Total Biomass	Mean Epiphyte Biomass per Stipe
2 m	1	0.8	0.8	0.51±0.18	0.51	8.4±3.3	8.4	0.06	1.7±0.6			
	2	1.0±0.18	0.2	0.87±0.68	1.36							
	3	2.8±1.52	1.8	4±2.48	3.1	22		0.18	4.8	9.7	11.6	
	4	8.8±5.8	6	20.8±11.8	16.8							
	5	21.2±8.8	12.4	42.7±12.8	21.9	78±4.7		0.54	85±19.3	118.4	148	
	6	32±30	11	59.6±15	16.9	90±30	12	0.66	122±10	149.9	213.6	
	7	32±8	0	60.3±9.2	0.7	101±8.7	11	0.6	155±54.7	155.7	247	20±8.6
5 m	1	0.4		0.4±0.1	0.4	4.5±0.7	4.5	0.08	1.2		3.4	
	2	0.8		0.8	0.4	10	5.5	0.08	2.2±0.6	3.4	8.5	
	3	1.5±0.5	1.1	2.8±0.4	2.0	25±2.1	15	0.11	4.2	7.3	42.3	
	4	3.7	2.2	10.6±5.3	7.8	52±10	27	0.2	28±10	42.3	72	
	5	9.0±3.2	5.3	27±1.6	16.4	72±5	20	0.37	36	57.7	201	
	6	26.2	17.2	57±15	30	95±14	23	0.6	118	165	202	
	7	27.6±9.6	1.4	67±5.6	10	109±9.6	14	0.61	108±11.5	119		18±7.2
12 m	1			0.3	0.3	6	6	0.05	1.2			
	2			0.8	0.5	11	5	0.07	2.4			
	3	1.0		1.6	0.8	17	6	0.094	3.6		6.2	
	4											
	5	7.8±4.2		21±2.8	4.0	55±7.5		0.38	33.3±3.3		62.1	
	6	15±7	7.2	25±6.4	24	62±5	7	0.4	76±10.8	82.7	116	
	7	24±13.6	9.0	49±10.4		82±3.1	20	0.59	90±13.4	123	163	6±4.6
18 m	1	1.0		0.56±0.24		5.7±2.2	11.3	0.09	0.8±0.6		3.8	
	2	1.0		1.6±0.6	1.04	17±3	8.0	0.09	1.2±0.8		7.0	
	3			4.8±1.4	3.2	25±3.2	2.0	0.19	42±4			
	4			6.4±1.3	1.6	27±4.6		0.31	10±8			
	5											
	6											
	7	14.4±1.5		18±4.6	0.36	50±7	0.36	0.36	17.2±1.8	0.36	49.6	2±1.8

