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

Whittock, Alan

Whittock, Alan (1969) *The kelp forest ecosystem at Petticoe Wick Bay lat 55 55'N. Long 2 09'W: an ecological study*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/10263/

THE KELP FOREST ECOSYSTEM AT PETTICOE WICK BAY

LAT 55°55'N. LONG 2°09'W

AN ECOLOGICAL STUDY

by

ALAN WHITTICK

A thesis submitted to the
University of Durham for
the Degree of Master of
Science.

AUGUST 1969

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 Whittick.

CONTENTS

ACKNOWLEDGEMENTS

I wish to thank Professor D. Boulter for the provision of working facilities in the Botany Department at Durham University during the period of this investigation; and to my supervisor, Dr. D.J.Bellamy, my sincerest thanks for his interest and encouragement throughout the course of this research.

I would also like to thank the following: Dr. D.M.John, for help with the identification of some algal species; Mr. D.J.Jones and Mr. E.Walker who accompanied me on many of my dives; various members of the Durham City Branch of the British Sub-Aqua Club and the Durham University Sub-Aqua Club who participated in certain parts of this work; Mr. A. Jamieson for photographic assistance; Mrs. J. Bailey for typing the manuscript and to my wife for her help and encouragement throughout.

This work was carried out under staff regulations of the University of Durham for the degree of Master of Science while the author was employed as a Research Assistant in the Department of Botany under a grant from the National Environmental Research Council.

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, Neushull 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 $[C^{14}]$ 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 *Macroystis pyrifera* (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 *in toto*.

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 *Laminaria hyperborea* (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

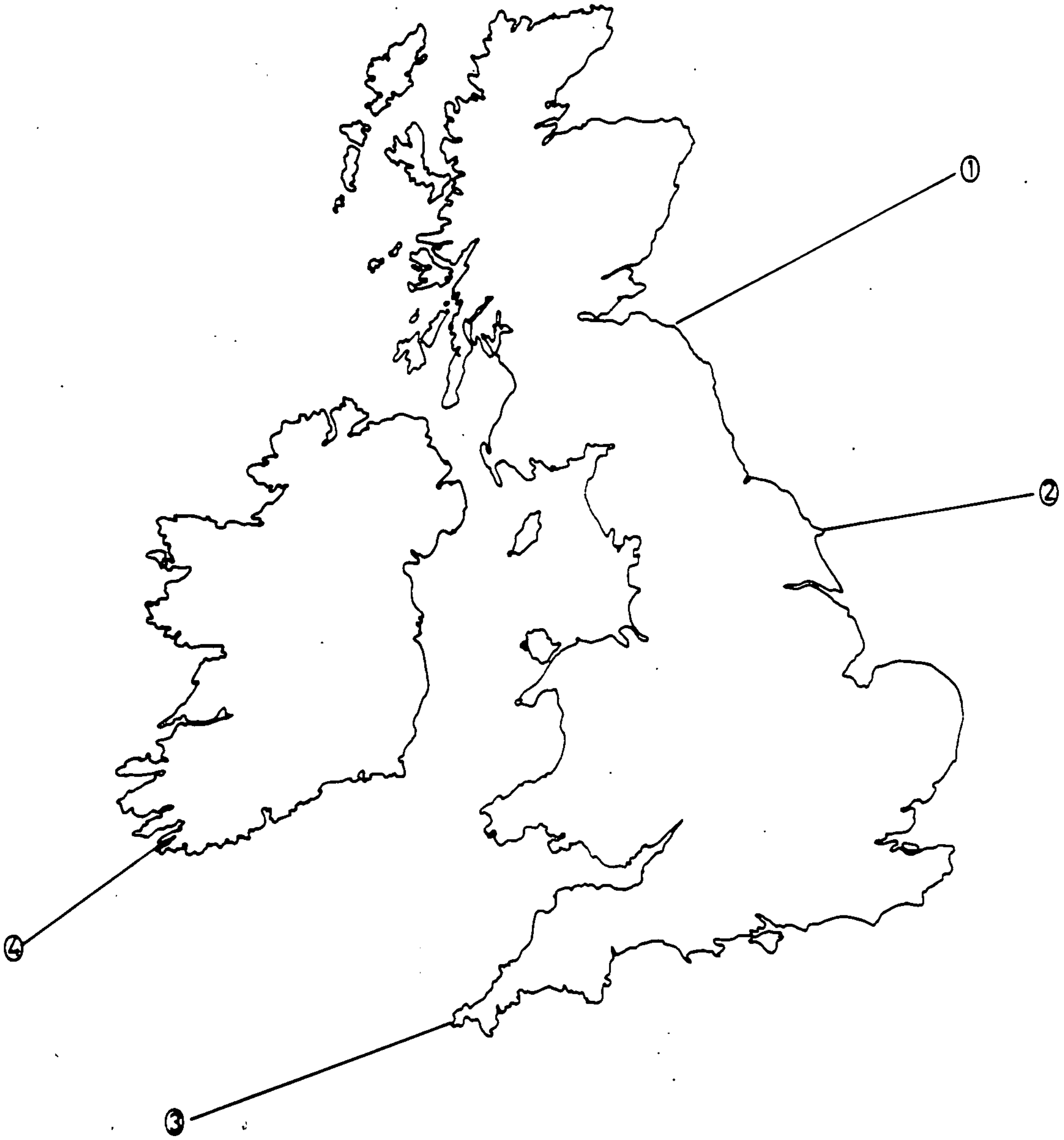
The sites studied:

(1) Main study site - Petticoe Wick Bay.

(2) Flamborough Head

(3) Sennen Cove

(4) Dunmanus Bay.



①
②
③
④

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. Abb's 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. Laminaria digitata
2. Laminaria hyperborea
3. Laminaria saccharina
4. Halidrys siliquosa

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) *Laminaria digitata*

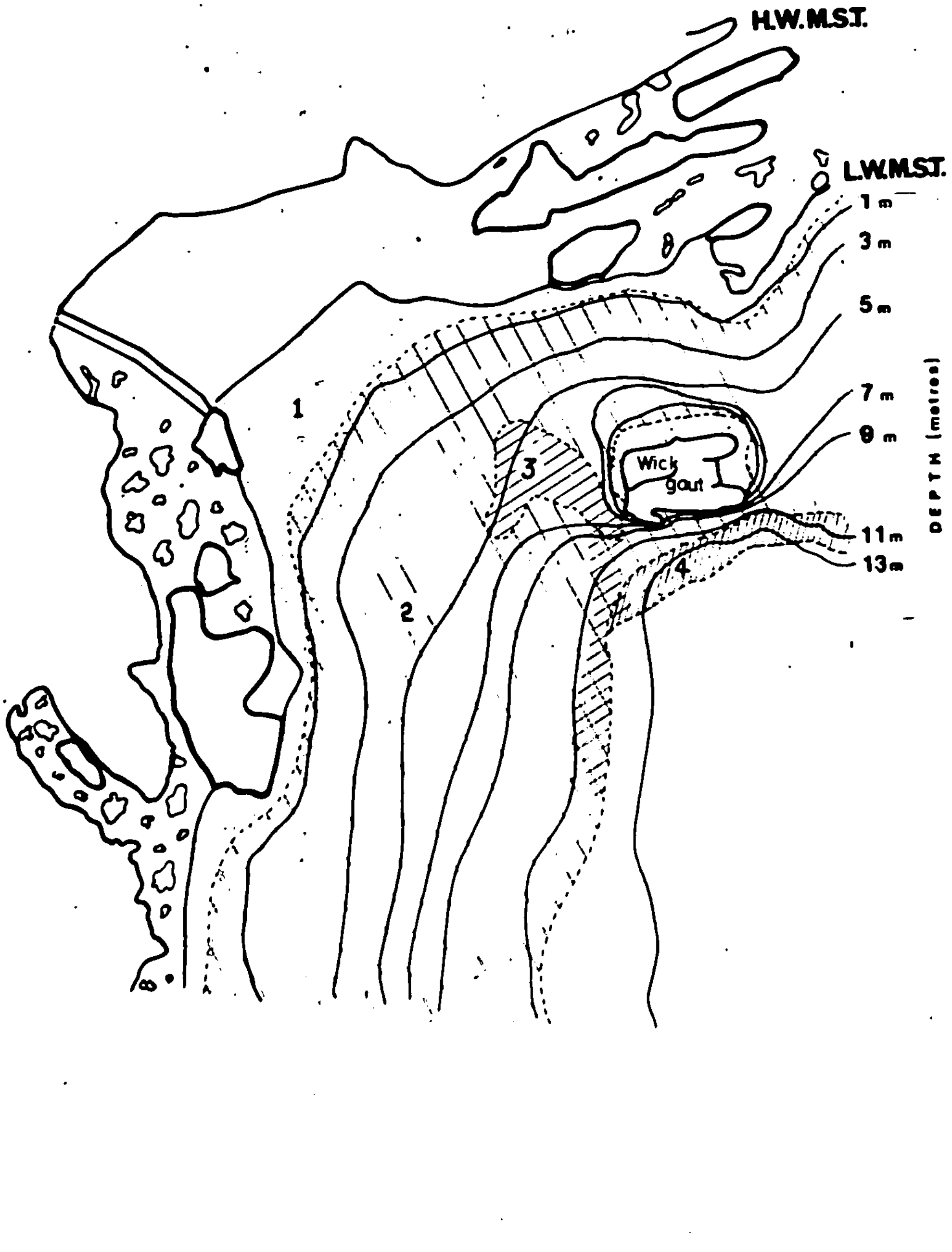
(2) *Laminaria hyperborea*

(3) *Laminaria saccharina*

(4) *Halidrys siliquosa*

Scale 1:2000

PETTICOE WICK BAY

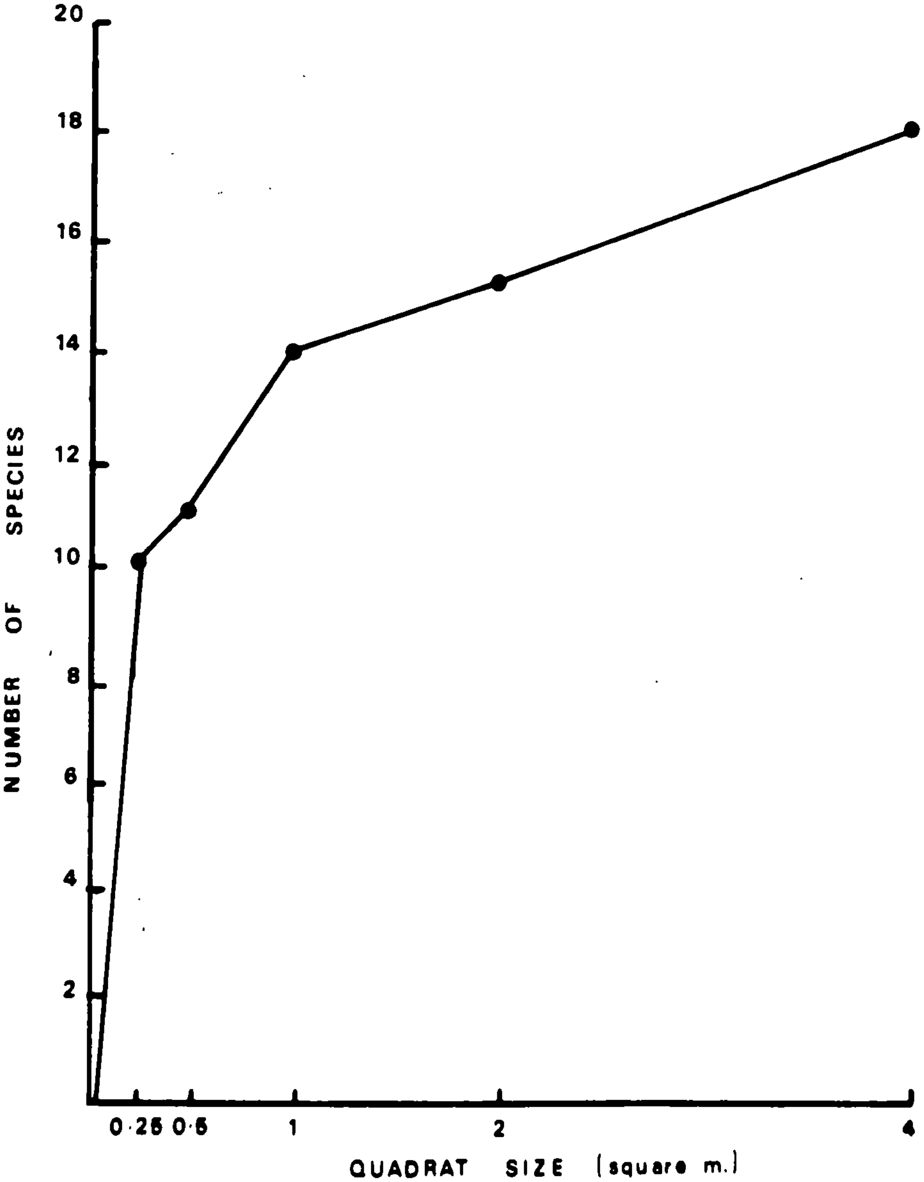


The results are shown in (Fig. 4). The minimal area is supposedly reached when the curve flattens out and no further species are added with increase in quadrat size. As pointed out by Hopkins (1957), this is an idealised case and rarely occurs in practice and in the present study it is seen that although 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.


NUMBER OF SPECIES
20
18
16
14
12
10
8
6
4
2
0·25
0·5
1
2
4
QUADRAT SIZE (square m.)

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) which 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 Kornas 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

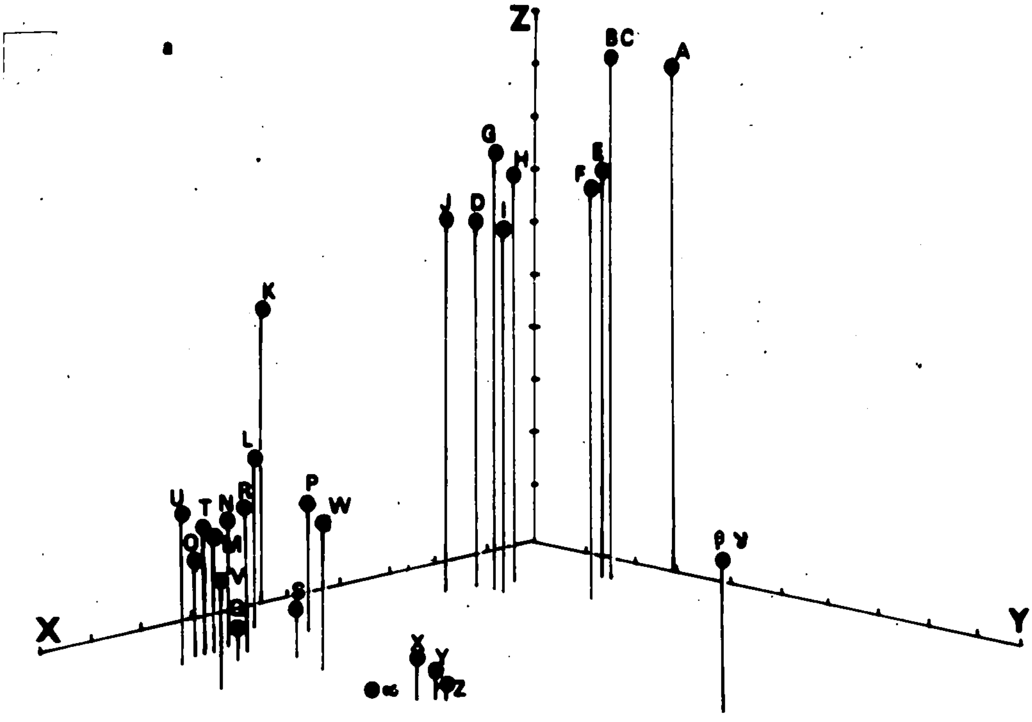
Pseudolithoderma extensum	+ X	Lithophyllum haplidioides	+ N	Lomentaria articulata	+ N
Ulva lactuca	+ V + U	Ectocarpus fasciculatus	+ T + 3 Y	Spongonema tomentosum	+ N
Cystoclonium purpureum	+ V + N	Chondrus crispus	+ Q	Acrosiphonia arcta	+ L
Enteromorpha prolifera	+ L	Heterosiphonia plumosa	+2O +2N	Sphacelaria 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

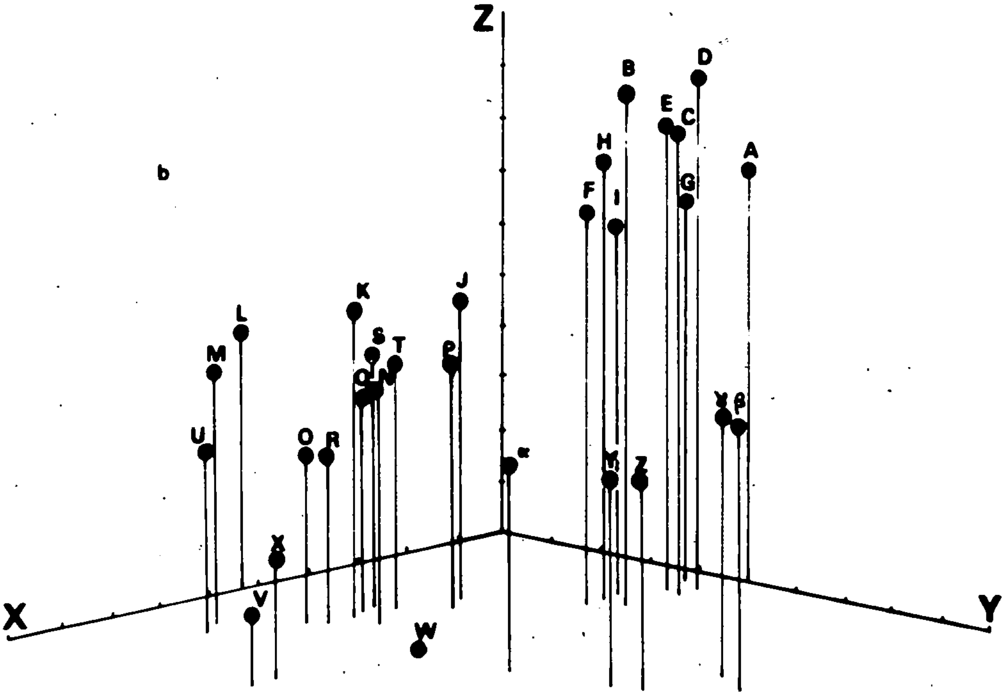
FIGURE 5

Three dimensional ordinations

(a) unloaded data

(b) loaded data


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


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

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 *Laminaria hyperborea* and *Halidrys siliquosa*, forming an open community at depths of 10 - 12 m.

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

Thus it would seem that the distribution of the dominant is dependent mainly on depth of immersion and on substrate type, *Laminaria digitata* and *L. hyperborea* being confined to stable substrates. In unstable areas, *L. hyperborea* is replaced by *L. saccharina* 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 *Halidrys silquosa* 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, obscure a great deal of detailed information. Their great 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 ofer 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 Laminaria hyperborea is the possibility and accuracy of aging the organism.

Problems of Aging L. hyperborea

In all the perennial species of Laminaria, 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 holdfast 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 face 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 labonatory mill to pass to 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 <u>Laminaria hyperborea</u>, 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*, *Ptilota 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 *Laminaria hyperborea*.

