Studies on littoral and sublittoral ecosystems

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Studies on Littoral and Sublittoral Ecosystems

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CONTENTS

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Abstract

The results of 93 phytosociological descriptions of five types of kelp forest from a number of phytogeographically distinct regions are presented.

Methods are described for the measurement of a complex of meaningful ecosystem parameters which fall into three groups; inidividual performance, ecosystem performance and ecosystem potential.

The results of such measurements in the phytosociologically defined units are presented. The validity of these results and the phytometer approach is discussed and tentative conclusions are drawn from the results regarding the biotic and abiotic components of the ecosystems.

TABLE 1

The locality and site data

Key

Exposure (Lewis 1964)		Substrate	
Very sheltered	A	Continuous rock	X
Moderately sheltered	B	Stable boulders	V
Exposed	C	Unstable boulders	W
Moderately exposed	D		
Very exposed	E		
Current surge	F		

Natural allochthonous material/Pollution		Water turbidity (m.)	
Little	+	0 - 5	0
Moderate	++	6 -15	1
Heavy	+++	16 -30	2
Very heavy	++++	31 +	3

Part I

INTRODUCTION

Introduction

The ultimate limit to the biological production of an ecological system is dependent on, "the total effective solar energy falling annually in the area, by the efficiency with which plants in the ecosystem* are able to transform this energy into organic components, and by those physical factors of the environment which effect the rate of photosynthesis." (Dice, 1952). A knowledge of these overall rates of energy fixation, release and accumulation, are necessary so as to provide a basis for integrating the diverse processes which are concerned in energy flow at all trophic levels in the system (Lindeman, 1942). The "performance" of such a system can be measured as the net rate of production, which is the change in material or energy stored in the system or its parts, this being equal to the rate of income minus the rate of loss. This is in contrast to gross production which is only arrived at after all sources of loss are taken into consideration.

Westlake's review of the literature (Westlake, 1963) indicates that in general, temperature macrophytic communities, including the emergent vegetation of ponds, deltas and coastal marshes and sublittoral seaweed beds, are amongst the most productive natural ecosystems in the world. Their standing crop and primary productivity far exceeding

*"A unit of vegetation considered as such a system includes not only the plants of which it is composed, but the animals habitually associated with them, and also all the physical and chemical components of the immediate environment or habitat which together form a recognisable self-contained entity." (Tansley, 1953).

that of the plankton of the open ocean. However, possibly due to their apparent lack of economic importance, the statement of Blinks (1955) still remains true "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."

During the past 50 years the majority of the studies of the phytobenthes have been purely descriptive and at the best record seasonal occurrence and growth. More recently quantitative studies of the evaluation type have been undertaken in commercially valuable species (MacFarlane, 1952; Hutchinson, 1949; Walker, 1955).

The methods employed, although some appear highly sophisticated (Grenager, 1952, 1954, 1955, 1958a,b; Walker, 1952, 1954a, b,c,d, 1955, 1956a,b, 1958a,b; Baardseth, 1954, 1955, 1958; Walker and Richardson, 1955, 1956, 1957a,b; et al) are extremely crude and produce only very approximate estimates of cropping potential. They all involve the use of grabs and whether random or patterned sampling is used the mean values obtained can at the best be regarded as crude estimates of production for a whole series of algal communities from different depths, substrate type, degree of exposure etc., each of which could be considered as a separate definitive ecosystem.

Knight and Parke (1950) and Sargent and Lantrip (1952) have been more exacting in their studies and have measured changes in standing crop with time but have not followed this development over a complete seasonal cycle of growth.

Kireeva and Schapova (1938), Tikhovskaya (1940), Kuznetzov (1946), Parke (1948a) and Sundene (1962, 1964) have shown the importance of this aspect in their studies in which they measured the seasonal variation in growth rate and in some cases the net production and photosynthesis of the Laminarian species.

The pioneer work of Gislén (1930) using "hard hat" diving techniques, must be regarded as a classic in inshore marine ecology. He attempted a blanket survey in which sociological structure, biomass and seasonal aspects were all studied in respect to substrate type, depth, degree of exposure, etc. His work, together with that of Cornover (1958), McFarland and Prescott (1959), North (1961) and Neushul and Haxo (1963), represent the core of meaningful ecological work in this field. Gislén described and measured attributes of ecosystems which he could see and therefore define. The comparatively recent development of SCUBA diving techniques has made possible more detailed work of this type. SCUBA has "opened up" to the ecologist the inshore marine fringe, with its distinct zonation of environmental conditions and the associated zonation of the various ecosystems. It is this distinct zonation and supposed interrelationships of environment and ecosystem (abiotic and biotic) which promises a fruitful field for work on the environmental control of the structure and the performance of ecosystems and their component species.

This thesis presents the results of a basic study of this type and is as much concerned with technique as with the ecological interpretation of the results. X

The aims of the study were as follows:-

(1) To describe the kelp forest ecosystems over as large a geographical range as possible.

(2) To measure the following ecosystem parameters

(a) Standing crop; total and component,

(b) Net annual production; total and component,

(c) Seasonal growth,

(d) Performance of individual species over distinct environmental gradients such as depth, exposure*, pollution, temperature and so forth.

*Throughout this work this term "exposure" is used as meaning "subject to wave action".

The Ecosystems

The ecosystems selected for study were the kelp forests, these being the most widespread and striking feature of the sub-littoral fringe in North Temperate waters.

The European kelp forests are dominated by one (more rarely co-dominated by two or more) of five species belonging to two genera of the Laminarials namely *Laminaria hyperborea* (Gunn.) Fosl., *Laminaria digitata* (Huds.) Lamour, *Laminaria saccharina* (L.) Lamour, *Laminaria ochroleuca* Pyl. and *Saccorhiza polyschides* (Lightf.) Batt. The general distribution of these species is given below.

Northern forms:	Northward limit	Southward limit	Other limits
Laminaria hyperborea	Arctic Circle	Portugal	Iceland
Laminaria digitata	Arctic Circle	N.W.Spain	N.E. American Continent
Laminaria saccharina	Arctic Circle	Portugal	N.E. and N.W. American Continent
Southern forms:			
Laminaria ochroleuca	S. England	N. Africa	Mediterranean
Saccorhiza polyschides	W. Norway	N. Africa	Mediterranean

The detailed distributions of these species are discussed in Appendix 1 and are based on the accounts of a number of workers including Harvey (1851); Batters (1890); Sauvageau (1897, 1918); Børgesen and Jonsson (1905); De Beauchamp (1907); Børgesen (1905);

Hamel (1928, 1931-1939); Flerov and Karsakoff (1932); Miranda (1934); Feldmann (1934); Lami (1943, 1954); Lunde (1947); Parke (1948b); Dangeard (1949); Spooner (1951); Molinier and Picard (1953); Station Biologique de Roscoff (1954); Fischer-Piette (1955, 1958); Ardré (1957, 1961); Taylor (1957); Ardré et al (1958); Crisp and Southward (1958); Gayral (1958); Huvé (1958); Den Hartog (1959); Jones (1960); Seoane-Camba (1960, 1966); Dixon (1961); Davy de Virville (1963); Zenkevitch (1963); Druehl (1968); Norton (1968) and John (1969).

Extent of the study

The investigation was centred on the British Isles and Fig. 1 shows the localities in which studies were made.

A detailed study was made in the near vicinity of, and within the Ria de Aldan on the Atlantic coast of Spain (Lat. 42°16'-20', Long. 8°49'-52'), in an attempt to gain data for the two most southerly distributed of the species studied, namely *Laminaria ochroleuca* and *Saccorhiza polyschides*. Fig. 2 shows the localities which were studied in North West Spain.

The sites for study in each of the localities were chosen so as to cover as full a range of depth and exposure to direct onshore wave action and current surge as possible. Exposure to direct onshore wave action was estimated in two ways. Firstly, by using the more objective exposure index of Grenager and Baardseth (1966) and secondly, by considering the presence of "indicator" species on the littoral (Lewis, 1964). The two methods were usually used in conjunction.

FIGURE 1

The localities studied in the British Isles

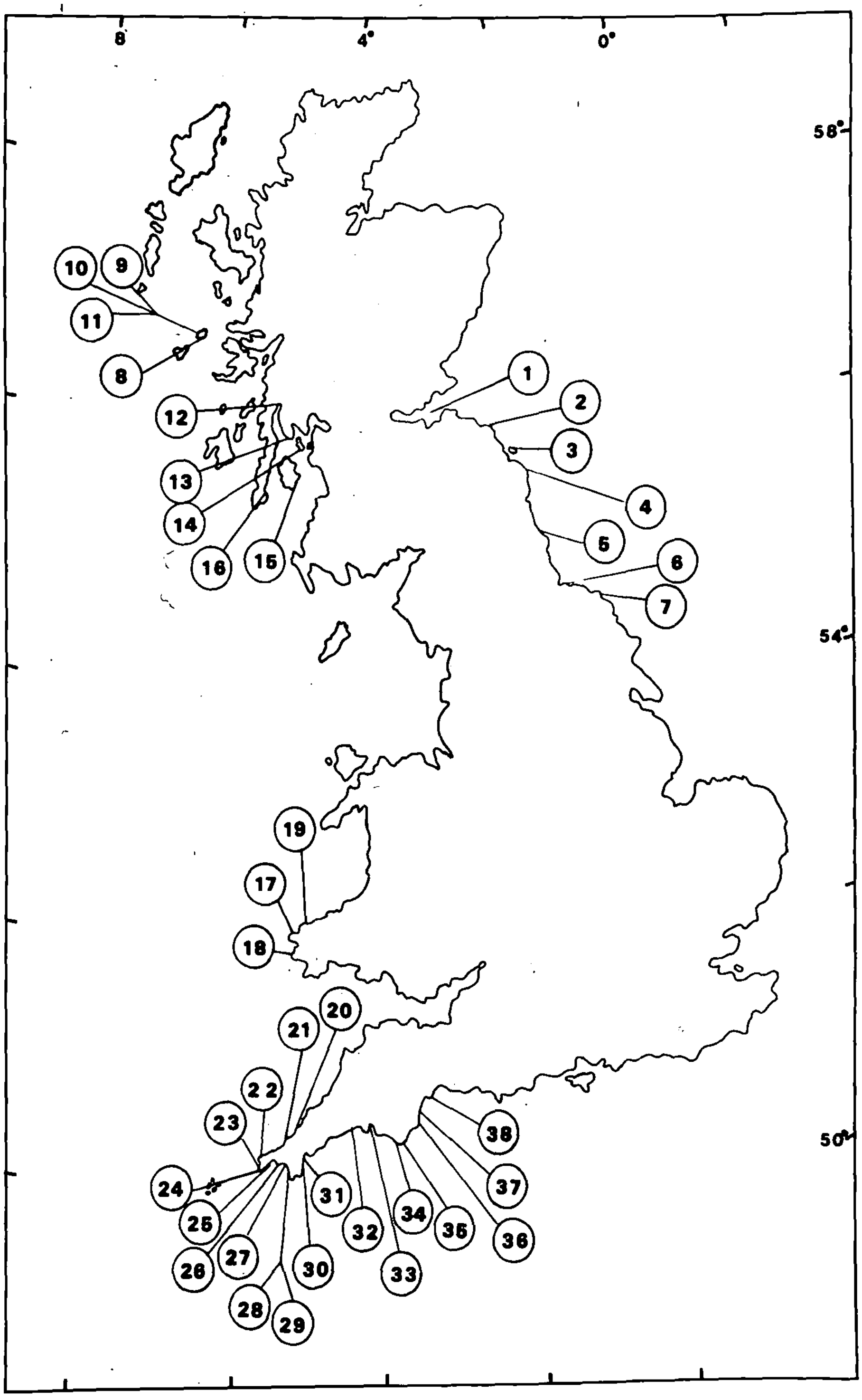
8°
4°
0°
58°
54°
50°
1
2
3
4
5
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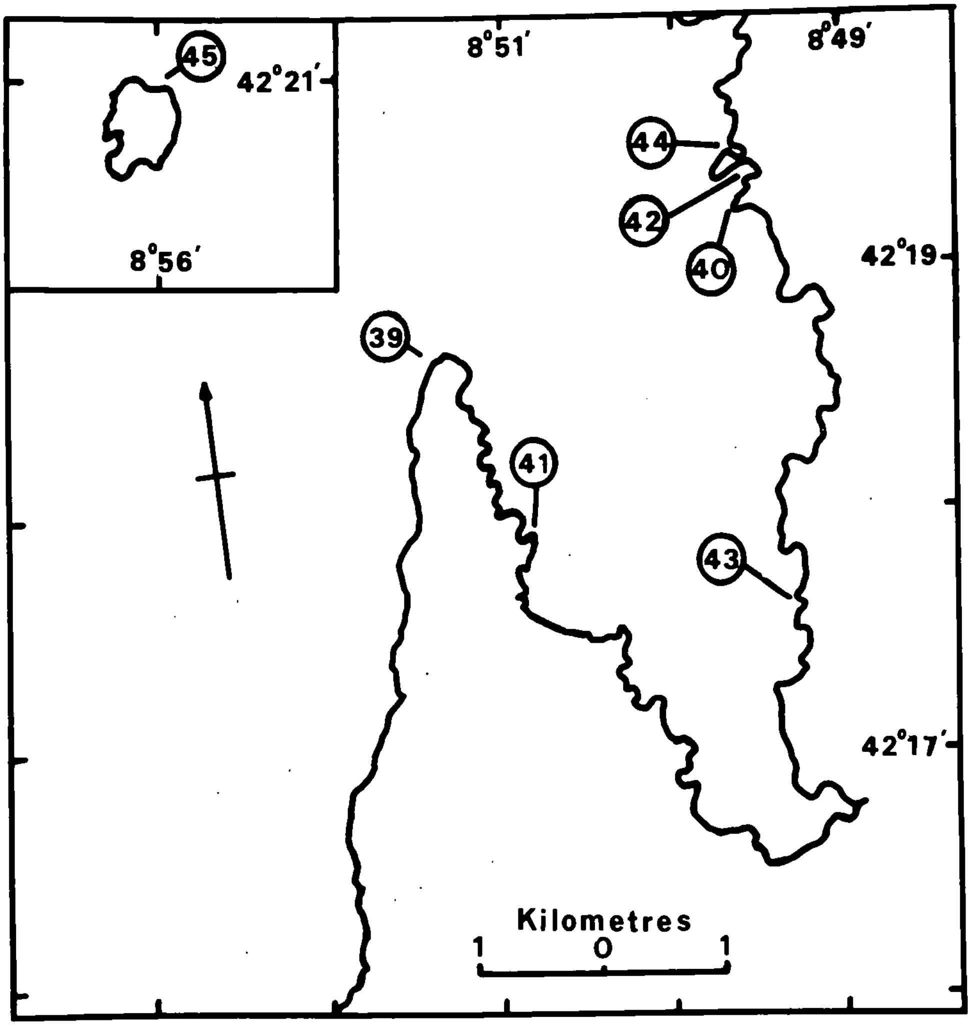
FIGURE 2

The localities studied in North West Spain


45
42°21′
8°56′
8°51′
8°49′
44
42
40
42°19
39
41
43
42°17′
Kilometres
1 0 1

The difficulties entailed in assessing the type and degree of water movement, the sources and the amounts of natural allochthonous material and pollution as well as turbidity are enumerated in Appendix 2.

Table 1 shows the site matrix for each locality together with all the relevant data.

TABLE 1

The locality and site data

Reference Code		Localities and Sites	Lat.	Long.	Grid Reference	Exposure Type	Exposure Scale	Depth ranges of kelp forests (m.-C.D.) Laminaria hyperborea	Laminaria saccharina	Laminaria ochroleuca	Saccorhiza polyschides	Substrate L. hyp.	L. dig.	L. sacc.	L. ochr.	S. polys.	Natural Allochthonous Material	Pollution	Water turbidity
		I NORTH EAST ENGLAND																	
1		Inchkeith	56°02'	3°08'	NT294826	F/A	2	-	0-6.1$^+$	-	-	-	-	IV	-	-	++++	++++	0
2		St. Abb's Head																	
	P	Petico Wick	55°55'	2°09'	NU907692	D	12	1.5-15.2	1.5-15.2	-	-	IV	IV	IVV	-	-	+	+	2
	H	Harbour	55°54'	2°08'	NU920674	F/B	0	2.0-3.1$^+$	3.1$^+$	-	-	IV	IV	IVV	-	-	+	+	2
3	H	Holy Island																	
		Castlehead Rocks	55°41'	1°47'	NU133440	D	17	2.0-6.1$^+$	-	-	-	IV	I	-	-	-	++	++	1
4		Beadnell																	
	L	Lady's Hole (Inlet)	55°33'	1°37'	NU240289	B	0	.5-10.0	2.0-7.6$^+$	-	-	I	I	IVV	-	-	+++	++	1
	P	Lady's Hole (Pool)	55°33'	1°37'	NU240289	B	0	-	MTL	-	-	-	I	IV	-	-	+++	++	1
	S	Lady's Hole (Surge)	55°33'	1°37'	NU240289	F/C	0	-	-	-	-	-	I	-	-	-	+++	++	1
	E	Ebbe's Snook	55°33'	1°37'	NU240289	D	16	2.0-10.7	-	-	-	IV	I	-	-	-	+++	++	1
5	M	Marsden																	
		Byer's Hole	54°58'	1°21'	NZ638412	D	18	1.6-6.0	-	-	-	IV	I	-	-	-	+++	++++	0
6	R	Redcar																	
		Salt Scar	54°38'	1°02'	NZ617264	D	13	1.6-7.2	-	-	-	IV	-	-	-	-	++++	+++	0
7	S	Staithes																	
		Cowbar Nab	54°33'	0°47'	NZ787191	D	18	1.6-7.0	-	-	-	IV	I	-	-	-	+++	++	0
		II INNER HEBRIDES																	
		Island of Coll																	
8		Loch Eatharna	56°37'	6°32'	NM229568	F/A	0	-	0-9.0$^+$	-	-	-	-	I	-	-	++	+	2
9		Coalas Soa	56°34'	7°40'	NM153519	F/C	2	2.0-5.0$^+$	5.0$^+$	-	-	I	I	VV	-	-	+	+	3
10		Island of Soa																	
		Eastside	56°34'	7°39'	NM158513	C	12	2.0-35.0	1.0-36.0	-	-	IV	I	IV	-	-	+	+	3
11		Eilean Iomallach																	
		Westside	56°33'	7°39'	NM156508	E	15	2.0-35.0	4.0-36.0	-	-	IV	I	IV	-	-	+	+	3
		III WEST SCOTLAND																	
12		Inveraray																	
		Strone Point	56°14'	5°04'	NN111088	A	0	-	0-13.0$^+$	-	-	-	IV	IV	-	-	+++	++	1
13		Sgat Mor	55°51'	5°19'	NR930667	F/B	0	2.0-6.0$^+$	2.0-13.0$^+$	-	-	IV	I	IV	-	-	+++	+	1
14		Island of Bute																	
		Rubh'n Amair	55°46'	5°05'	NS031619	E	0	2.0-8.0$^+$	2.0-13.0$^+$	-	-	IV	IV	IV	-	-	+++	+	1
15		Island of Arran																	
		Sannox Bay	55°40'	5°10'	NS020459	C	8	-	0-12.0$^+$	-	-	-	IV	-	-	-	+++	+	2
16		Peninsula of Kintyre																	
		Saddell Bay	55°32'	5°30'	NR797317	D	7	1.5-6.5$^+$	6.5-7.0$^+$	-	-	I	-	VV	-	-	++	+	2
		IV WEST WALES																	
17		Abereiddy																	
	Q	Quarry	51°56'	5°13'	SM795315	A	0	-	0*-5.0(10)	-	-	-	I	IV	-	-	++++	+	1
	E	Entrance	51°56'	5°13'	SM795315	F/B	0	-	0*	-	-	-	I	I	-	-	+++	+	1
18		Martin's Haven	51°44'	5°14'	SM761093	C	4	-	1.8-6.1$^+$	-	-	-	I	VV	-	-	+++	+	1
19		Cardigan Island																	
		Southside	52°08'	4°42'	SN159514	D	10	1.0-12.0	2.0-8.2$^+$	-	-	IV	-	VV	-	-	+++	+	1
		V SOUTH WEST ENGLAND																	
20	P	Porthmeor	50°30'	5°03'	SW847717	D	14	2.0-10.0$^+$	-	-	-	IV	I	-	-	-	++	+	2
21	P	Porthtreath																	
		Gull Rock	50°26'	5°18'	SW648456	F/B	2	1.5-6.0$^+$	1.0-8.0$^+$	-	2.0-8.0$^+$	IV	I	IVV	-	IVV	++	+	2
22	C	Cape Cornwall																	
		Priest's Hole	50°07'	5°41'	SW350316	E	12	2.0-24.0$^+$	-	-	2.0-25.0$^+$	IV	IV	-	-	IVV	+	+	3
23	S	Sennen Cove	50°05'	5°41'	SW349265	F/D	8	2.0-40.0	-	-	2.0-35.0$^+$	IV	I	-	-	IVV	+	+	3
24	L	Lamorna	50°03'	5°33'	SW451240	E	13	2.0-35.0$^+$	-	-	1.0-15.0$^+$	IV	V	-	-	IVV	+	+	3
25	E	Kaskilly	50°05'	5°31'	SW473273	C	8	1.6-13.0$^+$	1.0-13.0$^+$	3.0-13.0$^+$	2.0-13.0$^+$	IV	IV	IVV	IV	IVV	++	++	1
26	H	Hoe Point	50°06'	5°22'	SW573277	E	12	2.0-14.0$^+$	3.0-14.0$^+$	-	-	IV	I	IVV	-	IVV	+	+	3
27	P	Porthleven	50°04'	5°17'	SW627254	C	12	-	-	-	-	-	I	-	-	-	++	++	2
28	P	Porthmellin	50°01'	5°15'	SW667178	C	1	2.0-6.8$^+$	2.0-6.0$^+$	-	2.0-6.0$^+$	IV	I	IVV	-	IVV	++	+	2
29	M	Mullion Island																	
		Westside	50°10'	5°15'	SW659175	E	14	2.0-36.5	-	-	-	IV	I	-	-	-	+	+	3
30	P	Porthallow/Porthkerris	50°03'	5°04'	SW804233	B	9	-	-	2.5-5.0$^+$	-	-	-	-	IV	-	+++	+	1
31		Dennis Head	50°04'	5°05'	SW789255	F/B	6	-	-	2.5-6.0$^+$	-	-	-	-	IV	-	+++	+	1
32	L	West Looe	50°21'	4°27'	SX251518	B	11	1.8-6.0$^+$	-	-	-	IV	-	-	-	-	++	++	1
33		Drake's Island	50°21'	4°09'	SX470529	F/B	0	-	-	0-3.5$^+$	-	-	-	-	IV	-	++++	+++	0
34	H	Hope Cove	50°12'	3°51'	SX674401	C	6	3.0-8.0$^+$	1.8-8.0$^+$	-	-	IV	-	VV	-	-	+++	+	1
35	S	South Sands	50°14'	3°47'	SX730378	B	1	1.6-6.3$^+$	1.6-6.3$^+$	-	-	IV	-	IV	-	-	+++	++	1
36	B	Brixham																	
		Shoalstone Point	50°24'	3°29'	SX936569	E	8	2.0-6.6$^+$	2.0-10.6$^+$	-	-	IV	-	IV	-	-	+++	+++	1
37	C	Saltern Cove	50°22'	3°32'	SX896586	C	6	0-5.1$^+$	-	-	-	IV	-	-	-	-	+++	+++	0
38	A	Torquay																	
		Ansteys Cove	50°28'	3°30'	SX938646	B	6	2.0-6.0$^+$	1.0-6.0$^+$	-	-	IV	-	IV	-	-	+++	+++	1
		VI NORTH WEST SPAIN																	
39	L	Las Osas																	
		Westside	42°18'	8°51'	-	E	25	-	-	9.1-12.2$^+$	1.5-9.1$^+$	-	-	-	IV	I	+	+	3
40	T	Punta Testada	42°19'	8°50'	-	D	14	-	-	6.1-24.4$^+$	0-6.1	-	-	-	IV	IV	+	+	3
41	A	Punta de Alada	42°18'	8°51'	-	C	9	-	-	2.5-9.2$^+$	0-2.5	-	-	-	IV	IV	+	+	3
42	L	Playa de Lago																	
		Inlet	40°19'	8°50'	-	C	4	-	-	2.0-9.2$^+$	0-2.0	-	-	-	IV	IV	+	+	3
43	M	Punta de Menduina	42°17'	8°49'	-	F/B	5	-	-	-	1.0-3.6	-	-	-	-	IV	+	+	3
44		Playa de Lago																	
	L	Lagoon	40°19'	8°50'	-	A	0	-	-	0-4.0	-	-	-	-	IV	-	+	+	2
	C	Channels	40°19'	8°50'	-	F/C	0	-	-	-	0-4.0	-	-	-	-	I	++	+	2
45	I	Isla Onza																	
		Punta Cocinadoiro	42°21'	8°56'	-	F/C	10	-	-	8.6$^+$	0-8.6	-	-	-	IV	IV	+	+	3

*Quarry low water

The Description of the Kelp Forests

Laminaria hyperborea

This kelp forest is found on stable boulders and continuous rock surfaces in exposed and semi-exposed situations being usually absent where there are conditions of low salinity.

The lower limit of its depth distribution is dependent on geographical as well as local environmental conditions. The lower limit of its vertical distribution is much greater in regions or localities where the water is comparatively clear, viz. 36.0 m. at Soa and Eilean Iomallach (Inner Hebrides), 40.0 m. Mullion Island and Sennen Cove (South West England) and 15.2 m. St. Abb's Head (South East Scotland), whilst it is much reduced where the turbidity of the water is high due to chronic pollution and/or a high proportion of allochthonous material in suspension, viz. pollution; 6.0 m. Byer's Hole, 7.2 m. Salt Scar (North East England), allochthonous material 10.7 m. Beadnell (North East England), 8.2 m. Cardigan Island (West Wales). This kelp forest is usually relatively dense in shallow water and tends to open out with increase in depth into what Kitching (1941) has referred to as the "park" area.

Typically this kelp forest consists of a crustaceous layer, a ground layer, an epiphyte layer and a layer consisting of the dominant. The layer of the dominant may be divided into a canopy, an understorey of maturing individuals and a ground layer of sporelings. The microscopic gametophyte generation can be detected by direct observation or culturing samples of the substrate in the laboratory.

One of the most striking features of this type of kelp forest is the abundance of the epiphytic algae. These are especially abundant on the stipes and haptera of older individuals, a fact which has been associated with the scabrous surfaces of these organs.

The morphology of the stipe is influenced by certain factors in the environment. It has been found in this study that there is a decrease in the thickness of the stipe with increase in depth and exposure, this phenomenon being unrelated to the level of stipe production. only in part.

Laminaria digitata

This kelp forest is found in very sheltered and moderately exposed situations on stable boulders or continuous rock surfaces. In very exposed situations it is often replaced by *Alaria esculenta*. This kelp forest ecosystem in the British Isles usually forms a relatively narrow zone on the lower littoral and immediate sublittoral and yet in other parts of its geographical range it may form extensive forests in the sublittoral.

It has a wide range of tolerance to changes in salinity and so occurs in the upper reaches of the Scottish sea-lochs and the Norwegian Fjords. The extent of its penetration in such areas is not always governed by salinity but by the high summer water temperature (Sundene, 1964).

This kelp forest has a similar structure to that dominated by *Laminaria hyperborea* except that the epiphyte layer is not nearly so well developed.

The morphology of the lamina in this species has been shown by Sundene (1962, 1964) to be influenced by the degree of water movement. The form and breadth of the lamina could therefore be used as an indication of the degree and type of water movement to which an ecosystem is subjected, viz. broad, undivided, crisp and easily damaged laminae - very sheltered (Abereiddy Quarry in West Wales); narrow, digitate, tough and leathery laminae - very exposed (Eilean Iomalloch in the Inner Hebrides). It is possible with experience to differentiate between the current and the previous seasons' laminae; usually the old one is gradually eroded away only to be finally lost from May to July. It was found in this study that the morphology of the stipe is effected by the degree of exposure. The thickness of the stipe appears to be governed by the degree of water movement as well as the actual level of production so that, under very exposed conditions, the stipe is relatively thin.