TABLE 22

SENNEN COVE   MEAN CROPPING AND PRODUCTION FIGURES

Depth	Age	Holdfast Biomass	Holdfast Annual Increment	Stipe Biomass	Stipe Annual Increment	Stipe Length	Stipe Length Annual Increment	Biomass/Unit Length	Lamina Biomass	Net Annual Production	Total Biomass per sq.m.	No.Plants per sq.m.	Mean Epiphyte Biomass per stipe
3 m	1												
	2											2	
	3	5.5±0.9		8.5±4.3		35±10.2		0.24	16.5±2.5		30.5	4	
	4	12±4.3	6.5	22±6.2	13.5	63±12.3	28	0.35	37±10.4	57	71	10	
	5	18±3.5	6.0	45±6.4	23	80±7.6	17	0.57	98±48	127	161	6	6.3±2.5
	6	22±6.2	4.0	46±4	1	71±10.6	-9	0.64	103±31	108	171	2	
	7	30	8.0	69	23	83	22	0.83	107±10.7	138	206	1	
7 m	1												
	2	3±0.8		2.7±1.17		17.2±4.0		0.15	5±4.2		10.7	8	
	3	5.6±1.2	2.6	11±2.6	8.3	35±10.2	17.8	0.32	12	22.9	28.6	4	
	4	11.6±0.72	6	19±3.8	8	52±5.2	17	0.37	22±4.0	36	52.6	10	
	5	21±2.6	9.4	38±2	19	77±6.0	25	0.49	82±4.2	102.4	141	7	19.1±7.4
	6	28±5.5	7	51±2.6	13	86±5	9	0.59	100±38	120	179	7	
	7	35±6	7	76±14	25	93±10	7	0.81	142±34	174	253	7	
10 m	1												
	2	2.7±0.43		3.1±1.4		18±5.6		0.17	5.6±0.72		11.4	4	
	3	7.1±0.97	4.4	12±1.4	8.9	45±2.5	27	0.26	12.5±2.5	25.8	31.6	4	
	4	13±1.0	5.9	22±1.4	10	54±9.7	9	0.4	23±0.72	38.9	58	4	
	5	18±3.1	5	32±9.5	10	60±3.3	6	0.53	56±10	71	106	5	20±8.6
	6	25±5.7	7	39±14	7	75±14	15	0.52	92±17	106	156	5	
	7	34±10	9	45±13	6	81±11.5	6	0.56	117±15	132	196	4	
13 m	1												
	2			1.5		8.8		0.17	1.5			2	
	3	3.9±8.7		5.3	3.8	23±6.7	14.2	0.23	7.5±3.2			10	
	4	7±2.6	3.1	17.4±5.8	12.1	34±8.6	11	0.51	17.6±5.3	32.8	42	7	
	5	10±3.5	3	29±2.8	11.6	62±6.1	28	0.46	27.5±9.5	42.1	66.5	8	8.3±2.1
	6	16±10.8	6	33±7	4	66±14	4	0.5	42±17.5	62	101	11	
	7	18±12.2	2	34±5.8	1	73±18	17	0.48	57±17	60	109	6	

TABLE 22 (Continued)

SENNEN COVE   MEAN CROPPING AND PRODUCTION FIGURES

Depth	Age	Holdfast Biomass	Holdfast Annual Increment	Biomass	Annual Increment	Length	Annual Increment	Stipe Biomass/Unit Length	Stipe Lamina Biomass	Net Annual Production	Total Biomass per sq.m.	No.Plants per sq.m.	Mean Epiphyte Biomass per Stipe
23 m	1	1.1		0.7		8		0.08	4.6		6.4	2	7.6±1.9
	2	2.2	1.1	1.5	0.8	12.2	4.2	0.12	6	7.9	9.7	5	
	3	5.1	2.9	8	6.5	26	13.8	0.3	12.6	22	25.7	5	
	4	6.7±2	1.6	12±9.4	4	36±11.2	10	0.32	15.2±12.6	20.8	33.6	3	
	5	11±2.1	4.3	25±14	13	52±15	16	0.48	19±7.7	36.3	55	3	
	6	15±6.8	4	23±8.8	2	48±14	-4	0.48	26±11.6	32	64	2	
	7												
30 m	1												
	2												
	3)												
	4	1.2		1.5		15		0.1	2		4.7	2	
	5	3.5±0.5	5.3	3.8±1.9	2.3	20	5	0.19	4	11.6	11.3	1	
	6	4	0.5	16	11.2	48	28	0.33	11	22.7	31	1	
	7	9	5	20	4	45	-3	0.44	11	20	40	1	
37 m	1												
	2												
	3	1.9		0.7		9		0.08	2.1		4.7	2	
	4	2.9	1	1.2	0.5	12	3	0.1	2.2	3.7	6.3	1	
	5	3.9	1	2.2	1.0	15	3	0.14	2.9	4.9	9.0	1	
	6	4.5	0.6	2.3±1.1	0.1	16.6±4	1.6	0.14	2.3±0.7	3.0	9.1	1	