CHAPTER 4

PERFORMANCE RESULTS FROM PETTICOE WICK

(1) *Laminaria hyperborea*[*]

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	•——•

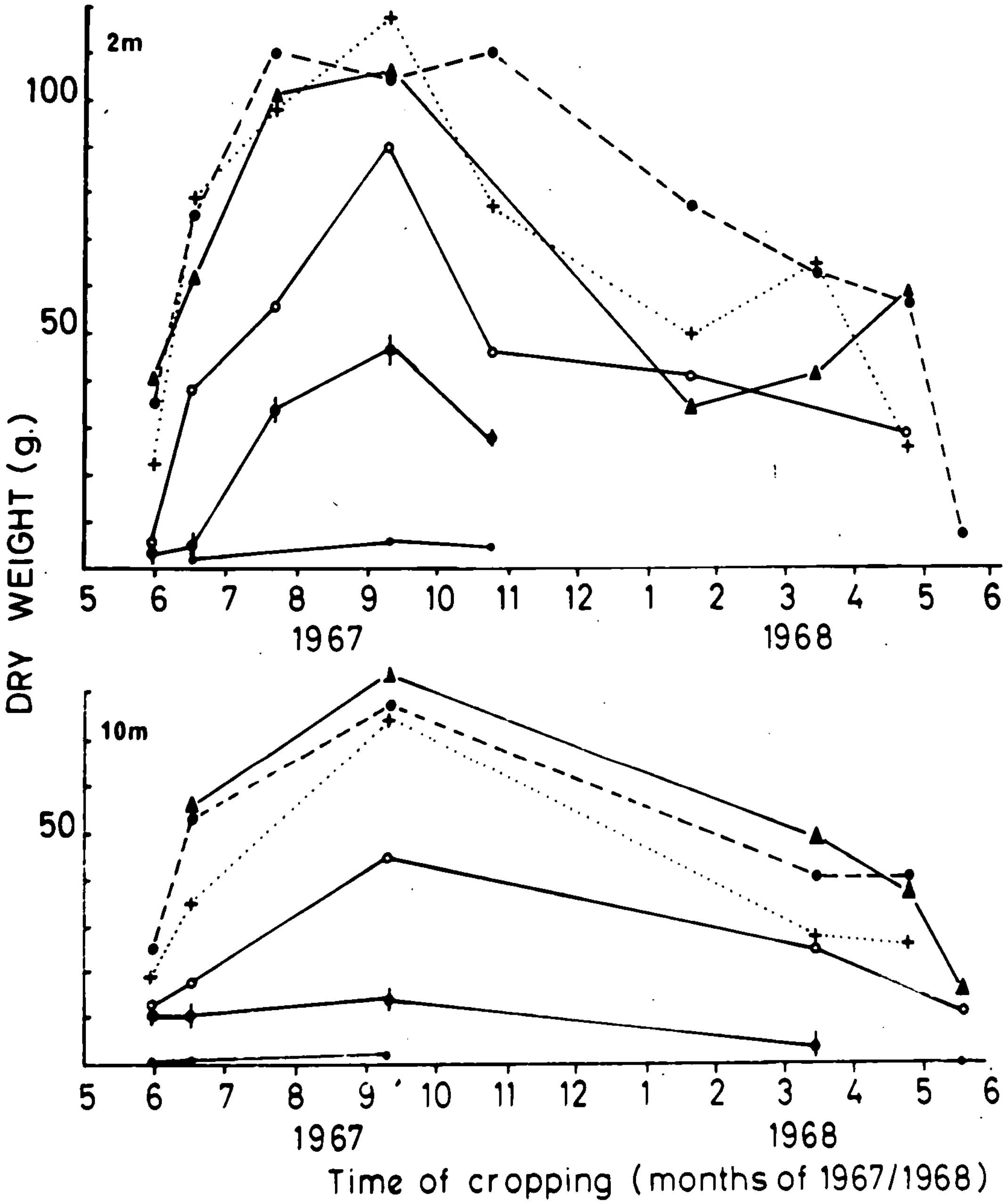

2m
100
50
DRY WEIGHT (g.)
5 6 7 8 9 10 11 12 1 2 3 4 5 6
1967
1968
10m
50
5 6 7 8 9 10 11 12 1 2 3 4 5 6
1967
1968
Time of cropping (months of 1967/1968)

FIGURE 7

Seasonal variation in lamina biomass for the five depths sampled at Petticoe Wick Bay.

Age in years	
7	▲———▲
6	●- - - -●
5	+·······+
4	o———o
3	ɸ———ɸ
2	•———•

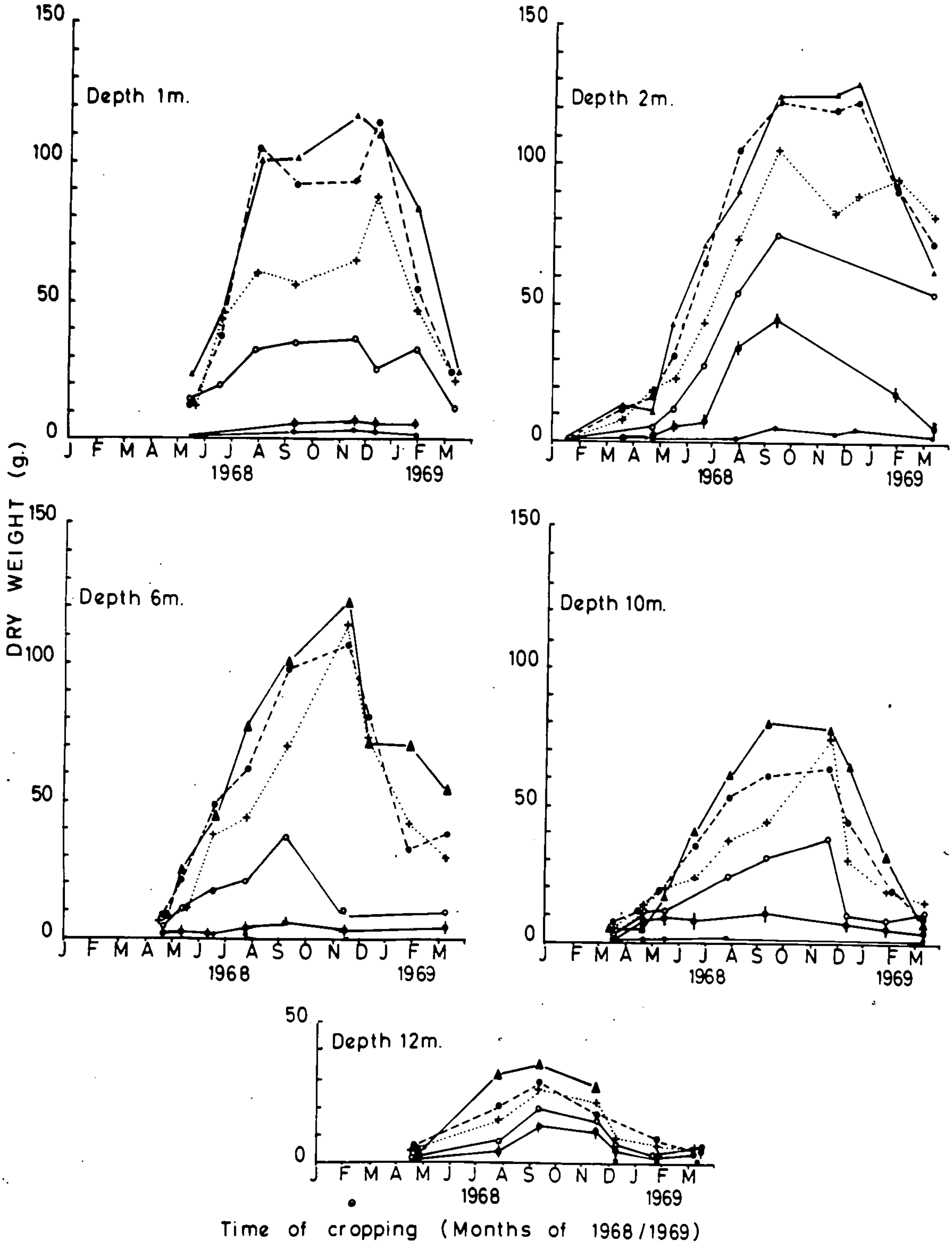
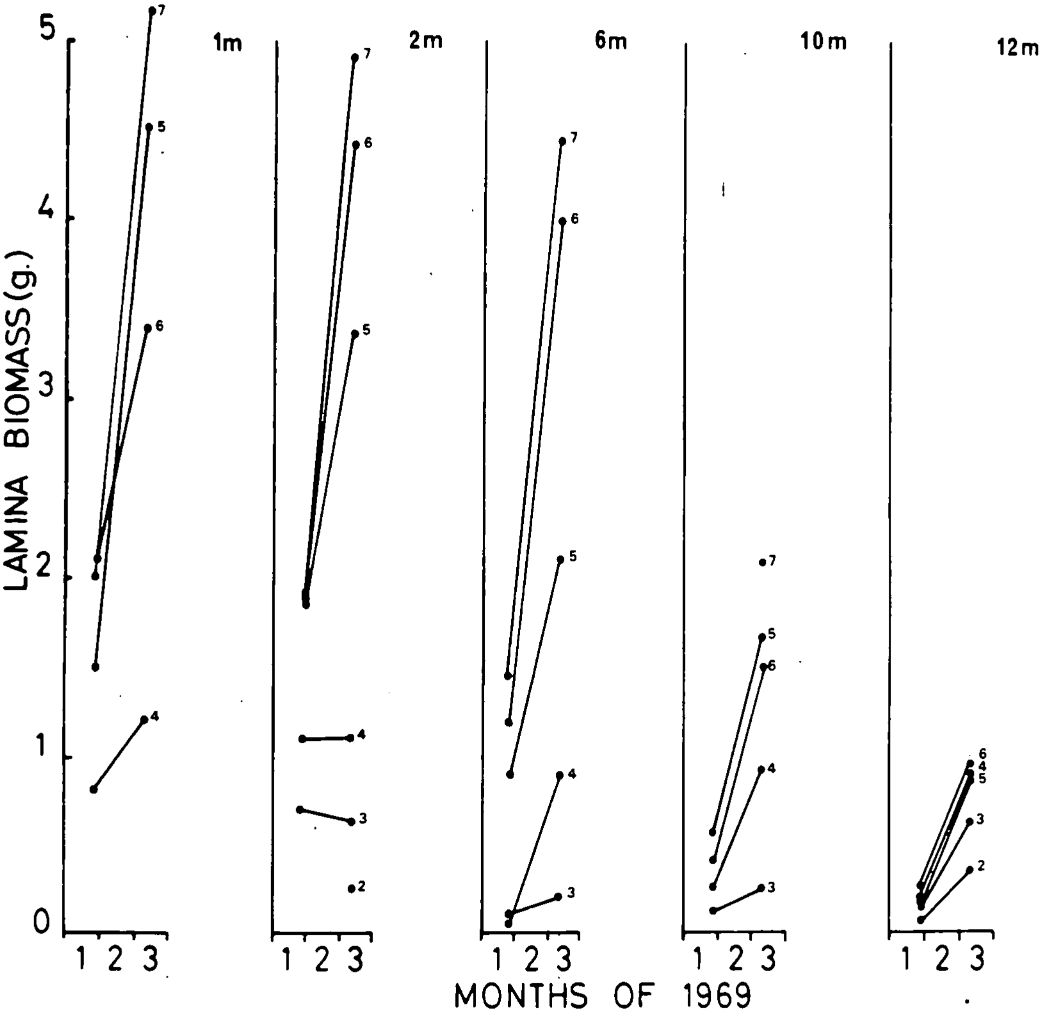

Depth 1m.
Depth 2m.
Depth 6m.
Depth 10m.
Depth 12m.
DRY WEIGHT (g.)
150
100
50
0
J F M A M J J A S O N D J F M
1968
1969
Time of cropping (Months of 1968/1969)

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.)
5
4
3
2
1
0
1m
7
5
6
4
2m
7
6
5
4
3
2
6m
7
6
5
4
3
10m
7
5
6
4
3
12m
6
4
5
3
2
1 2 3
1 2 3
1 2 3
1 2 3
1 2 3
MONTHS OF 1969

FIGURE 9

Peak lamina biomass (1968) at the five depths sampled at Petticoe Wick Bay.

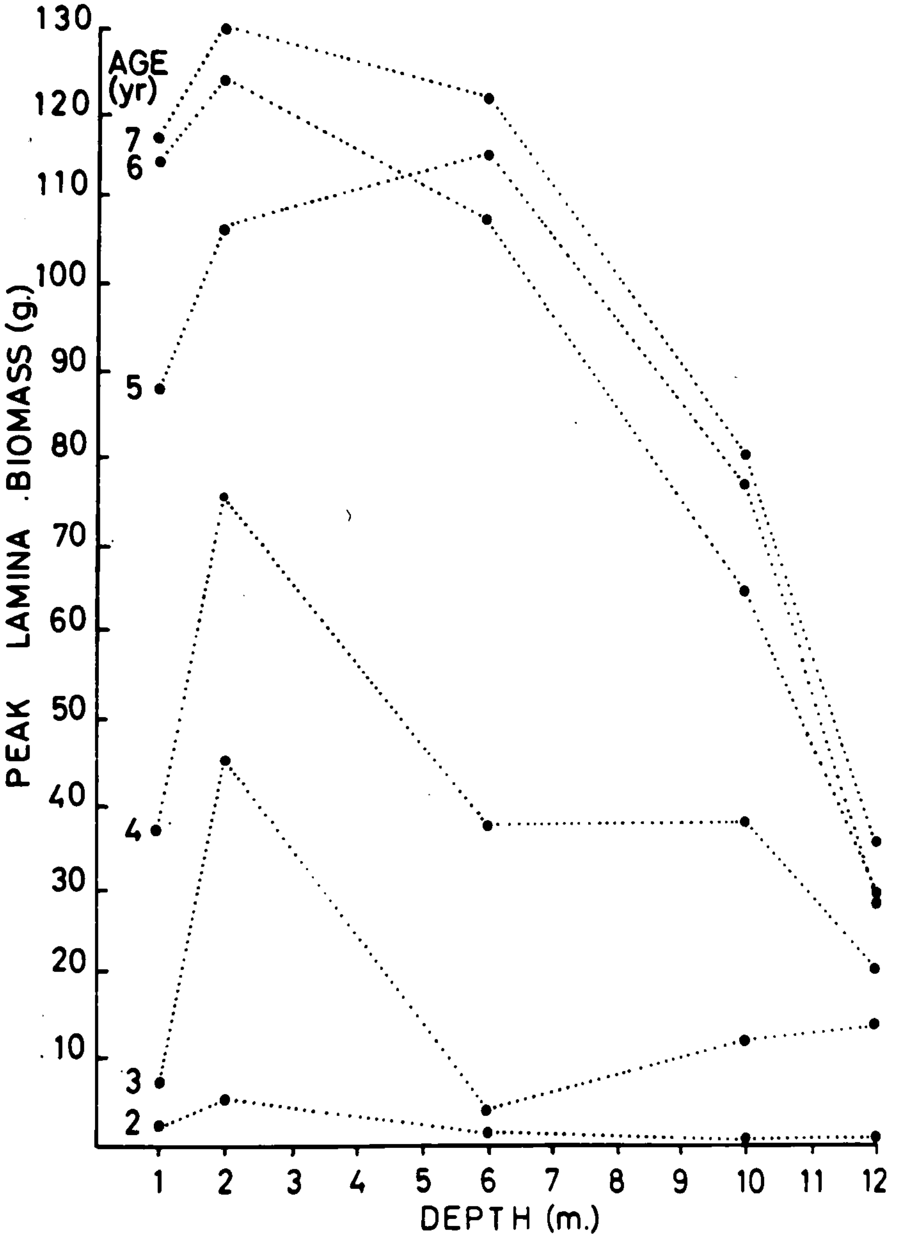

130
120
110
100
90
80
70
60
50
40
30
20
10
AGE (yr)
7
6
5
4
3
2
PEAK LAMINA BIOMASS (g.)
1
2
3
4
5
6
7
8
9
10
11
12
DEPTH (m.)

Fig. 10a 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

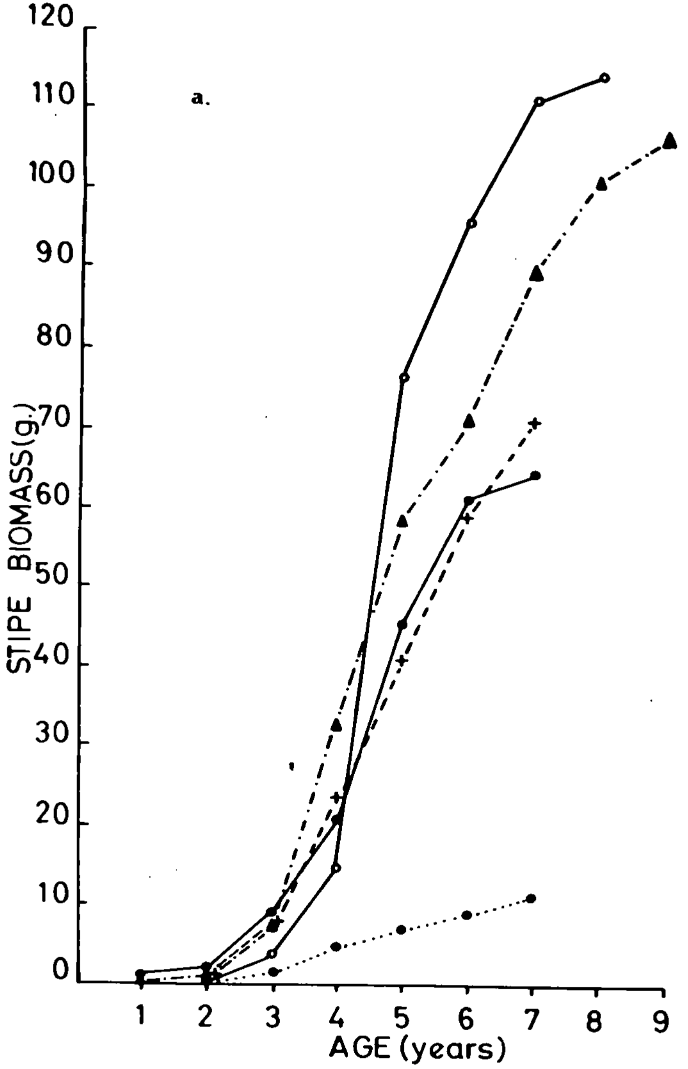
Stipe biomass shows a progressive increase with age from all depths. There is an initial "lag period" followed by a period of rapid growth in three, four and five year old plants and a progressive tailing off in growth with further increases in age. This holds for all depths sampled except at 12 m where 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	●·······●


a.
STIPE BIOMASS(g.)
120
110
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
AGE (years)

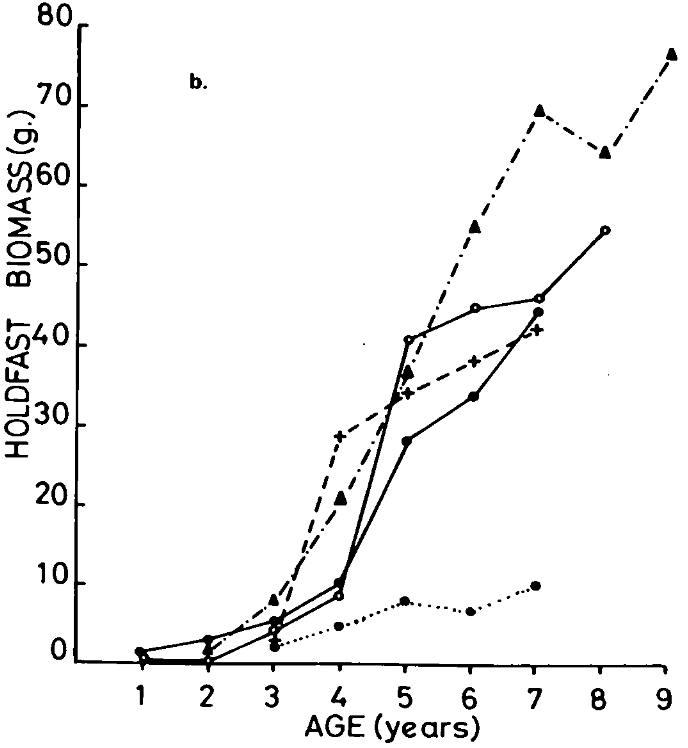

b.
HOLDFAST BIOMASS(g.)
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
AGE (years)

FIGURE 11

Stipe length at five depths sampled at Petticoe Wick Bay.