Laminaria saccharina

The kelp forest is best developed on unstable substrates in sheltered or moderately exposed situations. Loose lying and relatively open populations attached to sand grains or small pebbles are only found in very sheltered situations, viz. in deep water at the entrance and also in relatively shallow water in the upper reaches of Loch Fyne (West Scotland). This species dominates the kelp forests on stable surfaces only in either very sheltered situations in shallow water (Abereiddy Quarry in West Wales) or in ones which are sheltered due to depth, viz. 14.0 m. at Petico Wick in South East Scotland, or where the salinity is low (Strone Point in Loch Fyne). Its success on stable surfaces in these localities might be partly the result of the absence of competition from Laminaria hyperborea.

The habitat conditions in which it is usually found together with its comparatively short life-span (3 years) means that this kelp forest has a relatively simple structure with no obvious layers. The morphology of the lamina is governed by its rate of growth (Parke, 1948) whilst it was found that the thickness of the stipe is usually dependent soley on its level of production. The previous season's lamina is easily recognised from the current one and it was found that it is lost from May to September depending on the exposure of a particular locality to water movement.

Laminaria ochroleuca

This kelp forest is found on stable boulders and continuous rock surfaces and has the same depth range as that dominated by Laminaria hyperborea. It is usually found only as a mixed forest on the northern edge of its geographical range in South West England. A depression of the upper limit of its bathymetric range was found to occur in North West Spain (in response to exposure to wave action). In very sheltered localities it extends onto the lower littoral (lagoon at the Playa de Lago), whilst it only occurs in excess of 9.1 m. in very exposed situations (Las Osas). A similar phenomenon is also found on the South West peninsula of England and has been noted in the Scilly Islands (Norton, 1968). This forest has a similar structure to that dominated by Laminaria hyperborea except for the almost complete lack of an epiphyte layer, a fact which may be related to the smooth and mucilagenous nature of its stipe and hapteron.

Saccorhiza polyschides

In North West Spain it usually forms a very distinctive zone above the kelp forest dominated by Laminaria ochroleuca. The zone of transition between these two distinct kelp forests becomes deeper as exposure to water movement increases. It may form extensive forests in certain situation where there is considerable current surge (entrance to Lagoon at the Playa de Lago).

The extensive sublittoral forests in this region, in which it is often the sole dominant, lend themselves admirably for the study of plot performance. There is much evidence to suggest that these kelp forests are largely annual (Phillips, 1896; Sauvageau, 1918; Spence, 1918; Norton, 1967) and so peak biomass can be equated with net annual production. The lamina of this species shows a marked degree of morphological plasticity in response to the physical effects of water movement. The morphology of the lamina can therefore be used as an indication of the degree and type of water movement to which an ecosystem is subjected, viz. broad, flimsy, curved and non-digitate laminae - Punta de Alada (moderately sheltered); long, tough, flat and very digitate - entrance to lagoon at the Playa de Lago (current surge); short, tough, flat and few digitations - Las Osas (very exposed).

Part 2

PHYTOSOCIOLOGY

Introduction

Throughout this study the methods of the Zurich-Montpellier School of phytosociology were used and are discussed in Appendix 3 The ninety three unit descriptions or aufnahmen were made and sorted using the methods of this School. The results are shown in the form of association tables (Tables 5-9 in Appendix 4) and are summarised as a table of presence (Table 2) in the main text.

It must be emphasised that even if all the previous published phytosociological descriptions of marine ecosystems are taken into consideration only very tentative conclusions could be drawn regarding the rank of the defined phytosociological units and the validity of the characteristic and differential species. Much more descriptive work is needed and the following discussion and conclusions are only of temporary importance. However as phytosociology is a synthetic discipline they can be regarded as foundations for future field work. The units delimited in this study can be looked for in the field and their validity tested in more comprehensive tables.

All the ecosystems described can be included in the Alliance *Laminarion*.

The character species of this Alliance are shown in Table 3 of these *Delesseria sanguinea* and *Phycodrys rubens* may be found as components of littoral tide pool communities and therefore are of doubtful use as character species at the Alliance level. Also many of the Alliance character species have low constancy in ecosystems dominated by *Laminaria digitata*. Presumably this fact can be explained

TABLE 2

Table of presence (III - V)

Number of Aufnahmen	41	20	5	12	15
Character species of association					
A Laminaria hyperborea	V	II	I	-	IV
Differentials of subassociation Typicum					
Polysiphonia brodiaei	IV	I	I	-	-
Ptilota plumosa	IV	-	-	-	-
Differentials of subassociation Desmarestrietosum					
A Giffordia hincksiae	IV	III	III	-	V
Asparagopsis armata (tetra.)	III	IV	-	II	III
Polyneura hilliae	III	I	-	III	III
A Desmarestria ligulata	III	III	-	I	III
Phyllophora brodiaei	III	-	-	II	II
Character species of association					
A Laminaria digitata	I	V	I	-	II
Differentials of subassociation Asparagopsietosum					
A Cryptopleura ramosa	II	III	III	II	III
Halurus equisetifolius	II	III	-	-	I
Mesophyllum lichenoides	I	III	-	II	-
Rhodochorton purpureum	I	III	-	-	-
Character species of association					
A Laminaria saccharina	III	I	V	II	II
Character species of association					
A Laminaria ochroleuca	I	-	-	V	II
Differentials of subassociation Cystoseiretosum					
A Cystoseira foeniculacea	I	I	I	V	I
A Cystoseira tamariscifolia	-	-	-	II	-
A Dilsea carnosa	IV	II	I	III	II
Plocamium vulgare	IV	I	V	II	-
Ulva lactuca	I	III	IV	II	II
Character species of association					
A Saccorhiza polyschides	IV	III	III	-	V
Differentials of subassociation Typicum					
Pterosiphonia complanata	-	-	-	III	V
Gelidium sesquipedale	-	-	-	II	IV
Codium tomentosum	-	I	-	II	IV
Differentials of subassociation Alarietosum					
Membranoptera alata	IV	II	-	-	IV
A Callophyllis laciniata	IV	I	I	V	III
Lithophyllum pustulatum	III	II	III	-	III
Cladostephus verticillatus	II	I	III	-	III
A Desmarestria aculeata	I	-	I	II	III
Himanthalia elongata	II	-	-	II	III
A Phycodrys rubens	IV	-	-	-	III
Alaria esculenta	-	III	I	-	III
Nitophyllum punctatum	I	I	I	-	III
Lomentaria articulata	II	I	-	-	III
Hypoglossum woodwardii	I	II	-	-	III
Polysiphonia urceolata	-	I	-	-	III
A Character species of alliance Laminarion					
Dictyota dichotoma	III	[illegible]	IV	III	III
Delesseria sanguinea	V	II	I	-	II
Dictyopteris membranacea	I	-	I	III	-
Ptilothamnion pluma	II	-	-	I	I
Odonthalia dentata	II	-	-	-	-
Taonia atomaria	I	-	I	-	-
Companions					
Lithothamnion spp.	V	V	III	V	V
Chondrus crispus	IV	III	III	IV	IV
Ceramium rubrum	IV	III	V	III	IV
Corallina officinalis	III	IV	-	III	V
Rhodymenia palmata	V	IV	IV	-	-
Heterosiphonia plumosa	II	I	-	III	III
Cladophora rupestris	I	III	-	-	II
Enteromorpha compressa	-	II	IV	-	I
Fucus serratus	II	III	-	-	-
Gigartina stellata	-	IV	-	-	-
Phyllophora membranfolia	III	-	-	-	I
Chorda filum	I	-	III	-	-
Gracilaria verrucosa	-	-	III	-	-

Table 3

The character species of the Alliance Laminarion

Phaeophyceae	Rhodophyceae
Laminaria hyperborea	Callophyllis laciniata
Laminaria digitata	Phycodrys rubens
Laminaria saccharina	Delesseria sanguinea
Laminaria ochroleuca	Dilsea carnosa
Saccorhiza polyschides	Ptilothamnion plumosa
Cystoseira foeniculacea	Odonthalia dentata
Giffordia hinksiae	Cryptopleura ramosa
Desmarestria ligulata	
Desmarestria aculeata	
Dictyota dichotoma	
Dictyopteris membranacea	
Taonia atomaria	

by the intolerance of these species for those environmental factors associated with life in the lower littoral and immediate sublittoral, viz. high light intensity, emmersion at spring tide and exposure to direct wave action. The long list of companion species includes a number which have high constancy in all the ecosystems studied. However they are usually common and often abundant components of the littoral ecosystems and some have been used as character species for littoral associations. A list of these is given in Table 4 For these reasons it would be best to use only the term "presumed character species".

Associations

The aufnahmen fall into five distinct groups but the study has revealed no true character species of these groups except for the dominant kelp species. It is suggested that very detailed study of microscopic epi- and endophytes might reveal good character species and that until the necessary work is carried out only the category of provisional association can be used. Similarly many more examples of mixed kelp ecosystems must be studied in order to ascertain their exact status. For instance Den Hartog (1959) has found on the coast of the Netherlands that *Laminaria digitata* and *Laminaria saccharina* rarely occur as pure stands, in fact he has erected an association *Laminarietum digitata-saccharinae* and recognised pure stands only as facies of the association. This fact emphasises the impossibility of drawing strict phytosociological conclusions from regional studies and

Table 4

The character species of some of the littoral associations

in Norway and the Netherlands

Association	Character Species	Authority
Chondrus-Phyllophora membranifolia	Chondrus crispus	Sundene (1953)
	Phyllophora membranifolia	
Phyllophora brodiaei	Phyllophora brodiaei	Sundene (1953)
Lomentarieto-Plumarietum	Lomentaria articulata	Den Hartog (1958)
	Plumaria elegans	
	Gelidium pusillum	
Polysiphoneto-Chaetomorphetum	Polysiphonia urecolata f. roseola	Van Goor (1922, 1923)
	Chaetomorpha aerea	Den Hartog (1958)
Cladophoreto-Polysiphonietum	Polysiphonia urceolata f. formosa	Den Hartog (1958)
	Ceramium diaphanium	

shows that much more basic descriptive work is needed. It also emphasises that the main importance of this part of the study is the recognition of subassociations, facies and variants of the provisional associations within the regions under investigation.

Subdivisions of the Provisional Associations

Laminarietum hyperboreae, Ass. Prov. (Table 5)

The constancy of a number of species of epiphyte to this association is in all probability linked to the scabrous nature of the stipe of this species of kelp. However they cannot be regarded as character species as all of them occur in other delimited associations.

Two phytogeographical subassociations are recognisable. One, which has its main development in the South West of the British Isles, can be differentiated by four groups of species.

(1) The constancy of *Polyneura hilliae*, *Asparagopsis armata*, *Mesophyllum lichenoides* and *Jania rubens*, these are all Lusitanian and/or Mediterranean species which find their northern limit on the South and West coasts of Britain.

(2) The constancy of *Saccorhiza polyschides* and *Halurus equisetifolius*, both species which occur on the North East coast of Britain and yet are very rare in that region.

(3) The presence of *Fucus serratus* and *Himanthalia elongata*, species which are usually confined to the lower littoral zone on the coast

of North East Britain.

(4) The absence of two northern species Ptilota plumosa and Odonthalia dentata. The presence of these two species and the absence of those in the first three categories distinguishes the more northern subassociation Typicum from that of the south west, which is best referred to as the subassociation Desmarestrietosum due to the constancy and characteristic life form of Desmarestria ligulata in this region.

All the above named species can be regarded as regional differentials for the two subassociations.

There is an indication of a depth variant in the subassociations which is only recognised by the low cover of the dominant. There is a distinctive species poor subgroup composed of aufnahmen taken from the coast of South Northumberland, Durham and North Yorkshire. A comparison with the species lists of Brady (1861a,b, 1862, 1863, 1864) indicated a drastic loss in species diversity over the last 100 years. It has been suggested that this loss is due to pollution concomitant with the industrialization and urbanization of the adjacent coastal plain (Bellamy et al, 1967a). The variant is therefore referred to as the anthropogenic variant.

Re-arrangement of the data on the subassociation Desmarestrietosum indicates no true differentiation of exposed and sheltered ecosystems. One group with a high cover of Laminaria saccharina is associated with a mixed substratum of stable and unstable boulders, whether this ranks variant status is in doubt and there is much to indicate that a smaller sample size should be used in such mosaic communities. Likewise it is difficult to show any difference in the subassociation with increasing depth. There appears to be a gradual loss of species with increasing depth associated with an opening out of the canopy. In depths in excess of 15 m. the kelp forest takes on a "park" like appearance within which the most abundant species are often Dictyota dichotoma, Cryptopleura ramosa and Dictyopteris membranacea, a fact which is corroborated by the work of Norton (1968).

Laminarietum digitatae, Ass. Prov. (Table 6)

The dominant is again the only true characteristic species, other species such as Bifurcaria bifurcata and Gastroclonium ovatum are absent from deeper water and are of rare occurrence in the Laminarietum hyperboreae, however they also occur as constant members of a number of littoral associations and so cannot be used as character species only as differentials. Similarly the deeper water plants such as Dictyota dichotoma and Dictyopteris membranacea and the typical epiphytes such as Phycodrys rubens and Ptitothamnion pluma are usually absent from this association.

Regional subassociations are recognisable. That of the coast of South West England has a number of good differentials which fall into three groups.

(1) Lusitanian-Mediterranean species such as *Asparagopsis armata*, *Bifurcaria bifurcata* and *Mesophyllum lichenoides*.

(2) Species of wide distribution which however were not found in the *Laminaria digitata* belt on the North East coast of Britain; viz. *Plumaria elegans*, *Callithamnion granulatum* and *Lithophyllum pustulatum*.

(3) The constancy and high cover abundance of *Himanthalia elongata* which is usually found above this belt on the North East coast.

The subassociation in the South West coast is provisionally named the *Asparagopsietosum*. The more northerly subassociation *Typicum* lacks the above differentials and appears to have none of its own.

The high constancy of such species as *Saccorhiza polyschides*, *Himanthalia elongata* and *Alaria esculenta*, particularly on the South West coast, indicates that many of the ecosystems described are in exposed situations (Lewis, 1964).

Laminarietum saccharinae, Ass. Prov. (Table 7)

Very few examples of this association were studied and the association table is far too incomplete to allow conclusions to be drawn. There are however indications of a variant with *Halidrys siliquosa* characteristic of stable substrates and turbid water, and a very fragmentary one with abundant ephemeral and pseudoperennial species found in situations with very unstable boulder substrates. Gislén (1930) has described a sublittoral *Halidrys* association but this is confined to localities with strong water movement, all other described associations characterised by *Halidrys* are confined to the littoral (Sundene, 1953; Den Hartog, 1959). It is suggested that further study may reveal a separate subassociation of Laminarietum saccharinae with Halidrys as a differential species.

Laminarietum ochroleucae, Ass. Prov. (Table 8)

This association is present on the South West peninsula of the British Isles but finds its maximum expression on the Atlantic coast of Spain. The following tentative conclusions refer solely to the populations which were described on the coast of Spain.

Two distinct subassociations are recognisable, Typicum and Cystoseiretosum foeniculaceae. The subassociation Cystoseiretosum foeniculaceae is found in relatively sheltered situations and can be recognised by three groups of species.

(1) The presence with high constancy and cover abundance of Cystoseira foeniculacea and Cystoseira tamariscifolia.

(2) A number of differentials with low constancy which include Champia parvula, Plocamium vulgare and Liagora viscida.

(3) The low cover abundance of the dominant species.

The subassociation can be further subdivided into a relatively sheltered and a more exposed variant. The exposed variant is distinguished from the sheltered one by the low cover-abundance of Cystoseira foeniculacea, the high cover abundance of Laminaria ochroleuca and the presence of such species as Gigartina teedii, Scinaia turgida. The sheltered variant has a number of species which are absent from the more exposed one, these include Jania rubens, Mesophyllum lichenoides and Halidrys siliquosa. The Typicum subassociation is recognised by the high cover abundance of the dominant and the absence of any good differential species. A deep water variant (in excess of 18.0 m.) is characterised by the low cover abundance of Laminaria ochroleuca, a low species diversity and the presence of Bonnemaisonii asparagoides, and Polysiphonia nigrescens.

It is possible that under very sheltered conditions the species of Cystoseira might give rise to a separate association, Cystoseiretum tamariscifolio-foeniculaceae.

Saccorhizetum polyschides, Ass. Prov. (Table 9)

This association is characterised by the life form of the dominant.

Two regional subassociations are indicated, Typicum and Alarietosum esculentae. The more northerly one can be recognised by the following differential species or groups of species.

(1) The constancy of Alaria esculenta whose southern range does not extend as far as North West Spain.

(2) The constancy of a number of species which include Membranoptera alata, Polysiphonia urceolata, Lithophyllum pustulatum and Hypoglossum woodwardii, all of which occur in North West Spain but do not occur in this association in South West Britain.

The more southerly Typicum subassociation has the following differential species: Pterosiphonia complanata, Gelidium sesquipedale and Codium tomentosum. A very exposed variant can be recognised in this subassociation by the decrease in cover of the dominant and a fall-off in species diversity.

This association gives way in more sheltered situations, often related to increase in depth, to the association dominated by <u>Laminaria hyperborea</u> in Britain and <u>Laminaria ochroleuca</u> in Spain.

Part 3

PERFORMANCE

Introduction

The Phytometer Approach

The growth of any organism can be regarded as an integrated measure of the effects of the in "topo" environment on that organism.

The use of growth parameters of a particular plant species to monitor environmental factors has long been a dream if not a tool of the terrestrial plant ecologist. Its most ambitious application to date is perhaps that of Paterson in his "Phyochorology of Norden" (Paterson, 1961).

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

The perennial species of kelp would appear ideal for this type of work.

Estimates of the net annual production of the perennial parts (stipe and hapteron) can be obtained from a simple age/biomass relationship based on increment cropping (Wiegert and Evans, 1964; Bellamy and Holland, 1966). The figures so obtained could 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 the laminae of perennial ones could be regarded as a measure of performance in relation to the environment over the current year. It should be possible to obtain a meaningful comparison of the performance of each kelp species within the phytosociological units delimited in the first section of the thesis. There is only one proviso to be considered when measuring the performance of kelp plants and that is whether it is possible to age them.

The Problems of Ageing the Kelps.

In all the perennial species of *Laminaria* there is a secondary meristem situated in the outer cortex of the stipe some 4-8 cells beneath the meristoderm. This meristem brings about the progressive increase in thickness of the stipe by producing radially arranged columns of cells.

The rate of division and growth is rapid at the beginning of each year and the cortical cells produced are large and translucent. Later in the year as growth slows down, small, dense and opaque cells are formed. The difference between the two types of cell are obvious both in a longitudinal and transverse section even to the naked eye.

Le Jolis (1855) was one of the first workers to suggest that enumeration of these contrast zones (growth rings) could be used to age individuals. More recent work (Parke, 1948a; Black et al, 1959) has investigated the validity of this method and Kain (1963, 1967) has summarised some of the problems and the precautions necessary when working with *Laminaria hyperborea*.

They may be summarised as follows:

(a) Interference zones may be produced due to disturbances other than seasonal.

(b) Tissues may be removed in the holdfast region by grazing organisms especially Patina pellucida.

(c) Favourable conditions for growth during the normally slow growth period may result in no discernable slow growth line being formed.

(d) Old individuals may not produce discernable secondary tissue during the fast growth season so that no zone is produced.

The following notes discuss some of the problems found in this study.

Laminaria hyperborea

The table shows the relationship between the number of growth rings and haptera whorls as the composite data for all the individuals studied on the coast of North East England and South East Scotland.

The relationship between the number of dark lines (L.S.) and haptera levels

Age determined by line counts

1	2	3	4	5	6	7
2.6	2.6	1.4	1.1	1.1	.9	.9

It may be seen that there is no strict proportionality in the first three years but after this the 1:1 relationship is good. As a number of the previously mentioned workers have shown that the rings are annual phenomena, and so the bad correlation can only be explained by the fact that more than one haptera whorl is produced in the first two or three years, some of these disappear with time. This is bourne out by the observation that the small attenuated haptera branches, typical of one and two year old individuals, were never found in older individuals.

The procedure for ageing individuals was the same as that described by Kain (1963), that was to follow the dark lines in order to determine whether or not they were associated with a hapteron level, this prevented the boundary of the medulla being mistaken for a growth line and allowed for the recognition of what are purely interference lines. Where this was not possible the number of growth lines was taken as the measure of minimum age.

<u>Laminaria digitata</u>

In all the individuals studied rings were discernable in a transverse section of the lower stipe region. A study of a population known to be three years old growing in a previously cleared area at Petico Wick (South East Scotland) showed that the majority of the largest members of the population had three clear growth rings; some however had less distinct rings which might be comparable to the interference rings described above. The lack of distinct whorls of haptera branches makes it impossible to distinguish between the true growth rings and the supposed interference ones. The individuals from a large sample of a population could be grouped into five classes based on the length of the stipe alone. The individuals were subsequently aged using only the distinct rings and it was found that length groupings were indeed age classes with there being a more than 90% correlation in all cases. However occasionally there were found relatively large plants with only one or two discernable growth rings. Ignoring these it would seem feasible to conclude that the majority of the individuals in all the populations studied can be placed into age classes.

<u>Laminaria saccharina</u>

Detailed study of populations on the coast of North East England and South West Scotland showed that although more than one hapteron whorl may be produced in a growing season only one main concentric growth zone or ring is produced. Other lines (cf. the interference lines of Kain) can be formed but these are usually much narrower than the true growth rings.

Therefore it would seem feasible, as suggested by Parke (1948a), that age can be determined by counting the number of distinct broad growth rings seen in a transverse section of the base of the stipe.

<u>Laminaria ochroleuca</u>

Sauvageau (1918) describes the holdfast of this species as being in the form of an inverted cone from which a number of branch levels arise, the whole structure being often as large as that of <u>Laminaria hyperborea</u>. The similarity of the hapteron of these two species also extends to their internal anatomy. In a transverse section of the lower stipe region a number of dark rings are apparent even to the naked eye. These rings are composed of small densely packed cells which abut directly onto large less dense layers and appear as a pair of lines in longitudinal section. The haptera are composed of the large less dense layers of cells with each new whorl being exterior to all previous pairs of dark lines (L.S.) It would seem that the growth phenomena in this species are similar to those described by Kain (1963, 1967) for Laminaria hyperborea. The dark rings must therefore correspond to successive periods of slow growth during which time no new whorls of haptera are produced.

The table shows the relationship between the number of growth rings and haptera whorls in individuals from South West England. The ratios would indicate that more than one haptera level

The relationship between the number of dark lines (L.S.) and haptera levels

Age determined by line counts

1	2	3	4	5	6	7
3.2	1.8	1.3	1.1	.9	.9	.8

is produced in the first, second and third years but after this the 1:1 relationship is good. The species was therefore aged using the same method and precautions as described for Laminaria hyperborea.

The Measurement of Net Annual Production

Methods

Field. A cropping team would dive within the study area and subjectively select a uniform stand of kelp forest for study. The exact position was fixed from the shore and six figure grid references were given for each site. The depth of the substratum was recorded using capillary gauges, the state of the tide was taken into consideration so that the exact depth could be calculated by reference to Admiralty Tide Tables (1966, 1967, 1968). The values for depth were always expressed in metres below Chart Datum.

Two cropping techniques were used.

(1) Random cropping of approximately 50 individuals ranging from sporelings to canopy plants from well within the boundaries of the chosen stand. In all cases where increment cropping was used care was taken not to sample exactly the same area more than once.

(2) Cropping all individuals from within a series of metre square quadrats (constructed from light alloy) placed well within the stand. This method was always employed when studying *Saccorhiza polyschides*.

The crops were packed into linen bags or wire baskets which were labelled before being brought to the surface.

Where possible the crops were brought directly to the laboratory for further study. Storage when necessary was at 5°C in a cold room. Appendix 5 gives details of modified field methods.

Laboratory

(1) On return to the laboratory each individual was treated as follows:

(a) all epiphytic and epizoic organisms were removed by careful scraping and as far as was practicable the hapteron was cleaned of all adhering matter;

(b) the condition of each plant was recorded, infestation by Patina pellucida, breakdown of the lamina and the presence of the previous years' lamina being noted;

(c) the total length of the stipe (from the point of expansion of the lamina to the upper limit of the haptera branches) was measured;

(d) the plant was divided into three parts; lamina, stipe and hapteron, in cases where the previous years' lamina was still present this was cut off and treated separately;

(e) the hapteron was cut longitudinally into two halves and the number of branch levels counted (only in Laminaria hyperborea and Laminaria ochroleuca);

(f) a longitudinal and/or transverse section of the base of the stipe was cut and the number of growth lines or rings were counted;

(g) the various parts of the plant were treated separately and dried to constant weight at 100°C in air-circulating ovens.

(2) A subsample was removed from a range of the plant parts in each age class and this was ashed in a muffle furnace for 14 hours at

$440^{o}C$. In some cases a series of subsamples were burnt in oxygen at 25 atmospheres in a Gallenkamp CB-370 Adiabatic Bomb Calorimeter in order to determine the calorific value of the plant tissue.

(3) Saccorhiza polyschides was treated in the same way but the whole crop was treated as a single plant instead of the individual plants being dealt with separately.

Results

The object of the work was simply to gain comparable data of performance in relation to the environment.

It was realised from the start that differential losses (due to damage, disease or grazing) between sites could obscure any real differences of performance. To overcome this the data on individuals which were damaged in any way were omitted from the calculation of performance. In organisms with the simple morphology of a kelp plant this is a perfectly objective approach. For similar reasons it was decided to calculate separate figures for stipe and hapteron performance. There is no morphological or anatomical reason for dealing with these parts separately. However it was realised from the start that serious errors might arise when calculating performance due to the difficulties entailed in cleaning the hapteron. Therefore, it was decided to treat the two separately as working with the stipe presents no such difficulty. It is realised that all the measured attributes (stipe length, stipe biomass, hapteron biomass) only have a meaning within the context of the methods of study employed, they have no meaning sensu stricto. It is suggested for these various reasons that the stipe values give the most accurate measure for comparative study.

Individual Performance Figures

The graphs of the mean values for stipe length, stipe biomass and hapteron biomass against age were plotted using only the organic (ash-free) dry weight data of healthy and undamaged individuals. The following growth increments for each age class could be calculated directly from the results or from the slopes of the appropriate portions of the graphs.

Net annual stipe biomass increment for year x in grams, N.A.S.B.I.

Annual stipe length increment for year x in cms, A.S.L.I.

Net annual hapteron biomass increment for year x in grams, N.A.H.B.I.

These figures could be used directly for detailed comparison. Plotting weight per unit length of stipe also allows a comparison of stipe morphology.

It was found that comparison of columns of up to 10 figures was very difficult so it was decided that a first approximation of overall performance would be useful. This can be accomplished in one of two ways.

(1) By calculating the mean net annual production figure from the overall slope of the graph. Mean net annual stipe production, M.N.A.S.P. 0-7 years in gram/years in Laminaria hyperborea and Laminaria ochroleuca, 0-5 years in Laminaria digitata.

(2) By taking the area beneath the growth curve ($\int_0^T$ wdt) in each case as an integrated figure of performance over the whole life span of a population. Integrated stipe or hapteron performance, I.S.P. or I.H.P. 0-7 or 0-5 gram/years. The composite values for the perennial parts can be obtained by adding any set of these values for the stipe and hapteron. Similarly integrated figures of stipe length, I.S.L. cm. years, and even the weight per unit length I.W./U.L. grams/cm. years can be calculated.

Lamina performance can also be treated in a number of ways for comparative purposes.

(1) The peak lamina biomass for each age class, net annual lamina production, N.A.L.P. for year x in grams can be directly compared. This figure added to the appropriate age class figures for net stipe and hapteron production can produce a figure for individual net annual production, I.N.A.P. for year x in grams (again long columns of figures are difficult to use for comparative purposes).

(2) Graphs of mean lamina biomass plotted against age, although in themselves meaningless, can be used to gain a visual impression of site differences. Similarly the area beneath such a growth curve $\int_0^T$ wdt could be regarded as an integrated figure of performance for comparative purposes. Integrated lamina performance, I.L.P., 0-x years.

Ecosystem Performance Figures

It was possible where the mean values for the number of individuals in each age class per unit of area was calculated, to determine the figures for net annual plot production, N.A.P.P. grams/m^2, by multiplication of the appropriate values. This was the only meaningful figure obtainable for comparative work in the case of Saccorhiza polyschides. These figures are summarised as follows.