TABLE 23

EPIPHYTE BIOMASS PER STIPE AS A FUNCTION OF STIPE AGE

Age (yrs)	1	2	3	4	5	6	7
Depth							
2 m							
Rhodymenia palmata				1.5 ± 1.08	33.6 ± 29	47 ± 25	42 ± 20.9
Ptilotia plumosa			0.17 ± 0.16	0.4 ± 0.52	8.7 ± 8.6	12.5 ± 5.3	7.5 ± 3.6
Phycodrys rubens			0.7 ± 0.89	0.8 ± 1.0	0.1 ± 0.24	0.6 ± 0.58	1.0 ± 0.74
Membranoptera alata			0.07 ± 0.16	0.4 ± 0.56	0.06 ± 0.037	1.4 ± 0.75	1.4 ± 0.96
TOTAL:			0.94 ± 1.15	3.4 ± 1.6	42.5 ± 37	61.5 ± 30	51.9 ± 21
10 m							
Ptilotia plumosa			0.329 ± 0.23	0.3 ± 0.57	2.03 ± 1.5	1.57± 3.4	1.34± 1.05
Phycodrys rubens				1.0 ± 2.2	3.29± 2.67	5.5 ± 4.7	5.2 ± 3.65
Membranoptera alata			0.16 ± 0.23	0.9 ± 2.5	1.97± 1.12	0.72± 1.08	1.9 ± 1.38
TOTAL:			0.49 ± 0.3	2.4 ± 2.6	7.3 ± 3.9	7.8 ± 6.08	8.4 ± 5.4

TABLE 24

PETTICOE WICK   EPIPHYTE BIOMASS (PER STIPE)

Depth	24.4.68	15.5.68	19.6.68	30.7.68	11.9.68	17.11.68	9.12.69	29.1.69	11.3.69
1 m									
Rhodymenia palmata		15±5.1	22±5.2	20±3.6	37.7±10.4	33.8±12.8	13±4.8	8.2 ±6.8	2.4 ±0.84
Ptilotia plumosa		0.1±0.06	0.2±0.14	0.5±0.2	0.24±0.22	0.6±0.52	0.9±0.63	0.37±0.39	1.2 ±0.39
Phycodrys rubens		0.2±0.15	0.2±0.07	0.4±0.16	0.6 ±0.6	0.62±0.48	0.48±0.22	0.12±0.22	0.29±0.17
Membranoptera alata		0.1±0.037	0.1±0.02	0.1±0.04	0.3 ±0.15	0.37±0.21	0.12±0.04	0.3 ±0.22	0.28+_0.12
Total:		15.4	22.5	21				8.9	
2 m									
Rhodymenia palmata	4±1.6	13.3±5.6	14.1±6.1	33.5±14.8	44 ±12	50±24	23.2±6.1	2.1±0.13	5.6±1.6
Ptilotia plumosa	3.8±2.1	6.2±3.2	12.2±4.4	16.9±6.3	12.8±3.1	3.3±0.92	3.3±0.1	1.9±0.2	2.4±0.76
Phycodrys rubens	0.6±0.3	0.5±0.29	4±0.99	3.6±0.87	6±3.2	1.17±0.6	0.8±0.37	0.23±0.19	0.2±0.08
Membranoptera alata	0.1±0.056	0.2±0.116	3.9±2.2	4.5±2	2±1.8	2.2 ±1.6	0.37±0.18	0.2 ±0.1	0.15±0.1
Total:	8.5	20.2	34.2	58,5	64.8	56.67	27.7	4.43	8.3
6 m									
Ptilotia plumosa	2.13±1.27	5.7±2.7	11.6±4.3	13.9±4.7	6±3.1	2.3±1.1	0.56±0.09	1.2±1.1	0.16±0.1
Phycodrys rubens	3.1 ±1.46	2.5±0.82	2.4±1.1	8.3±3.3	24 ±5.6	13.6±4.6	3.8 ±1.2	5.2±0.96	4.6 ±2.6
Membranoptera alata	1.5 ±0.9	4±1.4	6±3	6.7±3.1	20 ±13.1	3.8±1.92	1.0 ±0.12	1.3±0.8	1.8±1.04
Total:	6.7	12.2	20	28.9	50	19.7	5.4	8.7	6.6
10 m									
Ptilotia plumosa	2.13±1.4	4.0±1.7	5.2±3	1.3±0.43	1.6±0.82	1.73±1.26	0.32±0.17	0.01	0.12±0.062
Phycodrys rubens	3.1 ±0.19	0.6±0.31	1.0±0.57	4.2±1.7	12.9±5.4	4.35±2.6	0.48±0.1	0.37±0.35	0.28±0.08
Membranoptera alata	1.5 ±0.09	0.8±0.47	0.8±0.38	1.9±0.91	4.6±1.9	1.57±0.94	0.6 ±0.13	0.03±0.021	0.12±0.04
Total:	3.4	5.4	7	7.4	19.1	7.7	1.4	0.41	0.52
12 m									
Phycodrys rubens				1.3±1.7	1.6±0.6	0.05±0.64		0.05±0.05	0.26±0.178
Membranoptera alata				0.4±0.2	0.38±0.19	0.01±0.01			0.07±0.06
				1.7	1.98	0.06		0.05	0.33