Depth (m)	
1	●———●
2	▲-·-·-▲
6	○———○
10	+- - - -+
12	●······●

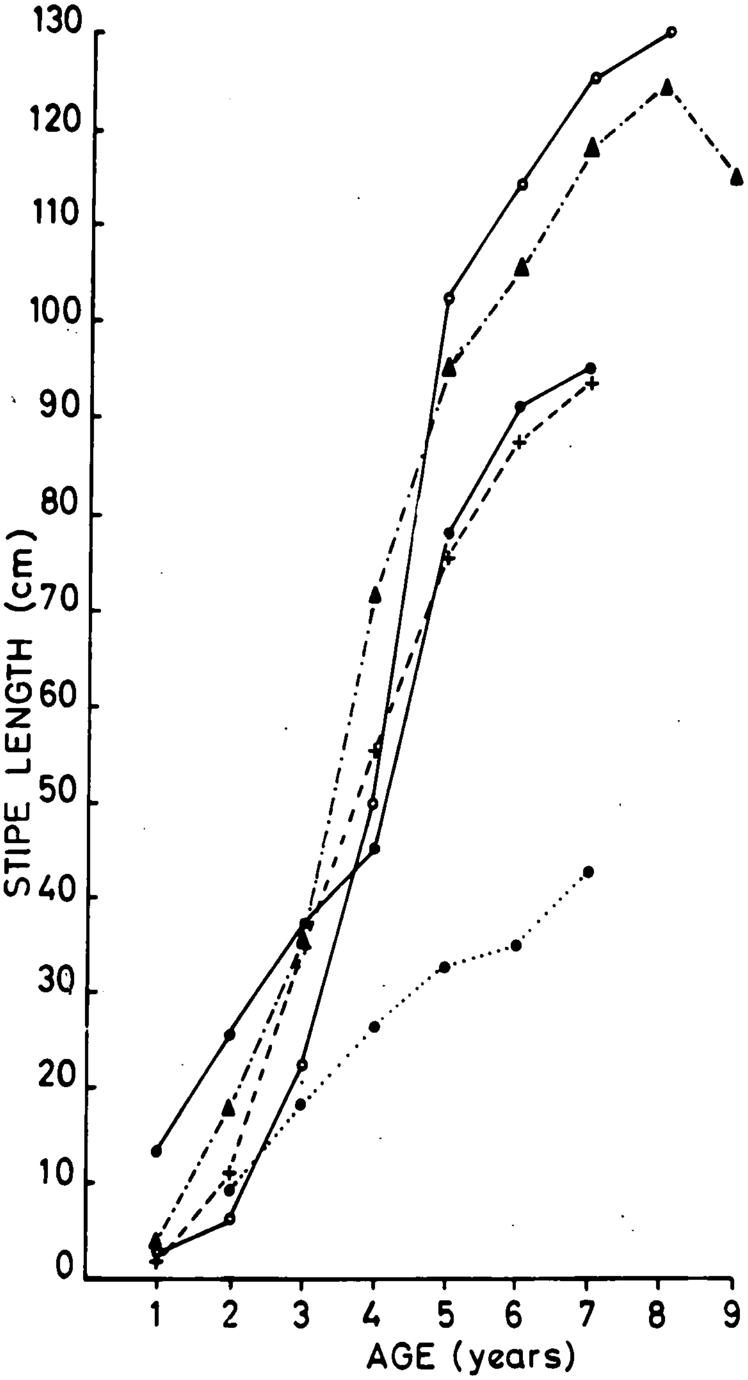
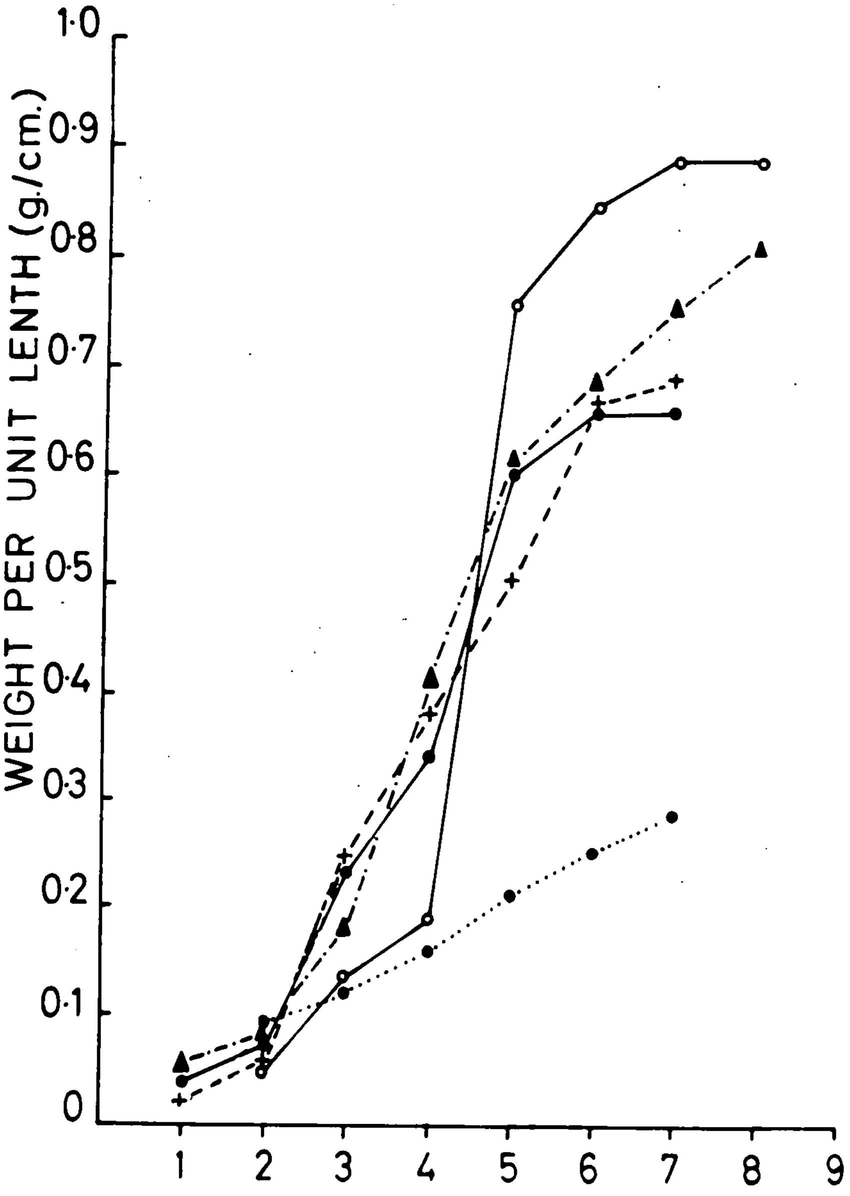

130
120
110
100
90
80
70
60
50
40
30
20
10
0
STIPE LENGTH (cm)
1
2
3
4
5
6
7
8
9
AGE (years)

FIGURE 12

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

Depth (m)	
1	●———●
2	▲-·-·▲
6	○———○
10	+- - -+
12	●······●


WEIGHT PER UNIT LENTH (g./cm.)
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
1
2
3
4
5
6
7
8
9
AGE (years)

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	+	+			
Ptilota 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			+		

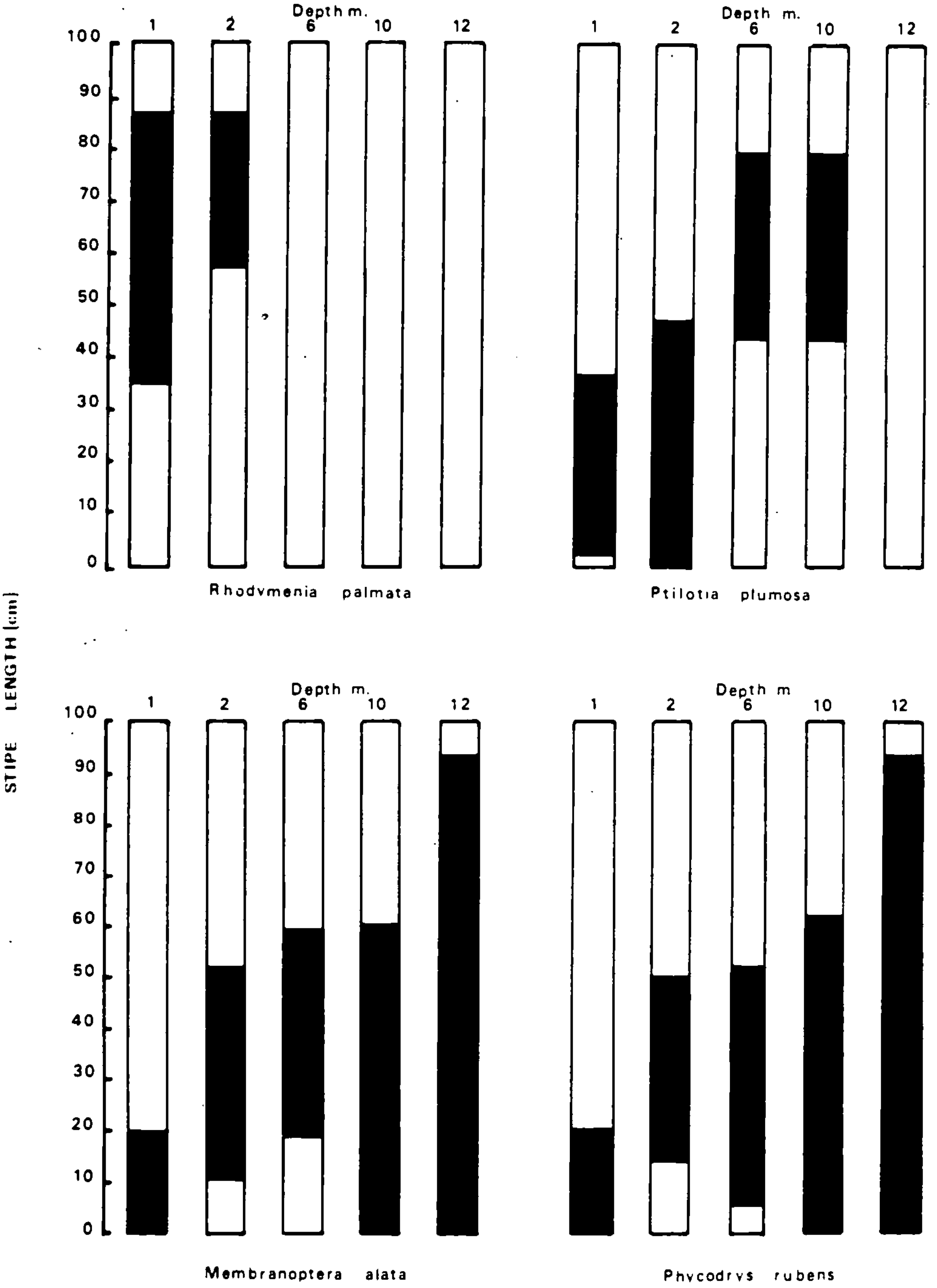
palmata, Membranoptera alata, Ptilotia plumosa and Phycodrys rubens make up over 99 per cent of the total epiphyte biomass and two of these Membranoptera alata and Phycodrys rubens are present as epiphytes throughout the depth range of Laminaria hyperborea. It was decided therefore to concentrate on 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.


STIPE LENGTH (cm)
Depth m.
1
2
6
10
12
100
90
80
70
60
50
40
30
20
10
0
Rhodymenia palmata
Ptilota plumosa
Membranoptera alata
Phycodrys 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 $p = 0.05$.

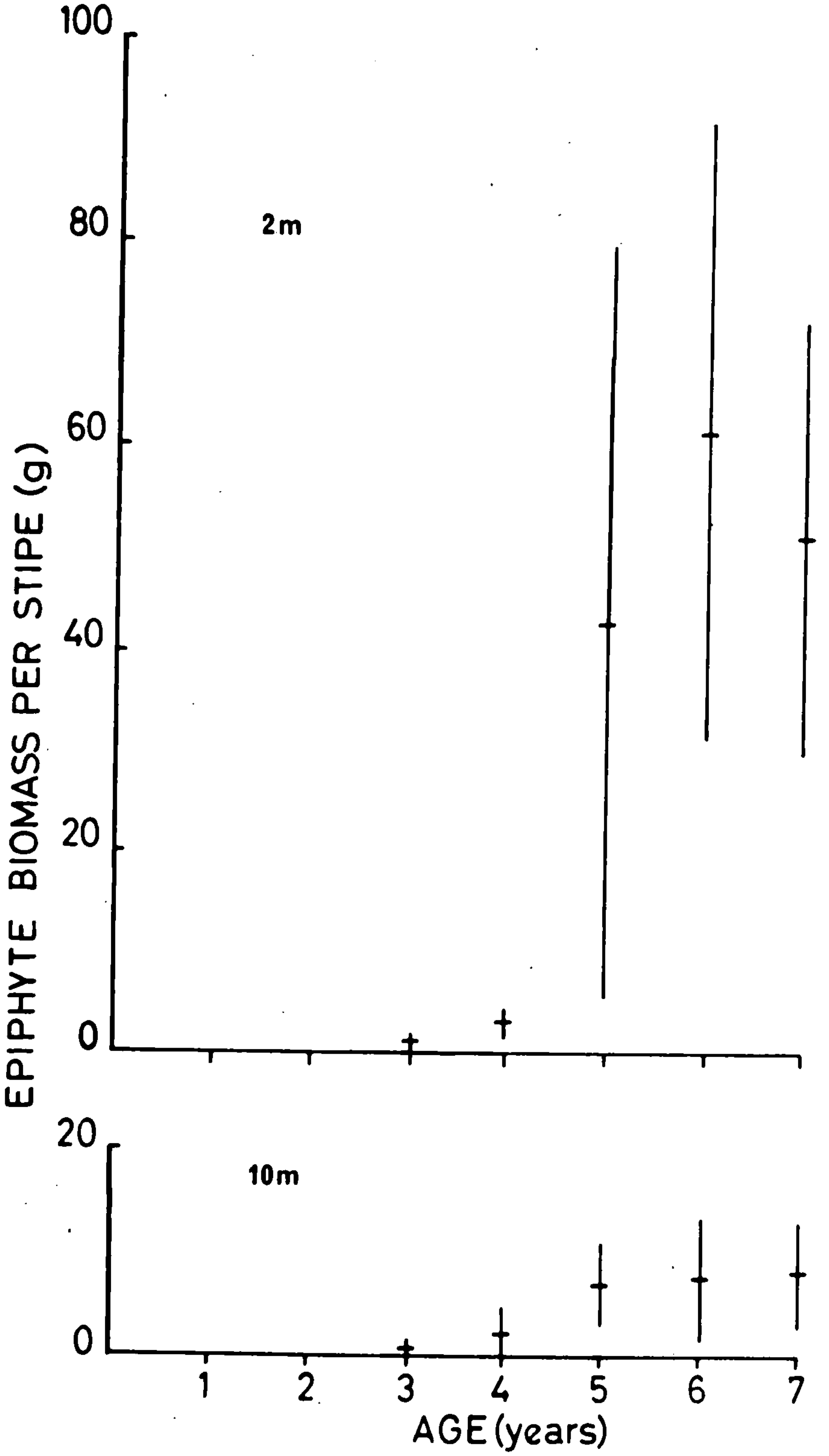

100
80
60
40
20
0
2m
EPIPHYTE BIOMASS PER STIPE (g)
20
0
10m
1
2
3
4
5
6
7
AGE (years)

FIGURE 15

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

Total epiphytes	●——●
Rhodymenia palmata	o----o
Ptilotia plumosa	+·········+
Phycodrys rubens	+–·–·–+
Membranoptera alata	o——o

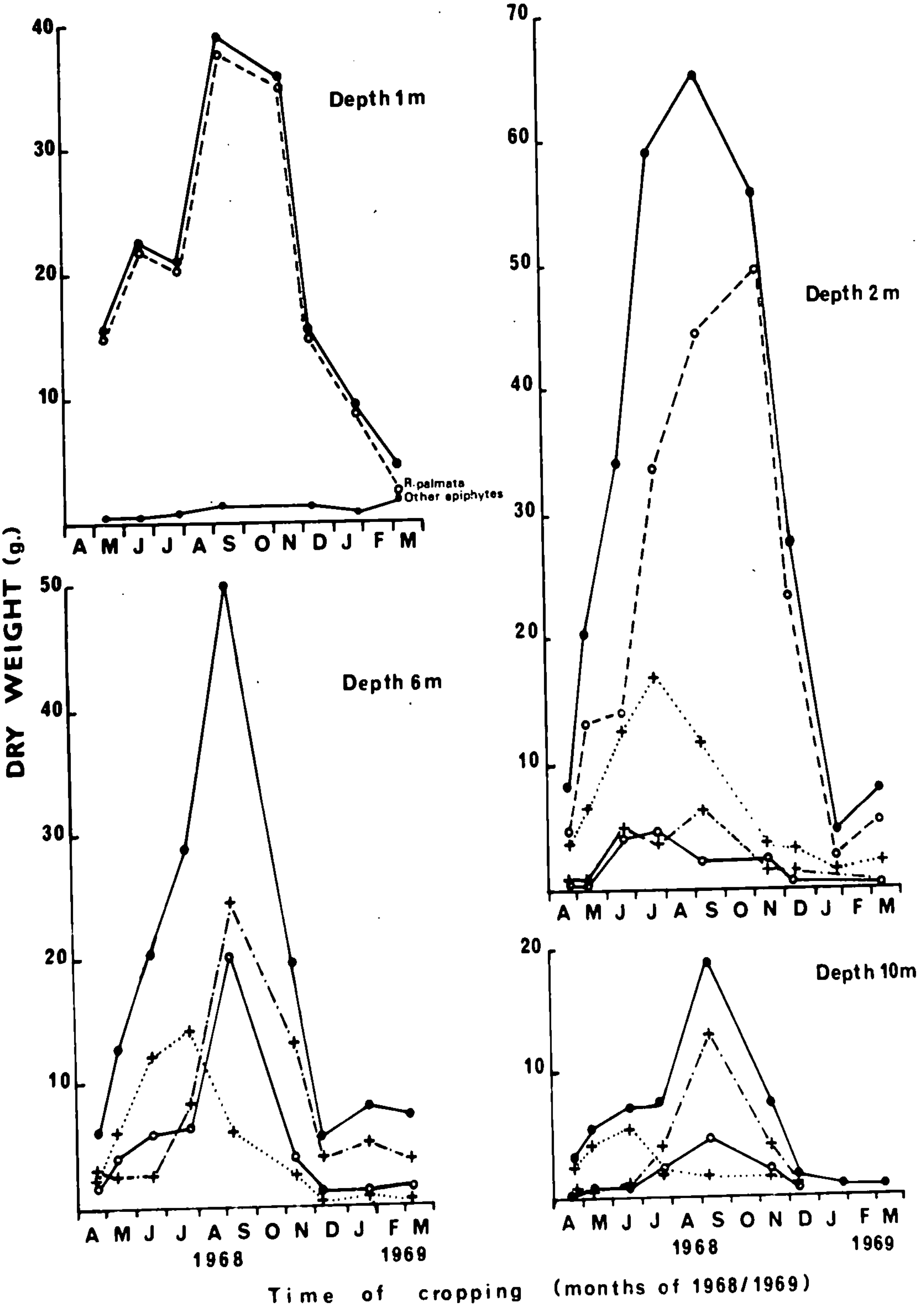
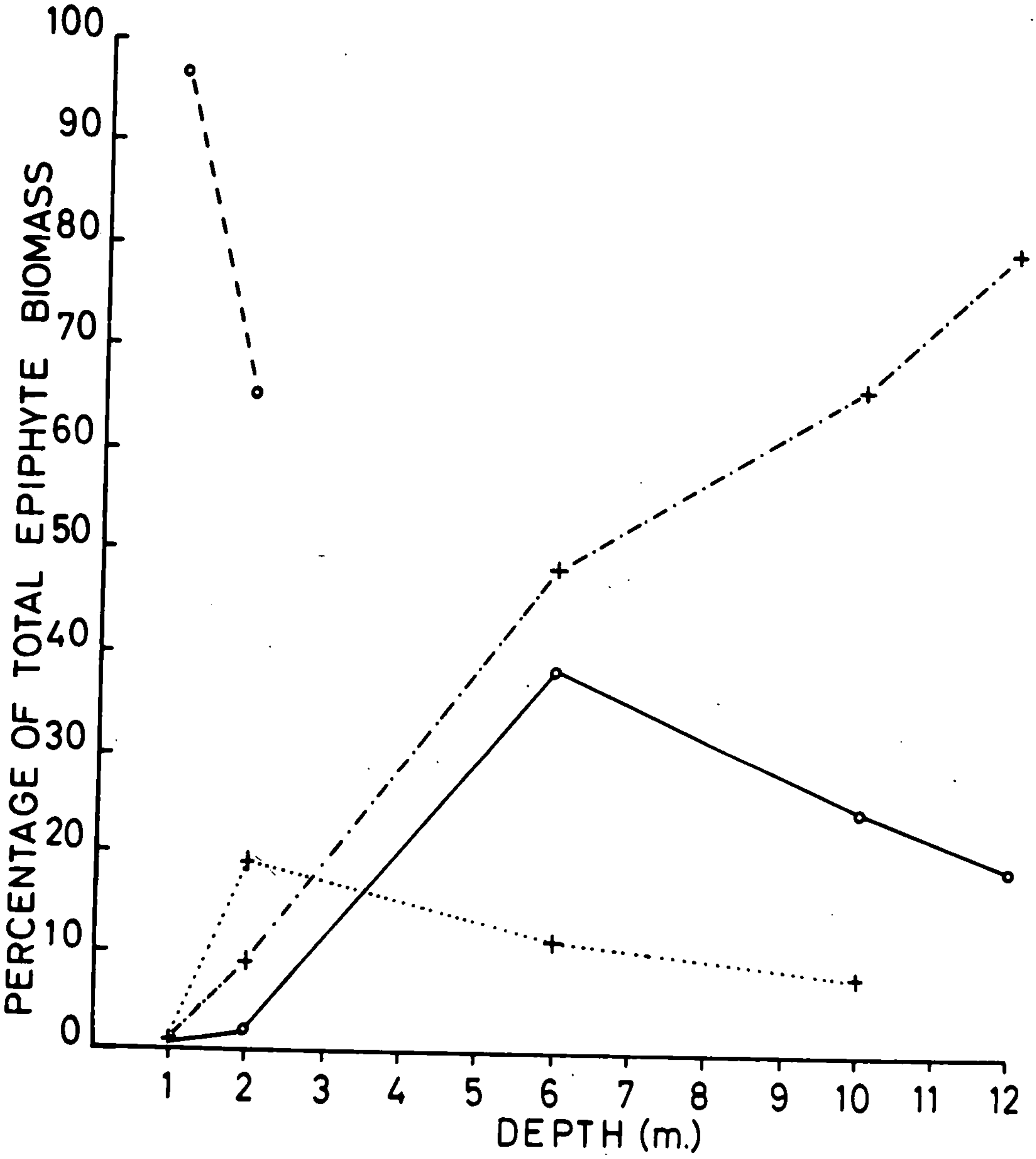

DRY WEIGHT (g.)
Depth 1m
40
30
20
10
R. palmata
Other epiphytes
A M J J A S O N D J F M
Depth 2m
70
60
50
40
30
20
10
A M J J A S O N D J F M
Depth 6m
50
40
30
20
10
A M J J A S O N D J F M
1968
1969
Depth 10m
20
10
A M J J A S O N D J F M
1968
1969
Time of cropping (months of 1968/1969)

FIGURE 16

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

Rhodymenia palmata	o- - - - -o
Ptilotia plumosa	+·········+
Membranoptera alata	o———o
Phycodrys rubens	+—·—·—+


PERCENTAGE OF TOTAL EPIPHYTE BIOMASS
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
DEPTH (m.)