Individual Performance Figures

N.A.S.B.I.	Net annual stipe biomass increment for each year.
A.S.L.I.	Annual stipe length increment for each year.
N.A.H.B.I.	Net annual hapteron biomass increment for each year.
M.N.A.S.P.	Mean net annual stipe production 0-x years.
I.S.P.	Integrated stipe performance 0-x years.
M.N.A.H.P.	Mean net annual hapteron production 0-x years.
I.H.P.	Integrated hapteron performance 0-x years.
N.A.L.P.	Net annual lamina production for each year.
I.N.A.P.	Individual net annual production for each year.
I.L.P.	Integrated lamina performance 0-x years.
I.S.L.	Integrated stipe length cm.years.
I.W./U.L.	Integrated stipe weight per unit length grams/cm.

Ecosystem Peformance Figures

N.A.P.P.	Net annual plot production grams per metre square.

It must be emphasised that all the figures only have meaning within the context of the methods described and have their main use for comparative study. All the results are presented as grams organic (ash-free) dry weight. This fact is of extreme importance owing to the great variations in the ash content of Laminaria spp. and Saccorhiza polyschides with the season as reported by a number of workers including Lapique (1919), Lunde (1937), Trofimov (1938), Black (1948a,b, 1950a,b, 1954), Haug and Jensen (1954) and Jensen and Haug (1956).

Laminaria hyperborea

The composite mean cropping data for all the sites is given in Appendix 6 and Tables 10 - 19. In an attempt to highlight the most significant trends the integrated performance figures are presented in the main text tables. The integrated figures and the relevant site data are given in table 20.

Summary tables

The effect of increasing depth on the integrated figures is shown in Table 21.

There is a general decrease in the I.S.P., I.S.L. and I.W./U.L. with increase in depth with the decrease in I.W./U.L. being only partly related to the lower values for I.S.P.

The effects of exposure to water movement on the integrated figures for the ecosystems in each of the regions is shown in Table 22

I South East Scotland and North East England

There is a trend in the shallow water ecosystems for an increase in I.S.P. and I.S.L. with increase in exposure to wave action with the exception of the moderately exposed ecosystem subjected to current surge (4E). It is possible that this trend is related to factors other than exposure (see table 23). There are no significant trends in I.W./U.L. with differences in exposure.

II Inner Hebrides

The values for I.S.P. and I.S.L. are higher in the exposed ecosystem than in the ones subjected to current surge or severe wave

Table 20

The relevant site data and integrated figures

Region	Site	Exposure Type	Exposure Scale	Pollution	Natural allochthonous material	Turbidity	Depth (m.-C.D.)	I.H.P.	I.S.P.	I.L.P.	I.S.L.	I.W./U.L.
	2P	D	12	+	+	2	3.0	85	154	328	422	14
	2P	D	12	+	+	2	7.6	83	125	255	369	15
	2P	D	12	+	+	2	10.6	30	49	-	228	7
	2P	D	12	+	+	2	13.7	9	8	-	110	2
	2H	F/B	0	+	+	2	3.0	-	101	-	192	10
I	4L	B	0	++	+++	1	3.0	70	131	208	446	12
	4L	B	0	++	+++	1	7.6	73	127	156	412	13
	4E	D	16	++	+++	1	3.0	35	64	101	251	7
	4E	D	16	++	+++	1	7.6	76	48	-	266	9
	5M	D	18	++++	+++	0	2.0	63	169	204	583	10
	5M	D	18	++++	+++	0	3.7	37	61	182	301	6
	6R	D	13	+++	++++	0	2.0	64	167	126	575	4
	6R	D	13	++	++++	0	4.2	30	102	36	571	7
	9	F/C	2	+	+	3	4.6	-	38	-	309	5
	10	C	12	+	+	3	4.6	-	94	-	434	8
II	10	C	12	+	+	3	18.3	-	27	-	241	5
	11	E	15	+	+	3	4.6	-	36	-	261	6
	11	E	15	+	+	3	18.3	-	15	-	180	3
III	14	B	0	+	+++	1	3.6	-	26	-	159	7
	16	D	7	+	++	2	3.6	-	55	-	285	7
IV	19	D	10	+	+++	1	3.6	-	44	-	275	8
V	23S	F/D	8	+	+	3	3.0	-	98	-	281	11
	23S	F/D	8	+	+	3	12.2	-	64	-	246	14

Table 20

The relevant site data and integrated figures

Region	Site	Exposure Type	Exposure Scale	Pollution	Natural allochthonous material	Turbidity	Depth (m.-C.D.)	I.H.P.	I.S.P.	I.L.P.	I.S.L.	I.W./U.L.
	2P	D	12	+	+	2	3.0	85	154	328	422	14
	2P	D	12	+	+	2	7.6	83	125	255	369	15
	2P	D	12	+	+	2	10.6	30	49	-	228	7
	2P	D	12	+	+	2	13.7	9	8	-	110	2
	2H	F/B	0	+	+	2	3.0	-	101	-	192	10
	4L	B	0	++	+++	1	3.0	70	131	208	446	12
I	4L	B	0	++	+++	1	7.6	73	127	156	412	13
	4E	D	16	++	+++	1	3.0	35	64	101	251	7
	4E	D	16	++	+++	1	7.6	76	48	-	266	9
	5M	D	18	++++	+++	0	2.0	63	169	204	583	10
	5M	D	18	++++	+++	0	3.7	37	61	182	301	6
	6R	D	13	+++	++++	0	2.0	64	167	126	575	4
	6R	D	13	++	++++	0	4.2	30	102	36	571	7
	9	F/C	2	+	+	3	4.6	-	38	-	309	5
	10	C	12	+	+	3	4.6	-	94	-	434	8
II	10	C	12	+	+	3	18.3	-	27	-	241	5
	11	E	15	+	+	3	4.6	-	36	-	261	6
	11	E	15	+	+	3	18.3	-	15	-	180	3
III	14	B	0	+	+++	1	3.6	-	26	-	159	7
	16	D	7	+	++	2	3.6	-	55	-	285	7
IV	19	D	10	+	+++	1	3.6	-	44	-	275	8
V	23S	F/D	8	+	+	3	3.0	-	98	-	281	11
	23S	F/D	8	+	+	3	12.2	-	64	-	246	14

Table 21

The effect of increase in depth

Association	Laminarietum hyperboreae
Subassociation	T. Typicum
Variant	(tp.) typicum
	(at.) anthropogenic
	(dp.) deep water
Subassociation	D. Desmarestrietosum
Variant	(tp.) typicum

	T (tp.)	T (tp.)	T (at.)	T (at.)	T (tp.)			D (tp.)	
Region			I			II		V	
Site	4L	2P	5M	6R	4E	10	11	23S	
Exposure	B	D	D	D	F/D	C	E	F/D	
0-3.1	131	154	169	167	64	-	-	98	
3.2-6.1	-	-	61	102	-	94	36	-	(at.Dp.)
6.2-9.1	127	125	-	-	48	-	-	-	(tp.Dp.)
9.2-13.1	-	49	-	-	-	-	-	-	
13.2-20.1	-	8	-	-	-	-	-	64	
20.2-26.1	-	-	-	-	-	27	15	-	

I.S.P.

0-3.1	446	422	583	575	251	-	-	281
3.2-6.1	-	-	301	571	-	434	261	-
6.2-9.1	412	369	-	-	266	-	-	-
9.2-13.1	-	228	-	-	-	-	-	-
13.2-20.1	-	40	-	-	-	-	-	246
20.2-26.1	-	-	-	-	-	241	180	-

I.S.L.

0-3.1	13	14	10	14	7	-	-	11
3.2-6.1	-	-	6	7	-	8	6	-
6.2-9.1	12	15	-	-	9	-	-	-
9.2-13.1	-	7	-	-	-	-	-	-
13.2-20.1	-	2	-	-	-	-	-	14
20.2-26.1	-	-	-	-	-	5	3	-

Table 22

The effect of exposure in each of the regions

Association: Laminarietum hyperboreae
Subassociation: T. Typicum
Variant:
(tp.) typicum
(at.) anthropogenic
(dp.) deep water

		T (tp.)	T (tp.)	T (at.)	T (at.)	T (tp.)					
Region				I				II			III
Site	2H	4L	2P	5M	6R	4E	10	9	11	14	16
Exposure	F/B	F/B	D	D	D	F/D	C	F/C	E	B	C
0-3.1	101	131	154	169	167	64	-	-	-	-	-
3.2-6.1	-	-	-	61	102	-	94	38	36	26	55
6.2-9.1	-	127	125	-	-	48	-	-	-	-	-
9.2-13.1	-	-	49	-	-	-	-	-	-	-	-
13.2-20.1	-	-	8	-	-	-	-	-	-	-	-
20.2-26.1	-	-	-	-	-	-	27	15	-	-	-
						I.S.P.					
0-3.1	192	446	422	583	575	251	-	-	-	-	-
3.2-6.1	-	-	-	301	571	-	434	309	261	159	285
6.2-9.1	-	412	369	-	-	266	-	-	-	-	-
9.2-13.1	-	-	228	-	-	-	-	-	-	-	-
13.2-20.1	-	-	110	-	-	-	-	-	-	-	-
20.2-26.1	-	-	-	-	-	-	241	-	180	-	-
						I.S.L.					
0-3.1	10	13	14	10	14	7	-	-	-	-	-
3.2-6.1	-	-	-	6	7	-	8	5	6	7	7
6.2-9.1	-	12	15	-	-	9	-	-	-	-	-
9.2-13.1	-	-	7	-	-	-	-	-	-	-	-
13.2-20.1	-	-	2	-	-	-	-	-	-	-	-
20.2-26.1	-	-	-	-	-	-	5	-	3	-	-
						I.W./U.L.					

action. The lowest values for I.S.L. are found in the ecosystem exposed to severe wave action whilst those for I.S.P. are similar in this ecosystem and the one subjected to current surge.

III West Scotland

The values for I.S.P. and I.S.L. are higher in the exposed ecosystem than the moderately sheltered one.

The effect of natural allochthonous material and pollution on the integrated figures for moderately exposed ecosystems along the coast of North East England and South West Scotland are given in Table 23.

The values for I.S.L. are significantly higher in the shallow water ecosystems in the two most effected sites (6R and 5M).

There is a very marked decrease in I.W./U.L. with only a very small increase in depth range at the ecosystems which are most effected (6R and 5M), this being related only in part to the fall-off in I.S.P. with depth.

The values for I.H.P. and I.L.P. are significantly lower in the ecosystems which are particularly effected by pollution and natural allochthonous material (6R and 5M). There is no significant difference in the values for I.S.P. in the shallow water ecosystems although there is a very much more rapid decrease in these values with increase in depth in the most effected ones (6R and 5M).

Phytogeographical differences in the integrated figures in nearly equivalent ecosystems are given in Table 24.

Table 23

The effect of natural allochthonous material and pollution

Subassociation T. Typicum
Variant (tp.) typicum
(at.) anthropogenic
(dp.) deep water

	T (tp.)	T (at.)	T (at.)	
Site	2P	6R	5M	
Pollution	+	+++	++++	
Natural allochthonous Material	+	++++	+++	
Turbidity	2	0	0	
0-3.1	85	64	63	
3.2-6.1	-	30	37	(at.Dp.)
6.2-9.1	83	-	-	
9.2-13.1	30	-	-	
13.2-20.1	9	-	-	
		I.H.P.		
0-3.1	154	167	169	
3.2-6.1	-	102	61	
6.2-9.1	125	-	-	
9.2-13.1	49	-	-	
13.2-20.1	8	-	-	
		I.S.P.		
Depth (m.-C.D.) 0-3.1	328	126	204	
3.2-6.1	-	36	182	
6.2-9.1	255	-	-	
9.2-13.1	-	-	-	
13.2-20.1	-	-	-	
		I.L.P.		
0-3.1	422	575	583	
3.2-6.1	-	571	301	
6.2-9.1	369	-	-	
9.2-13.1	228	-	-	
13.2-20.1	110	-	-	
		I.S.L.		
0-3.1	14	14	10	
3.2-6.1	-	7	6	
6.2-9.1	15	-	-	
9.2-13.1	7	-	-	
13.2-20.1	2	-	-	
		I.W./U.L.		

Table 24

Phytogeographical differences in nearly equivalent ecosystems

Subassociation T. Typicum
Variant (tp.) typicum
(at.) anthropogenic
(Dp.) deep water
Subassociation D. Desmarestrietosum
(tp.) typicum

		T (tp.)	D (tp.)				T (tp.)			D (tp.)		
Region	III	I	I	III	II	II	I	IV	I	V	II	
Site	14	4L	2H	16	10	9	2P	19	4E	23S	11	
Exposure	B	B	F/B	C	C	F/C	D	D	F/D	F/D	E	
Pollution	++	+++	+	++	+	+	+	+++	+++	+	+	
Natural Allochthonous material	+	+++	+	++	+	+	+	+++	+++	+	+	
Turbidity	1	1	2	2	3	3	2	1	1	3	3	
0-3.1	-	131	101	-	-	-	154	-	64	98	-	
3.2-6.1	26	-	-	55	94	38	-	44	-	-	36	
6.2-9.1	-	127	-	-	-	-	125	-	48	-	-	(tp.Dp.)
9.2-13.1	-	-	-	-	-	-	49	-	-	-	-	
13.2-20.1	-	-	-	-	-	-	8	-	-	64	-	
20.2-26.1	-	-	-	-	27	-	-	-	-	-	15	
I.S.P.												
0-3.1	-	446	192	-	-	-	422	-	251	281	-	
3.2-6.1	159	-	-	285	488	309	-	275	-	-	302	
6.2-9.1	-	412	-	-	-	-	369	-	266	-	-	
9.2-13.1	-	-	-	-	-	-	228	-	-	-	-	
13.2-20.1	-	-	-	-	-	-	110	-	-	-	-	
20.2-26.1	-	-	-	-	241	-	-	-	-	246	180	
I.S.L.												
0-3.1	-	13	11	-	-	-	14	-	7	11	-	
3.2-6.1	7	-	-	7	8	-	-	8	-	-	6	
6.2-9.1	-	12	-	-	-	-	15	-	9	-	-	
9.2-13.1	-	-	-	-	-	-	7	-	-	-	-	
13.2-20.1	-	-	-	-	-	-	2	-	-	14	3	
20.2-26.1	-	-	-	-	55	-	-	-	-	-	-	
I.W./U.L.												

The values for I.S.P. and I.S.L. and I.W./U.L. show considerable variations within the ecosystems in each category of exposure so much so that no overall pattern emerges when the sites are considered as a whole.

Laminaria digitata

The composite data from all the sites is given in Appendix 6 Tables 25-32. In an attempt to highlight the most significant trends the integrated performance figures are presented in the main text tables. The relevant site and integrated data is given in Table 33.

Summary tables

The effect of exposure to water movement on the integrated figures for the ecosystems in each of the regions is shown in Table 34

I South East Scotland and North East England

The values for I.S.P. and I.S.L. are significantly higher in the moderately sheltered ecosystems with the notable exception of the tide pool (4P). There is no significant trend in the values for I.S.P. and I.S.L. in the exposed to moderately exposed ecosystems. The values for I.L.P. show little relationship with the other measured attributes of I.S.P. and I.S.L. There are no significant trends in I.H.P. and I.W./U.L. with changes in exposure although there is a certain relationship between I.W./U.L. and I.S.P.

II Inner Hebrides

There is no significant difference in the I.S.P. between the exposed and severely exposed ecosystems. The severely exposed ecosystem has the highest I.S.L. and the lowest values for I.W./U.L. There is a general trend towards an increase in I.W./U.L. with increase in exposure.

III West Scotland

The I.S.P. and I.S.L. are highest in the very sheltered and

Table 33

The relevant site data and integrated figures

Region	Site	Exposure Type	Exposure Scale	Pollution	Natural allochthonous material	Turbidity	I.H.P.	I.S.P.	I.L.P.	I.S.L.	I.W./U.L.
I	2P	D	12	+	+	2	5	11	110	123	2
	2H	F/B	0	+	+	2	5	21	149	188	3
	4P	B	0	++	+++	1	5	7	125	70	2
	4L	B	0	++	+++	1	7	24	68	181	4
	4E	D	16	++	+++	1	6	14	90	163	3
	5M	D	18	++++	+++	0	7	14	65	127	3
II	9	F/C	2	+	+	3	-	13	-	121	3
	10	C		+	+	3	-	14	-	132	14
	11	E	15	+	+	3	-	13	-	200	2
III	12	A	0	++	+++	1	-	16	-	157	3
	13	F/B	0	+	+++	1	-	10	-	119	3
	14	B	0	+	+++	1	-	5	-	63	3
IV	17Q	A	0	+	++++	1	-	9	-	127	3
	17E	F/B	0	+	+++	1	-	12	-	158	2
	18	C	4	+	+++	1	-	14	-	149	3
V	20P	D	14	+	++	2	-	18	-	152	4
	24L	E	13	+	+	3	-	25	-	179	6
	25R	C	8	++	++	1	-	25	-	145	6
	26M	E	12	+	+	3	-	15	-	199	3
	27P	E	12	++	++	2	-	2	-	60	2
	29M	E	14	+	+	3	-	18	-	141	4

Table 34

The effects of increase in exposure to water movement on the integrated figures in each of the regions

Association Laminarietum digitatae
Subassociation Typicum; Asparagopsietosum
Variant (Sh.) Sheltered, (Ex.) Exposed

Subassociation	Typicum																		Asparagopsietosum			
Variant																		(Sh.)		(Ex.)	(Ex.)	
Region				I					II			III			IV				V			
Site	4L	4P	2H	4S	2P	4E	5M	10	9	11	12	14	13	17Q	17E	18	25R	27P	20P	26H	24L	29H
Exposure	B	B	F/B	F/C	D	D	D	C	F/C	E	A	B	F/B	A	F/B	C	C	C	D	E	E	E
I.H.P.	7	5	5	8	5	6	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I.S.P.	24	7	21	14	11	14	14	14	13	13	16	5	10	9	12	14	25	2	18	15	25	18
I.L.P.	68	125	149	106	110	90	65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I.S.L.	181	90	188	142	123	163	127	132	121	200	157	63	119	127	158	149	145	60	152	199	179	141
I.W./U.L.	4	2	3	3	2	3	3	4	3	2	3	3	3	3	2	3	6	2	4	3	6	4

lowest in the moderately exposed ecosystem, whilst the one exposed to current surge has somewhat intermediate values. There is no significant difference in I.W./U.L. between the ecosystems.

IV West Wales

The values for I.S.P. and I.S.L. are highest in the more exposed ecosystem with the exception of the high values for I.S.L. in the one subjected to current surge. The ecosystem subjected to current surge also has lower values for I.W./U.L. than the other two.

V South West England

There emerge no significant trend in the values for I.S.P., I.S.L. or I.W./U.L. between the exposed to severely exposed ecosystems with the notable exception of the very low values in the one sampled at a high level on the lower littoral (27P). There is a certain relationship between the values for I.W./U.L. and those for I.S.P.

The effect of natural allochthonous material and pollution on the integrated figures for the moderately exposed ecosystem along the coast of South East Scotland and North East England is given below.

Association Subassociation	Laminarietum digitatae Typicum	
Site	2P	5M
Pollution	+	++++
Natural allochthonous material	+	+++
Turbidity	2	0
I.H.P.	5	7
I.S.P.	11	14
I.E.P.	110	65
I.S.L.	123	127
I.W./U.L.	2	3

There is a trend towards an increase in the values for I.H.P., I.S.P. and I.W./U.L. with increase in turbidity related to the amount of natural allochthonous material and pollution. There is little difference in I.S.L. and hence the I.W./U.L. is higher in most effected ecosystems. In fact I.W./U.L. appears to be related to the values for I.S.P. The I.L.P. is lower in the less effected ecosystem (2P).

Phytogeographical units (where known) in nearly equivalent ecosystems are given in Table 35 and Fig. 3. The measurements show considerable variations within each category of exposure so much so that no overall trend related to this factor emerges for the regions as a whole.

Table 35

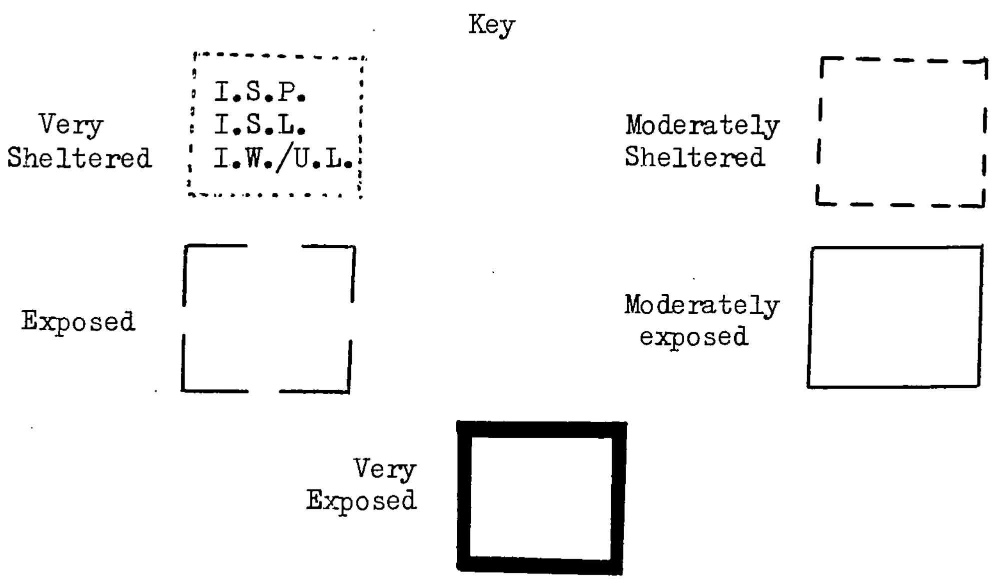
Phytogeographical differences in equivalent ecosystems

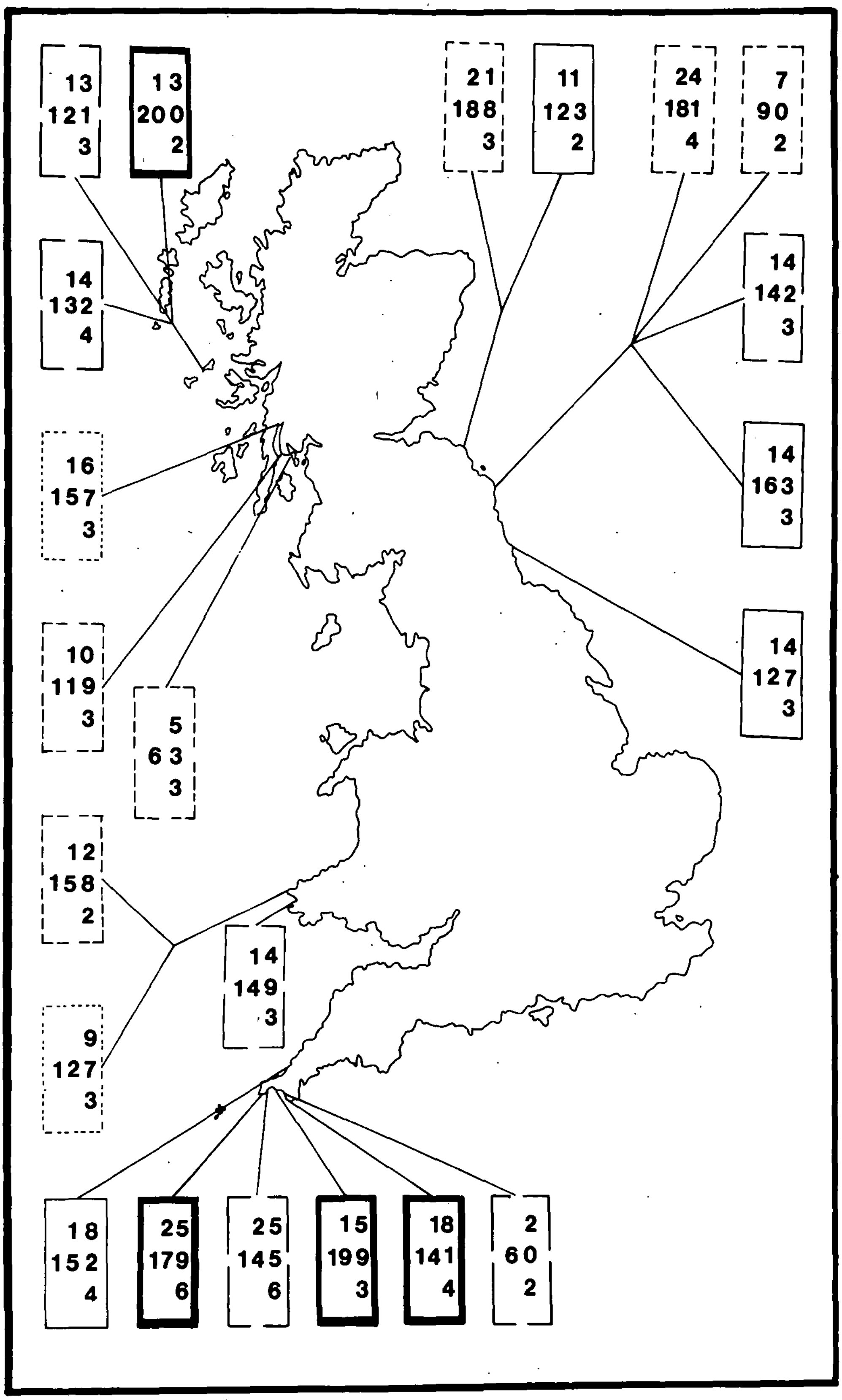
Association Laminarietum digitatae
Subassociation T - Typcium, A - Asparagopsietosum
Variants (Sh.) Sheltered, (Ex.) Exposed

Region	III	IV	T I	T I	III	T I	IV	II	V	A (Sh.) V	T I	T I	T I	A V	II	(Ex.) V	(Ex.) V	A V	III	IV	T I	II
Site	12	17Q	4L	2H	14	4P	18	10	25R	27P	2P	4E	5M	20P	11	26H	24L	29M	13	17E	4S	9
Exposure	A	A	B	B	B	B	C	C	C	C	D	D	D	D	E	E	E	E	F/B	F/B	F/C	F/C
I.H.P.	-	-	7	5	-	-	5	-	-	-	5	6	7	-	-	-	-	-	-	-	8	-
I.S.P.	16	9	24	21	5	7	14	14	25	2	11	14	14	18	13	15	25	18	10	12	14	13
I.L.P.	-	-	68	149	-	125	-	-	-	-	110	90	65	-	-	-	-	-	-	-	106	-
I.S.L.	157	127	181	188	63	90	149	132	145	60	123	163	127	152	200	199	179	141	119	158	142	121
I.W./U.L.	3	3	4	3	3	2	3	4	6	2	2	3	3	4	2	3	6	4	3	2	3	3

FIGURE 3

The integrated figures for stipe production, stipe length and weight/unit length in *Laminaria digitata*

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90
2
14
142
3
14
163
3
14
127
3
18
152
4
25
179
6
25
145
6
15
199
3
18
141
4
2
60
2

Laminaria saccharina

The composite data from all the sites is given in Appendix 6 and Tables 36-40. The most significant trends are highlighted by the biomass of the stipe and lamina, length and the weight/unit length of stipe in two year old individuals and are presented together with the relevant site data in Table 41.

Summary tables

The effect of increasing depth on the biomass, length and weight per unit length of stipe in the two year old individuals is given below.

Region	I	II	II	III
Site	2P	10	11	12
Exposure	D	C	E	A
0-4.1	1.2	-	-	.9
4.2-7.1	-	1.5	1.2	-
7.2-10.1	1.0	-	-	1.4
10.2-22.1	-	.8	1.0	-

Stipe biomass (2 yrs.)

0-4.1	30.3	-	-	24.0
4.2-7.1	-	26.6	25.6	-
7.2-10.1	25.5	-	-	26.7
10.2-22.1	-	16.7	21.0	-

Stipe length (2 yrs.)

0-4.1	.4	-	-	.4
4.2-7.1	-	.6	.5	-
7.2-10.1	.4	-	-	.5
10.2-22.1	-	.5	.4	-

Wt./unit length of stipe (2 yrs.)

There is a trend towards a decrease in the values for stipe biomass and length with the notable exception of Strone Point (12).