TABLE 25

PETTICOE WICK   EPIPHYTE BIOMASS (INDIVIDUAL PLANTS)

Depth		15.5.68	30.7.68	11.9.68	17.11.68	29.1.69	11.3.69
2 m	Rhodymenia palmata	0.058±0.025	0.03 ±0.016	0.7 ±0.066	0.72 ±0.18	0.17 ±0.11	0.08 ±0.034
	Membranoptera alata	0.08 ±0.02	0.012±0.025	0.13 ±0.13	0.37 ±0.19	0.03 ±0.02	0.09 ±0.057
	Ptilotia plumosa	0.08 ±0.026	0.046±0.019	0.37 +_0.21	0.068±0.018	0.123±0.04	0.036±0.007
	Phycodrys rubens	0.014±0.011		0.025±0.019	0.15 ±0.07	0.046±0.02	0.012±0.0004
10 m.	Phycodrys rubens	0.016±0.003	0.028±0.054	0.66 ±0.22	0.28 ±0.08	0.081±0.04	0.005±0.001
	Membranoptera alata	0.022±0.008	0.081±0.16	0.18 ±0.117	0.16 ±0.58	0.043±0.03	0.024±0.0017
	Ptilotia plumosa	0.019±0.008	0.011±0.005	0.19 ±0.05	0.22 ±0.11	0.003±0.003	

TABLE 26

FLAMBROOUGH   EPIPHYTE BIOMASS (per stipe)

		%	Depth 5 m	%	8 m	%
Rhodymenia palmata	9.7±4.2	96	1.2±0.72	23		
Phycodrys rubens	0.3±0.28	3	3.0±1.5	58	2.2±1.1	51
Membranoptera alata	0.1±0.2	1	1.0±0.42	20	1.6±1.1	37
Cryptopleura ramosa					0.55±1.8	12
TOTAL:	10.1		5.2		4.35	

TABLE 27

SEASONAL VARIATION IN PERCENTAGE ASH IN LAMINARIA HYPERBOREA

Month	Lamina	Stipe
J	28 ± 2.4	32.6 ± 1.9
F	27.3 ± 0.96	33.6 ± 3.6
M	31.8 ± 4.2	38.4 ± 5.9
A	30.8 ± 2.3	36.5 ± 2.1
M	27.6 ± 2.1	$35 \quad \pm 2.8$
J	26.1 ± 1.6	$37 \quad \pm 2.2$
A	22.7 ± 2.9	
S	19 ± 1.9	$36 \quad \pm 3.5$
O	21 ± 3.9	
N	25 ± 4.4	
D	28.7 ± 7.4	33.6 ± 3.4
J	29.8 ± 4.6	
F		
M	33 ± 5.7	
A	31.2 ± 3.9	
M	33 ± 2.2	

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