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. Ptilota 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 Phycodrys rubens 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, *Rhodymenia palmata*, *Ptilotia plumosa*, *Membranoptera alata* and *Phycodrys rubens*; make up nearly all the total epiphyte biomass.

(10) The epiphytes show a zonation on the stipes with depth of submersion with *Rhodymenia palmata* at the top followed by *Ptilotia plumosa* and with *Phycodrys* rubens and *Membranoptera alata* 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) *Ptilotia plumosa* reaches its maximum biomass earlier than the other species.

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

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

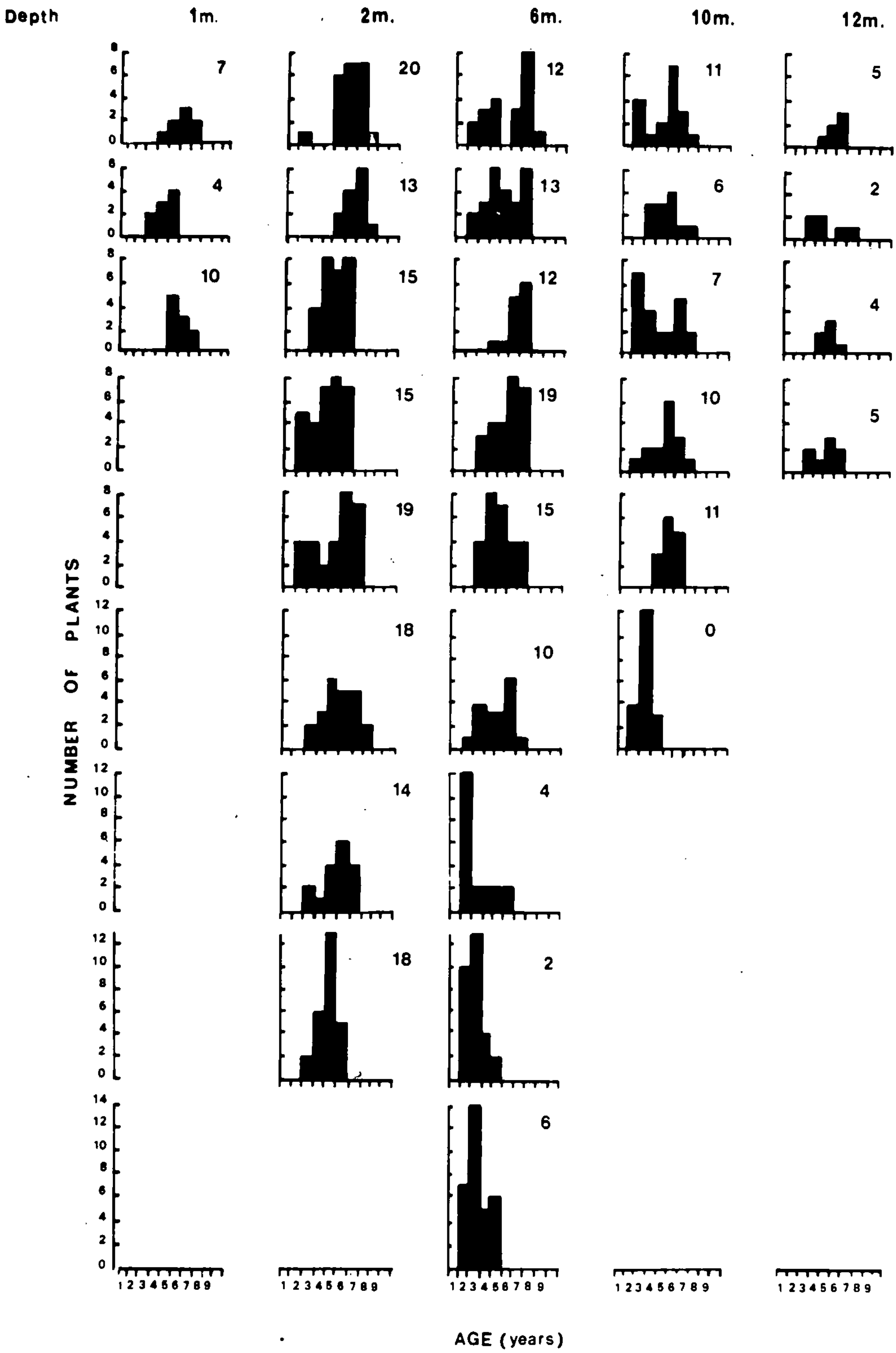
Plants of one year of age and less were discarded as cropping was carried out at different times over a period of two years and owing to the extended reproductive season of Laminaria hyperborea comparisons of the density of these "sporlings" would be meaningless. The results are shown in the form of 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.
7
20
12
11
5
4
13
13
6
2
10
15
12
7
4
15
19
10
5
19
15
11
18
10
0
14
4
18
2
6
NUMBER OF PLANTS
0 2 4 6 8
0 2 4 6 8 10 12
0 2 4 6 8 10 12 14
1 2 3 4 5 6 7 8 9
AGE (years)

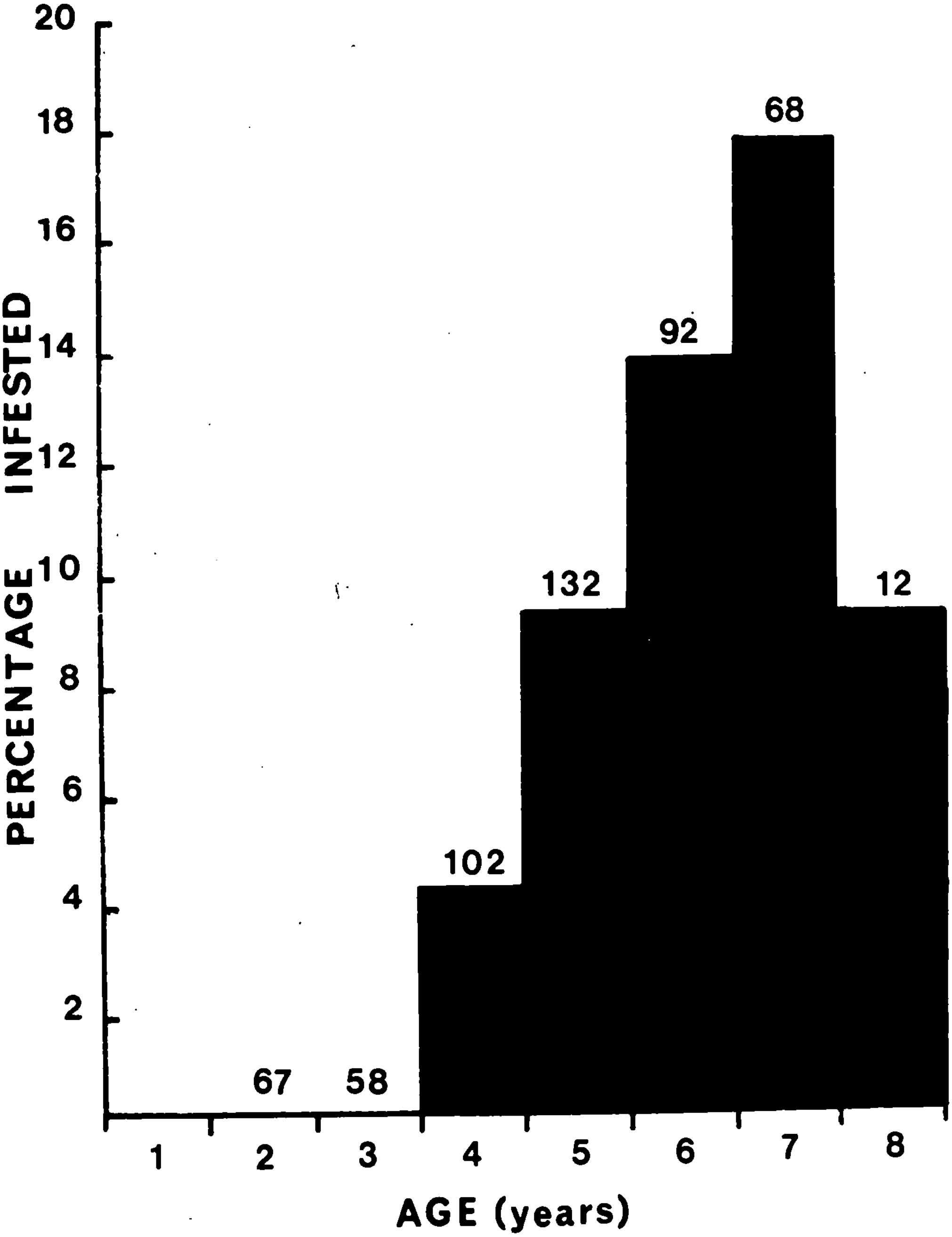
in depth. One pattern that emerges from Fig. 17 is that in the quadrats cropped which include a large number of older canopy plants the number of younger plants is reduced in comparison with quadrats containing fewer old plants.

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

Percentage infestation *by Patina pellucida* of individuals of *Laminaria hyperborea* in each age class. The figure above each column indicates the number of individuals sampled in that age class.


PERCENTAGE INFESTED
20
18
16
14
12
10
8
6
4
2
67
58
102
132
92
68
12
1
2
3
4
5
6
7
8
AGE (years)

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 L. hyperborea in the understorey plants; ~~in~~ stands containing a large number of canopy plants the numbers of understorey individuals are reduced.

(3) Infestation levels of the holdfasts of _Laminaria hyperborea_ by _Patina pellucida_ 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.

<u>Site 1</u>: <u>North Landing Flamborough</u>

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. <u>Laminaria hyperborea</u> 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	▲– – –▲

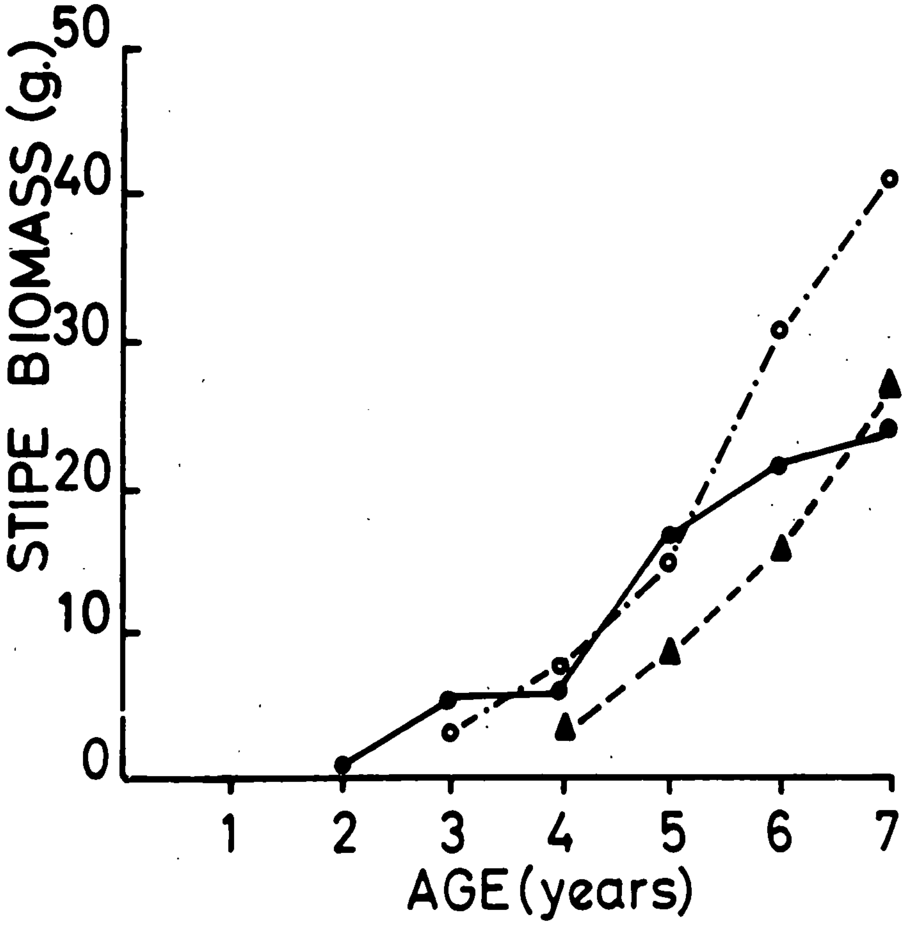

STIPE BIOMASS (g.)
50
40
30
20
10
0
1
2
3
4
5
6
7
AGE (years)

FIGURE 20

Lamina biomass at three depths sampled at Flamborough.

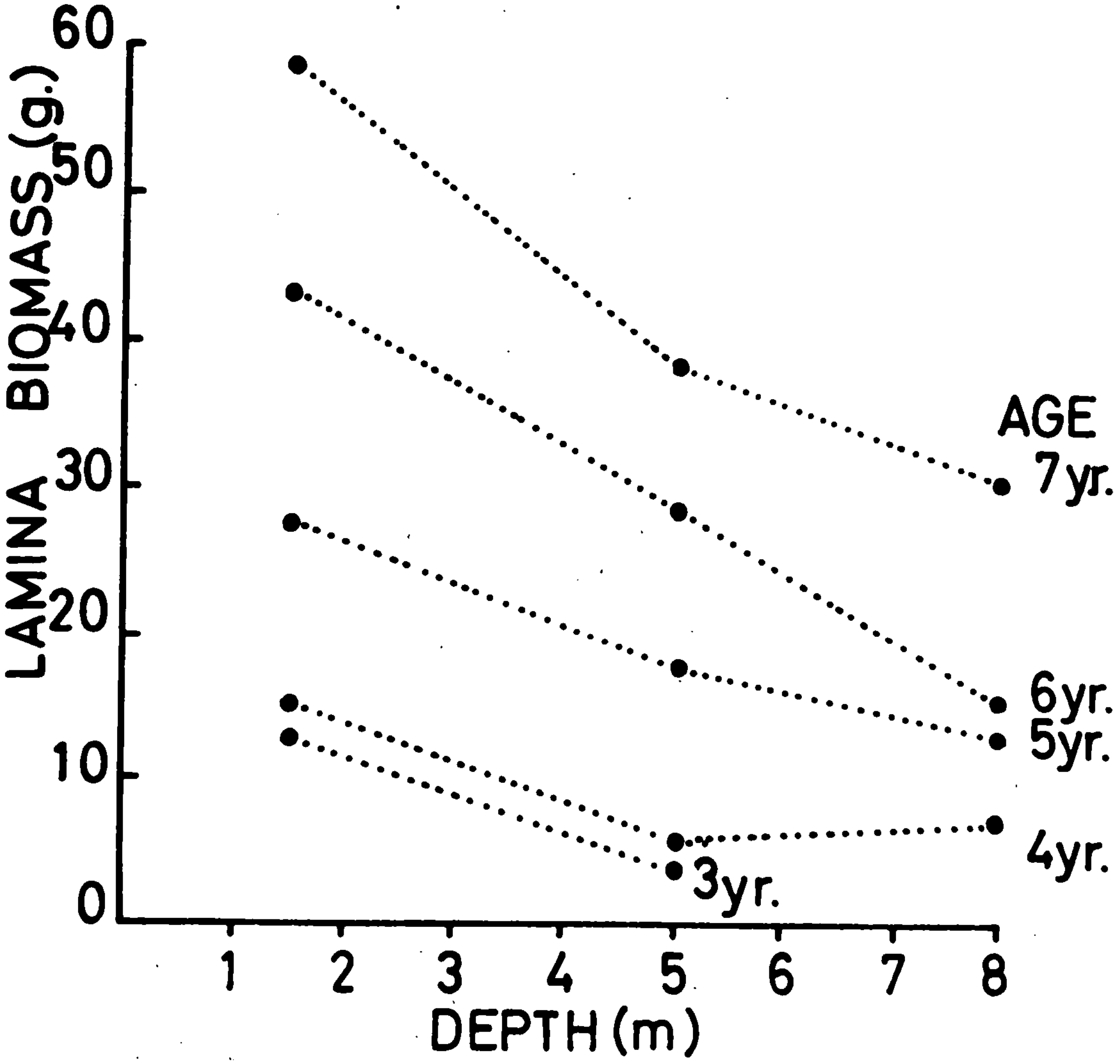
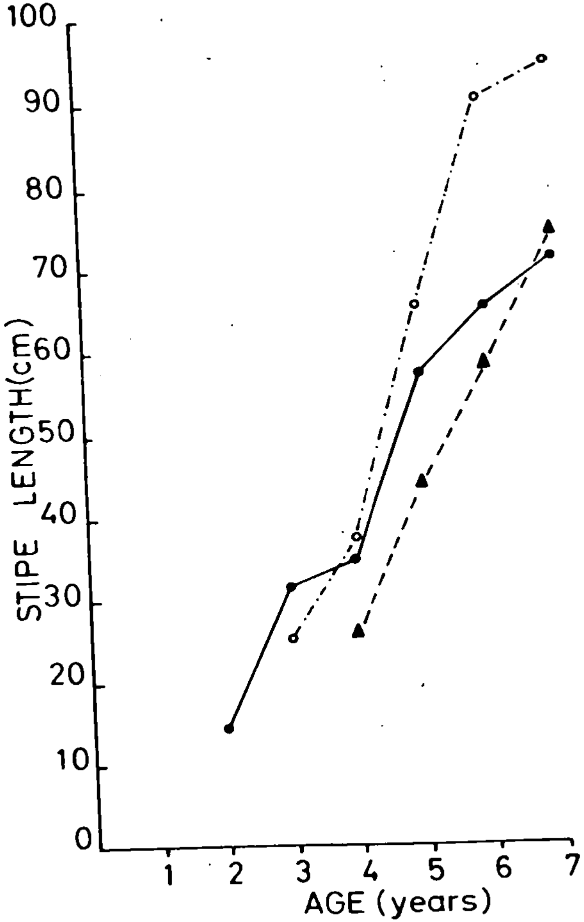
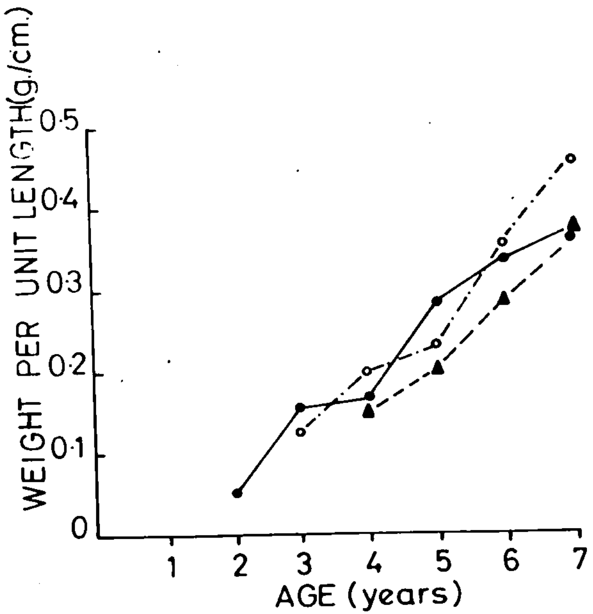

LAMINA BIOMASS (g.)
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
DEPTH (m)
AGE
7yr.
6yr.
5yr.
4yr.
3yr.

FIGURE 21

Stipe length at three depths sampled at Flamborough

Depth (m)	
1.5	●———●
5	○–·–·–○
8	▲----▲


STIPE LENGTH(cm)
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
AGE (years)


WEIGHT PER UNIT LENGTH(g./cm.)
0·5
0·4
0·3
0·2
0·1
0
1
2
3
4
5
6
7
AGE (years)

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 Ptilotia plumosa and the extension of the depth range of Rhodymenia palmata 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, Cryptopleura ramosa 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. Phycodrys rubens and Membranoptera alata reach their greatest biomass on the stipes from 5 and 8 m depth.