Table 41

The relevant site and biomass of stipe, lamina, length, and weight/unit length of site data

Region	Site	Exposure Type	Exposure Scale	Pollution	Natural allochthonous material	Turbidity	Depth (m.-C.D.)	Biomass Stipe	Biomass Lamina	Stipe Length	Stipe Wt./unit length
I	1	A	2	++++	++++	0	5.0	2.2	9.3	42.7	.5
	2P	D	12	+	+	2	3.0	1.2	19.0	30.3	.4
	2P	D	12	+	+	2	9.1	1.0	18.9	25.5	.4
	2H	F/B	0	+	+	2	2.4	.9	39.1	23.5	.4
	4L	B	0	++	+++	1	2.0	.9	37.1	25.6	.2
	4P	B	0	++	+++	1	MTL	.3	40.0	11.7	.3
II	8	F/A	0	+	++	3	6.1	9.5	69.5	71.0	1.3
	10	C	12	+	+	3	6.1	1.5	21.4	26.6	.6
	10	C	12	+	+	3	21.4	.8	13.1	16.7	.5
	11	E	15	+	+	3	6.1	1.2	24.2	25.6	.5
	11	E	15	+	+	3	21.4	1.0	16.2	21.0	.4
III	12	A	0	++	+++	1	3.0	.9	34.1	24.0	.4
	12	A	0	++	+++	1	7.6	1.4	53.0	26.7	.5
	13	F/B	0	+	+++	1	3.6	1.6	32.4	36.8	.4
	14	B	0	+	+++	1	3.6	.7	45.0	20.5	.3
	15	C	8	+	+++	2	3.6	.9	137.1	24.4	.4
	16	D	7	+	++	2	3.6	1.0	34.7	19.2	.5
IV	17Q	A	0	+	++++	1	1.5	.5	22.1	17.9	.3
	17E	F/B	0	+	+++	1	0	.8	13.9	24.2	.3
	18	C	4	+	+++	1	3.0	1.1	36.3	33.3	.3
	19	D	10	+	+++	1	5.3	.4	-	12.3	.3

The weight per unit length of stipe is related to the figures for stipe biomass.

The effect of exposure to wave action on the biomass, length and weight/unit length of stipe of the ecosystem in each of the regions is shown in Table 42.

I South East Scotland and North East England

The highest values for the biomass, length and weight/unit length of stipe occur in the very sheltered ecosystem (1) which is subjected to current surge. There is little difference in the values for the biomass of the stipe and lamina and the length of the stipe in the moderately sheltered to moderately exposed ecosystems in shallow water with the notable exception of the tide pool (4P). There tends to be an increase in the weight/unit length of stipe with increase in exposure between the moderately sheltered and moderately exposed ecosystems.

II Inner Hebrides

There is a significant decrease in the biomass of the stipe and lamina and length with increase in exposure to water movement although there is no significant difference in stipe length between the exposed and the severely exposed one. The weight/unit length of stipe tends to decrease with increase in exposure and follows the same trend as stipe biomass.

III West Wales

There is an increase in the biomass of the stipe and lamina and the length of the stipe between the very sheltered and moderately

Table 42

The effects of increase in water movement on the integrated figures in each of the regions

Region			I				II				III				IV		
Site	1	4L	4P	2H	2P	8	10	11	12	14	13	15	16	17Q	18	17E	19
Exposure	F/A	B	B	F/B	D	F/A	C	E	A	B	F/B	C	D	A	B	F/B	D
0-4.1	9.3	37.1	40.0	39.1	19.0	69.5	-	-	34.1	45.0	32.4	137.1	34.7	22.1	36.3	13.9	-
4.2-7.1	-	-	-	-	-	-	21.4	24.2	53.0	-	-	-	-	-	-	-	-
7.2-10.1	-	-	-	-	18.9	-	-	-	-	-	-	-	-	-	-	-	-
10.2-22.1	-	-	-	-	-	-	13.1	16.2	-	-	-	-	-	-	-	-	-
Lamina biomass (2 yrs.)																	
0-4.1	2.2	.9	.3	.9	1.2	9.5	-	-	.9	.7	1.6	.9	1.0	.5	1.1	.8	.4
4.2-7.1	-	-	-	-	-	-	1.5	1.2	1.4	-	-	-	-	-	-	-	-
7.2-10.1	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-
10.2-22.1	-	-	-	-	-	-	1.8	1.0	-	-	-	-	-	-	-	-	-
Stipe biomass (2 yrs.)																	
0-4.1	42.7	25.6	11.7	23.5	30.3	71.0	-	-	24.0	20.5	36.8	24.4	19.2	17.9	33.3	24.2	12.3
4.2-7.1	-	-	-	-	-	-	26.6	25.6	26.7	-	-	-	-	-	-	-	-
7.2-10.1	-	-	-	-	25.5	-	-	-	-	-	-	-	-	-	-	-	-
10.2-22.1	-	-	-	-	-	-	16.7	21.0	-	-	-	-	-	-	-	-	-
Stipe length (2 yrs.)																	
0-4.1	1.5	.2	.3	.4	.4	-	-	-	.4	.3	.4	.4	.5	.3	.3	.3	.3
4.2-7.1	-	-	-	-	-	1.3	.6	.5	.5	-	-	-	-	-	-	-	-
7.2-10.1	-	-	-	-	.4	-	-	-	-	-	-	-	-	-	-	-	-
10.2-22.1	-	-	-	-	-	-	.5	.4	-	-	-	-	-	-	-	-	-
Wt./unit length (2 yrs.)																	

exposed ecosystems, these values are lowest in the more exposed ones. There is no significant difference in the weight/unit length of stipe between the various ecosystems.

Phytogeographical differences in the integrated figures (where known) in nearly equivalent ecosystems are given in Table 43.

The ecosystems which are very sheltered from direct onshore wave action and yet are subjected to a certain amount of current surge (8 and 1) have the highest values for biomass, length and weight/unit length of stipe. There is no significant trend in the values between the other ecosystems although they are subjected to very different types and degrees of exposure to water movement.

Table 43

Phytogeographical differences in equivalent ecosystems

Region	III	IV	I	I	I	III	IV	I	III	IV	II	III	III	IV	I	II
Site	12	17Q	1	8	4L	14	18	2H	13	17E	10	15	16	19	2P	11
Exposure	A	A	F/A	F/A	B	B	B	F/B	F/B	F/B	C	C	D	D	D	E
0-4.1	.9	.5	-	9.5	.9	.7	1.1	.9	1.6	.8	-	.9	1.0	.4	1.2	-
4.2-7.1	1.4	-	2.2	-	-	-	-	-	-	-	1.5	-	-	-	-	1.2
7.2-10.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-
10.2-22.1	-	-	-	-	-	-	-	-	-	-	.8	-	-	-	-	1.0
Stipe biomass (2 yrs.)																
0-4.1	24.0	17.9	-	71.0	25.6	20.5	33.3	23.5	36.8	24.2	-	24.4	19.2	12.3	30.3	-
4.2-7.1	26.7	-	42.7	-	-	-	-	-	-	-	26.6	-	-	-	-	25.6
7.2-10.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25.5	-
10.2-22.1	-	-	-	-	-	-	-	-	-	-	16.7	-	-	-	-	21.0
Stipe length (2 yrs.)																
0-4.1	.4	.3	-	1.3	.2	.3	.3	.4	.4	.3	-	.4	.5	.3	.4	-
4.2-7.1	.5	-	.5	-	-	-	-	-	-	-	.6	-	-	-	-	.5
7.2-10.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.4	
10.2-22.1	-	-	-	-	-	-	-	-	-	-	.5	-	-	-	-	.4
Wt./unit length (2 yrs.)																

Laminaria ochroleuca

The composite data and production figures are given in Table 44 in Appendix 6 and represent the mean values for all of the ecosystems sampled between 1.8-8.4 m. on the coasts of North West Spain and South West England. The results are summarised as integrated figures below.

	North West Spain	South West England
I.H.P.	22	40
I.S.P.	56	35
I.L.P.	218	163
I.S.L.	184	275
I.W./U.L.	20	7

The I.S.P. and I.L.P. are significantly higher in the individuals from the ecosystems in North West Spain. The ecosystems on the English coast in fact have higher values for stipe production between 1 and 4 years of age and significantly lower ones above these age classes. However, as the calorific values per gram of organic matter are much higher in the English material (5138 $\pm$ 415) than in the Spanish (3619 $\pm$ 183), the differential effect in the upper age classes appears to be much less in terms of "net calories stored". The I.S.L. is significantly higher in the ecosystems from the English coast and the I.W./U.L. is therefore much lower. The I.H.P. is higher in the ecosystems on the English than the Spanish coast.

The Seasonal Changes in Lamina Performance

The increment cropping data for the production of the lamina for the three species of Laminaria on the North East of England and South East Scotland are given in Tables 45-53 in Appendix 6 and are summarised in graph form in figure 4.

Laminaria hyperborea

The peak seasonal production of the lamina is usually reached from July to September with a decrease occuring after this month.

Laminaria digitata

The old and new laminae were not separated when cropping in 1967 but since the maximum biomass usually occurs between July to September after the old lamina is lost, then this can be considered as representing the peak seasonal production.

Laminaria saccharina

The peak seasonal production of the lamina is usually reached in August and September. The values for the seasonal production of the laminae can show considerable fluctuations between consecutive years in the same ecosystem.

FIGURE 4

The seasonal changes in lamina production

St. Abb's Head: (2P) Petico Wick; (2H) Harbour.

Beadnell: (4P) Tide pool; (4L) Lady's Hole (Inlet);
(4S) Lady's Hole (current surge); (4E) Ebbe's Snook.

Marsden; (5M) Byer's Hole.

Key

<u>*Laminaria hyperborea*</u>

New lamina

2P 3.0 ○

2P 7.6 ●

4L 3.0 △

4L 7.6 ▲

5M 2.4 □

5M 3.7 ■

<u>*Laminaria digitata*</u>

New & Old lamina

New lamina

2P	○	4P	▲
2H	●	4L	▲
4S	+	5M	□
4E	■		

<u>*Laminaria saccharina*</u>

New lamina

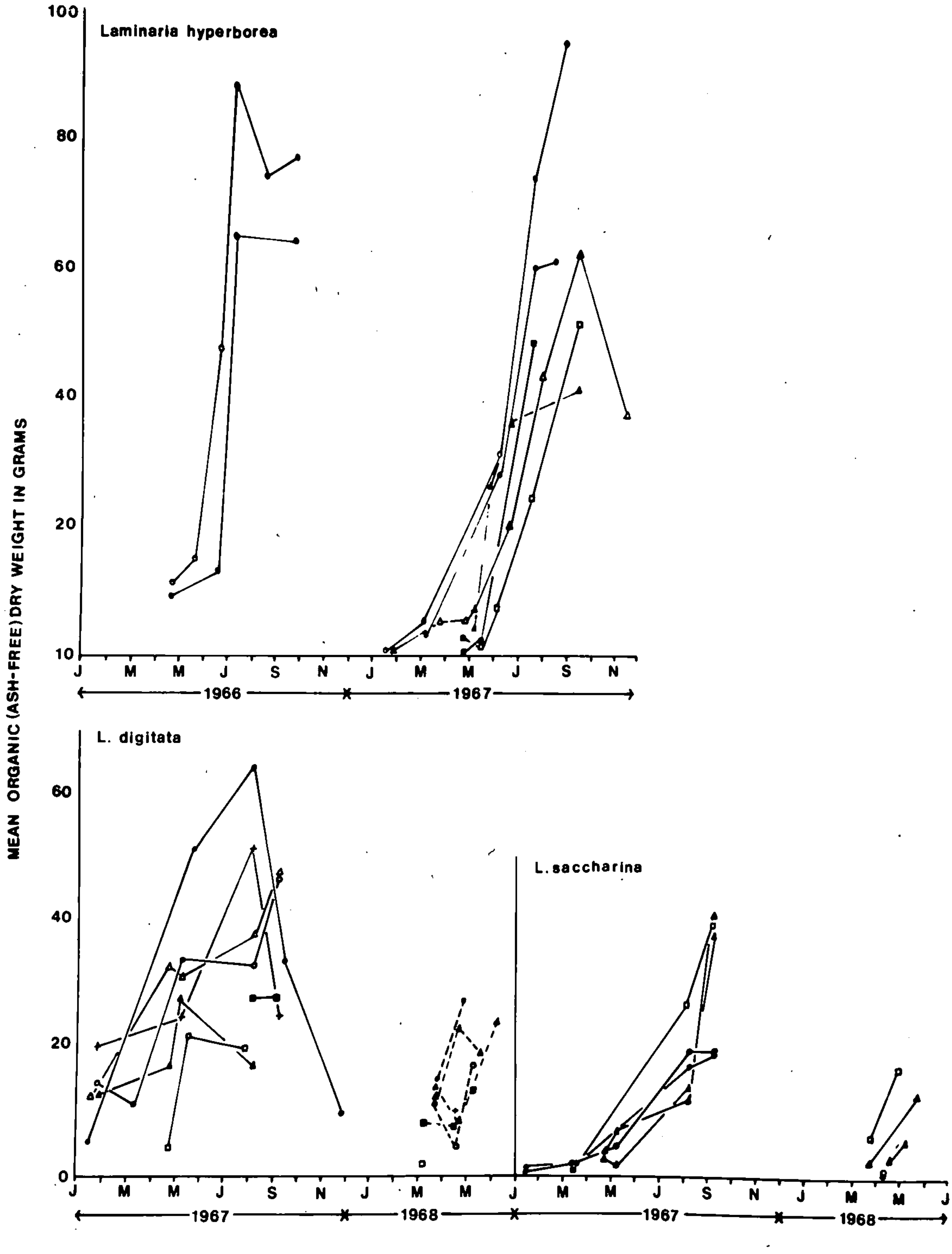
2P ○

2P ●

2H □

4P △

4L ▲



Laminaria hyperborea
L. digitata
L. saccharina
MEAN ORGANIC (ASH-FREE) DRY WEIGHT IN GRAMS
100
80
60
40
20
10
0
J M M J S N J M M J S N
1966
1967
1968
MONTH

Ecosystem Performance

Laminaria hyperborea

The percentages and the mean number of individuals within each age class per metre square from two depths at Petico Wick (South East Scotland) are shown in Fig. 5. There is a relatively even age distribution within each of the ecosystems with there being two relatively high peaks in age classes one and two.

The net annual production per metre square in the ecosystems at the two depths are given below.

Depth (m.-C.D.)	Hapteron	Stipe	Lamina	Total
3.0	131	236	1743	2110
7.6	95	119	698	912

Mean organic (ash-free) dry weight

There is a significant decrease in N.A.P.P. with increase in depth.

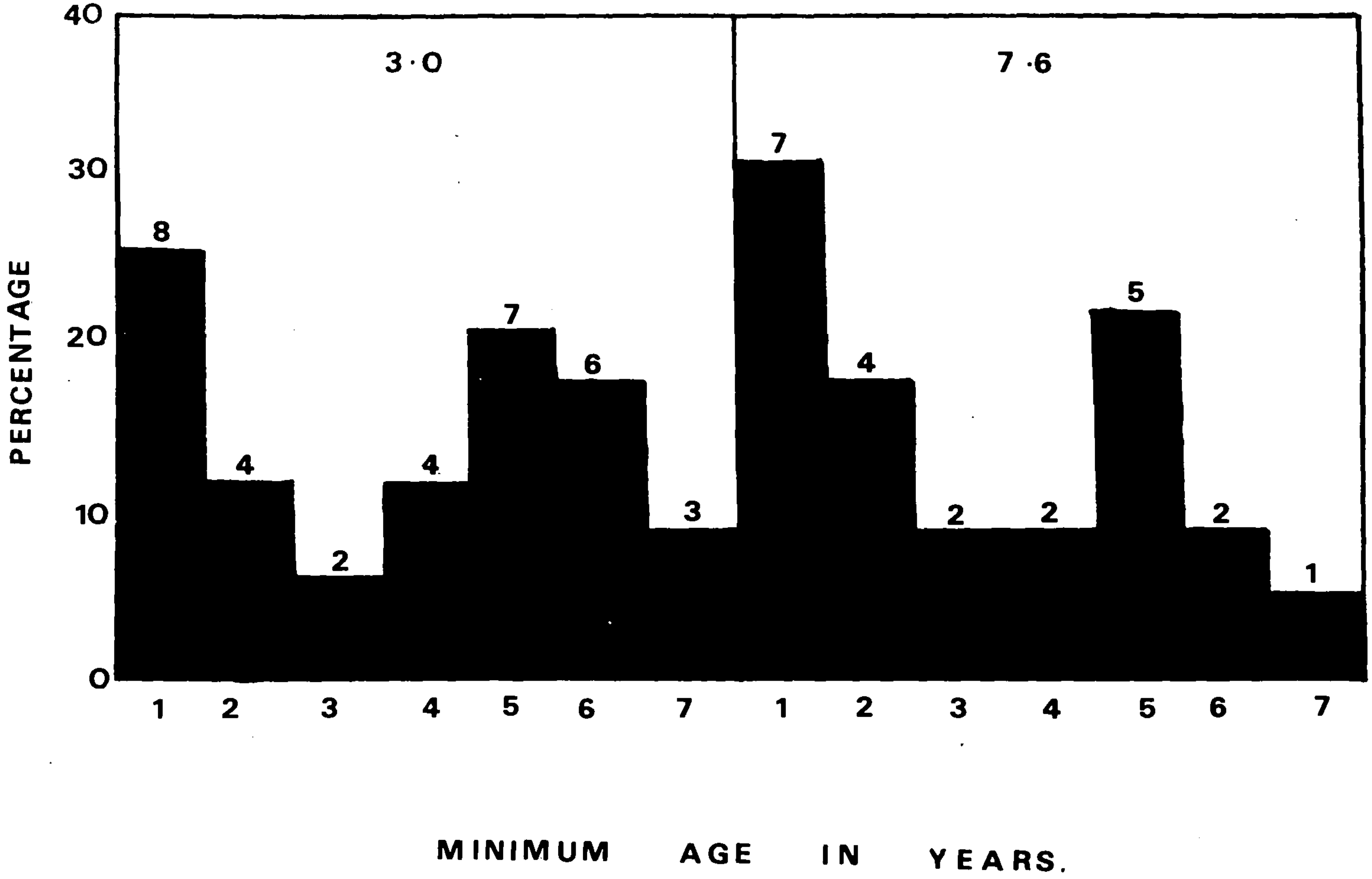
Laminaria ochroleuca

The percentages and the number of individuals within each age class per metre square in a number of ecosystems on the coast of North West Spain are shown in Fig. 6.

Many of the ecosystems have even age distributions with no large proportion of individuals which had arisen during one period (41A, 5.0; 42L, 5.0; 29L, 11.8; 41A, 8.4). An irregular age structure

FIGURE 5

The percentage and mean number of individuals in a metre square (mean of 10 samples) from two depths

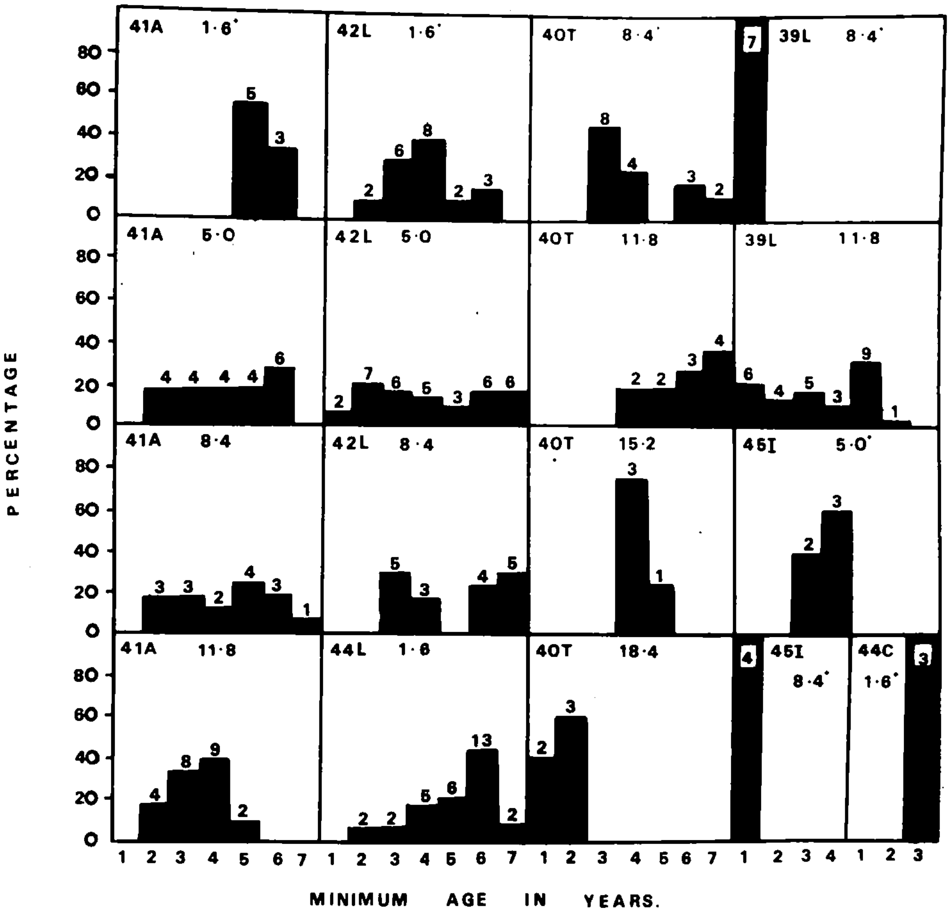


40
30
20
10
0
PERCENTAGE
3·0
7·6
8
4
2
4
7
6
3
7
4
2
2
5
2
1
1 2 3 4 5 6 7 1 2 3 4 5 6 7
MINIMUM AGE IN YEARS.

FIGURE 6

The percentage and mean number of individuals in a metre square

(mean of two samples)



PERCENTAGE
41A 1·6
42L 1·6
40T 8·4
39L 8·4
41A 5·0
42L 5·0
40T 11·8
39L 11·8
41A 8·4
42L 8·4
40T 15·2
45I 5·0
41A 11·8
44L 1·6
40T 18·4
45I 8·4
44C 1·6
MINIMUM AGE IN YEARS.

is usually associated with deep water ecosystems or ones in which Saccorhiza polyschides is co-dominant. The N.A.P.P. is determined from the stipe and lamina production figures given in Appendix 7 and Tables 54-55. The production figures for the haptera are obtained from the summed data from all the ecosystems.

The site and composite plot production data is given in Table 56 and the main trends are summarised in the following table.

Association Laminarietum ochroleucae

Subassociation T. Typicum, C. Cystoseiretosum

Variant (Dp.) Deep water, (Ex.) Exposed
(tp.) typicum, (sh.) sheltered

	C (sh.)	C (sh.)		T	T (tp.)		C (sh.)	
Site	44L	41A	42L	40T	39L	45I	44C	
Exposure	A	C	C	D	E	F/C	F/C	
Depth (m.-C.D.) 1.6	1662	541*	444*	-	-	-	19*	(T.tp.)
5.0	-	799	1146	-	-	71*	-	(T.tp.)
8.4	-	752	1096	564*	3	84*	-	(T.tp.)
11.8	-	387	-	565	570	-	-	(T.tp.)
15.2	-	-	-	74	-	-	-	(T.tp.)
18.4	-	-	-	30	-	-	-	(T.dp.)

*mixed ecosystems

N.A.P.P.

The highest values for N.A.P.P. are found in the very sheltered shallow water ecosystems in the lagoon at the Playa de Lago.

Table 56

The relevant site and plot production per metre square

Site	Exposure Type	Exposure Scale	Pollution	Natural allochthonous material	Turbidity	Depth (m.-C.D.)	Hapteron	Stipe	Lamina	Total
44L	A	0	+	+	2	1.6	86	456	1066	1662
41A	C	9	+	+	3	1.6*	23	31	487	541
						5.0	41	60	698	799
						8.4	40	59	653	752
						11.8	21	30	336	387
42L	C	4	+	+	3	1.6*	37	115	292	444
						5.0	75	171	900	1146
						8.4	51	204	840	1096
40T	D	14	+	+	3	8.4*	33	91	440	564
						11.8	42	136	412	565
						15.2	7	6	61	74
						18.4	.5	1	29	30
39L	E	25	+	+	3	8.4	.7	.3	2	3
						11.8	32	90	448	570
45I	F/C	10	+	+	3	5.0*	6	4	61	71
						8.4*	.4	1	6	7
44C	F/C	0	+	+	3	1.6*	.5	.5	18	19

*mixed ecosystem

There is a general trend towards a progressive decrease in plot performance with increase in exposure to water movement and increase in depth below a certain level. A low plot performance is only found in shallow water where the ecosystem is co-dominated by Saccorhiza polyschides.

Saccorhiza polyschides

The data for the net annual production per metre square is given in Table 57 and the most significant trends in N.A.P.P. are highlighted in the following table.

Association Saccorhizetum polyschides

Subassociation Typicum

Variant (Ex.) Exposed, (Tp.) Typicum

Site Exposure	Tp. 41A C	Tp. 42L C	Tp. 40T D	Ex. 39L E	45I F/C	44C F/C
1.6	807*	1472*	998*	1088	3269	3882*
3.6	-	-	1214	1821	-	-
5.0	-	-	-	-	2042*	-
7.6	-	-	[illegible]82	1934	-	-
8.4	-	-	-	-	489*	-

*mixed ecosystems

The highest values for N.A.P.P. in the ecosystems subjected to onshore wave action occur in those which are exposed. The highest values for N.A.P.P. in this region are found in those ecosystems which

Table 57

The relevant site and plot production per metre square

Site	Exposure Type	Exposure Scale	Pollution	Natural allochthonous material	Turbidity	Depth (m.-C.D.)	Hapteron and Stipe	Lamina	Debris	Total
41A	C	9	+	+	3	1.6*	366	409	32	807
42L	C	4	+	+	3	1.6*	878	572	22	1472
40T	D	14	+	+	3	1.6*	466	486	46	998
						3.6	654	546	14	1214
						7.6	29	53	0	82
39L	E	25	+	+	3	1.6	593	479	16	1088
						3.6	1114	707	0	1821
						7.6	1069	851	14	1934
45I	F/C	10	+	+	3	1.6	2159	1110	0	3269
						5.0*	910	921	211	2042
						8.4*	246	231	12	489
44C	F/C	0	+	+	3	1.6*	2047	1718	117	3882

*mixed ecosystem

are exposed to and also subjected to considerable current surge.

Part IV

GRAZING EXPERIMENTS

Introduction

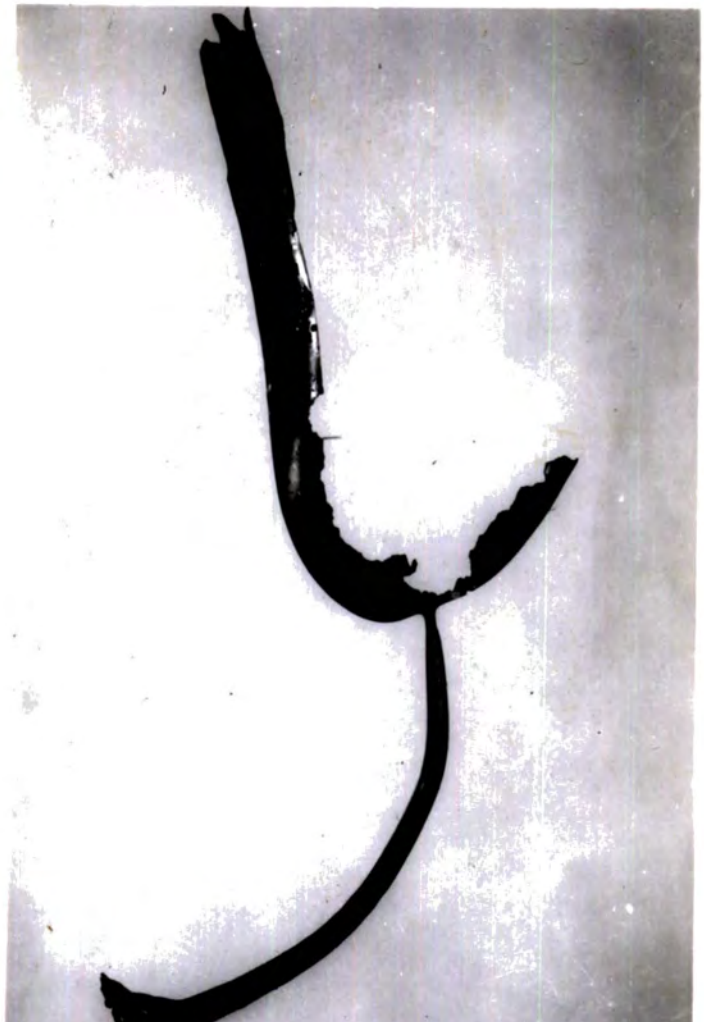
The methods used in the comparative work described above were specifically designed to eliminate the effects of grazing within the ecosystems studied. However, during the course of this study much data were gained regarding the effect of grazing organisms and these together with certain skeletal experimental studies are described in this section.