Site 2: Dunmanus Bay

At this site Laminaria hyperborea 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 L.hyperborea 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	●——●
Rhodymenia palmata	○- - - -○
Phycodrys rubens	+—·—·—+
Membranoptera alata	○——○
Cryptopleura ramosa	▲

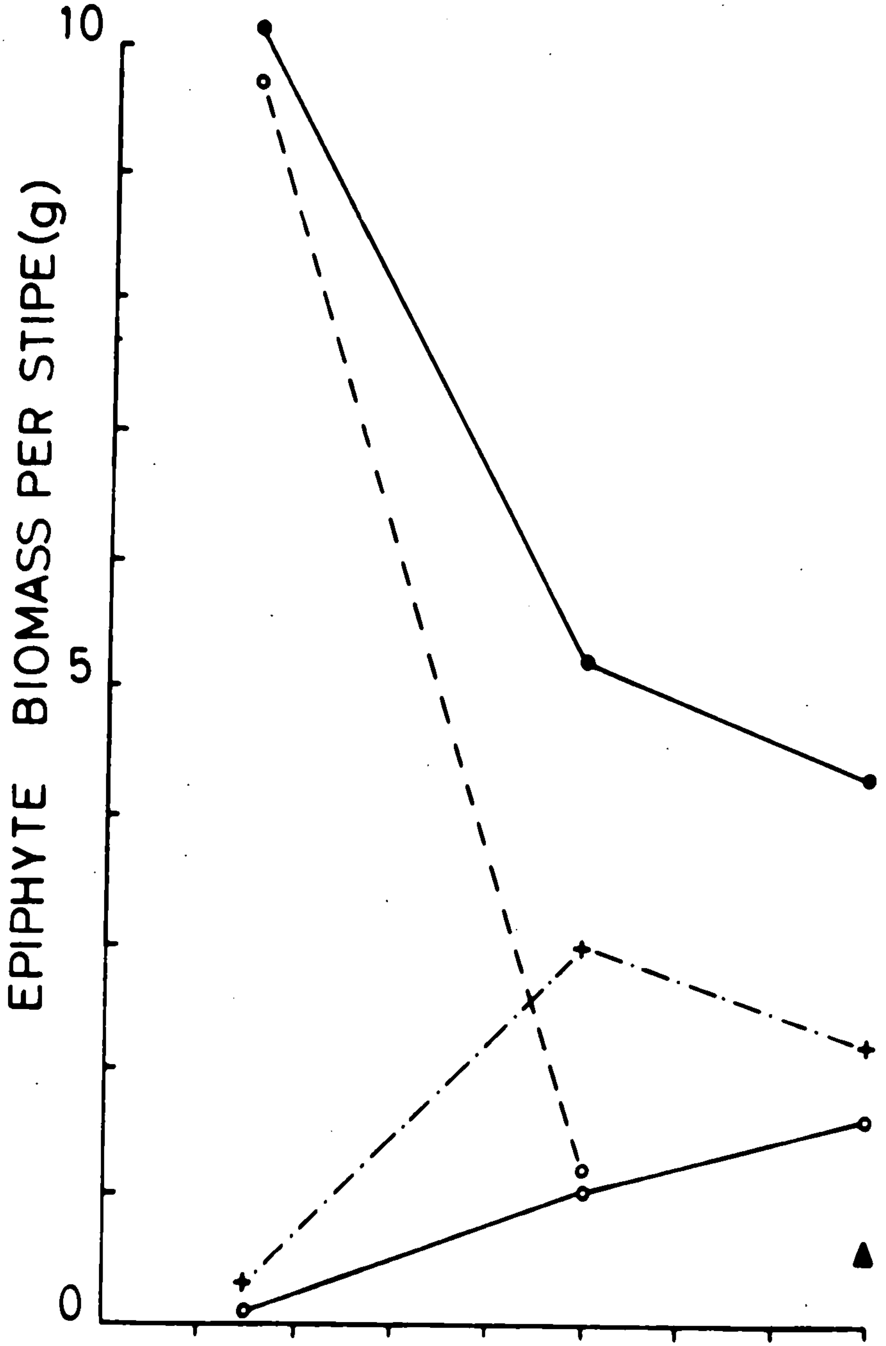

10
5
0
EPIPHYTE BIOMASS PER STIPE (g)
1
2
3
4
5
6
7
8
DEPTH(m)

FIGURE 23

Percentage of total epiphyte biomass at the three depths sampled at Flamborough

Rhodymenia palmata	o----o
Phycodrys rubens	+-·-·-+
Membranoptera alata	o———o

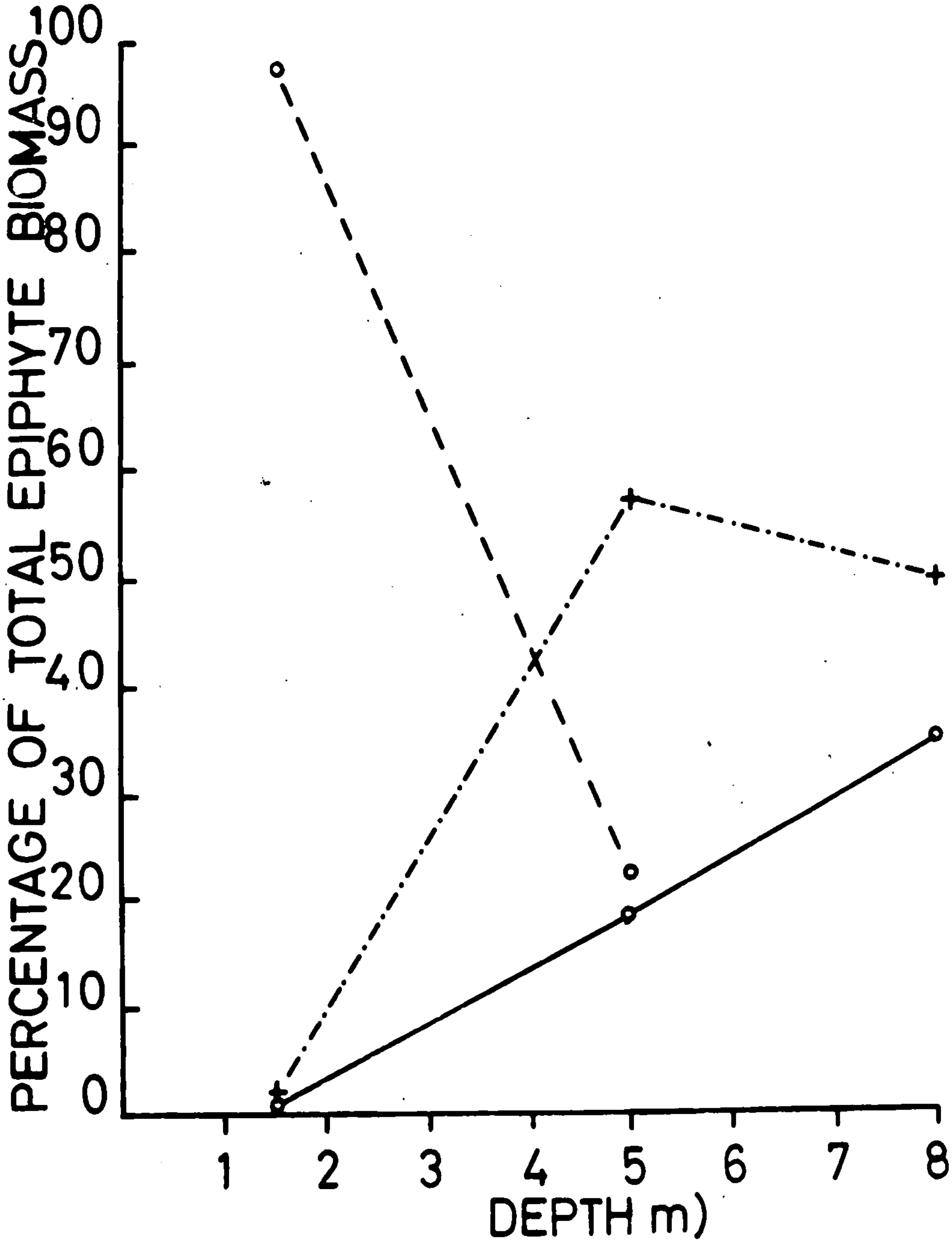

PERCENTAGE OF TOTAL EPIPHYTE BIOMASS
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
DEPTH m)

FIGURE 24

Stipe biomass at four depths sampled at Dunmanus Bay

Depth (m)	
2	●———●
5	▲– – –▲
12	○–·–·–○
18	●·······●

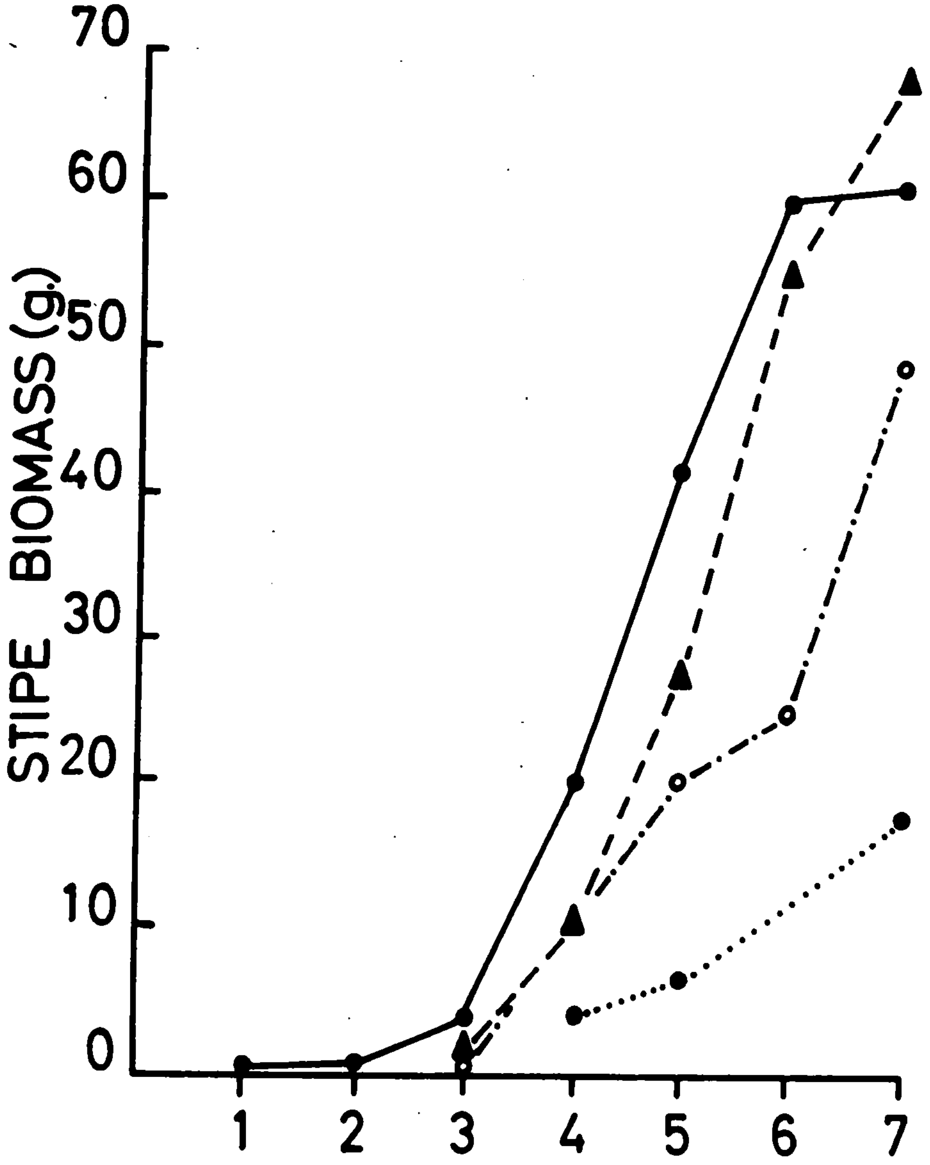

STIPE BIOMASS (g)
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
AGE (years)

FIGURE 25

Stipe length at four depths sampled at Dunmanus Bay.

Depth (m)	
2	●———●
5	▲- - -▲
12	○—·—·—○
18	●·······●

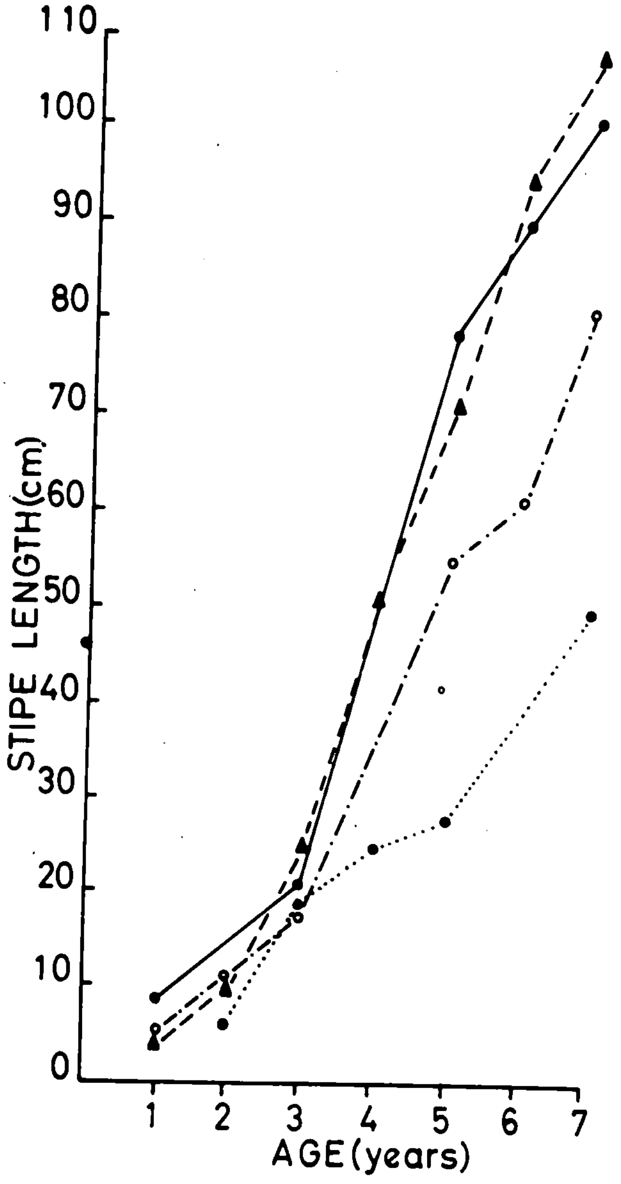

STIPE LENGTH (cm)
110
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
AGE (years)

FIGURE 26

Lamina biomass at the four depth sampled at Dunmanus Bay.

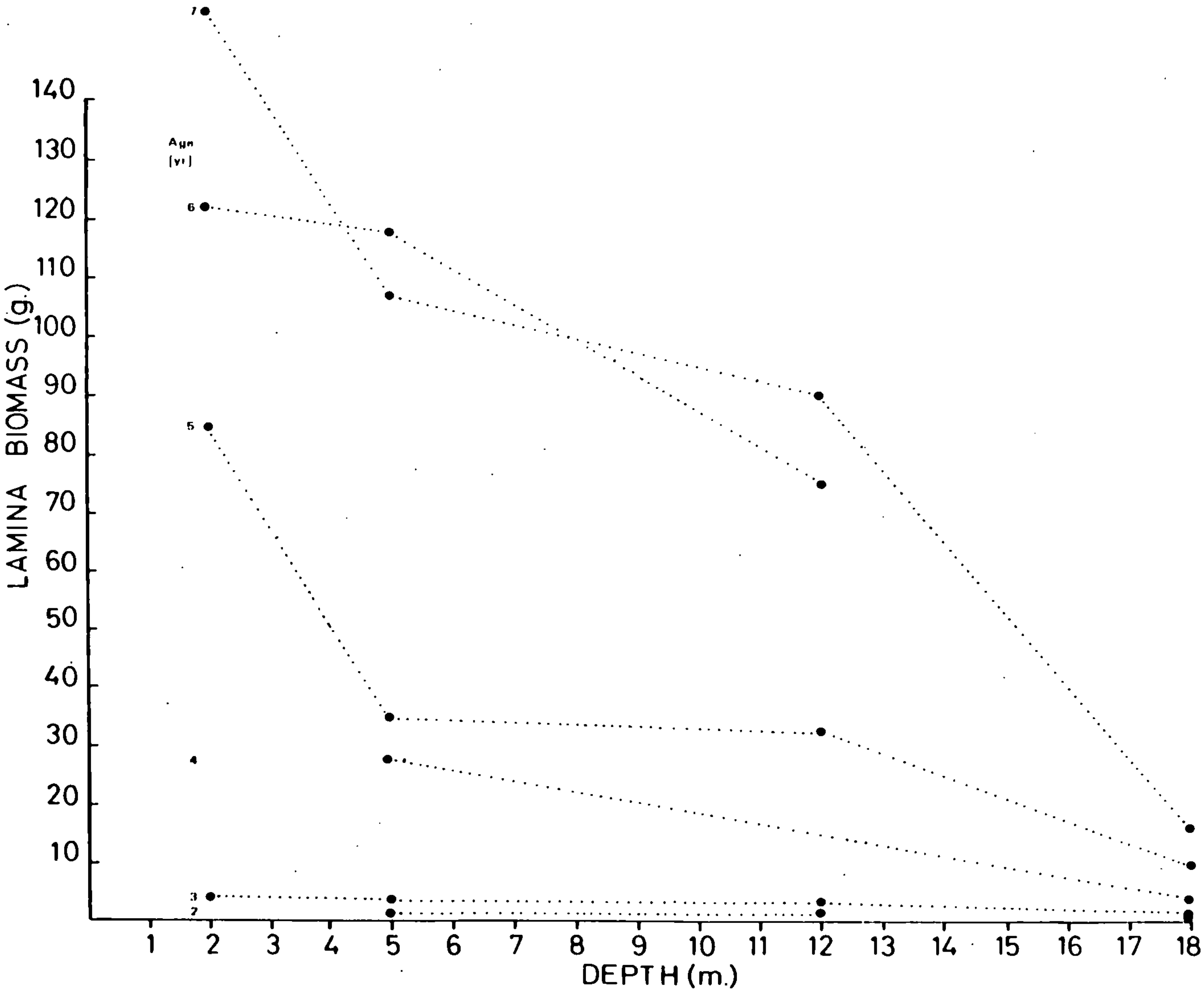
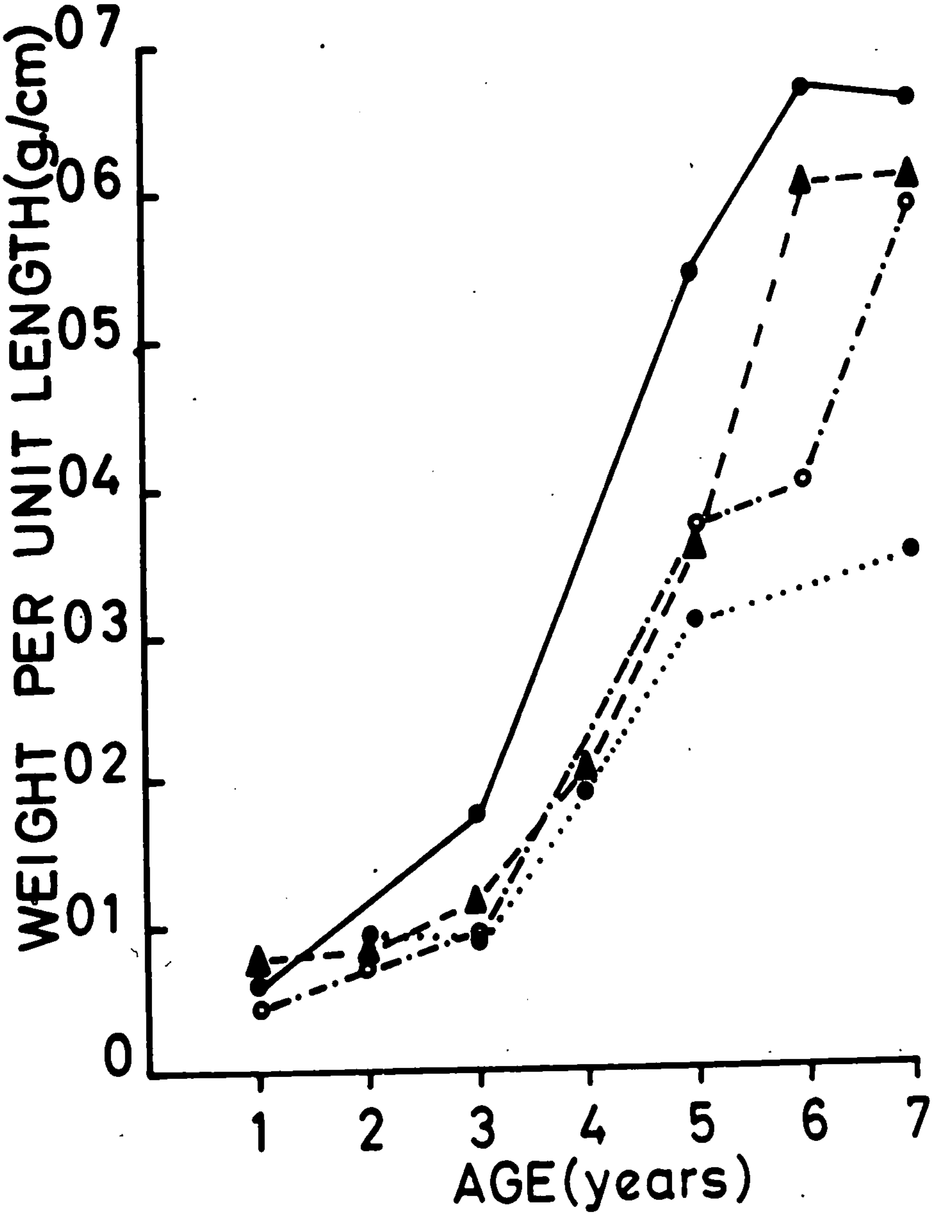

Age (yr)
7
6
5
4
3
2
LAMINA BIOMASS (g.)
140
130
120
110
100
90
80
70
60
50
40
30
20
10
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
DEPTH (m.)

FIGURE 27

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

Depth (m)	
2	●———●
5	▲----▲
12	○-·-·-○
18	●·······●


WEIGHT PER UNIT LENGTH(g/cm)
0
01
02
03
04
05
06
07
1
2
3
4
5
6
7
AGE(years)

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.

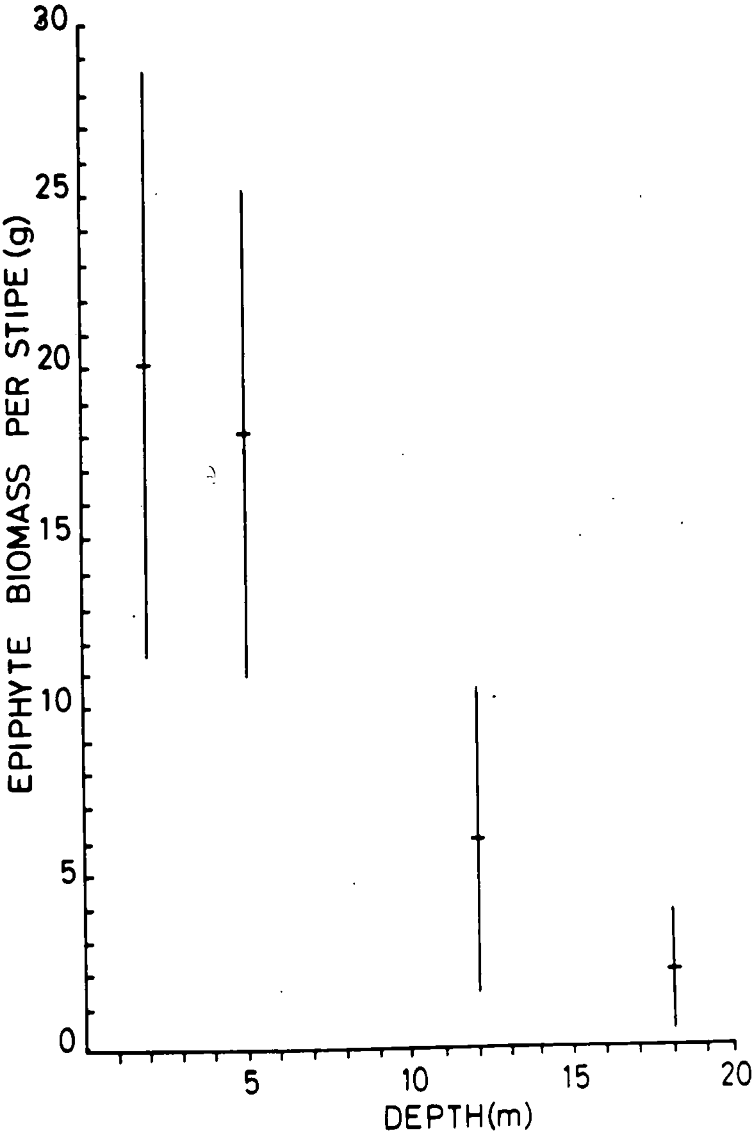

EPIPHYTE BIOMASS PER STIPE (g)
30
25
20
15
10
5
0
5
10
15
20
DEPTH(m)

FIGURE 29

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

Depth (m)	
3	●——●
7	○- - -○
10	▲-·-·-▲
13	●·········●
23	○——○
30	+——+
37	●- - -●

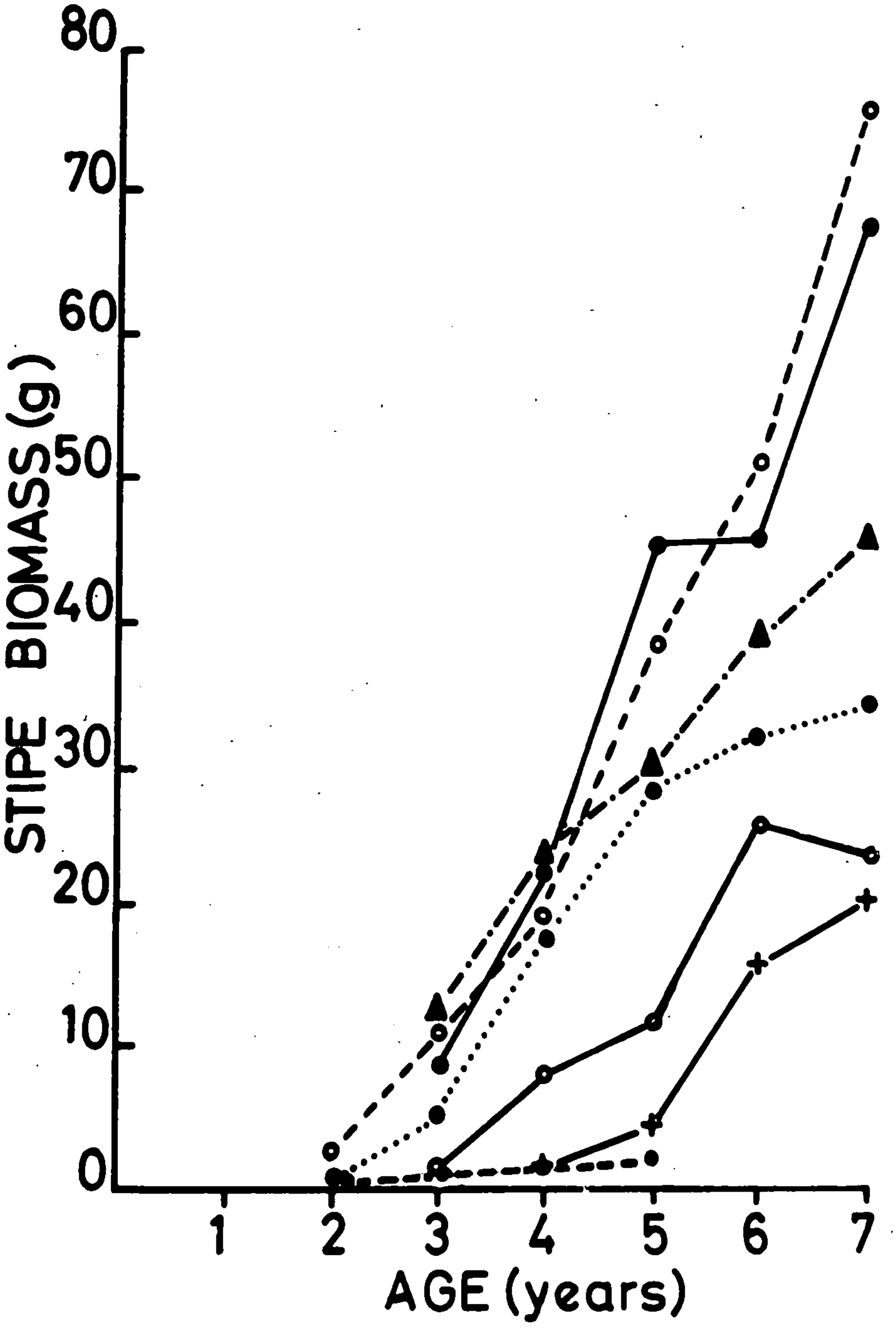

STIPE BIOMASS (g)
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
AGE (years)

FIGURE 30

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

Depth (m)	
3	●——●
7	○– – –○
10	▲–·–·–▲
13	●·······●
23	○——○
30	+——+
37	●– – –●

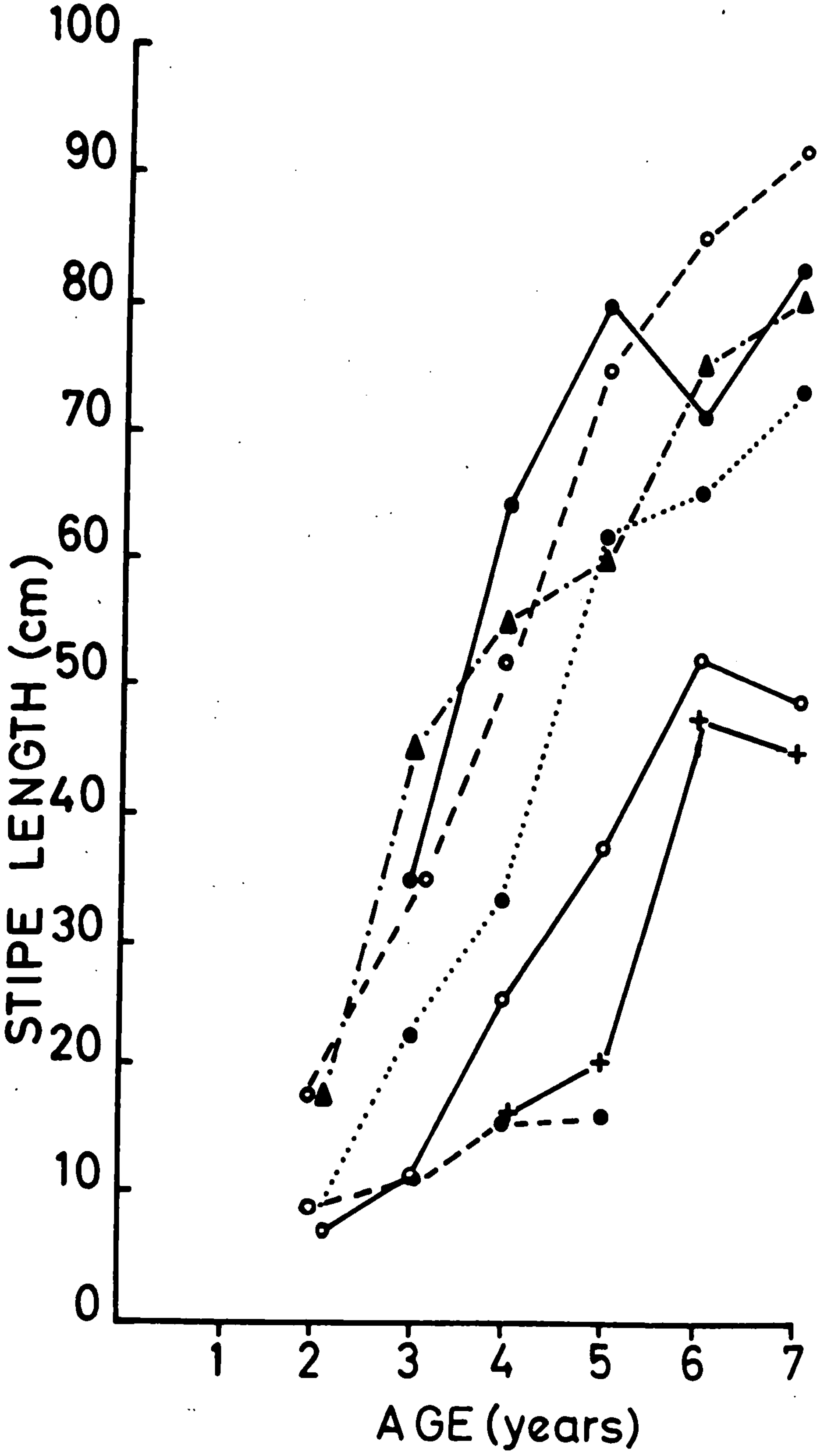

STIPE LENGTH (cm)
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
AGE (years)

FIGURE 31

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

Depth (m)	
3	●———●
7	○- - - -○
10	▲—·—·—▲
13	●·······●
23	○———○
30	+———+
37	●– – –●

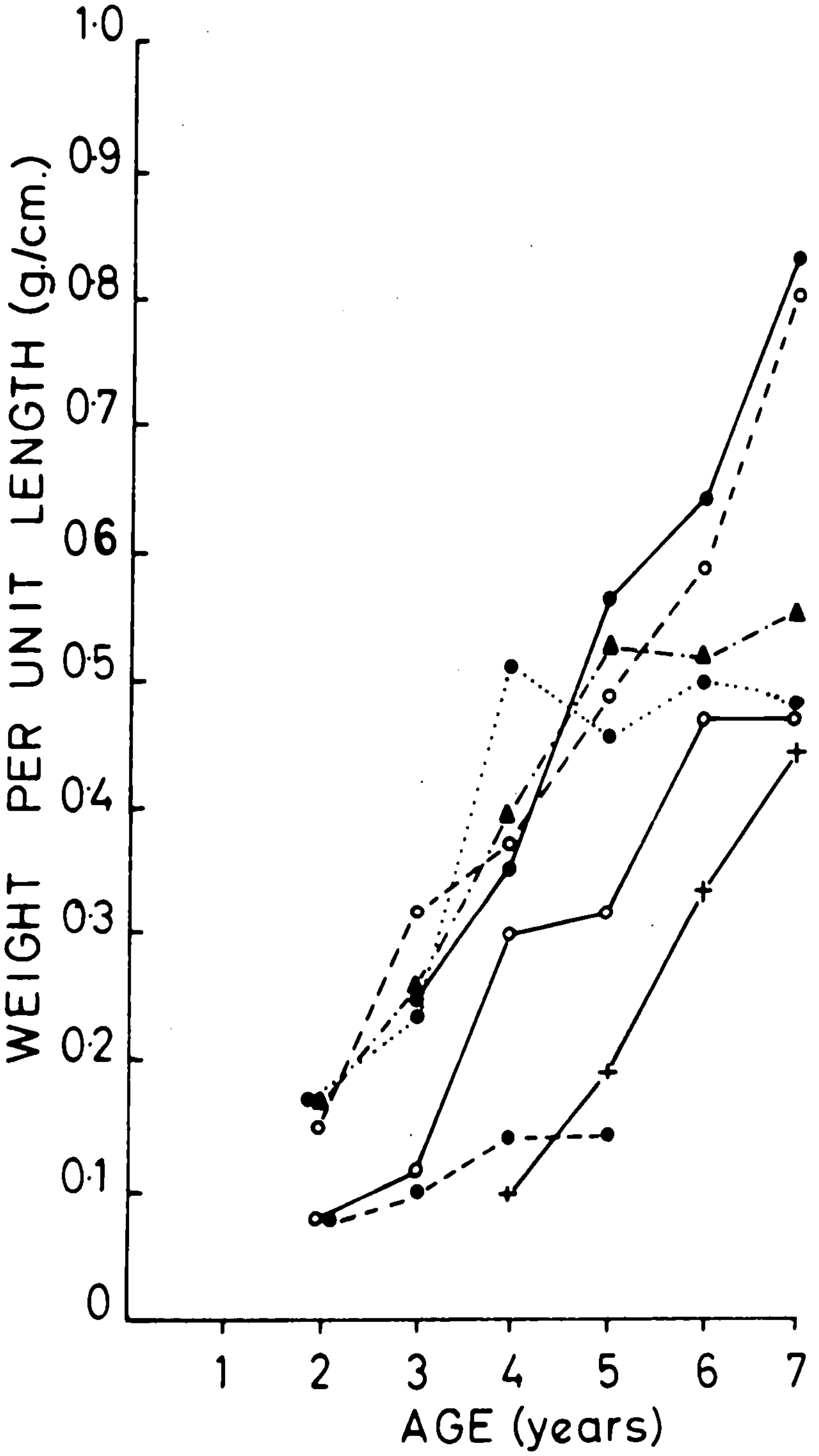
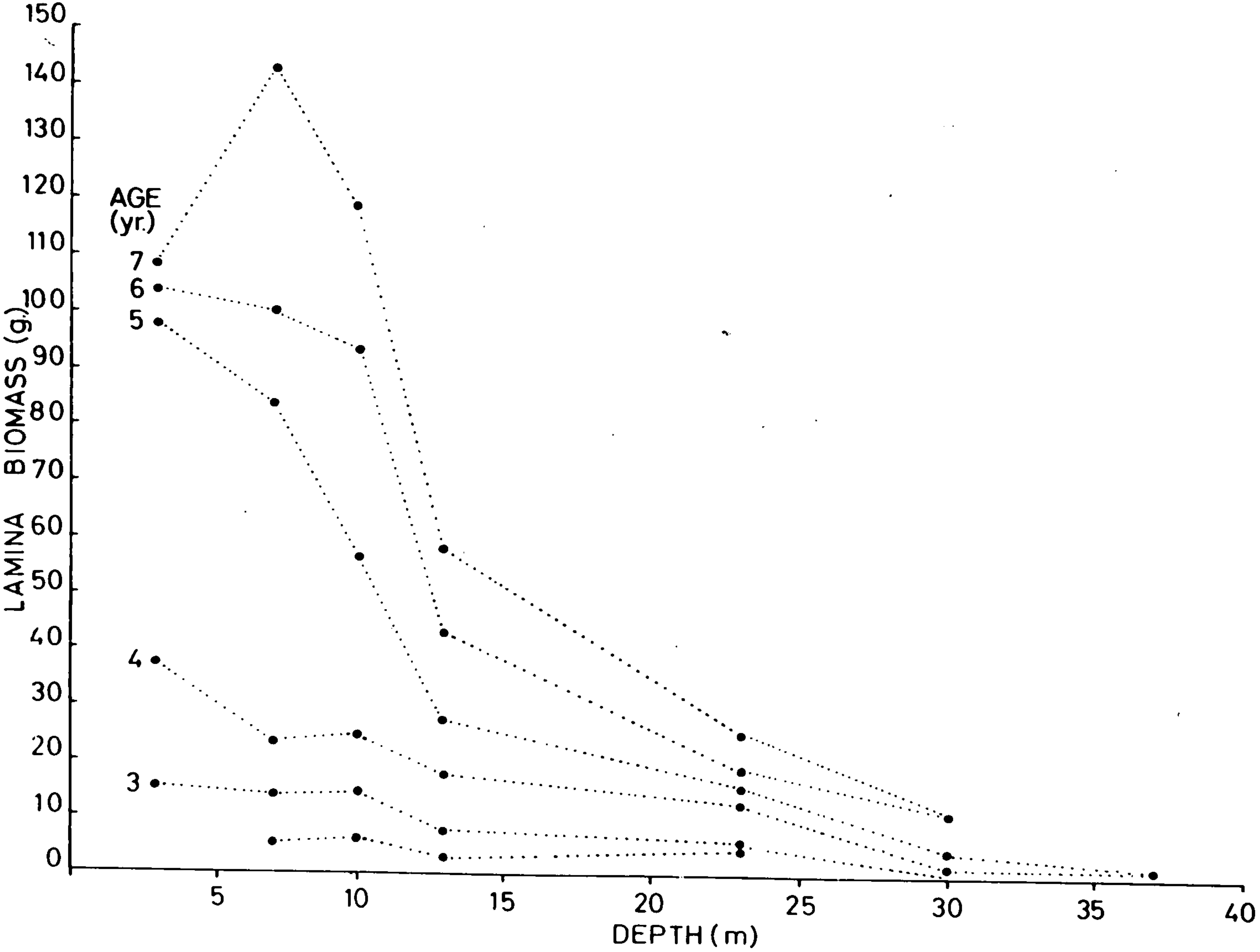

WEIGHT PER UNIT LENGTH (g./cm.)
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
1
2
3
4
5
6
7
AGE (years)

FIGURE 32

Lamina biomass at the seven depths sampled at Sennen Cove.


LAMINA BIOMASS (g)
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
AGE (yr.)
7
6
5
4
3
5
10
15
20
25
30
35
40
DEPTH (m)

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.