The Problem

Two groups of organisms appear to be the main kelp grazers in the British Isles. Echinoderms, mainly Echinus esculentus and Paracentrotus lividus; and limpets, especially Patella spp. and Patina pellucida. The experimental removal of Echinoderms in a number of widely separated regions (Neuschul, 1958; Kitching and Ebling, 1961; Leighton, et al, 1966; Neill and Larkum, 1966; Jones and Kain, 1967) have indicated the important role of these browsers in the ecesis of kelp sporophytes. Similar evidence was obtained from a study of the "Torrey Canyon" disaster area where, in localities badly effected by oil and detergent, much of the browser populations were destroyed and dense populations of kelp forest seedling developed (Bellamy et al, 1967b). Jones and Kain (1967) have presented experimental evidence to show that the lower limit of the Laminaria hyperborea forest may be determined by the grazing pressure of Echinus. Similarly Kain (1964) has suggested that grazing by Patina pellucida could be an important factor controlling the performance of the kelp forest.

FIGURE 7

The effect of grazing by *Echinus* on the lamina of *Laminaria hyperborea*



Patina can effect species of *Laminaria* 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 branches. Secondly, infestation of the laminae and its consequent damage.

Observations

Echinus esculentus

Throughout the whole study only one case of active grazing of adult individuals of *Laminaria* by *Echinus* was recorded. Fig. 7 (included by kind permission of D. Jones) shows a 3 year old individual from a forest in which the understorey had been completely decimated by a dense population of *Echinus* (20-50 /m^2). However in this case none of the canopy plants had been damaged.

It would seem that *Echinus* grazing must therefore have its main effect on the haplophase and the sporeling stage of the diplophase and so in order to gain first hand information on this the enclosure experiment described below was set up.

Patina pellucida

Laminaria hyperborea. The level of infestation was recorded in all the ecosystems studied (any individual with one or more cavities at the base of the stipe, whether occupied or not, was counted as infested and was therefore omitted from the production calculations). The composite results of the percentage infestation are given in Fig. 8. They show that the level of infestation is very low and is mainly confined to the upper age classes. This is in agreement with Kain's (1964) findings in which she concludes that the larger surface area of the hapteron and the longer time of exposure of the individual to "spat falls" can explain the susceptibility of the older individuals. The expected fall-off in the infestation of individuals from the highest age classes, due to the differential loss of the infested individuals from the population, was not found in those studied.

In none of the ecosystems studied was *Patina* infestation greater than 38% in any age class, whilst Kain (1963) found infestation to be as high as 40-50%.

Laminaria digitata. The data for the percentage infestation of all ecosystems studied are given in Fig. 9. The very high infestation level is very striking when compared to the *Laminaria hyperborea* forest. This is in itself noteworthy as individuals of *Laminaria digitata* are rarely found older than 5 years and therefore the hypothesis of increased chance of infestation with longevity of about 5 years is in some doubt. Similarly it would be expected that loss of infested individuals would be much more likely in the immediate sublittoral (*Laminaria digitata* forest belt) than in the deeper *Laminaria hyperborea* forest. Fig. 10 gives comparative infestation levels for the ecosystems at Beadnell.

FIGURE 8

The percentage infestation in individuals of each age class from all the ecosystems dominated by this species. The figure above each column indicated the numbers of individuals in that age class.

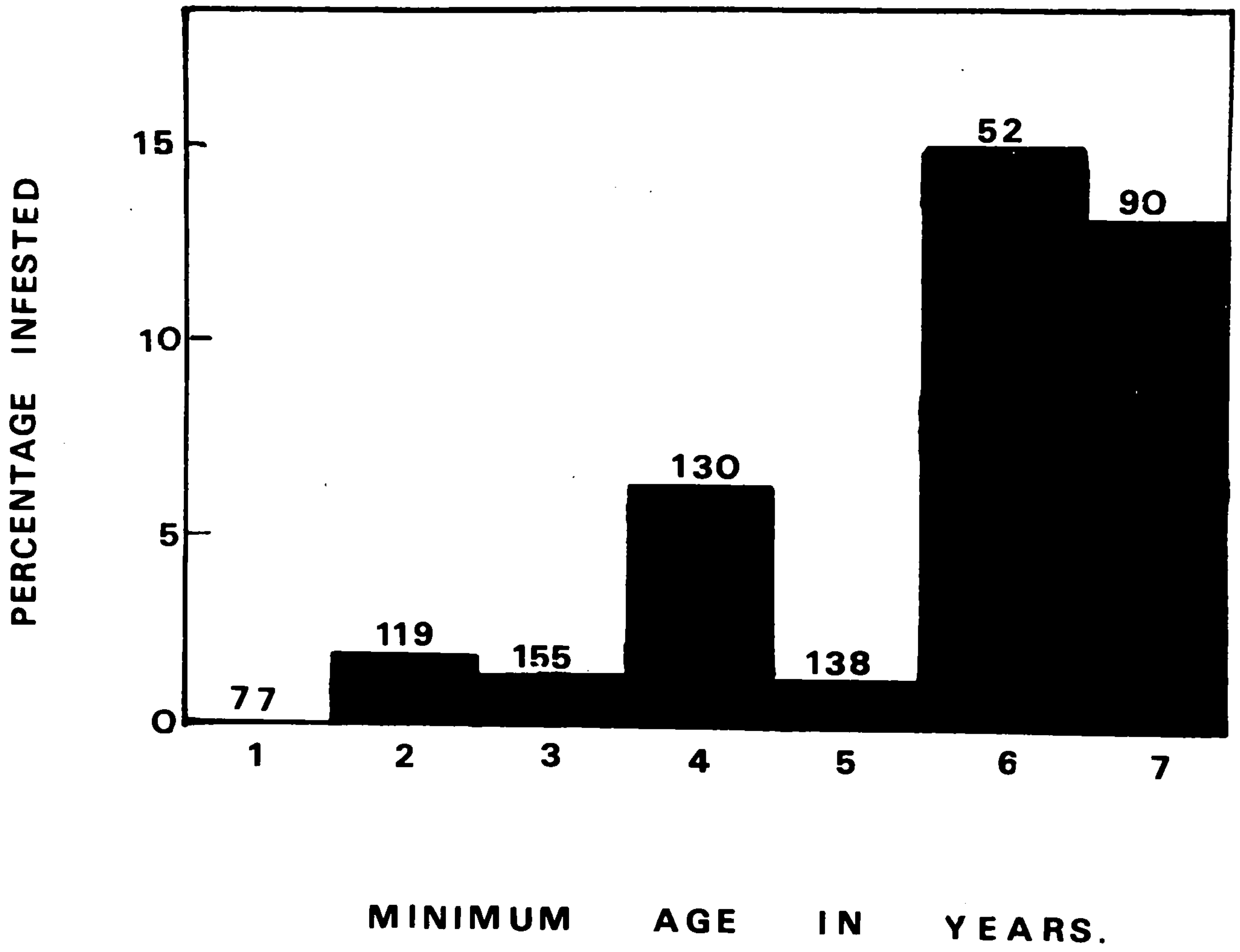

PERCENTAGE INFESTED
15
10
5
0
77
119
155
130
138
52
90
1
2
3
4
5
6
7
MINIMUM AGE IN YEARS.

FIGURE 9

The percentage infestation in individuals of each age class from all the ecosystems dominated by this species. The figure above each column indicates the numbers of individuals in that age class.

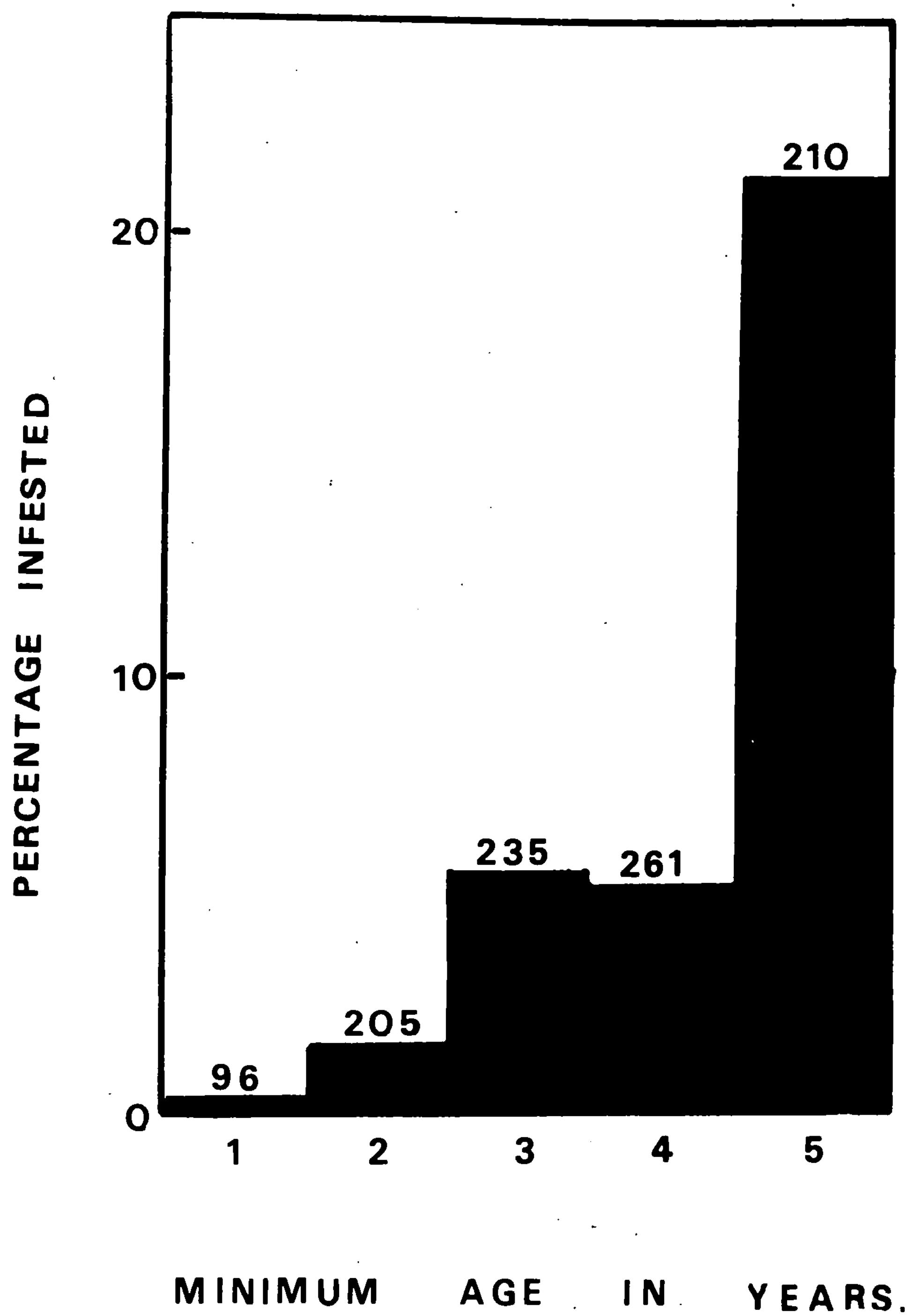
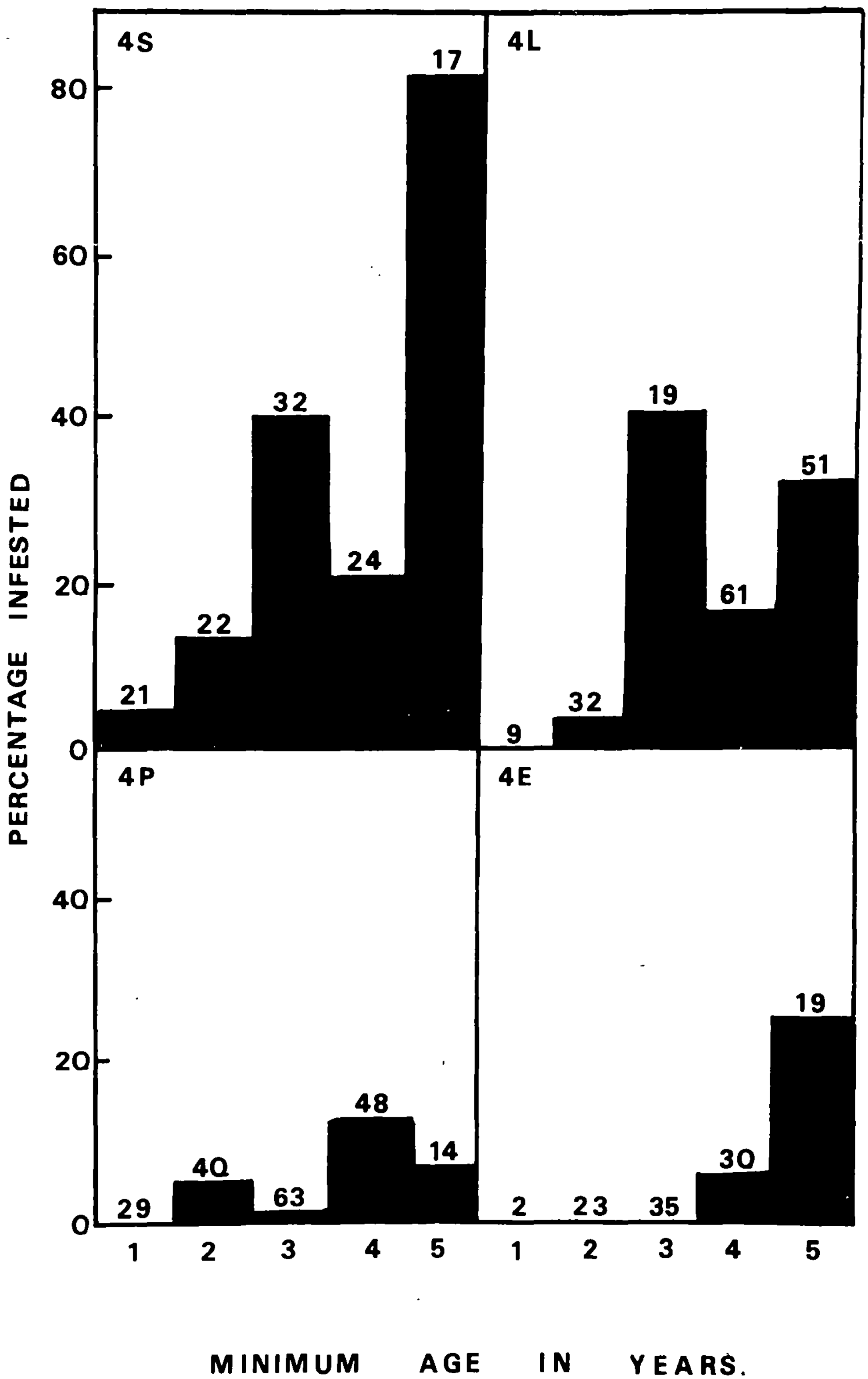

PERCENTAGE INFESTED
20
10
0
96
205
235
261
210
1
2
3
4
5
MINIMUM AGE IN YEARS.

FIGURE 10

The percentage infestation in individuals of each age class from four ecosystems at Beadnell: (4S) Current surge; (4L) Inlet; (4P) Tide pool; (4E) Ebbe's Snook


4S
4L
4P
4E
80
60
40
20
0
40
20
0
17
32
24
22
21
19
51
61
32
9
48
40
63
14
29
19
30
2
23
35
1 2 3 4 5 1 2 3 4 5
PERCENTAGE INFESTED
MINIMUM AGE IN YEARS.

There is considerable variation in the figures but it is evident that in general the highest values are from ecosystems in sheltered or current surge situations. This contrasts with the results of Kitching (1941) who found that the greatest density of Patina was to be found on the most exposed side of Carsaig Island (West Scotland).

Laminaria saccharina. Less than 1% of the individuals studied were found to be infested with Patina and it would therefore seem reasonable to conclude that Patina is not important in the kelp forest dominated by Laminaria saccharina. Similarly careful observation showed that Echinus was very rarely present in the ecosystems dominated by Laminaria saccharina, and it is suggested that this is due to the habitat preference of this species being unstable boulders often lying on sand. The sand offering no grazing and the unstable boulders being a hazard to any slow moving organism during rough sea conditions.

Experimental Work

Enclosure experiments

Two plots were selected at Petico Wick (South East Scotland), one "shallow" at 3.0 m in a dense Laminaria hyperborea forest and the other "deep" at 13.1 m in an open forest. All macrophytic algae and benthic fauna were removed from approximately 10 $/m^2$ of continuous rock surface at each depth. Enclosures, constructed as shown in

Appendix 8 were erected to one side of each cleared plot. They were visited at regular intervals and any small animals which had been able to gain entry were removed. Unfortunately the deep enclosure was lost during stormy weather early in 1967. Therefore results were only obtained from the shallow water plot. The density of the first year laminarians was estimated inside and outside the enclosures after a period of one year (October 1966 to October 1967) by using 10 overlapping $\frac{1}{2}$ metre square quadrats to sample the whole area in each case. The results show no marked difference with there being 10 to 17 individuals of Laminaria hyperborea per square metre within the enclosure and 14 to 19 outside. Likewise a nearly equivalent number of scattered individuals of Laminaria saccharina were found inside and outside the enclosure. Therefore it would seem that grazing by Echinus during the period of the study had no effect on the performance of the Laminaria hyperborea forest studied. The only inference which can be drawn is that much more data are required concerning the population dynamics and movement of Echinus.

Lamina experiments

The following experiments were set up to investigate the effect of lamina grazing by Patina.

Two forests of Laminaria digitata were sellected, one in a moderately exposed situation in Petico Wick (South East Scotland), and the other in a sheltered inlet at Lady's Hole, Beadnell (North East England).

The individuals for study at each locality were selected and tagged with "Darvic" bird rings. The basal 10 cms of each lamina was removed in December 1966 from half of the tagged individuals. Regular observations were made. It was found that by March 1967 all the lamina, both of untreated and treated individuals, were infested with Patina (5-25 /5sq. cms) at Petico Wick, whereas those at Beadnell were devoid of Patina although being in a more sheltered situation.

All infested laminae showed distinct signs of grazing. The untreated plants were otherwise quite healthy and are still surviving in the population. This is in marked contrast to the treated plants which were bleached and appeared to be in a decidedly moribund state, being lost from the population by May 1967. At Beadnell, where there had been no infestation, both treated and untreated plants remained in a healthy state and were still present in the population late in 1967.

Therefore it is suggested that either the slow rate of growth of the small laminae of treated plants was insufficient to keep pace with the rate of grazing, or that in the absence of the old lamina grazing was concentrated on the lower regions and the intercalary meristem was effected.

The results indicate that grazing by Patina may have a severe effect on both individual and plot production of Laminaria digitata especially in years of heavy spat fall.

Part V

TRANSPLANT EXPERIMENTS

Introduction

It was realised early in the investigation that in situ measurements of the performance of individuals within the complex kelp forest ecosystems can only give indications of the factors causing the observed differences. Proof can only be obtained in the culture tank under accurately controlled conditions. As a step towards this it was decided to set up growth experiments in the field where at least a number of the variables could be eliminated.

Experiment to measure the performance of 1st year individuals of *Laminaria hyperborea*, *Laminaria digitata* and *Laminaria saccharina* at three different depths.

Methods

First year individuals of the three species were collected from sublittoral kelp forests at the beginning of the period of fast growth (January 1966). After removal of the old lamina and measurement (see below), they were attached to polythene frames which were secured to platforms suspended at 1.5, 7.6 and 13.7 m at Petico Wick. The method of attachment of the individuals to the frames and the details of the constructuion of the platforms is given in Appendix 9. The frames were left in position until June 1967 when all the plants were removed and brought back to the laboratory for measurement.

Measurements and Manipulation

Initial

(1) The areas of the new laminae were determined using an E.E.L.

area meter with a correction being made for the amount of light transmitted through the organ. Other laminae of known area were dried to constant weight at 100°C and ashed at 440°C so that the original organic (ash-free) dry weight of each lamina could be calculated.

(2) The lengths of the stipes and laminae were measured.

(3) Certain individuals of each transplant population were treated in the following way. Holes were punched at 1 cm intervals from the tip of the base of the lamina and a record of the number punched was kept.

(4) All the individuals could be recognised at the end of the experiment by the position they occupy on each frame (see Appendix 9).

Final

(1) The organic (ash-free) dry weights of the laminae were determined and their increment obtained.

(2) Similarly stipe and lamina lengths were measured and the increment calculated.

(3) The number of holes remaining in the laminae of the marked individuals were counted and a measure of the amount of material lost by erosion from the tip of the lamina was obtained.

Results

The composite data for individuals of each species are given in Tables 56-58 in Appendix 10.

Although there is a certain amount of variation in the growth "performance" of individuals from the same depth they all still show the same overall trends which are summarised below.

(1) The performance of the individuals of all three species decreases significantly with depth. The only exception is the length of the laminae of Laminaria digitata from the 1.5 and 7.6 m. levels.

(2) There are indications that the loss of tissues from the laminae is greater in the shallow water treatments.

(3) Erosion of the laminae of Laminaria digitata is markedly less than for the other two species.

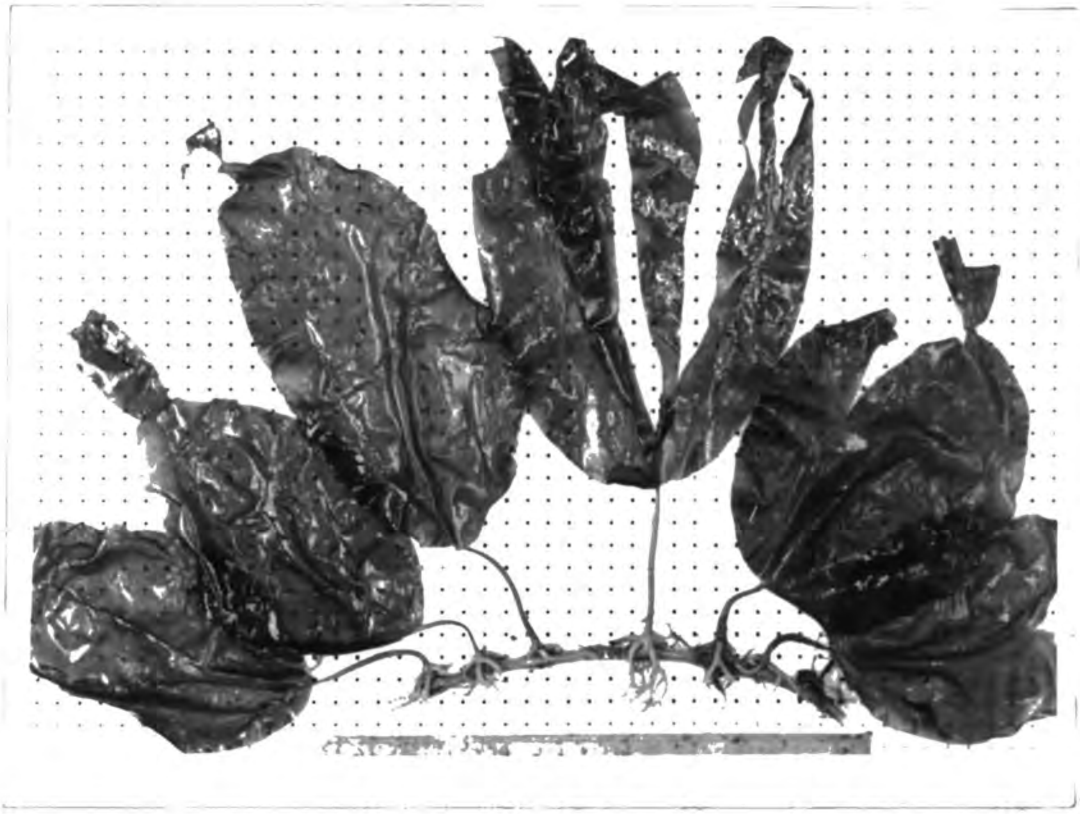
Discussion

The data is insufficient to drawy any firm conclusions; all that can be said is "that there are indications that". The findings are consistent with the accepted ideas of ecological control in inshore marine ecosystems. The attenuation of light with depth could well explain the fall-off in performance with depth. Similarly the increased effect of water movement nearer the surface could explain the greater erosion of the laminae at the 1.5 m. level, although more rapid lamina growth producing a "weaker" lamina must not be overlooked. The indication of greater "strength" of the lamina in Laminaria digitata is not inconsistent with its usual position on the shore. The similarity in the length of the laminae of the individuals of Laminaria digitata at 1.5 and 7.6 m. levels appears to be due to a change in morphology (fig. 11).

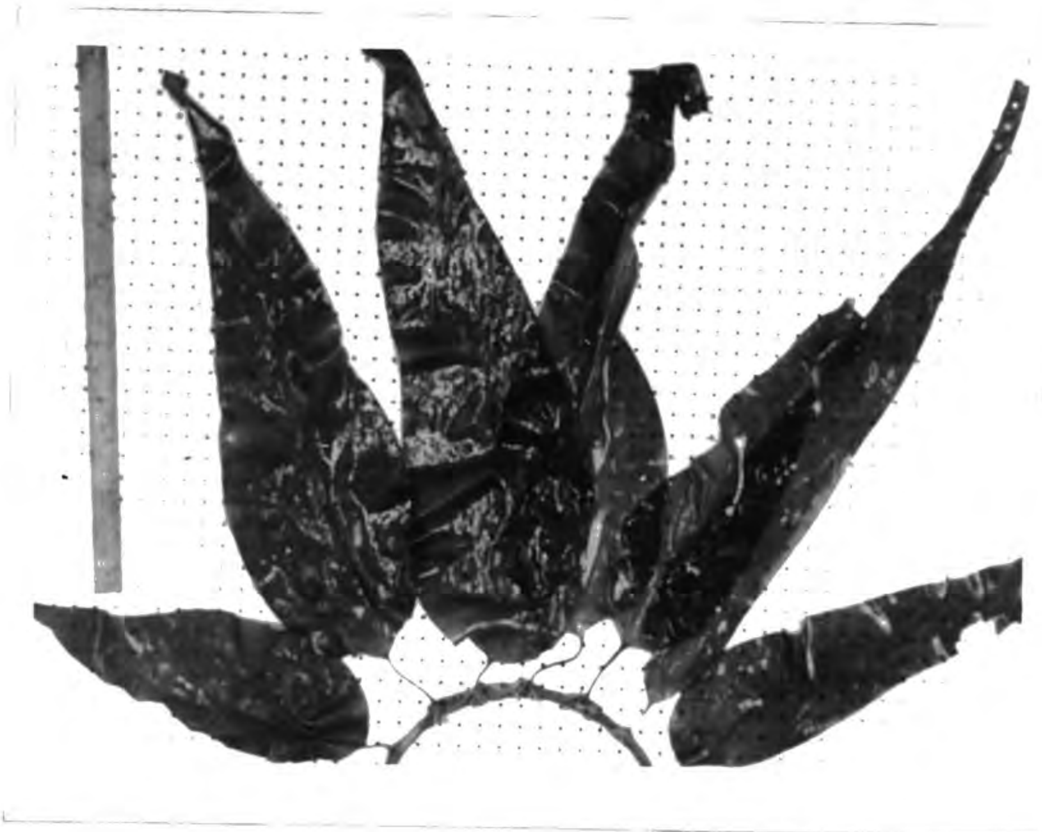
FIGURE 11

The change in morphology of the lamina with depth

1.5 m.



7.6 m.



Part VI

THE ORGANIC (ASH-FREE) DRY WEIGHT

Introduction

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

To investigate this further the data from the regularly sampled ecosystems on the coasts of North East England and South East Scotland are discussed below.

Methods

Sub-samples of all the plants' parts were removed, dried to constant weights at 100°C and then ashed in a muffle furnace at 440°C. The results for organic (ash-free) dry weight are presented as a percentage of the total dry weight.

The composite results for stipes and laminae in each age class are given in Table 59. There appears to be no significant difference between age classes when an ecosystem is sampled at one time in the year.

It would therefore seem reasonable when studying seasonal variation to select individuals of any age for comparison.

Lamina data

Laminaria digitata

The comparable data for ecosystems from three localities

Table 59

Variations in the lamina and stipe between individuals from a number of age classes

Laminaria hyperborea

	Minimum age in years					
	2	3	4	5	6	7
Stipe	65	62	66	63	67	64
	61	59	63	61	62	63
	69	71	67	69	67	67
New lamina	74	74	72	70	76	76
	68	67	70	66	65	70
	74	74	72	73	72	74
Old lamina	66	68	60	71	67	70
	69	69	75	75	64	68
	81	82	66	82	83	81

Laminaria saccharina / Laminaria digitata

	L. saccharina 1	2	3	*L. digitata* 2	3	4	5
Stipe	55	61	70	60	63	67	66
	74	70	70	64	64	67	65
	71	67	67	60	60	69	63
New lamina	54	60	60	65	66	65	67
	64	61	59	65	67	67	66
	62	60	60	63	66	71	64
Old lamina	54	61	63				
	67	60	62				
	53	60	57				

Mean organic (ash-free) dry weight as a percentage of the dry weight are presented in Table 60 in Appendix 11 and summarised in graph form in Figure 12. The ecosystems at the two more southerly localities (Marsden and Beadnell) have a minima early in the year (January to July) and a maxima at the end of the growing season (September to December). In the more northerly locality at St. Abb's Head there is a seasonal maxima in May and a minima in December in the ecosystem at the harbour (St. Abb's Head), whilst the maxima is from January to September and the minima is from March to August in the one at Petico Wick.

It is interesting to note that the same pattern of change is shown by each ecosystem in two consecutive years indicating that these are real and not chance differences.

Laminaria hyperborea

The results are presented in Table 61 in Appendix 11 and summarised in Figure 13. In all ecosystems studied the maximum values for organic (ash-free) dry weight (80.0-84.2) are obtained by September and the minima (60.0-65.2) from March to April. There are no significant differences between these values and the seasonal changes in the deep and shallow water ecosystems at any locality. Again there was found to be no difference between the means and the trends over two seasons and therefore only the composite data is presented.

The results show that as the new lamina develops the organic content of the old one falls, this could indicate that there is either translocation of material between the two and/or an actual loss of organic material due to the breakdown and continued sporogenesis of the old lamina. The importance of the further investigation of this

FIGURE 12

Seasonal variation in the new and old laminae of

Laminaria digitata.

Beadnell: (4P Tide pool; (4L) Lady's Hole (Inlet);

(4S) Lady's Hole (Current surge); (4E) Ebbe's Snook.

St. Abb's Head: (2) Harbour; (2P) Petico Wick.

Marsden: (5M) Byer's Hole.

Key

o 1967

• 1968

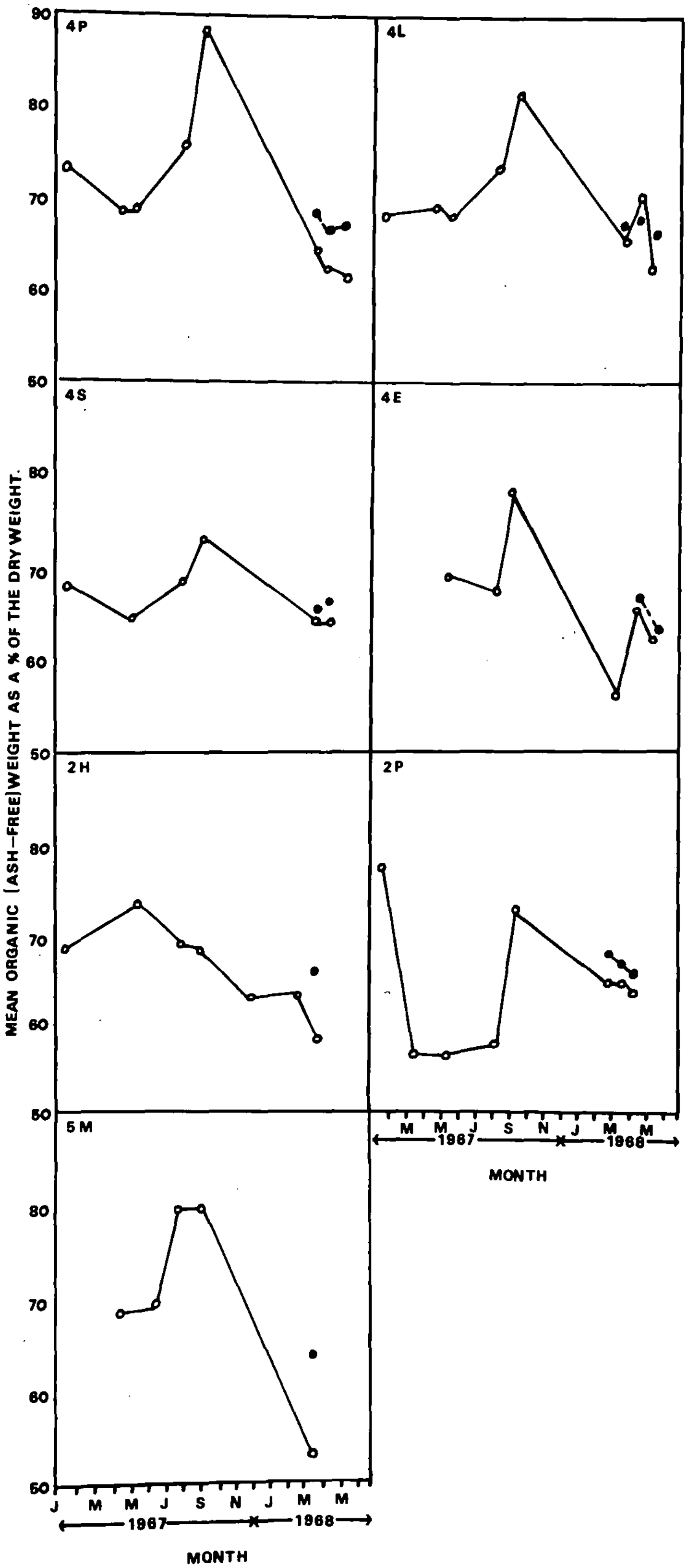

4P
4L
4S
4E
2H
2P
5M
90
80
70
60
50
MEAN ORGANIC (ASH-FREE) WEIGHT AS A % OF THE DRY WEIGHT.
J M M J S N J M M
1967 1968
MONTH

FIGURE 13

Seasonal variation in the new and old laminae of

Laminaria hyperborea.

Beadnell: (4L) Lady's Hole (Inlet).

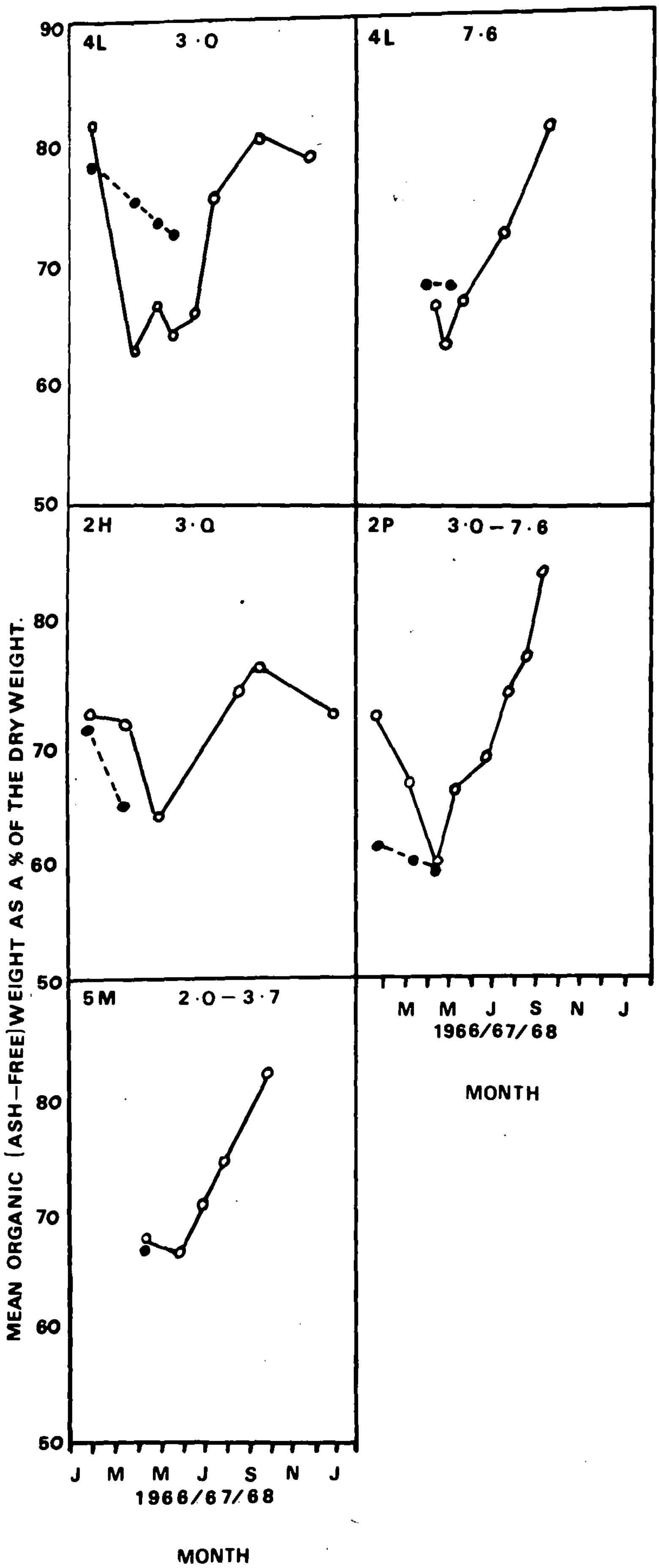
St. Abb's Head: (2H) Harbour; (2P) Petico Wick.

Marsden: (5M) Byer's Hole.

Key

o New lamina

● Old lamina



4L 3·0
4L 7·6
2H 3·0
2P 3·0 – 7·6
5M 2·0 – 3·7
90
80
70
60
50
MEAN ORGANIC (ASH–FREE) WEIGHT AS A % OF THE DRY WEIGHT.
J M M J S N J
1966/67/68
MONTH

phenomenon in relation to the measurements of actual production is indicated.

Laminaria saccharina

The results are presented in Table 62 in Appendix 11 and are summarised in Figure 14. There is again no significant difference between the values for consecutive years.

The seasonal maxima (75.2-85.1) is reached in all the ecosystems from August to September whilst minimal values (57.5-63.1) are found in March.

Discussion

The values for organic (ash-free) dry weight and the main trends of variation with the season are in good agreement with those found by other investigators working in widely separate geographical regions. However the variations do indicate that it is essential to reduce all measurements to organic (ash-free) dry weight (organic content) for comparative work.

Saccorhiza polyschides

Comparison of the organic (ash-free) dry weight of the stipe plus bulbate holdfast and lamina give results which are not consistent with those obtained by Black (1948b). There being found to be no significant difference in the organic (ash-free) weight of the stipe and bulbate hapteron (78.8 $\pm$ 5.9) and the lamina (82.3 $\pm$ 8.1) at the time of peak production.

FIGURE 14

Seasonal variation in the new and old laminae of

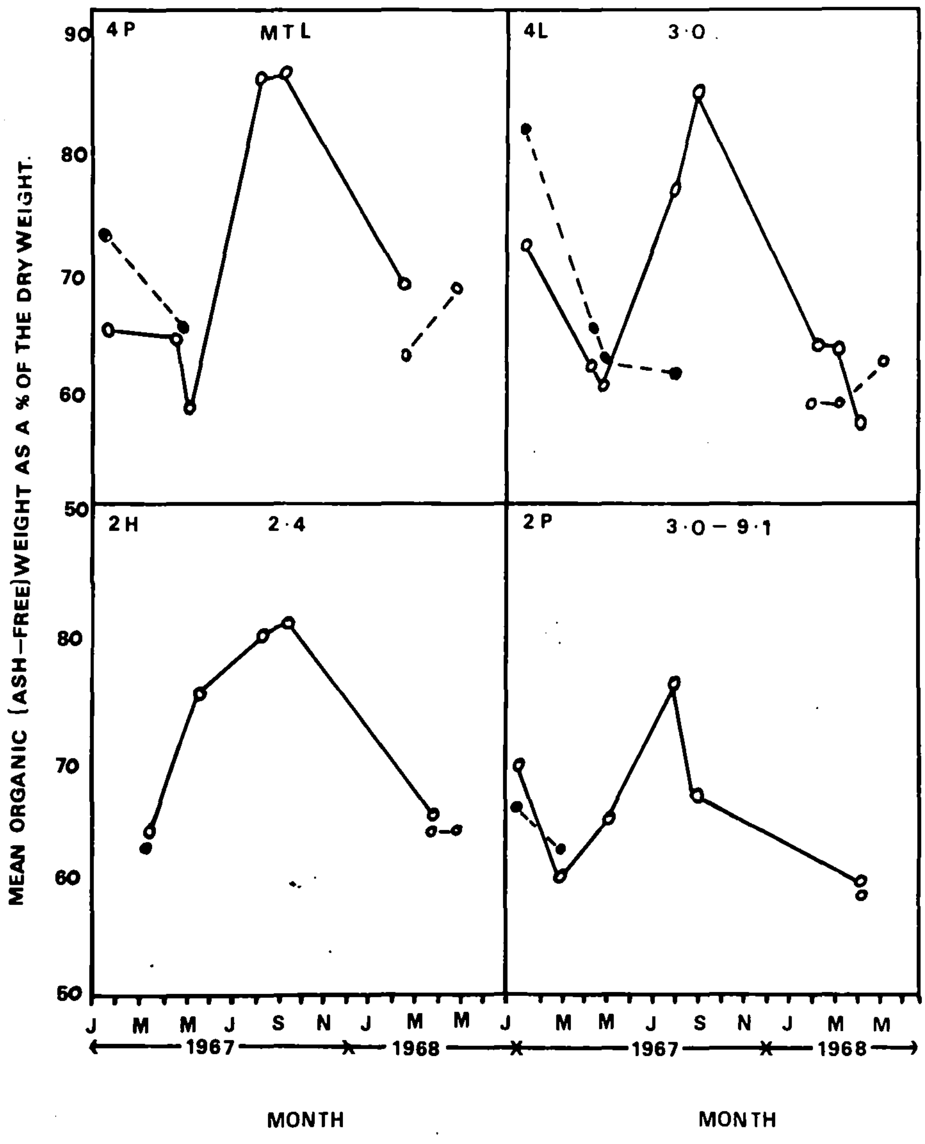
<u>Laminaria saccharina</u>.

Beadnell: (4P) Tide pool; (4L) Lady's Hole (Inlet).

St. Abb's Head: (2H) Harbour; (2P) Petico Wick.

Key

--●--	1966
—o—	1967
--o--	1968



MEAN ORGANIC (ASH-FREE) WEIGHT AS A % OF THE DRY WEIGHT.
4 P
MTL
4L
3·0
2 H
2·4
2 P
3·0 – 9·1
90
80
70
60
50
J M M J S N J M M
1967
1968
MONTH
MONTH

Stipe Data

The results for *Laminaria digitata* and *Laminaria saccharina* are presented in Tables 63-64 in Appendix 11 and summarised in Figures 15-16. It can be seen that there are fluctuations in the values but no significant seasonal variations, this is consistent with the findings of Black (1948b, 1950a,b), Black et al (1959), Haug and Jensen (1954) and Jensen and Haug (1956). These results again indicate the importance of ash determination in comparative studies of this type.

Hapteron Data

The difficulties of cleaning all extraneous mineral matter from the hapteron has been discussed above. It was necessary to ascertain as to whether the values for the hapteron differ from those of the stipe. In certain cases new haptera branches were selected or old ones were meticulously cleaned and then their ash weight determined. In no case was there any significant deviation from the stipe values.

Differences between Geographical Regions

The mean organic (ash-free) dry weight content of all the species sampled from the different localities are shown in Tables 65-67 in Appendix 11. The variations are not great and there are no consistent trends between regions except in the case of *Laminaria ochroleuca*

	Spain	England
Stipe	71.5 ± 2.3	56.3 ± 2.0
Lamina at peak biomass	70.8 ± 1.6	76.1 ± 2.5

FIGURE 15

The seasonal variations in the stipe of

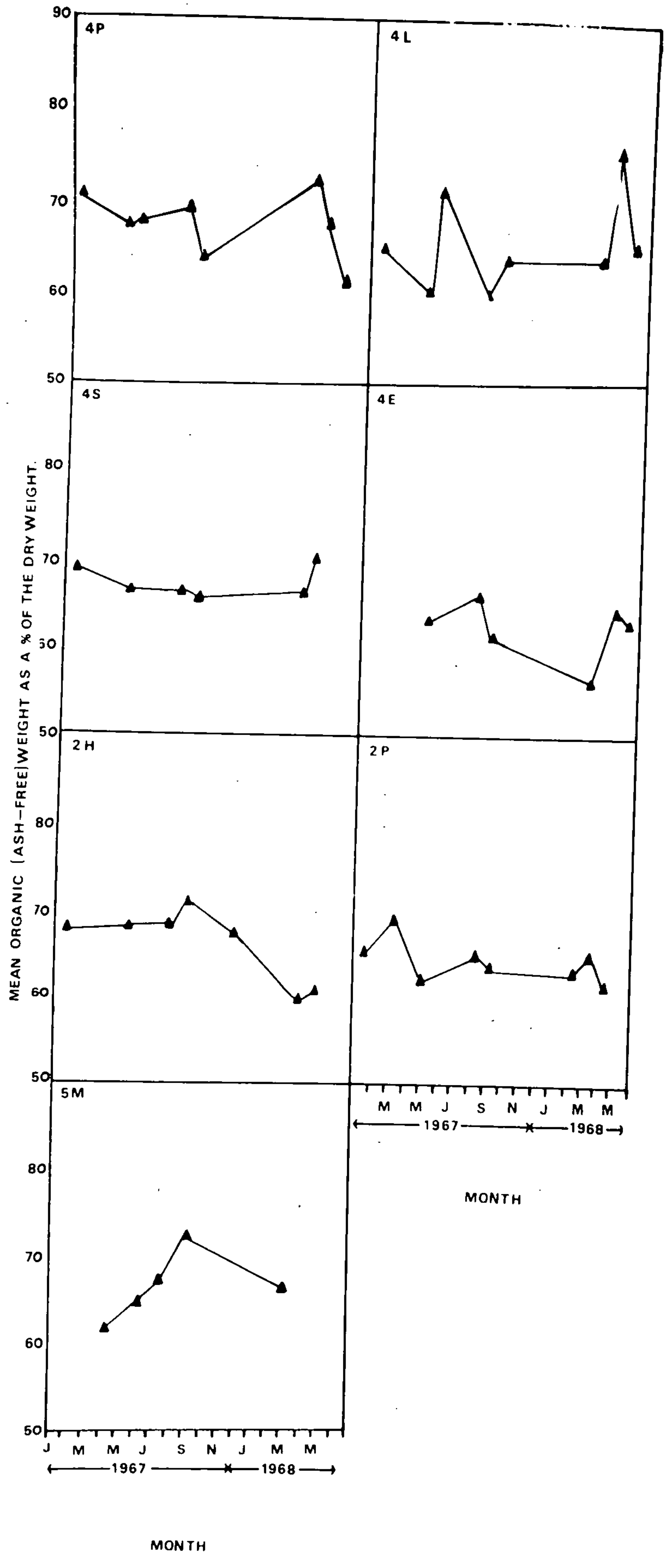
Laminaria digitata.

Beadnell: (4P) Tide pool; (4L) Lady's Hole (Inlet)

(4S) Lady's Hole (Current surge); (4E) Ebbe's Snook.

St. Abb's Head: (2H) Harbour; (2P) Petico Wick.

Marsden: (5M) Byer's Hole.



4P
4L
4S
4E
2H
2P
5M
MEAN ORGANIC (ASH-FREE) WEIGHT AS A % OF THE DRY WEIGHT.
90
80
70
60
50
J M M J S N J M M
1967
1968
MONTH

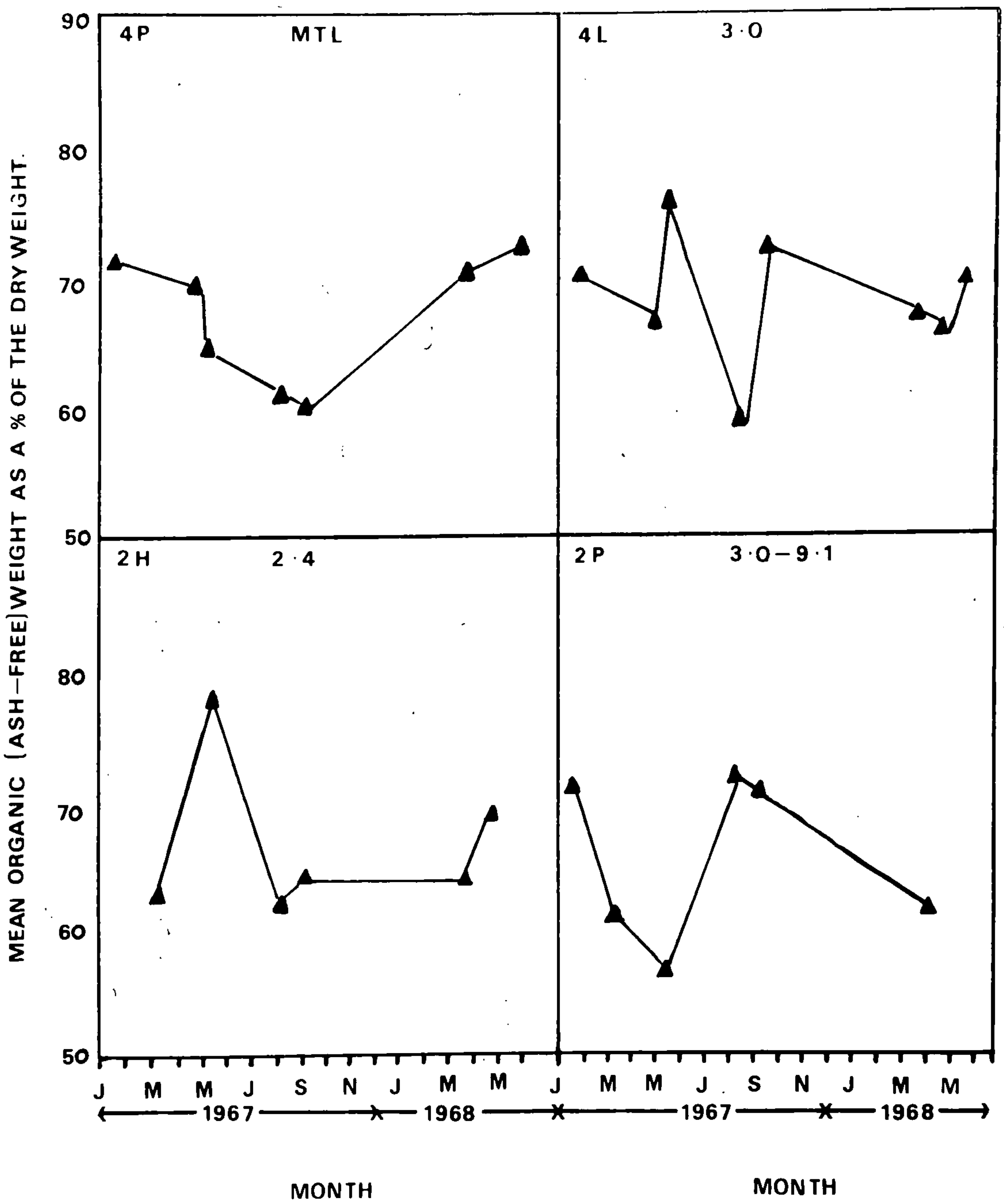
FIGURE 16

Seasonal variations in the stipe of

Laminaria saccharina.

Beadnell: (4P) Tide pool; (4L) Lady's Hole (Inlet).

St. Abb's Head: (2H) Harbour; (2P) Petico Wick.


4P
MTL
4L
3·0
2H
2·4
2P
3·0—9·1
90
80
70
60
50
MEAN ORGANIC (ASH—FREE) WEIGHT AS A % OF THE DRY WEIGHT.
J M M J S N J M M
1967
1968
MONTH

These differences are discussed in the appropriate section. It can only be concluded that the observed variations need much more study before explanations can be put forward to account for them. They do however show that determination of organic (ash-free) dry weights is essential for all comparative work of the type described in this thesis.

It is interesting to note that there is a certain correlation between the values for organic (ash-free) dry weight and the seasonal changes in lamina production.

Part VII

GENERAL DISCUSSION

The inshore marine ecologist is faced with two major problems; the great variation in environmental conditions over very short stretches of coast, and the element of chance in the recruitment and establishment of species whose dispersal phases are planktonic. These would appear to make a meaningful ecological comparison between sites very difficult. Figure 17 summaries some of the complex factors acting within and on the kelp forest ecosystem. Measurement of the environmental parameters; viz. current surge, wave action, turbidity, sedimentation and incident light energy, all require the development of integrating data logging equipment. The effects of damage and removal of individuals from the kelp forest both by grazing and wave action require long-term and detailed study. Similarly, measurements of the levels of nutrient and toxic substances require regular and detailed analysis to avoid drawing wrong conclusions from freak conditions.

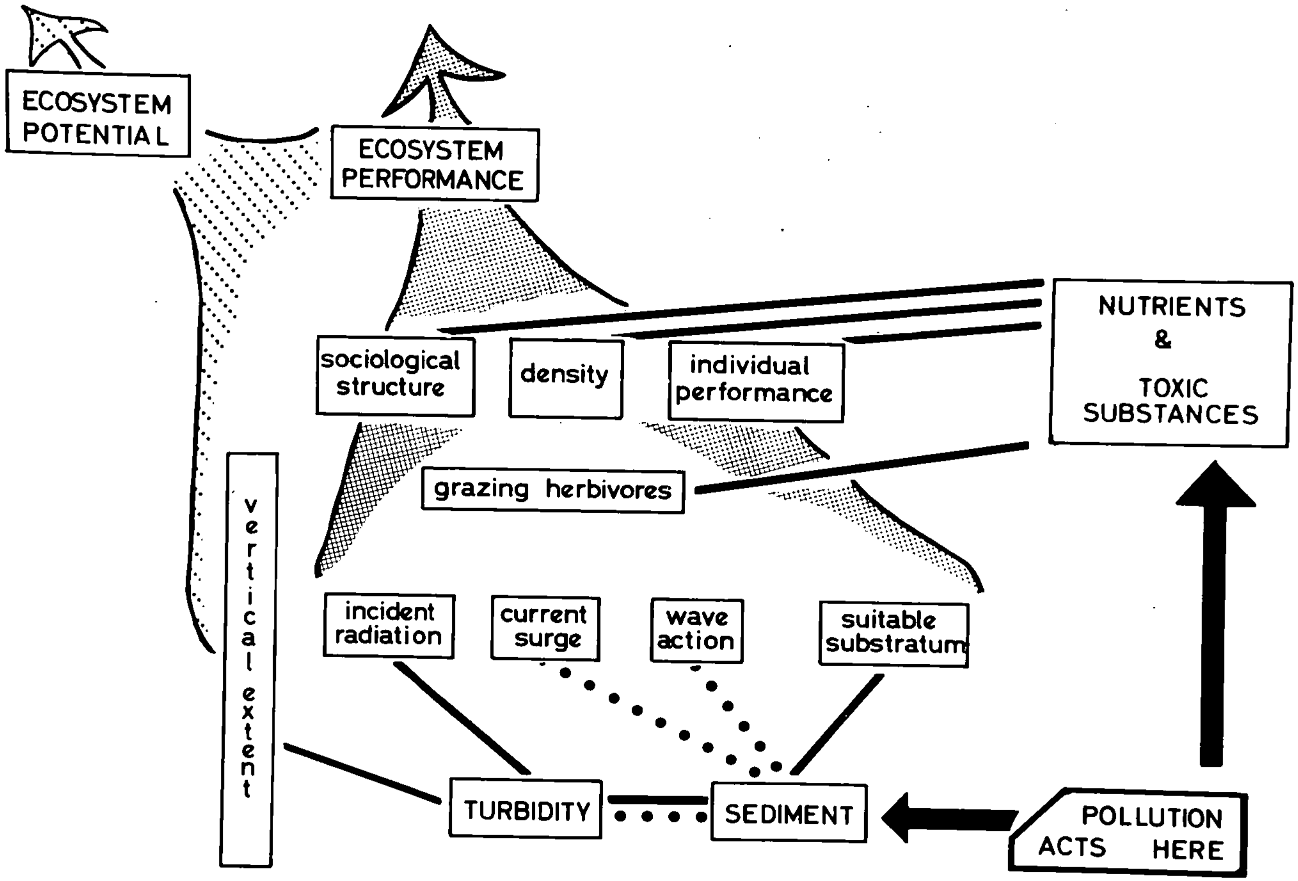
The work described in this thesis has shown that the ecosystem parametres summarised in Figure 17 can be measured simply and moderately accurately. The work thus indicates the possible role of the phytometer approach in an understanding of the factors controlling sublittoral ecosystems.