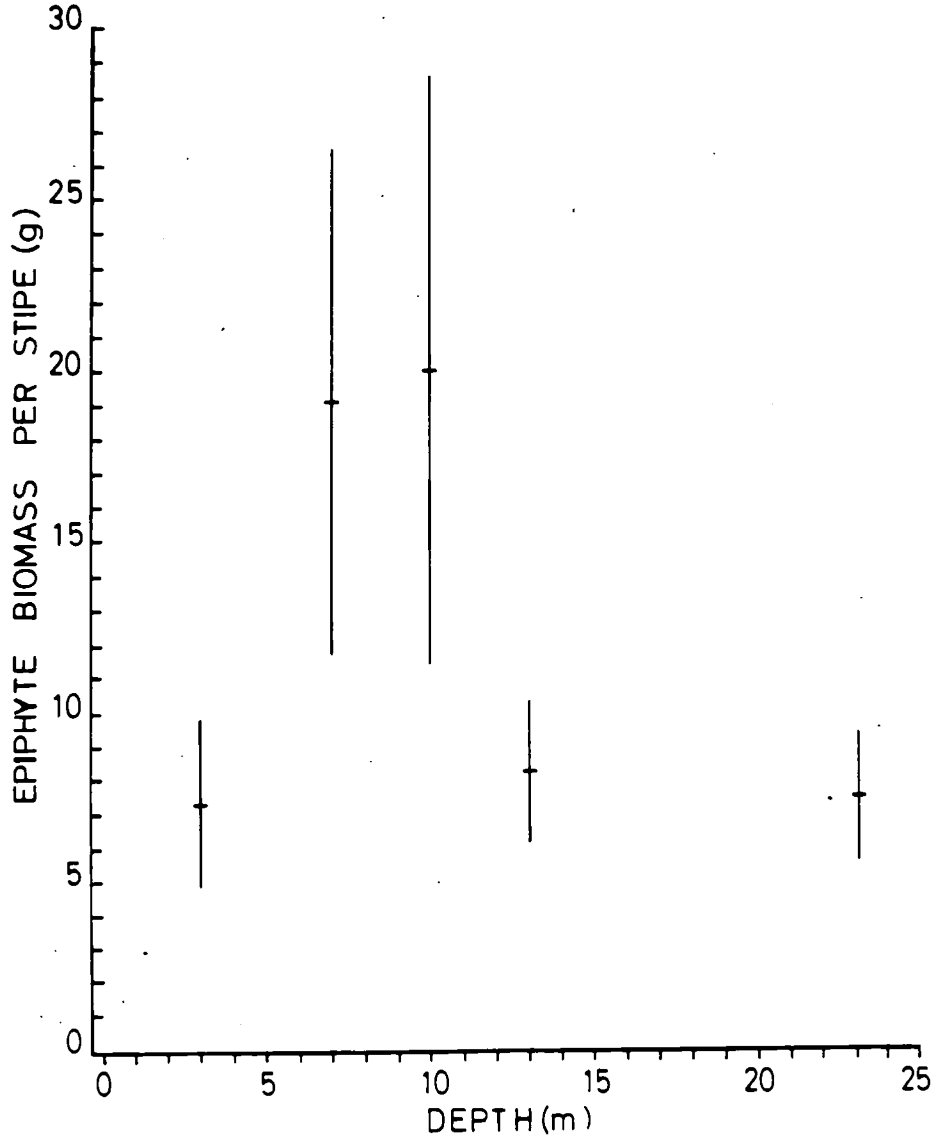

EPIPHYTE BIOMASS PER STIPE (g)
30
25
20
15
10
5
0
0
5
10
15
20
25
DEPTH (m)

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:

$$\int_{0}^{7} w dt$$

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) Laminaria hyperborea 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; Rhodymenia palmata 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°C. This ground dried material was then ashed to constant weight at 440°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

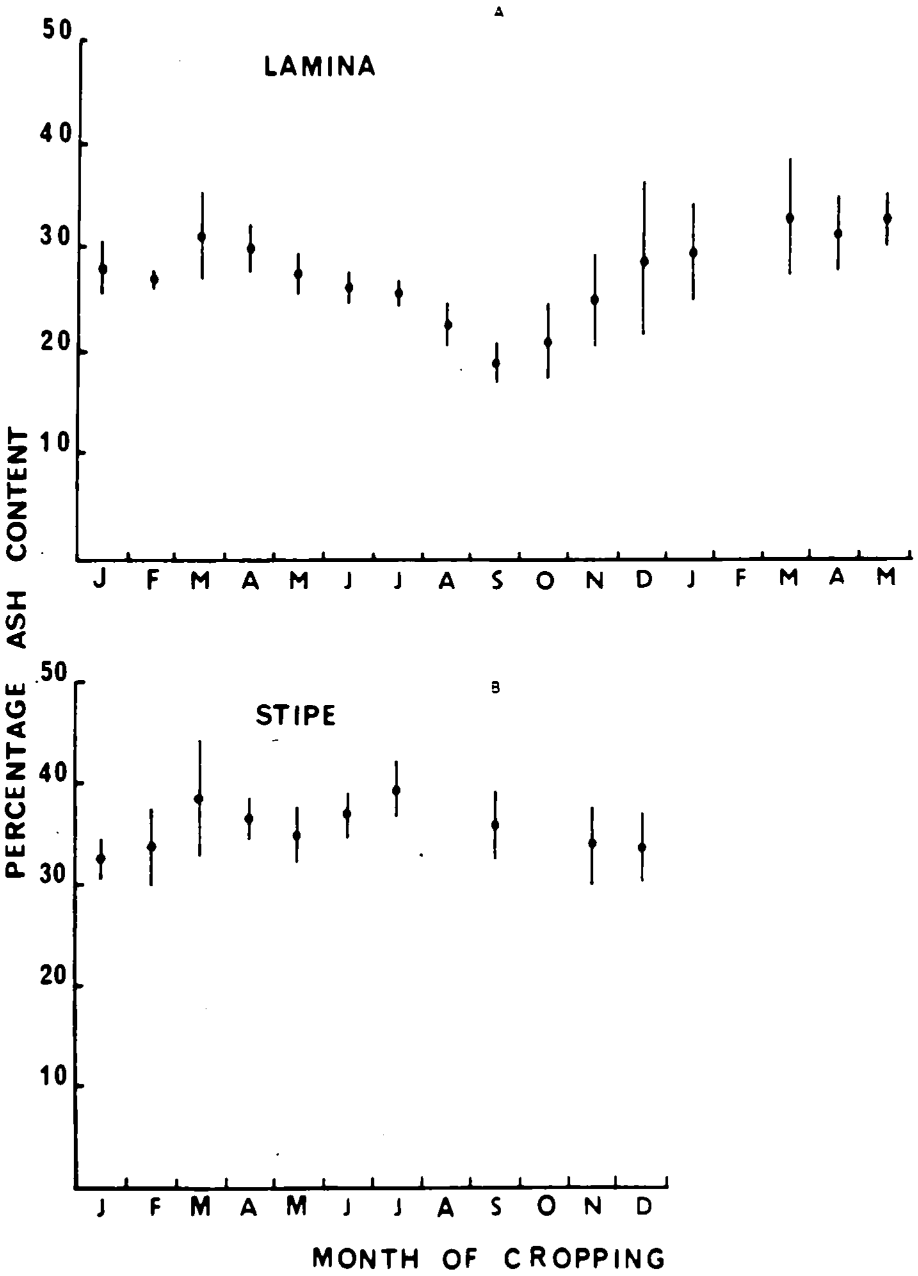
	Lamina	Stipe
Sennen Cove	18.6 ± 3.6	35.4 ± 2.6
Flamborough	17.3 ± 4.3	37.4 ± 4.8
Dunmanus Bay	20.4 ± 2.2	36.6 ± 3.7

FIGURE 34

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

A. Lamina
B. Stipe

AT PETTICOE WICK

A
LAMINA
50
40
30
20
10
PERCENTAGE ASH CONTENT
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
B
STIPE
50
40
30
20
10
J
F
M
A
M
J
J
A
S
O
N
D
MONTH OF CROPPING

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 *Laminaria hyperborea*. Table 11 shows percentage ash content of the epiphytes at five times throughout the years 1968 and 1969, (mean ± standard error).

TABLE 11

	Month				
	April	July	Sept.	Nov.	Jan.
Rhodymenia palmata	27±2.6	31±1.8	32±2.4	25.8	26±3.8
Membranoptera alata	37±4.2	35.9±5.7		45±3.6	34.8±1.5
Ptilotia plumosa	35.9±3.6	35±2	33±7.1	41±6	30±7
Phycodrys rubens	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 o~~f~~r lamina of *Laminaria hyperborea* 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 *Laminaria hyperborea* 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

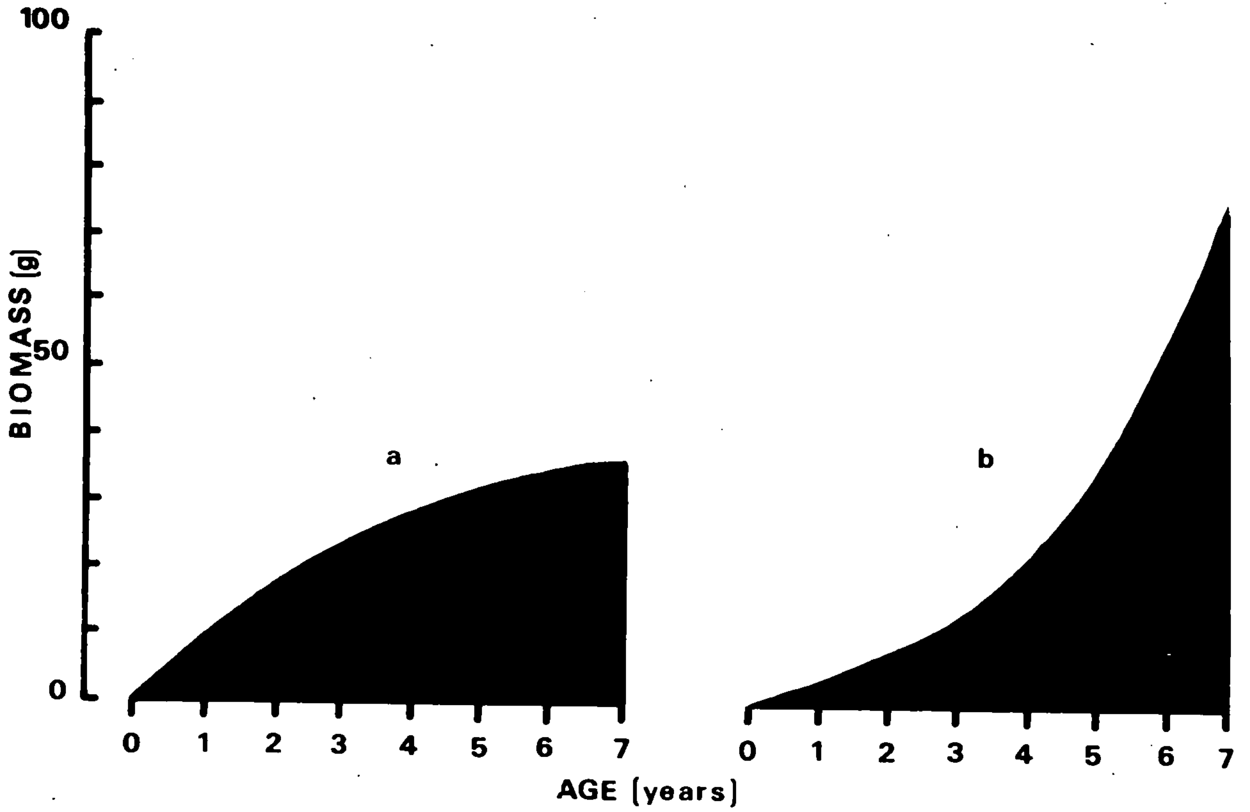
METHODS

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.


100
50
0
BIOMASS [g]
a
b
0
1
2
3
4
5
6
7
0
1
2
3
4
5
6
7
AGE [years]

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 _Laminaria hyperborea_ 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 _Laminaria hyperborea_ 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 _in toto_ 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 <u>Laminaria saccharina</u> 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 etiolation in terrestmal 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 Laminaria hyperborea, with a more rapid decline occurring in deeper water. Not all the component species grow at the same rate; it is very noticeable that Ptilotia plumosa 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 Ptilotia plumosa 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 *Laminaria hyperborea* and *L. digitata* 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 individuals. At the upper limit of growth in the immediate sublittoral competition for space with *Laminaria digitata* 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, *Patina pellucida* and *Echinus esculentus L*. Kain (1963) reported infestation levels of the holdfasts of *Laminaria hyperborea* 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 *Patina* infesting the holdfasts of *Laminaria hyperborea* 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 Echinus esculentus on the lamina of Laminaria hyperborea.

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 Laminaria hyperborea 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 seem 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 <u>Laminaria hyperborea</u> 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 presence 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 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	33	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	06	0			
∞	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	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	∝	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. 37that 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 (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 intersection 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.C.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	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	∞	β
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	623	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	9·1	90	97	73·4	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		
∞	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	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	99	100	95	44	35	50	30

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±13.8	27 ±7.9				
	4	5.3±2.8	39±17.2	57±10.8	90±16.7	46.1 ±20.8	41±54		29.2	
	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	28.4±20.4	
	6	36.3±3.3	76.2±25	110±11	104±16.3	110 ±19.3	76±19.3	63±21.9	56 ±18.3	7.6±14
	7	41.3±14.4	62 ±17.2	102±13.1	106±21.7		36±31	42.2±27.2	56.5±38	
10 m	1				0.45±0.2					
	2	0.8±0.4	1.6±2.8		2.2 ±1.3			2.2±2.0		0.3±0.2
	3	10.8±2.3	10.5±10.2		14.7 ±2.3			4 ±10		
	4	12.8±5.3	18.3± 5.8		46 ±6.2			26.5±6.3		12.1±10
	5	19.9±10.2	35.5± 6.1		75.8 ±7.9			28 ±20.2	26±4.6	
	6	25.4±9.4	54.4±17.2		78.8 ±22			41 ±8.6	41±18.7	
	7		56.6± 7.7		84 ±25			50	38±12.5	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							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	
1 m	4				13±4	20 ± 0	32±15	35 ± 5	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
	1		0.16			0.8		0.75±0.6				
	2	0.99	0.83	1.1			1.5±1.2	6±0.9	3.7	4.3±0.75		1.3±0.68
	3	0.14		2.8	6.4	8.6±1	35±4.5	45±5			19.6±3.7	6.7±0.26
2 m	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	96±16	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	Date of Cropping									
		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
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±0.06					0.2
	2	0.5±0.2	0.61±0.15	0.75±0.2		1.2±0.15					1.3
	3		9.9 ±0.61	10±3	9.5±46		12		7.5	6	5
	4	4.8±1.2	11.9 ±1.0	11±1		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	23.6±6	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	36±4.7	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	40±10.2	60±8	80	78±10.2	64.7±1.4	32±12	8±3
12 m	1										
	2		0.35±						1.4±0.8	1.05±0.4	1.3±0.6
	3		0.35			4.1±1.27	13.6±4.2	13±1.5	6.6±2.7	3.4 ±0.8	3.9±1.2
	4		1.5±0.42			9.4±22	20±7	16±2.5	7.2±3	3.4±0.78	7.6±1.3
	5		4.1±2.7			15.6±3.4	28±6.3	22±4.4	8±4.2	7.0±1.1	7.4±2.8
	6		5.4±0.46			21.0±5.1	29±4.8	17±5		9.1±1.0	5±2
	7		4.4±0.45			32±3.2	36±3	28±8			

TABLE 18

PETTICOE WICK GROWTH OF NEW LAMINA 1969

				Depths		
Date	Age	1 m	2 m	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	

Table 19

PETTICOE WICK MEAN CROPPING DATA AND PRODUCTION FIGURES

Depth	Age	Holdfast		Stipe					Peak Lamina Biomass		Total Biomass		Net Annual Production	
		Biomass	Annual Increment	Biomass	Annual Increment	Length	Annual Increment	Biomass /Unit Length	1967	1968	1967	1968	1967	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±8,5	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	89.9	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	193	194	99	95
12 m	1													
	2	0.8±0.8		0.87±0.42		10 ±1.04		0.08±0.017		1.4±0.8		2.97		
	3	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
	4	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
	5	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		[illegible]

TABLE 20

FLAMBOROUGH MEAN CROPPING DATA AND PRODUCTION FIGURES

		Holdfast		Stipe								
Depth	Age	Biomass	Annual Increment	Biomass	Annual Increment	Length	Annual Increment	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	4.8±1.2		5.1±0.6	4.35	32±2.1	18	0.153	13±3.7		22.9	2
	4	5.4±1.8	0.6	5.7±1.3	0.6	34±4.6	2	0.167	15.3±4.5	16.5	26.4	3
	5	5.6±4.5	0.2	16.4±6.0	10.7	57±10.1	23	0.29	27±8.2	37.9	49	5
	6	13.8±1.8	8.2	22±3.4	3.8	65±6.0	8	0.33	43±8.3	55	78.8	2
	7			25.6±4.2	3.6	71±3.5	6	0.36	58.4±4.7			3
5 m	1											
	2											
	3			3±1.3		25±5.3		0.12	4.2±1.1			3
	4	6.7		7.5±2	4.5	36±4.7	11	0.2	6.3±2.4		20.5	2
	5			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

		Holdfast		Stipe								
Depth	Age	Biomass	Annual Increment	Biomass	Annual Increment	Length	Annual Increment	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	20±8.6
	7	32 ±8	0	60.3 ±9.2	0.7	101±8.7	11	0.6	155±54.7	155.7	247	
5 m	1			0.4±0.1	0.4	4.5±0.7	4.5	0.08	1.2			
	2	0.4		0.8	0.4	10	5.5	0.08	2.2±0.6	3.4	3.4	
	3	1.5±0.5	1.1	2.8±0.4	2.0	25±2.1	15	0.11	4.2	7.3	8.5	
	4	3.7	2.2	10.6±5.3	7.8	52±10	27	0.2	28±10	42.3	42.3	
	5	9.0±3.2	5.3	27±1.6	16.4	72±5	20	0.37	36	57.7	72	
	6	26.2	17.2	57±15	30	95±14	23	0.6	118	165	201	
	7	27.6±9.6	1.4	67±5.6	10	109±9.6	14	0.61	108±11.5	119	202	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		55±7.5		0.38	33.3±3.3		62.1	
	6	15±7	7.2	25±6.4	4.0	62±5	7	0.4	76 ±10.8	82.7	116	6±4.6
	7	24± 13.6	9.0	49±10.4	24	82±3.1	20	0.59	90 ±13.4	123	163	
18 m	1											
	2			0.56±0.24		5.7±2.2		0.09	0.8±0.6			
	3	1.0		1.6 ±0.6	1.04	17±3	11.3	0.09	1.2±0.8		3.8	
	4	1.0		4.8±1.4	3.2	25±3.2	8.0	0.19	42±4		7.0	
	5			6.4±1.3	1.6	27±4.6	2.0	0.31	10±8			2±1.8
	6											
	7	14.4±1.5		18±4.6		50±7	0.36	0.36	17.2±1.8		49.6	

TABLE 22

SENNEN COVE MEAN CROPPING AND PRODUCTION FIGURES

Depth	Age	Holdfast		Stipe									
		Biomass	Annual Increment	Biomass	Annual Increment	Length	Annual Increment	Biomass /Unit Length	Lamina Biomass	Net Annual Production	Total Biomass	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	22±6.2	4.0	46±4	1	71±10.6	-9	0.64	103 ±31	108	171	2	6.3±2.5
	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	141	7	
	6	28±5.5	7	51±2.6	13	86±5	9	0.59	100±38	120	179	7	19.1±7.4
	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	
	6	25±5.7	7	39±14	7	75±14	15	0.52	92±17	106	156	5	20±8.6
	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	
	6	16±10.8	6	33±7	4	66±14	4	0.5	42±17.5	62	101	11	8.3±2.1
	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

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

TABLE 23

EPIPHYTE BIOMASS PER STIPE AS A FUNCTION STIPE AGE

Depth	Age (yrs)	1	2	3	4	5	6	7
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	3.2 ± 1.6	42.5 ± 37	61.5 ± 30	51.9 ± 21
10 m	Ptilotia plumosa				0.3 ± 0.57	2.03 ± 1.5	1.57 ± 3.4	1.34 ± 1.05
	Phycodrys rubens			0.329 ± 0.23	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
	Total				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

FLAMBOROUGH 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 ± 2.8
J	26.1 ± 1.6	37 ± 2.2
A	22.7 ± 2.9	
S	19 ± 1.9	36 ± 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	

BIBLIOGRAPHY

Admiralty Tide Tables (1967, 1968, 1969). European Waters. London: Hydrographic Department, Admiralty.

Ardré, F. (1957). Florule hivernale de La Ria de Vigo *Rev. Alg.N.S.*, *3*, 135-146.

Ardré, F. (1961). Algues du Portugal: Liste preliminaire. *Rev. Gen. Bot.*, *67*, 1-9.

Austin, M.P. and Orloci, L. (1966). Geometric methods in Ecology. An evaluation of some ordination techniques. *J. Ecol.*, *54*, 217-237.

Ballantine, W.J. (1962), A biologically defined exposure scale for comparative description of rocky shores. *Field Studies*, *1*(3), 1-19.

Bannister, P. (1968), An evaluation of some procedures used in simple ordinations. *J. Ecol.*, *56*, 27-34.

Becking, R.W. (1957). The Zurich-Montpelier School of Phytosociology. *Bot. Rev.*, *23*, 411-488.

Bellamy, D.J., Bellamy, S.R., John, D.M. and Whittick, A. (1967a). Some effects of pollution on rooted marine macrophytes on the North East coast of England. *Br. Phycol. Bull.*, *3*, 409.

Bellamy, D.J., Clarke, P.H., John, D.M., Jones, D.J. and Whittick, (1967b). Effects of pollution from the Torrey Canyon on Littoral and Sublittoral Ecosystems. *Nature*, *216*, 1170-1173.

Bellamy, D.J. and Whittick, A. (1968). Problems in the assessment of the effects of pollution on In shore Marine ecosystems dominated by attached macrophytes. *Field Studies.Symp*. Suppl. to Field Studies, 2, 49-54.

Bellamy, D., John, D.M. and Whittick, A. (1968). The "kelp forest ecosystem" as a phytometer in the study of polution of the inshore environment. *Underwater Association Report*. pp. 79-82.

Black, W.A.P. (1948a). Seasonal variation in chemical constitution of some common British Laminariales. *Nature*, *161*, 174.