The environment and the ecosystem are two interacting information matrices, either one can therefore be used to interpret the other.

FIGURE 17

Factors acting within and on the

kelp forest ecosystem


ECOSYSTEM POTENTIAL
ECOSYSTEM PERFORMANCE
sociological structure
density
individual performance
NUTRIENTS & TOXIC SUBSTANCES
grazing herbivores
vertical extent
incident radiation
current surge
wave action
suitable substratum
TURBIDITY
SEDIMENT
POLLUTION ACTS HERE

Interpretation of Key Factors from Ecosystem Parameters

A. Seasonal growth cycle and individual performance.

Laminaria hyperborea, *Laminaria digitata* and *Laminaria saccharina* on the coast of North East England and South West Scotland begin to produce new laminae in December and January. The new laminae undergo an intial period of rapid growth which gradually falls of towards the middle of the summer. The peak seasonal biomass is reached from July to September in *Laminaria digitata* and *Laminaria hyperborea*; being from August to September in *Laminaria saccharina*.

The seasonal variations in the rate of net annual production of the lamina has been observed by other investigators working on similar ecosystems in different parts of the Northern hemisphere. Kireeva and Schapova (1938) and Tikhovskaya (1940) investigating *Laminaria digitata* and *Laminaria saccharina* in the Barents and White Seas have found that the new lamina begins development in January and does not reach its peak seasonal biomass until August, after this month it gradually undergoes a decrease. Kuznetzov (1946), working on *Laminaria saccharina* in the same region, has found that the peak production of the lamina is reached in July with an actual decrease taking place in August, Parke (1948a) has found that the peak seasonal production of the lamina in *Laminaria saccharina* is reached in October on the coast of Argyllshire and a month earlier in Devon. Sundene (1964) has found that the growth of *Laminaria digitata* is at a minimum during the summer months in South Norway, whilst in North Norway it is at a minimum during the dayless winter months.

The remarkable similarity in the seasonal cycle of lamina production in regions which are so widely separated would suggest that the factors which control this growth rhythm are common to all or else there is some inherent factor within the species which governs it. If there is such an endogenous growth rhythm it must be subject to modification by environmental factors.

Kireeva and Schapova (1938) suggest that the stimulus for the development of the new lamina in Laminaria digitata and Laminaria saccharina is associated with the beginning of active assimilation since its appearance co-incides with the end of the polar night in very northerly latitudes.

In contrast Tikhovskaya (1940) has found that the new lamina in Laminaria saccharina may be produced actually during the polar night when no active assimilation is taking place. Kylin (1916) has noted the early development of the new lamina in species of Laminaria on the coast of Sweden and has suggested that this is due to the laminarin stored in the old lamina. Kireeva and Schapova (1938) refute this by arguing that since there is no polar night in this region weak assimilation might still occur. Kain (1963) has presented much evidence to suggest that its development does not take place at the expense of material stored in the stipe but is instead dependent on assimilation. It does seem likely that at certain times of the year translocation of photosynthate and other materials must occur, especially from the lamina to the stipe and hapteron, since it seems improbable that an often heavily encrusted stipe and hapteron could undergo any effective assimilation.

The importance of temperature and light on the quotient of respiration/assimilation and hence on the seasonal cycle of growth in Laminarian species has been emphasised by a number of workers. Sundene (1962, 1964) has suggested that the decrease in the growth rate of Laminaria digitata towards Autumn is related to the progressive increase in temperature. High summer water temperature has also been found to bring about the cessation of growth in Laminaria japonica Aresch, (Tseng et al, 1957) and Laminaria angustata Kjellm, (Hasegawa, 1962). Tseng et al have found that the effect of high summer water temperature may be partly offset by fertilizing the sea with nutrients. Kniep (1915-1916) and later Ehrke (1931) have found that many species of marine algae are capable of assimilation at low temperatures and light intensities and that with a small rise in temperature the rate of respiration increases much faster than the rate of photosynthesis. Therefore the quotient of assimilation/respiration is high at low temperatures. These findings have been further substantiated by the measurements of photosynthesis under field conditions by Tikhovskaya (1940). Therefore the rapid rate of growth observed during the early part of the year is probably related to the slow increase in water temperature and rapid one in light intensity. Tikhovskaya has found that the quotient of assimilation/respiration in *Laminaria saccharina* was at its maximum from February to May. The eventual increase in water temperature leads to the gradual lowering of the quotient of assimilation/respiration until a zero value is reached from July to September depending both on the species and the local conditions. The rate of loss is now greater than growth increment and so there is a gradual decrease in the net production of the lamina.

It would seem therefore that on consideration of the seasonal cycle of growth of the main photosynthetic organ that the most important factors controlling individual performance are incident light energy and water temperature. It is also evident that all the species studied respond in much the same way and therefore as a first approximation the general conclusions of the work apply to all the species studied.

B. Variations in individual performance with depth.

The most obvious ecosystem variable in a sublittoral depth transect is a decrease in the intensity and spectral quality of the light incident on the benthos. This is complicated by an overall decrease in the annual water temperature and its fluctuation and a decrease in the effect of water movement with increasing depth. Table 68 gives comparative data for indiviudal performance along 8 depth transects within the *Laminarietum hyperboreae* and indicates that light is the over-riding factor. This conclusion is substantiated

Table 68

A number of depth transects

Locality	Depth (m.-C.D.)					
	0-3.1	3.2-6.1	6.2-9.1	9.2-13.1	13.2-20.1	20.2-26.1
St. Abb's Head (2P)	154	-	125	49	8	-
Beadnell (4L)	131	-	127	-	-	-
" (4E)	64	-	48	-	-	-
Marsen (5M)	169	61	-	-	-	-
Redcar (6R)	167	102	-	-	-	-
Island of Soa (9)	-	94	-	-	-	27
Eilean Iomallach (11)	-	36	-	-	-	15
Sennen Cove (23S)	98	-	-	-	64	-

I.S.P.

by all the transplant experiments. A similar trend is also shown in the Desmarestrietosum subassociation on the South West peninsula.

The low individual performance of two species in a sheltered tide pool at Beadnell (Tables 34 and 42) could be due to high temperatures during the periods of low water or due to any or all of the other multitude of factors at work on the littoral.

Ecosystem performance

This study indicates that individual and ecosystem performance show similar trends, there being a general decrease in plot performance with depth. However there is no direct relationship between the two, the decrease in ecosystem performance is not simply due to the production of smaller plants, it is also due to a reduction in density of the canopy. The simplest explanation of this decrease is simply competition for light between the canopy and the gametophyte, sporeling and/or developing sporophytes.

The removal of individuals by increased frequency and intensity of grazing must be bourne in mind but without long term detailed study of a series of ecosystems it is just speculation.

Thus again it would appear that light is the most important factor controlling ecosystem performance measured as net annual production.

Ecosystem potential

Ecosystem potential measured as strip production may be considered to be dependent mainly on the bathymetric range of each of the species at each site. The main factors controlling this would be the availability of suitable substrate for the species under consideration. However in a number of the areas studied suitable substrates were found at depths in excess of the deepest occurrence of kelp forests. Even in the situations where the water clarity was good the Laminarietum hyperboreae subassociation Typicum extended only from 1.5-15.2 m. below Chart Datum, whereas in the subassociation Desmarestrietosum it was common to a depth of 2.0-40.0 m. This regional difference can be explained by the differences in solar altitude, incidence angle and hence reflection and absorption (Holmes, 1957). However the phytosociological differences, such as the lower limit of typically littoral species in the subassociation Desmarestrietosum, may indicate an effect of high temperature allowing these species to compete in the sublittoral.

The anthropogenic variant from the North East of England throws some light on the problems of the controlling factors. In all cases where the sea water is charged with particulate material, whether due to pollution (Bellamy et al, 1967a) or natural allochthonous material or both, the ecosystem potential is drastically reduced due to a major reduction in the depth range of the ecosystem. The details for a series of depth transects along the coast of North East England are summarised below and the actual gradient of pollution and natural allochthonous material along the coast is shown in Figure 18.

Locality	Pollution	Natural allochthonous material	Turbidity (m.)	Depth range of kelp forest (m.)
St. Abb's Head	+	+	2	1.5-15.2
Beadnell	++	+++	1	10.7
Marsden	++++	+++	0	1.6-6.0
Redcar	+++	++++	0	1.6-7.2
Staithes	++	+++	0	1.6-7.0

All indications point to an attenuation of light as being the effective factor bringing about a marked fall-off in individual and ecosystem performance over a short bathymetric range.

There is a dramatic decrease in individual performance and in the weight per unit length of stipe with only a small increase in depth in the most grossly polluted areas.

Tseng et al (1957) have noted that high nutrient levels can allow Laminaria japonica to be grown well outside its natural temperature range. It is suggested that the high levels of nutrients, especially phosphate and nitrate, found in the polluted areas may be the only factor allowing growth at depth in these very turbid waters.

FIGURE 18

The pollution gradient

(Bellamy, 1968; and unpublished data)

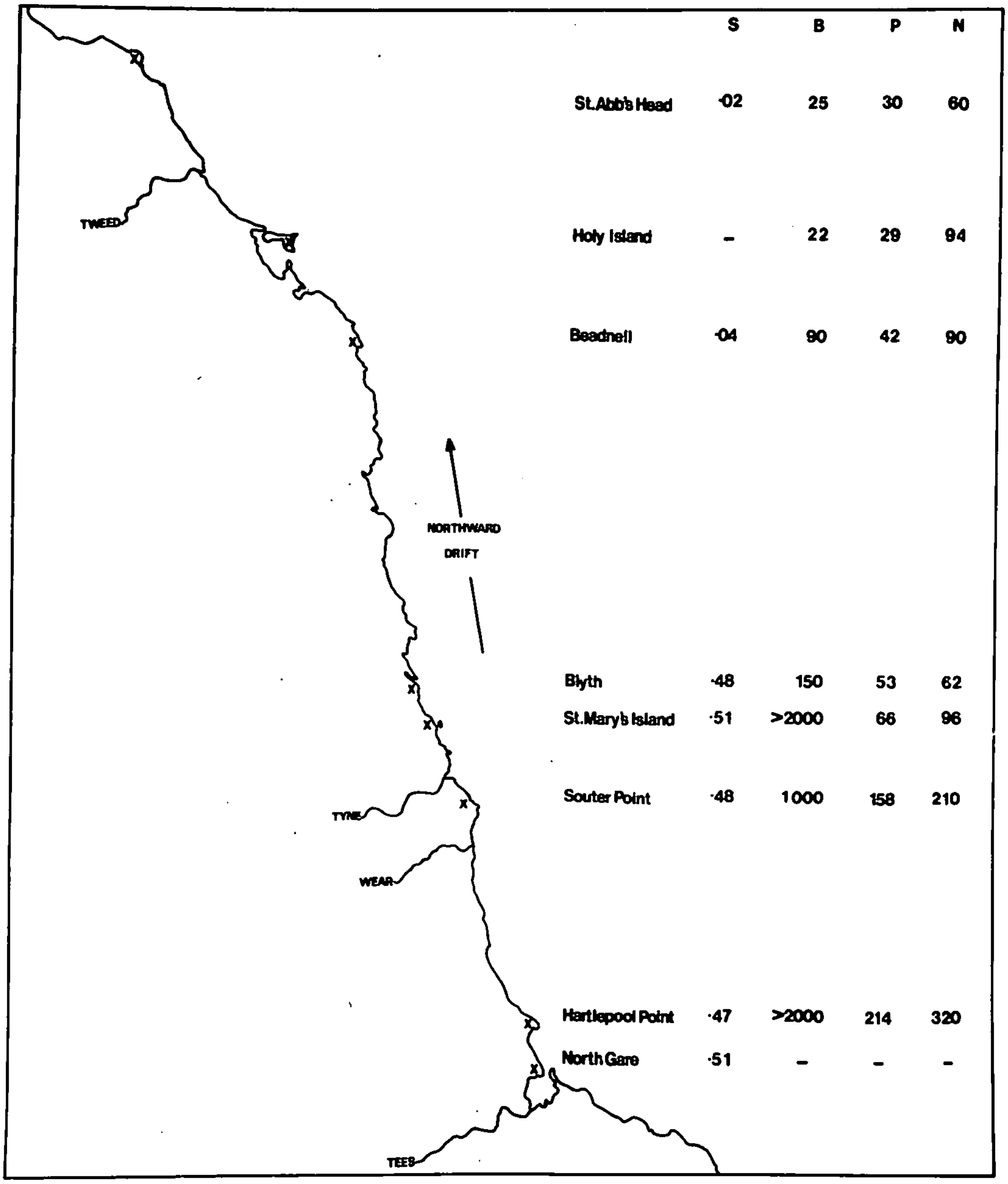
Key

S. Suspended material (Grams per litre)

B. Faecal bacteria (Mean probable number per 100 ml.)

P. Phosphate (Micrograms per litre)

N. Nitrate (Micrograms per litre)


S B P N
St.Abb's Head ·02 25 30 60
Holy Island – 22 29 94
Beadnell ·04 90 42 90
NORTHWARD
DRIFT
Blyth ·48 150 53 62
St.Mary's Island ·51 >2000 66 96
Souter Point ·48 1000 158 210
Hartlepool Point ·47 >2000 214 320
North Gare ·51 – – –
TWEED
TYNE
WEAR
TEES

Any particulate material in supension, be it natural or man made, must finally settle out and the sediment so formed can effect the ecosystem in a number of ways:

(1) Sediment settling on the surface of the photosynthetic organs will cause a reduction in the amount of light reaching the chloroplasts and hence reduce the rate of photosynthesis (Gislén, 1930) which will bring about a reduction in both, individual and and ecosystem performance and ecosystem potential.

(2) The settlement and establishment of many algae are dependent on the availability of suitable substrate; deposition of sediment could have a profound effect on the type of substrate and therefore limit the extent of the ecosystem. Since the rate of sedimentation will be greatest at depth and in sheltered localities, it would appear that detailed study of shallow, sheltered and current surge sites could help to differentiate between the various effects.

C. Effects of water movement, current surge and exposure to direct onshore wave action.

The individual performance figures obtained in this study show trends related to the type and degree of exposure to water movement, these trends do not necessarily mirror one another in the different regions. The individual performance of Laminaria hyperborea is usually greatest in moderately sheltered to moderately exposed ecosystems (exposure scale of Lewis, 1964) in relatively shallow water, whilst there is a tendency for a fall-off in these values in those which are very exposed.

Individual performance is highest in Laminaria digitata from the moderately sheltered ecosystems on the coast of North East England and South East Scotland, whilst in South West England it is highest in those which are very exposed. This might be related to the higher water temperature on the South West coast and the fact that water movement would prevent stratification of the water. There is no significant difference in individual performance between the exposed and severely exposed ecosystems in the Inner Hebrides.

The highest individual performances of Laminaria saccharina are found in shallow water ecosystems which are sheltered from direct onshore wave action but are subjected to a certain amount of current surge. In general there is a trend towards a decrease in individual performance with increase in exposure.

The decrease in individual performance in moderately to very exposed ecosystems occurs in every age class and so suggest that this fall-off is not due to sellection against individual which are near their maximum age and size.

The lower levels of individual performance in moderately to very exposed ecosystems is either dependent on the rate of erosion of the lamina and/or could be due to an actual slowing in the growth rate. In certain circumstances current surge might accentuate the effect of exposure to wave action by adding to the forces bringing about the erosion or tearing of tissues.

The low levels of individual performance of Laminaria digitata and Laminaria saccharina in very sheltered situations, especially where there is a high concentration of natural allochthonous material, is believed to be related to the physical effect of sediment deposition on the laminae.

The optimal conditions for sustaining a high level of individual performance in Laminaria saccharina are found in sheltered localities which are subjected to a certain amount of current surge. Similarly the highest values for plot performance in Saccorhiza polyschides occur in current surge sites.

A certain amount of water movement, whether it is wave action or current surge, may be advantageous for the following reasons:

(1) Prevents temperature and salinity stratification.

(2) Increases the supply of nutrient salts in a unit period of time (Odum and Hoskin, 1958).

(3) Allows for a high rate of gaseous exchange between the water and the atmosphere and so prevents deoxygenation and large fluctuations in pH.

(4) Leads to a steepening of the diffusion gradient and so brings about an increase in the rate of exchange of nutrient salts and gases.

(5) Prevents the fouling of surfaces and individuals by particulate matter coming out of suspension.

The beneficial effects of water movement will depend on its average strength, duration and maximum effective force.

The higher individual performance in current surge sites may be due to an actual increase in growth rate. A number of workers have found that oxygen consumed in the dark and the rate of photosynthesis of algae are increased in moving as compared to still water (Gessener, 1937; Steemen-Nielsen, 1947). Similarly a many fold increase in respiration has been observed in fresh-water algae under conditions of water movement (Whitford and Schumacher, 1961). Therefore water movement might directly influence performance by modifying the quotient of respiration/assimilation.

It is possible that the net annual plot production of Saccorhiza polyschides might be influenced by a higher density of individuals in the current surge sites since there is a greater likelihood that in such situations a larger number of viable spores will be brought into contact with a suitable surface in a unit period of time.

The low plot performance in sites exposed to severe wave-action can be explained by either the removal of mature individuals and/or the prevention of spore settlement and initial development.

Laminaria digitata presents a special problem since it is the only species which is more or less confined to the immediate sublittoral in the British Isles. Its flexuous stipe is undoubtedly well adapted to harsh wave action giving it a competitive advantage in the immediate sublittoral. The question is: what is the factor controlling its downward limit? Experimental data obtained in this study has shown that the species can grow at a depth far in excess of its normal range and yet it is usually confined in nature to a very narrow belt. It is suggested that Laminaria digitata can grow in deeper water and could compete on a productive basis with Laminaria hyperborea however as its life cycle is completed in 5 years as compared with 8 for Laminaria hyperborea; i.e. its turnover period is shorter, it will be at a competitive disadvantage in the more stable conditions of the deeper water.

Phytogeographical boundaries

The main phytogeographical boundary covered in this study is that between Laminaria hyperborea and Laminaria ochroleuca. Whatever the actual environmental factor or factors limiting the northward extension of the range of Laminaria ochroleuca one of the most important must be competition with Laminaria hyperborea, a species with a more northerly distribution. The comparable stipe production data for a "mixed" population at Roskilly (South West England) is shown in Figure 19. It appears that Laminaria hyperborea out performs Laminaria ochroleuca throughout the life of the sporophyte thus indicating that it would have a distinct advantage in a mixed population. Nevertheless it would appear that Laminaria ochroleuca can

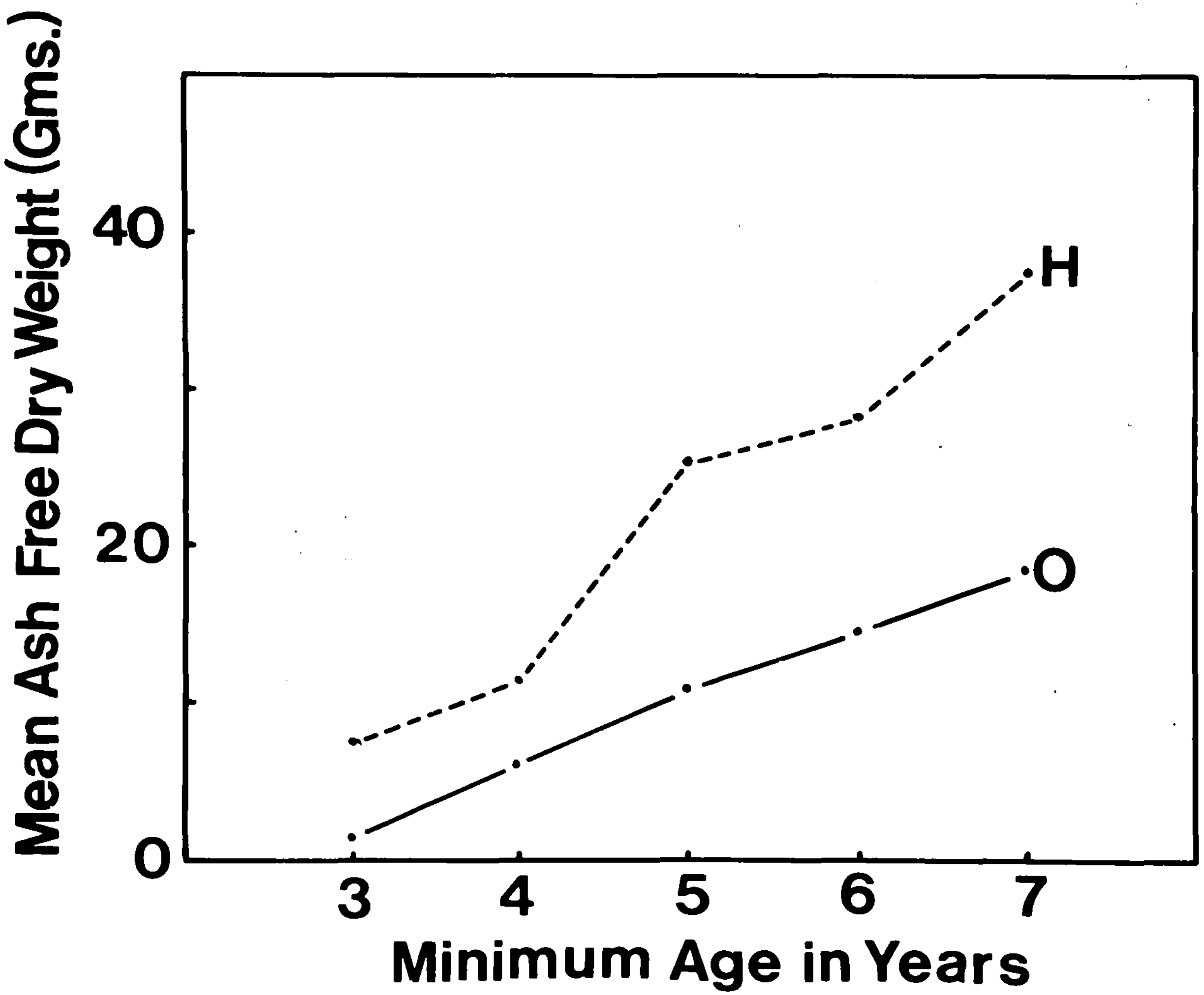
FIGURE 19

Mean individual biomass of stipe

Key

O. *Laminaria ochroleuca*

H. *Laminaria hyperborea*


Mean Ash Free Dry Weight (Gms.)
40
20
0
3
4
5
6
7
Minimum Age in Years
H
O

"hold its own" in a mixed kelp forest and can under certain conditions form nearly pure stands on the English coast.

It is interesting to note that *Laminaria ochroleuca* is the only species which shows a marked difference in individual performance over the geographical range studied. The individuals from the Spanish populations have very large laminae and a very high weight per unit length of stipe when compared with their age counterparts on the English coast. It is interesting to speculate on the change in performance. The further South the population the better should be the conditions for photosynthesis. However it would seem that the balance between photosynthetic biomass and respiratory biomass would become more critical the higher the average water temperature. It would be expected that passing South into the optimum range of the species that the individuals would be both more productive and have a larger lamina/stipe biomass than in the cooler waters. This is bourne out by the data obtained (see Figure 20). It would be interesting to measure these parameters at the southern limit of the species. There is sometimes a change in the morphology of the stipe in *Laminaria hyperborea* and *Laminaria digitata* when exposed to moderate to very exposed wave action and with also an increase in depth in *Laminaria hyperborea*.

The decrease in the thickness of the stipe is only partly explained by the level of production, it is possible that it might be related to a change in the ratio between photosynthetic (lamina) /non-photosynthetic (stipe) biomass.

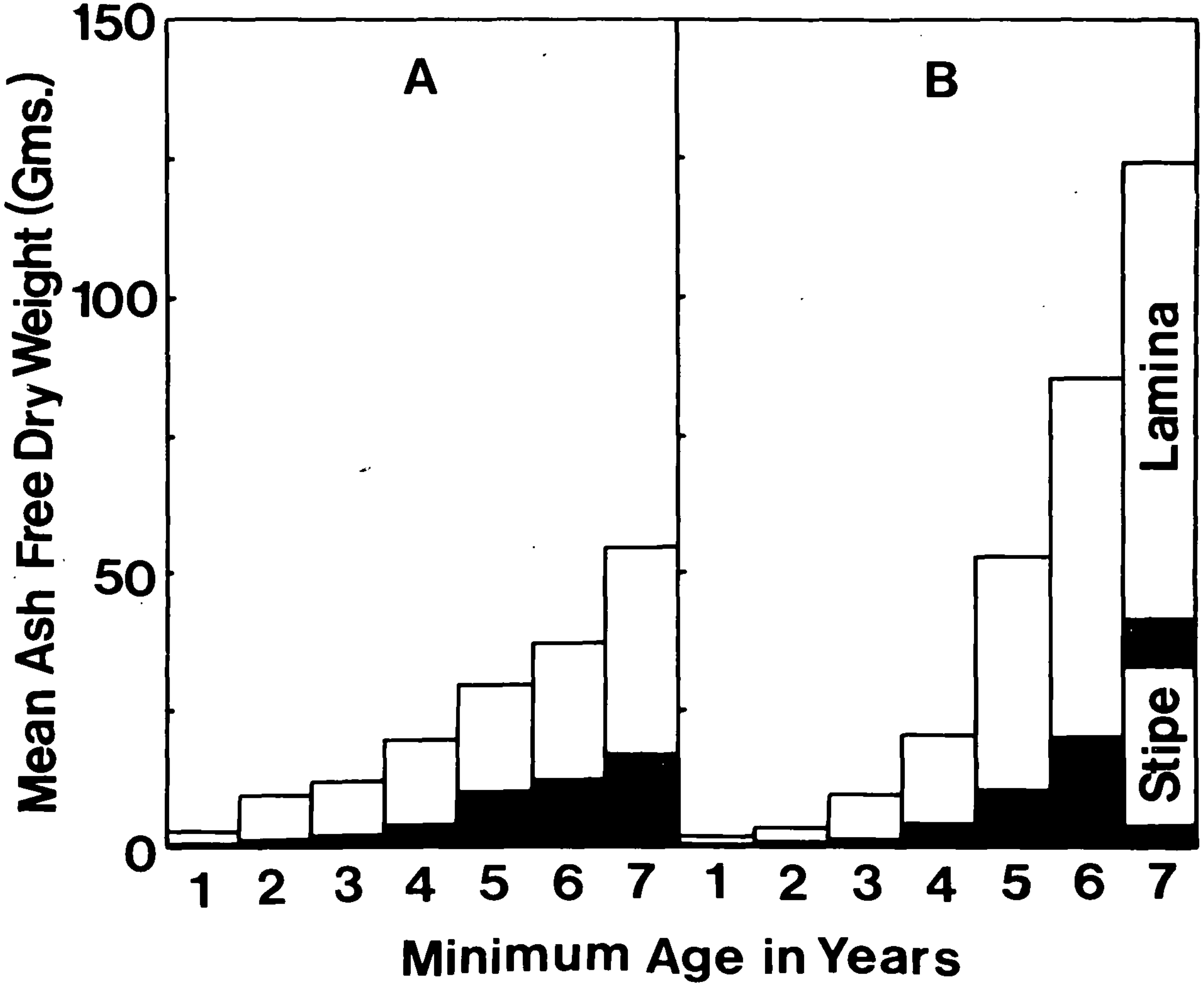
FIGURE 20

The biomass of stipe and lamina

Key

A. Population from the English Coast

B. Population from the Spanish Coast


A
B
Lamina
Stipe
Mean Ash Free Dry Weight (Gms.)
150
100
50
0
1 2 3 4 5 6 7 1 2 3 4 5 6 7
Minimum Age in Years

There is occasionally very little relationship between the level of lamina production and stipe biomass. It is not possible to determine as to whether this difference is due to atypical growing conditions over a single season or to there in fact being little relationship between stipe and lamina production. In fact the magnitude of the seasonal changes in lamina production has been shown to undergo significant differences between consecutive years.