Black, W.A.P. (1948b). The seasonal variation in chemical constitution of some of the sublittoral seaweeds common to Scotland. Pt. I. *Laminaria cloustoni*; Pt. 2, *Laminaria digitata*; Pt. 3, *Laminaria saccharina* and *Saccorhiza bulbosa*. *J. Soc.Chem. Ind.*, *67*, 165-176.

Black, W.A.P. (1950a). The effect of depth of immersion on the chemical constitution of some of the sublittoral seaweed beds common to Scotland. *J. Soc. Chem. Ind.* *69*, 161-165.

Black, W.A.P. (1950b). Seasonal variation in weight and chemical composition of some of the common British Laminariaceae. *J. mar.biol. Ass. U.K.*, *29*, 45-72.

Black, W.A.P. (1954). Concentration gradients and their significance in *Laminaria saccharina*. *J. mar.biol, Ass. U.K.*, *33*, 49-60.

Black, W.A.P., Richardson, W.D. and Walker, F.T. (1959). Chemical and growth gradients of *Laminaria cloustoni* Edm.(*L.hyperborea* Fosl.) *Econ. Proc. R. Soc. Dublin*, *4*, 137-149.

Blinks, L.R. (1955). Photosynthesis and marine algae. *J. Mar. Res.*, *14*, 363-373.

Borgesen, F. (1905). The algal vegetation of the Faeroese coasts, with remarks on the phyto-geography. *Bot. Faeröes Copenhagen*, *3*, 683-834.

Borgesen, F. and Johsson, H. (1905). The distribution of the marine algae in the Artic Sea and Northern most part of the Atlantic. *Bot. Faeröes Copenhagen*, *3*, 1-28.

Braun-Blanquet, J. (1927). *Pflanzensoziologie*. Springer, Wien.

Braun-Blanquet, J. (1951). *Pflanzensoziologie Grundzuge der vegetation-skunde*, 2 Aufl., S. Wien, Springer.

Bray, J.R. and Curtis, J.T. (1957). An ordination of the Upland forest communities of Southern Wisconsin. *Ecol. Monogr.* *27*, 325-349.

Burrows, E.M. (1958). Sublittoral algal population in Port Erin Bay, Isle of Man. *J. mar.biol.Ass. U.K.* *37*, 687-703.

Chapman, V.J. (1944), Methods of surveying Laminaria beds. J.Mar.Biol.Ass.U.K. 26, 37-60.

Conover, J.T. (1958), Seasonal growth of bethic marine plants as related to environmental factors in an estuary. Inst.Mar.Sci.Univ.Texas, 5, 97-147.

Conway, E.(1967). Aspects of Algal ecology. Br. phycol. Bull., 2, 161-174.

Crawford, R.M.M. and Wishart, D. (1968). A rapid classification and ordination method and its application to vegetation mapping. J.Ecol., 56, 385-404.

Crisp, D.J. and Southward, A.J. (1958). The distribution of intertidal organisms along the coasts of the English Channel. J.mar.biol.Ass.U.K., 37, 157-208.

Dagnelie, P. (1960). Contribution a l'etude des communautes vegetales par l'analyse factorielle. Bull. Serv. Carte phytogeogr. Ser. J., 5, 7-71; 93-195.

de Virelle, A. (1963). Contribution a l'etude de La Flore marine des Iles Anglo Normandes. Rev. Gen. Bot., 824, 1-62.

Den Hartog, C. (1955). A classification system for the epilithic algae communities of the Netherlands coast. Acta Bot. Neerl., 4, 126-135.

Den Hartog, C. (1959). The epilithic algal communities occurring along the coast of the Netherlands. Amsterdam: North Holland Publ. Comp.

Dice, L.R. (1945). Measures of the amount of ecologic association between species. Ecology, 26, 297-302.

Dixon, P.S. (1961). List of marine algae collected in the Channel Islands during the joint meeting of the British Phycological Society and the Societe Phycologique de France. Sept. 1960. Br. phycol. Bull., 11, 71-81.

Ehrke, G. (1929). Die Einwirkung der Temperatur und des Lichtes auf die Atmung und Assimilation der Meeresalgen. Planta, 9, 631-638.

Ernst, J. (1966). Donneses quantitatives au Sujet de La Repartition Verticale des Laminaires sur les Cotes Nord de la Bretagne. *C.R.Acad.Sc. Paris*, t *262*, 2715-2717.

Fallis, A.L. (1915). Growth in some Laminariaceae. *Puget Sound Marine Sta.Pub*., *1*, 137-155.

Forster, G.R.(1958). Underwater observations on the fauna of shallow rocky areas in the neighbourhood of Plymouth. *J.mar.biol.Ass.U.K*., *37*, 473-482.

Gail, F.W.(1918). Some experiments with *Fucus* to determine the factors controlling its vertical distribution. *Publ.Pudget Sd.Mar.(biol). St*., *2*, 287-306.

Gail, F.W.(1922). Photosynthesis in some red and brown algae as related to depth and light. *Publ.Puget Sd.Mar. (biol)St*., *3*, 177-193.

Gislen, T. (1930). Epibioses of the Gullmar Fjord II *Kristinebergs Zoologiska Station, 1877-1927 Uppsala*, *4*, 1-360.

Goodall,D.W.(1954). Objective methods for the classification of vegetation. III An essay in the use of factor analysis. *Aust. J.Bot*., *2*, 304-324.

Graham, A. and Fretter, V. (1947). The life history of *Patina pellucida* L. *J. mar. biol. Ass. U.K*., *26*, 59
601.

Hamel, G. (1931-1939). *Phéophycées de France*. 47, Paris.

Hasegawa, Y. (1962). An ecological study of *Laminaria angustata* Kjellman on the coast of Hikada Prov., Hokkaido. *Bull. Hokkaido. Reg. Fish.Res.Lab*., *24*, 116-138.

Haug, A. and Jensen, A.(1954). Seasonal variation in chemical composition of *Alaria esculenta*, *Laminaria saccharina* *L. hyperborea* and *L. digitata* from the Norwegian coast. *Rep. Norw. Inst. Seaweed Res*. *4*, 1-14.

Holmes, R.W. (1957). Solar radiation, Submarine Daylight and Photosynthesis. *In Treatise on Marine Ecology and Paleoeiology Ecology*. pp.109-128. *Geol. Soc.America, 67*.

Hopkins, B. (1957). The concept of the minimal area *J.Ecol.*, *43*, 564-594.

Jensen, A. and Haugh, A. (1956). Geographical and seasonal variation in the chemical composition of *Laminaria hyperborea* and *Laminaria digitata* from the Norwegian coast. *Rep. Norw.Inst.Seaweed.Res*.*14*,1-8.

Jerlov, N.G.(1951). Optical studies of ocean waters: *Swed: Deep Sea Exped. Reports, Physics and Chemistry*. *3*, 1-59.

John, D.M.(1969). An ecological study of *Laminaria Ochroleuca* *J. mar.biol.Ass. U.K.*, *49*, 175-187.

Johnston, C.S. and Cook, J.P. (1968). A preliminary assessment of the techniques for measuring primary production in macrophytic algae. *Experientia*, *24*, 1176-1177.

Jones, N.S. (1950). Marine bottom communities. *Biol.Rev*., *25*, 283-313.

Jones, N.S. and Kain, J.M. (1967). Subtidal algal colonisation following the removal of *Echinus*. *Helgoländer wiss. Meeresunters.*, *15*, 460-466.

Jones, W.E. (1959). Experiments on some effects of certain environmental factors in *Gracilaria verrucosa* Hudson) Papenfuss. *J.Mar.biol.Ass.U.K.*, *38*, 153-167.

Kain, J.M. (1961). Some sublittoral records. *Br. phycol.Bull*. *2*, 80-86.

Kain, J.M. (1962). Aspects of the biology of *Laminaria hyperborea*:I. Vertical distribution. *J. mar.biol.Ass.U.K*., *42*, 377-385.

Kain, J.M. (1963). Aspects of the biology of *Laminaria hyperborea:* II. Age, weight and length. *J.mar.biol.Ass.U.K.*, *43*, 129-151.

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

Kain, J.M.(1967). Populations of *Laminaria hyperborea* at various latitudes. *Helgoländer wiss Meeresunters*, *15*, 489-499.

Kirejava M. and Schapova, T. (1938). Rates of growth, age and spore-bearing of Laminaria saccharina and L. digitata in Kola Fjord. Trans.Inst.Mar.Fish.Oceanogr U.S.S.R., 7, 29-58.

X Kitching, J.A.(1941). Studies in Sublittoral Ecology III. Biol.Bull.Mar.Biol.Lab. Wood's Hole, 80, 324-337.

X Kitching, T.A., Lilly,S.J., Lodge, S.M., Sloane, J.F., Bassindale, R., and Ebling, F.J. (1952). The ecology of the Lough Ine Rapids with special reference to water currents III. The effect of the current on other environmental conditions. J.Ecol., 40, 179-201.

Klugh, A.B. and Martin, J.R. (1927). The growth rate of certain marine algae in relation to depth of submergence. Ecology, 8, 221-231.

Kornas, J. and Medmecka-Kornas, A. (1948). Podwodne zespoty roslinne zatoki Gdanskiej. Les associations vegetales. Sous marines dan le Golfe du Gdansk (Baltique polonaise). Bull. Int.Ac.Poln.Scet Lettres, 1, 71-88.

Kornas, J. and Medeweka-Kornas, A. (1949). Associations vegetales sous marine dans la Golfe de Gdansk. Vegetatio, 2, 120-128.

Kornas, J. and Medwecka-Kornas, A.(1950). Associations vegetales sous-marine dans le Golfe de Gdansk. Vegetatio, 3, 120-127.

Kornas, J., Panar, E. and Brezski, B. (1960). Studies on sea bottom vegetation in the Bay of Gdansk off Rowa. Fragm.Flor.Grebot., 6, 1-92.

Kulczynski, S. (1927). Die Pflanzenassoziationen der Pieninen. Bull.Intern.Acad.Pol.Sci.Lett.Cl. Sci. Math.Nat. B. (Sci.Nat.)., Suppl. 2, 57-203.

Kylin, H. (1916) Uber den Generationswechsel bei Laminaria digitata. Svensk bot Tidskr., 10, 551-561.

Lapique, D.M. (1919). Variation saisonnière dans la composition chemique des algues marines. C.r.hebd Séanc Acad Sci., Paris, 169, 1426-1428, Larkum, A.W.D., Drew, E.A. and Crossett, R.N. (1967). The vertical distribution of attached marine algae in Malta. J. Ecol., 55, 361-371.

Le Jolis, A. (1855). Examen des espèces confondues sousle nom de Laminaria digitata, Suivi de quelques observations sur le gendre Laminaria. Mém.Soc.Imp.Sci.Nat.Cherbourg, 3, 241-312.

Levring, T. (1947). Submarine daylight and the photosynthesis of Marine algae. Goteborgs Vetensk. Samh. Handl. IV Ser. B., 5:6, 1-89.

Lewis, J.R. (1964). The Ecology of Rocky Shores. English Univ. Press: London.

Lunde, G. (1937). Der meerestang als Rohstaff quelle. Angew. Chem. 50, 731-742.

Luning, K. (1969). Growth of amputated and dark exposed individuals of the brown alga Laminaria hyperborea. Mar. biol., 2, 218-223.

McAllister, H.A., Norton, T.A. and Conway, E. (1967). A preliminary list of sublittoral algae from the West of Scotland. Br.phycol.Bull., 2, 175-184.

McFarland, W.N. and Prescott, J. (1959). Standing crop, chlorophyll content and in Situ Metabolism of a giant kelp community in Southern California. Inst. Mar. Sci. Univ. Texas, 6, 109-132.

Marshall, W. (1960). An underwater study of the epiphytes of Laminaria hyperborea (Gunn).Fosl. Br.phycol.Bull. 2, 18-19.

Miranda, F. (1934). Materiales para une flora de las rias Bajas gallegas. Bol.Soc.Esp.Hist.Nat., 34, 165-180.

Molinier, R. and Picard, J. (1952). Recherches sur les herbiers de Phanerogames marines du littoral Méditerranean francais. Ann.Inst.Oceanogr., 27,157-2

Molinier, R. and Picard, J. (1953). Recherches analytique sur les peuplements littoraux Mediterraneans se developpant sur substrat solide. Rec.Trav. Stat.Mar. d'Endourne, 8, 1-18.

Malone, T.F.(1951). Compendium of meterology: American Meterological Soc., Baltimore, Waverley Press, Inc.

Neushull, M. (1967). Studies on Subtidal Marine vegetation in Western Washington. Ecology, 48, 83-94.

Neushull, M. and Haxo, F.T. (1963). Studies on the giant kelp Macrocystis I. Growth of young plants. Am. J. Bot., 50,349-353.

Newton, L. (1931). A handbook of British seaweeds pp. 478. British Museum (Natural History), London.

North, W.J. (1961). Experimental transplantation of the giant kelp, Macrocystis pyrifera 4th Inst. Seaweed Symp. 248-254.

Norton, T.A.(1968). Underwater observations on the vertical distribution of algae at St. Mary's Isles of Scilly. Br. phycol.Bull., 3, 585-588.

Norton, T.A. and Burrows, E.M. (1969). Studies on marine algae of the British Isles, 7. Saccorhiza polyschide (Light f.) Batt. Br. phycol.J., 4, 18-54.

Norton, T.A., McAllister, H.A., Conway, E. and Irvine, L.M. (1969). The marine algae of the Hebridean Island of Colonsay. Br. phycol.J., 4, 125-136.

Odum, E.P. (1960). Organic production and turnover in field succession. Ecology, 41, 34-49.

Odum, H.T. and Hodkins, C.Y.(1958). Comparative studies on metabolism of marine waters. Inst. Mar.Sci.Univ. Texas, 5, 16-46.

Orloci, L. (1966). Geometric models in ecology. I The Theory and Application of some Ordination Methods. J. Ecol.,54, 193-215.

Title Parke, M. (1948). Studies on British Laminaria saccharina (L) lamour. J.mar.biol.Ass.U.K., 27, 651-709.

Parke, M. and Dixon, P.S. (1968). Check list of British Marine Algae - second revision. J. mar. biol.Ass.U.K 48, 783-832.

Penfound, W.T. (1956). Primary production of vascularaquatic plants. *Limnol Oceanogr*., *1*, 92-101.

Petersen, C.G.J. (1911). Valuation of the sea. I. Animal life of the sea, its food and quantity. *Rep. Danish Biol. Sta.* *20*, 3.

Petersen, C.G.J. (1913). Valuation of the sea. II The animal communities of the sea bottom and their importance for marine zoogeography. *Rep. Danish biol. Sta.*, *21*, 1.

Petersen, C.G.J. (1915). On the animal communities of the sea bottom in the Skagerrak, the Christianiafjord and the Danish Waters. *Rep. Danish biol.Sta*., *23*, 3.

Petersen, C.G.J. (1918). The sea bottom andits production of fish food. *Rep. Danish biol. Sta.*, *25*, 1.

Printz, H. (1939). Uber die Kohlensaureassimilation der Meeresalgen in verschiedenen Tiefen. *Skr. norske Vidensk-Akad., Kl. I*, *1*, 1-101.

Rattray, J. (1886). The distribution of the marine algae of the Firth of Forth. *Trans. Proc.bot.Soc. Edinb.*, *16*, 420-466.

Sargent, M.C. and Lantrip, L.W. (1952). Photosynthesis, Growth and Translocation in Giant Kelp. *Am.J.Bot*., *39*, 99-107.

Seone-Cambra, J. (1960). Communidales algulesde la Ria de Vigo. *Bol. Soc.Esp.Hist.Nat.*, *58*, 371-374.

Seone-Cambra, J. (1966). Las Laminarias de Espana y su distrbution. *Publnes.tec.Junta. Eshid Pesca*, *5*, 425-436.

Sokal, R.R. and Sneath, P.H.A. (1963). Principles of *Numerical Taxomomy*. Freeman.

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to the analyses of the vegetation on Danish commons. *Biol.Skr*., *5*, 1-34.

South, G.R. and Burrows, E.M. (1968). Studies on marine algae of the British Isles. 5. *Chorda filum* (L) Stackh. *Br. phycol.Bull.*, *3*, 379-402.

Steeman-Nielsen, E.(1952). Use of radio-active carbon for measuring organic production in the sea. *J. Cons.Int.Explor.Mer.* *18*, 117-140. [C^{14}]

Sundene, O. (1953). The algal vegetation of Oslofjord *Skrifter Norshe-Vidensk-Ak. Oslo*, *2*, 1-244.

Sundene, O. (1962). Growth in the sea of *Laminaria digitata* sporophytes from culture. *Nytt. Mag.Bot.*, *9*, 5-24.

Sundene, O. (1964). The ecology of *Laminaria digitata*in Norway in view of transplant experiments. *Nytt.Mag.Bot.*, *11*, 83-107.

Svendsen, P. (1968). Regrowth of *Laminaria hyperborea* after harvesting. *Int. Seaweed Symp.*, *6*, (in press).

Sverdrup, H.U., Johnson, M.W. and Fleming, R.H. (1942). *The Oceans: Their physics, chemistry and general biology*: New York, Prentice-Hall, Inc.

Tikhovskaya, Z.P. (1940). Seasonal variations in the productivity and photosynthesis of *Laminaria saccharina* in the Dalne-Zelenetz Bay of the Barents Sea. *C.R.Acad.Sci.U.S.S.R.*, *29*, 120-124.

Tobler, F. (1908). Epiphyten der Laminarien. *Engler.Bot.Jahrb* *44*, 51-90.

Tokida, J. (1960). Marine algae epiphytic on Laminariales plants. *Bull.Fac.Fish.Hokkardo Univ.*, *11*, 73-105.

Trofimov, A.B. (1938). On the seasonal modifications of the iodine and chlorine content in *Laminaria* of the Kola fjord. *Trans.Inst.Fish and Oceanogr.U.S.S.R.*, *7*, 59-67.

Tseng, C.K. Wu,C.Y. and Sun, K.Y. (1957). The effect of temperature on the growth and development of Haitai (*Laminaria japonica*, Aresch.). *Acta. Bot.Sinica*, *6*, 124-130.

Waern, M. (1952). Rocky Shore Algae in the Öregrund Archipelago. Act. Phytogeogr.Suec., 30, 1-298.

Walker, F.T. (1947). Sublittoral seaweed survey. Part I, Development of the View Box - Spring Grab Technique for Sublittoral Weed survey. Part II. Survey of Orkney, Scapa Flow. Part III. Survey of Orkney, Bay of Firth. J. Ecol., 35, 166-185.

Walker, F.T. (1952). Sublittoral seaweed survey: Dunbar to Fast Castle, East Scotland, J.Ecol., 40, 74-83.

Walker, F.T. (1954a). Distribution of Laminariaceae around Scotland. J.Cons.Perm.Int.Explor.Mer., 20, 160-166.

Walker, F.T. (1954b) The laminariaceae off North Shapinsay changes from 1947-1953. Ann.Bot.Lond., 18, 483-494.

Walker, F.T. (1954c). Distribution of the Laminariaceae and their seasonal and cyclic changes around Scotland. Rapp.comm. Int.Bot.Congr., 17, 138-139.

Walker, F.T. (1954d). Distribution of Laminariaceae around Scotland. Nature, 173, 766-768.

Walker, F.T. (1955). A sub-littoral survey of Laminariaceae of little Loch Broom. Trans.Proc.Bot.Soc.Edinb., 36, 305-308

Walker, F.T. (1958a). An ecological study of the Laminariaceae of Ailsa Craig, Holy Island, Inchmarnock, May Island and Seaforth Island. Trans.Proc.Bot.Sci.Edinb., 37, 182-199.

Walker, F.T.(1958b). Some ecological factors conditioning the growth of the laminariaceae around Scotland. Acta Adriat, 8, 3-8.

Walker, F.T. and Richardson, W.D. (1955). An ecological investigation of Laminaria cloustoni Edm. (L. Hyperborea Fosl.) J.Ecol., 43, 26-38.

Walker, F.T. and Richardson, W.D. (1956). The Laminariaceae off North Shapinsay, Orkney Islands; Changes from 1947-1955. J. Mar.Res., 15, 123-133.

Walker F.T. and Richardson, W.D. (1957a). Survey of the Laminariaceae off the Island of Arran; Changes from 1952-1955. J. Ecol.,45, 225-232.

Walker, F.T. and Richardson, W.D. (1957b). Perennial changes of Laminaria cloustoni Edm. on the coasts of Scotland. J. cons. Perm. Int.Explor.Mer., 22, 298-308.

Watt, A.S.(1947). Pattern and process in the plant community. J. Ecol., 35, 1-22.

Westhoff, V. (1951). An analysis of some concepts and terms in vegetation study on phytocenology. Synthese, 8, 1 194-206.

Westlake, D.F. (1963). Comparisons of Plant productivity. Biol. Rev., 38, 385-425.

Whitford, L.A. and Schumacher, G.J. (1961). Effect of current on mineral uptake and respiration by a fresh water alga. Limnol. oceanogr. 6, 423-425.

Whittaker, R.H. (1967) Gradient analysis of vegetation. Biol.Rev., 49, 207-264.

Williams, W.T. and Lambert, J.M. (1959). Multivariate methods in plant ecology. I Association analysis in plant communities. J.Ecol., 47, 83-101.