There are no overall trends in individual performance between nearly ecologically equivalent ecosystems in different geographical regions with the exception of Laminaria ochroleuca.

In the other Laminaria species the variations brought about by geographical differences are not great enough to be detected and measured using the methods described. The relatively crude study made by Bellamy and Whittick (1967) has nevertheless shown that with sufficient data from widely separated regions a meaningful picture of kelp forest production can be obtained.

The variability and sometimes small inconsistencies in the results are no doubt due to the genetical non-uniformity which would be expected in a natural out-breeding population. Nevertheless the techniques which have been described and developed produced consistent and reproducible results when measuring the net annual performance of both the kelp forest ecosystem and the individuals it is composed of.

The work indicates the following general and somewhat "basic" relationship that the shorter the life span of a species the greater is its level of production; viz. the large size of individuals of the annual Saccorhiza polyschides, and the large lamina production of Laminaria saccharina under optimal conditions, it is suggested that this is an important factor governing the success of these short lived species. It is suggested that this would be a fruitful field for further work and speculation.

This thesis lays down the base line for a number of more detailed studies on the interpretation of growth parameters and using these for illucidating local and regional environmental agencies in the sublittoral kelp forest.

Conclusions

(1) The methods of the Zurich-Montpellier system of phytosociology is with some minor modifications applicable to the description and ecological classification of kelp forest ecosystems.

(2) The phytometer approach is applied to these systems and simple measurements of a complex of performance parameters can give an insight into the factors controlling sublittoral ecosystems both on a local and a regional scale.

(3) Much more purely descriptive work is needed in the inshore marine environment before more detailed studies of this type.

Part VIII

APPENDICES

Appendix 1

PHYTOGEOGRAPHICAL DISTRIBUTIONS

Northern Forms

Laminaria hyperborea

This has a somewhat localised distribution on the coasts of France, Spain and Portugal, being at the southern edge of its range in Portugal (Hamel, 1931-1939; Miranda, 1934; Station Biologique de Roscoff, 1954; Ardré, 1957, 1961; Seoane-Camba, 1960, 1966; Dixon, 1961; Davy de Virville, 1963; et al). It is very common on all but the south eastern coast of the British Isles. It is rarely found on the coast of the Netherlands but is very common in Heligoland (Den Hartog, 1959). It occurs along the coast of western Norway and reaches as far as the U.S.S.R. border (Baardseth, pers. comm. to Kain, 1967). It is found in the Faeroe Islands and is common on all but the East coast of Iceland (Børgesen and Jonsson, 1905, Børgesen, 1905).

Laminaria digitata

This is a northern Temperate species which has its most southerly limit on the coast of North West Spain (Sauvageau, 1918; Fischer-Piette, 1956; Ardré et al, 1958). It is common along much of the Atlantic sea-board of Europe and is found as far west as the Barents sea coast of Novaya Zemlya being also abundant on the White Sea coast of the U.S.S.R. mainland (Zenkevitch, 1963). It has been recorded for the Faeroe Islands, Iceland and Greenland (Børgesen and Jonsson, 1905; Børgesen, 1905). Its distribution on the North American continent is summarised by Taylor (1957) as "Staten Island, Long Island, Connecticut to southern Massachusetts, at a few exposed stations becoming common north of Cape Cod to the lower St. Lawrence, Hudson Bay and Ile Miquelon."

Laminaria saccharina

It is locally abundant on the Atlantic sea-board of Europe and has been found as far South as the coast of Portugal (Ardré, 1961). It occurs along the shores of the Barents and White Seas (Flerov and Karsakoff, 1932; Zenkevitch, 1963) and in deep water in the southern part of the Baltic (Lunde, 1947). Børgesen and Jonsson (1905) and Børgesen (1905) have recorded it for the Faeroe Islands, Greenland and Iceland. Taylor (1957) summarises its distribution for the North American Continent as "Northern Massachusetts to the lower St. Lawrence, Labrador, Newfoundland, Hudson Strait, Baffin Island and Cornwallis Island." On the North East Pacific coast it extends from Adak Island, Alaska to Coos Bay, Oregon (Druehl, 1968). Zenkevitch (1963) states that it is found in the sea of Japan. There exists the possibility that it is conspecific with Laminaria cordata Dawson (Druehl, 1968) and Laminaria agardhii Kjellman (Burrows, 1964a,b) and so its range may in fact be greater than that mentioned in this text.

Southern Forms

Laminaria ochroleuca

Mme. P. Gayral (1958) summarises the general phytogeographical distribution of this species as being "the Channel and South Atlantic, extending as far North as Brittany, being also found both on the Algerian and Moroccan coasts of the Mediterranean." On the French side of the Channel it has its eastern limit about Alderney and Barfleur being apparently absent from the Gulf of St. Malo and most of Contentin (Hamel, 1931-1939; Lami, 1943, 1954; Station Biologique de Roscoff, 1954; Crisp and Southward, 1958; Dixon, 1961; and Davy de Virville, 1963). The species has been recorded in three localities on the South West coast of Britain by Parke (1948b) and Spooner (1951). A number of new localities, mostly towards the tip of the Cornish peninsula, have been discovered recently (John, 1969). It has also now been recorded for the Scilly Islands (Norton, 1968).

Saccorhiza polyschides

It is common in relatively exposed localities on the coasts of Spain, Portugal, France and the Channel Islands (Sauvageau, 1897; De Beauchamp, 1907; Hamel, 1928; Miranda, 1934; Fischer-Piette, 1958; Davy de Virville, 1963; et al), its eastern limit on the French side of the Channel is Barfleur (Hamel, 1931-1939). It has been recorded in the southern part of Marocco (Dangeard, 1949) and it is probable that it is found as far south at Mauritania (Sourie: in Fischer-Piette, 1955). Gayral (1958) records it as being present in the Straites of Gibralter and Feldmann (1934) and later Molinier and Picard (1953) have found it as far east in the Mediterranean as Messina on the coast of Scilly. It has been recorded at a number of other localities in the Mediterranean and these are summarised by Huvé (1958).

It is locally abundant on the North, South and West coasts of the British Isles, whilst there are only a few records for its occurrence on the eastern side of the British Isles (Batters, 1890; Jones, 1960). According to Harvey (1851) it is also found on the coast of Norway and the Faeroe Islands.

Appendix 2

SITE DATA

Exposure

This was assessed in two ways. Firstly, a quantitative estimate of exposure to wave action was made using the method of Grenager and Baardseth (1966). A circle of a radius of 5 cms. and divided into 10^{o} sections was used on a 1/250,000 map. A certain amount of caution is necessary when assessing the degree of exposure based on this quantitative scale since a number of factors, other than coastal configuration and shore topography, might influence it, viz. inclination of the shore, extent of the shore, the presence of platforms and ledges, the angle of the waves, the direction of the prevailing winds. A more reliable indication of the exposure of a locality was obtained by referring to certain "indicator" species. The difficulties entailed in comparing the exposure of ecosystems in widely separated regions was partly overcome by employing the broad exposure categories and the geographical "indicator" species of Lewis (1964). Lewis considers that his biological exposure scale is applicable to the whole of the British Isles.

Pollution and Natural Allochthonous Material

Pollution may be anything produced by the activity of man which is discharged or finds its way into the sea and includes: toxic material, nutrient substances and suspensoides. Natural allochthonous material is taken to mean matter in suspension produced by natural processes of erosion. It was necessary to consider the geography and the geology of the region in which a site was studied in order to determine the source and the nature of these factors, viz. stability and erodability of the substrate, the proximity of estuaries and deltas, the location of large urban connubation, presence of local sewage outfalls, coal washing plants, factories and so forth.

Turbidity

This is directly related to the type and amount of natural allochthonous material and pollution of the water.

Turbidity was assessed by the distance a diver could see an object along a horizontal plane underwater, this may be referred to as "underwater visibility". Turbidity may undergo considerable fluctuations both in time and space, being dependent on a number of factors, viz. the state of the tide, the ambient sea conditions, the intensity of the incident illumination and the season of the year. The categories of turbidity based on underwater visibility were made as broad as possible so as to illiminate as far as possible very local differences prevailing at the time of making the assessment.

Appendix 3

THE ZURICH-MONTPELLIER SCHOOL OF PHYTOSOCIOLOGY

Introduction

The description and the classification of marine vegetation has in the past been based on geographical, physiognomic, ecological, successional or floristic characteristics.

In many of the early descriptions of such ecosystems much emphasis has been placed on them as physiognomic units with little importance being attached to their total floristic composition (Kjellman, 1878; Børgesen, 1905; Kylin, 1907; Jonsson, 1912 et al). A number of the early attempts at classification were based soley on the life form of the dominant (Oltmanns, 1922-23; Funk, 1927; Nienburg, 1930). A comprehensive review of much of the early work has been published by Gislén (1930). The study of Gislén itself represents one of the first attempts to define marine ecosystems both on a qualitative and quantitative basis.

Starting with the pioneer work of Berner (1931) and Feldmann (1938) a number of attempts have been made to apply the survey methods and taxonomic techniques of the Zurich-Montpellier and Uppsala schools of Phytosociology to marine ecosystems. Detailed appraisal of these two schools of phytosociology are given by Westhoff (1951), Becking (1957) and Whittacker (1962).

The chief workers responsible for adapting these systems to the study of marine environment have been Kornás and Medwecka-Kornás (1948, 1949, 1950); Kornás et al (1960); Waern (1952); Molinier and Picard (1953); Sundene (1953); Den Hartog (1955, 1959) and Taniguti (1962). A number of these workers have studied the sublittoral ecosystems using diving techniques and have stressed the importance of describing them in situ (Gislén, Waern, Kornás and Medwecka-Kornás, Molinier and Picard).

The Basic Concepts

The four synthetic characters of vegetation; fidelity, presence, constancy and dominance, can be used to varying degrees for the attainment of a workable classification of marine or terrestrial communities.

The fidelity of a species is a reflection of its preference for a specific vegetational unit. When considering the concept of fidelity other properties are often taken into consideration such as presence, cover-abundance, dominance, sociability and vitality. Five classes or degrees of fidelity and three categories of diagnostic species can be recognised and their relationship to one another is shown in Table 69.

The kelp forest ecosystems were studied from a number of widely separated phytogeographical regions since the diagnostic value of a character species for single associations and even alliances is dependent on the total range of the species as well as that of the vegetation unit.

A number of companion species of fidelity class II, especially the constant companions, may have diagnostic value for the distinction of vegetation units and these are known as differentials. These differential species are generally used for distinguishing subassociations

Table 69

Qualitative fidelity classes or degrees

(after Becking, 1957)

(a) Character species (Charakterarten, Kennarten)

Fidelity class

V Plant species exclusively or almost exclusively restricted to certain vegetation units.

IV Plant species with strong preference for a specific vegetation unit but also occurring in other vegetation units; however then it occurs sparingly, infrequent or rarely.

III Plant species often occurring in other vegetation units but with their optimum in one vegetation unit.

(b) Companions (Begleiter)

II Plant species without any definite preference for certain vegetation units.

(c) Strangers

I Plant species rare or accidental in the studied vegetation unit, an invading or relict species from other successional plant communities. These species usually have their definite optimum outside the considered vegetation unit.

and variants of the association. An assessment may be made of the position of a community along a particular environmental gradient; viz. exposure, depth, pollution, by referring to one or a combination of species which may delimit a variant of an association or a subassociation.

One of the criteria used in this study was presence. Presence is usually defined as the occurrence of a species in any stand of an association provided its size is greater than the minimal area and contains the characteristic combination of species. It differs from the concept of constancy in that determination is not made within plots of sharply delimited area.

Percentage classes for presence or constancy are given in the following table.

Percentage classes for presence or constancy
(after Becking, 1957)

I	- present in less than		20%	of the compared plots
II	- present in	20 to	40%	of the compared plots
III	- present in	40 to	60%	of the compared plots
IV	- present in	60 to	80%	of the compared plots
V	- present in	80 to	100%	of the compared plots

The species of presence V are known as the 'constants' of the association.

Dominance is used by the Zurich-Montpellier school to refer to the species within the community which show the greatest cover. In this study it was found that the dominant species was usually the one which gave the ecosystem its characteristic physiognomy and so in the following discussion dominancy refers to both cover-abundance and life form. The most readily delimited vegetation units are those in which the dominant is also the faithful species of the ecosystem. In fact, this was often found to be the case in the sublittoral ecosystems studied.

The System of Classification

It is usually possible to delimit the vegetation units for study by the dominant and the sharp boundaries between them. They may be considered to be associations in the sense of the Zurich-Montpellier school since they have character or combinations of character species. Such an association may be defined as a "plant community (abstract) identified by its characteristic species composition (or assemblage), including one or more (local) character or differentiating species". (Meijer Drees, 1951).

Den Hartog (1959), after studying marine communities in the Netherlands, believed that the sociation of the Upsalla school of phytosociology, i.e. "communities characterised by the presence of at least one dominant species" (Du Rietz, 1930; Westhoff, 1951), and the association are units of similar status. A similar stand-point was taken in this present study with as much emphasis being placed on the presence, dominance and structure of the marine ecosystems, as on the presence of character species.

The association can be united into groups of higher rank using the following prefixes to indicate their synsystematic rank:

Subassociation	- etosum
Association	- etum
Alliance	- ion
Order	- etalia
Class	- etea

The higher units (Alliance, Order, Class) are characterised by the fidelity of the groups of constant species. The highest units are initially chosen on the grounds of ecology and life form.

In each of the geographical regions a number of unit descriptions were also made of the littoral as well as the sublittoral ecosystems in order to ascertain the degree or class of fidelity of a species to a particular association.

The Methods of Survey

In this school of phytosociology more attention is focused on the floristic uniformity of the vegetation than on the concept of homogeneity*. Therefore the selection of each study unit or aufnahme

*A plant species is said to be homogeneously distributed within a certain area if the probability to catch a plant species within a test area of a given size is the same in all parts of the area. A plant community is said to be homogeneous if the individuals of the plant species which were used for the characterisation of the community of homogeneously distributed." Dahl and Hadac (1949).

was dependent on the uniform distribution of the dominant, the structure of the canopy and the habitat, as far as assessment was possible. This method of assessing homogeneity by eye is called "die pflanzensoziologische Blick".

The initial selection of a suitable survey plot was performed relatively quickly since swimming above the vegetation is akin to close range "aerial" survey.

In some instances it was possible to describe the whole stand of vegetation (the total area of vegetation in the field which has been discerned). When the stand was very large this proved to be impracticable and small sample plots were taken instead. The sample plots were selected near the middle of the stand of vegetation and the shape and size of these were so arranged as to permit the inclusion of the most "homogeneous" vegetation and to exceed its minimal area. The concept of the minimal area is based on the asynoptic curve constructed when the ratio of the number of species to the size of the analysed area are plotted together, it is reached when the curve flattens off with no further species being added.

The size of the minimal area has been found to be 1 square metre in the marine communities studied by Molinier and Picard (1952), Den Hartog (1959) and Kornas et al, (1960). This was similarly found to be the case in the majority of the kelp forests studied except in species poor communities where it was as small as $\frac{1}{2}$ metre square.

The completion of an aufnahme, depending on the density and diversity of the ground and epiphyte flora, the depth, clarity, temperature and turbulence of the water, took from between 10 to 25 minutes of diving time. Survey plots were described at various levels over the entire depth range of the vegetational unit in situ, occasionally a line transect was laid over a number of depth levels in an attempt to gain a clearer insight into the structure of the communities. The size of the survey plot was usually from 3-10 metres in extent. The aufnahmen were written on pads of roughened perspex using a wax crayon.

An aufnahme consisted of:

(a) A full list of all the species in the survey plot, all those which could not be identified in situ were numbered, bagged and labelled for subsequent laboratory determination.

(b) Indices of cover abundance and sociability were estimated for each species using the scales proposed by Szafer and Pawlowski (1927) and Braun-Blanquet (1928, 1951). These two scales are given in Table 70.

(c) The following ecological data were also added; the depth, the degree of exposure, the type, nature and stability of the substrate.

In each survey plot a number of individuals were collected and brought back to the laboratory where smaller algae, which might have escaped detection in the field, could be discovered and identified.

It was not possible to re-survey many of the communities and as a result some emphemeral or pseudo-perennial species might have been missed and hence were not included in the field lists at the time of survey.

Table 70

The scales of cover-abundance and sociability

Cover abundance

+ - occasional and less than 5% cover of total plot area.

1 - abundant or common but insignificant in cover, less than 5% cover of total plot area.

2 - very abundant or common but low in cover, 5-25% cover of total plot area.

3 - 25-50% cover of total plot area irrespective of number of specimens.

4 - 50-75% cover of total plot area irrespective of number of specimens.

5 - 75-100% cover of total plot area irrespective of number of specimens.

Sociability

1 - growing solitarily, 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 completely covering the whole plot area.

Sociability according to Pfeiffer (1962) "gives a more complete picture of the community structure and the communal organisation of the vegetation".

The information for each aufnahme was transferred from the writing pads onto 8 x 6 ins. file cards. On the top of each card was added the code number of the aufnahme, the data, locality, the actual depth (see page 28), as well as the ecological and floristic data.

Synthesis of Field Data

In the initial survey, when sufficient data had been amassed, they were summarised in the form of a composite table.

Such a table was arranged with all the species being listed along the left hand side and the plots listed horizontally along the top. The cover abundance and sociability figures of each species were recorded. The aufnahme number and the total number of species per aufnahme were also noted.

The 'raw' table laid out in this manner permitted the easy checking of species for their presence or absence in all of the aufnahmen simultaneously and to select those which appeared to be characteristic of the various ecosystems. The table was edited many times with the grouping of vegetation plots into one synthetic table by vertical rearrangement. It was also rearranged horizontally into new diagnostic groups until all the lists for homogeneous associations were together. On arriving at the final table, other properties of the vegetation were considered, especially presence, cover-abundance and dominance. These proved to be important in defining groupings lower than the association. The 'blocks' of mutually exclusive species were termed 'presumed' character and differential species. It was often found that many 'presumed' character species had to be demoted to differential or companions as more information was gathered.

In the final table each species was given its proper sociological rank. Ecological data were then included at the top of the table at this final stage. Once such a tentative classification had been determined for regional use further selection of stands for study was made rapidly.

Appendix 4

PHYTOSOCIOLOGICAL TABLES

(Tables 5-9)

TABLE 5

Laminarietum hyperboreae (Ass. Prov.)

Provisional

Alliance

Association

Subassociation — Typicum

Variant — typicum — Dp — D

(Dp - Deep Water)

Aufnahme Number	2P1	2P2	4BL1	4BL2	4BL4	4BL5	4BL6	4BL7	5M1	5M2	5
Depth (m.-C.D.)	3.6	6.1	6.1	5.2	.9	10.0	8.4	8.4	2.4	4.8	4
Exposure	D	D	B	B	B	B	B	B	D	D	D
Substrate	XV	XV	X	X	X	X	X	X	XV	XV	X
Total cover (%)	80	90	70	90	90	90	60	40	75	70	6
Species number	20	18	14	18	16	14	21	13	13	11	1
Character species of association											
Laminaria hyperborea	45	44	44	33	33	33	23	+1	33	23	+
***Differentials of regional subassociation Typicum**											
Variant typicum											
Polysiphonia brodiaei	+1			+1			13*	12	12	+3	1
Anthropogenic variant											
Ptilota plumosa	•	•	•	•	•	•	•	•	•	•	•
****Differentials of regional subassociation Desmarestrietosum ligulatae**											
Unstable variant											
A Polyneura hilliae											
A Cladostephus verticillatus											
Variant typicum											
A Asparagopsis armata (tetra.)											
C Fucus serratus											
C Plumaria elegans											
C Halurus equisetifolius											
C Nitophyllum punctatum											
A Asparagopsis armata (diplo.)											
C Himanthalia elongata											
C Halopteris filicina											
C Callithamnion granulatum											
A Mesophyllum lichenoides											
A Jania rubens											
C Griffithsia flosculosa											
C Rhodochorton purpureum											
A Schizymenia dubyi											
A Rhadicilingua thysanorhizans											
Character species of alliance											
Delesseria sanguinea	12	23	+1*	+2	+2	23	+2	+2	23	12*	1
Phycodrys rubens	•	•	•	•	•	•	•		•		•
Dilsea carnosa	+2	+2			+2	+2	+1	+2	+2	+2	
Callophyllis laciniata	+1*	+3*				+3*	+3*	13			
C**Saccorhiza polyschides											
C**Giffordia hincksiae											
Dictyota dichotoma	+1										
Laminaria saccharina	13	+1	+1								
Cryptopleura ramosa	+1*				+1						
Ptilothamnion pluma					•						
C**Desmarestria ligulata											
C**Phyllophora brodiaei											
Desmarestria aculeata	+2	+2	+1				+1				
A**Sphondylothamnion multifidum											
* Odonthalia dentata	23	24		12	23	+1	+1	+1			
Laminaria digitata			+1								
A**Taonia atomaria											
Dictyopteris membranacea										+1	
A**Laminaria ochroleuca											
C**Cystoseira foeniculacea											
A**Callocolax neglectus											
Companions											
Lithothamnion spp.	13	13	22	13	44	44	33	+3	23	44	1
Rhodymenia palmata		+2*	+2*		+3*		+1*		+2*	+3*	+
Membranoptera alata	+1*		+2*	+2*	+2*	+2*	+2*		+2*		+
Chondrus crispus		+2	+2	+2	+2	+2	+2	+2		+2	
Plocamium vulgare	+1*	+3		+3*	+2	+2	+3	12			
Ceramium rubrum	+1	+2	+2	+2	+2	+2	+2	+2	+2		
Corallina officinalis		+3	+3	+3	+2		+2	+2	+3		+
Lithophyllum pustulatum				•	•	•	•		•		
Phyllophora membranifolia	+2			+2		13	23	+3	+3	+3	+
Heterosiphonia plumosa							+2				
Lomentaria articulata	+2*										
Ulva lactuca	+1										+
Hypoglossum woodwardii										+2	
Ahnfeldia plicata		+2		+1							
Halidrys siliquosa	+2	+2	+2								
Furcellaria fastigiata		+1		+3			23				
Cladophora rupestris				+2	+2						
Polyides rotundus				+2			+3				

***Subassociation Typicum**

Variant typicum

Distribution	Aufnahme No.	Species with low presence	
C	4BL2	Rhodomela confervoides	•

****Subassociation Desmarestrietosum ligulatae**

Differentials of subassociation
Variant typicum

A	25R2	Cladophora sericea	+2
C	25R2	Ectocarpus fasciculatus	•
C	25R2	Rhodophyllis divaricata	+2
A	21P1	Callithamnion tetricum	+2
A	21P1	Ceramium strictum	•
A	23S1	Gastroclonium ovatum	+1
C	23S1	Porphyra umbilicalis	•
A	22C1 23S1	Sphaerococcus coronopifolius	+2
A	22C3	Gelidium latifolium	+2
A	2C1	Polyneura spp.	+1*
C	20P1	Mesogloia vermiculata	+1
C	20P1	Antithamnion plumula	•
C	20P1	Bryopsis hypnoides	+2
C	20P1	Gigartina stellata	+2
C	20P1	Bonnemaisonia aspargoides	+2
C	20P1	Spermothamnion repens	+2*
C	28P2	Scytosiphon lomentarius	+1
C	28P2	Sphacelaria pennata	•
C	28P2	Chorda filum	+2
A	29M3	Erythroglossum sandrianum	•
C	23S1	Halopteris scoparia	+2
A	29M5 23S1	Dictyopteris membranacea	+1
C	24L1	Ceramium echionotum	+2*
C	34H1	Halarachnion ligulatum	+1

Unstable v

Distributi
C
C
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C
A
r

Companions
A

Phytogeog
A Recor
B Recor
C Recor

TABLE 6

Laminarietum digitatae (Ass. prov.)

Provisional																				
Alliance	Laminarion																			
Association	Laminarietum digitatae																			
Subassociation	Typicum											Asparagopsietosum								
Variant												Sh.			Exp.					
Aufnahme Number	2P1	3H1	3H2	4B11	4B12	5H1	5M2	5M2	5M2	7B1	7B2	28P1	25P2	27P1	26H1	24L1	23S1	23S2	22C1	21P4
Depth (m.-C.D.)	0	0	0	1.2	0	.9	.9	.9	.9	.9	0	.9	0	0	.9	.9	1.5	.9	.9	.9
Exposure	D	D	D	B	B	D	D	D	D	D	D	C	C	C	E	E	F/D	F/D	E	F/B
Substrate	XV	X	X	X	X	X	X	X	X	X	X	X	X	X	X	V	X	X	XV	X
Total cover (%)	90	80	100	100	90	70	95	90	90	80	75	80	80	70	80	80	80	80	85	80
Species Number	11	13	21	11	6	14	10	7	8	13	9	22	17	15	26	16	28	36	26	28
Character species of association																				
Laminaria digitata	33	23	23	33	12	33	33	23	23	33	13	23	33	23	23	13	13	23	23	13
Differentials of regional sub-association Asparagopsietosum armatae (tetra.)																				
(Sh.) **Moderately sheltered variant**																				
B Asparagopsis armata (tetra.)												•	•		•	•	•	•		•
C Rhodochorton purpureum												•							•	•
B Mesophyllum lichenoides												+2	+2			+3	+2	+1		
C Halurus equisetifolius														+2			+2	+2	+2	+2
(Exp.) **Exposed variant**																				
C Lithophyllum pustulatum															•	•	•			
B Bifurcaria bifurcata															+1		13	+2		
C Plumaria elegans																		+2°	+2°	+2°
C Callithamnion granulatum																		+2°	+2°	+2°
Character species of alliance																				
Laminaria hyperborea				+1							+1	+1	+1					+1	+1	+1
C** Desmarestia ligulata													+1		+2	+1		+2		+2
(Exp.) C** Saccorhiza polyschides															+1	+2	+1		+1	+2
(Exp.) C** Giffordia hincksiae															•	•	•		•	•
(Exp.) C Delesseria sanguinea							+1	+2	13	+2										+2
C** Cryptopleura ramosa												•	+1				+2		+1	
Laminaria saccharina	+1					+1								+2						
(Exp.) C** Dilsea carnosa															+2	+2				
C** Dictyota dichotoma												+2	+2							
(Exp.) C Cystoseira foeniculacea						+1														
(Exp.) C** Callophyllis laciniata																		+1		
Companions																				
Lithothamnion spp.	34	33	23	55	55	23	33	55	30	44	13	33	23	23	23	23	44	34	34	34
Corallina officinalis	+2	+3	34	+2		+2				+2	+3	40	44	44	44	44	13	23	44	24
Rhodymenia palmata	+2°		+2°	+2°	+2°	+2°	13°	13°	13°	+3°		+1°			+1°		+1°	+1°	13°	+2°
Gigartina stellata	13		+2	13	12				+2	+2			+2	23	+3	23	13	13		+2
Ceramium rubrum		12	13			+2	+1			+2	+3	+2		23	+2°	+2°		+2		+3
Himanthalia elongata			+1						+2			24	12	13	13	13	13	23	13	23
Alaria esculenta		23		+3						35			+1	+2	+1	+1	+2		+3	+2
Fucus serratus	+1		+4	+2	+2	23	+2	+2						+2	+2			+2		+2
Cladophora rupestris		+2	+2	+2	+2	+2					+2	+2	+2					+2	+2	+2
Ulva lactuca	+1	+2				+1				+1	+1			+3		+1	+1°	+1	+1	
Chondrus crispus							+2	+2					+2		+2	23	+2	13	+2	+2
Laurencia pinnatifida	+2											+3	+2	+2	+2		+2	+3		+2
Porphyra umbilicalis	+1			+1						+1				+1			+1	+1	+2°	+3
Ectocarpus fasciculatus																				
Polysiphonia urceolata		+2				+3				+2		•						+2		+2
Membranoptera alata		+1	+1	+1°			+1			+1							+1°			
Enteromorpha compressa		+1				+2	+2					+3°			+2			13		
Elachista fucicola	•		•			•	•	•				•								
Hypoglossum woodwardii									+2				+2					12	+2	+2
Spongonema tomentosoides		•	•			•									•					
Lomentaria articulata			•											+2			+2	+2		
Enteromorpha intestinalis		+2									+1							13		
Dumontia incrassata			+1						+1								+1			

Subassociation Typicum

Distribution	Aufnahme No.	Species of low presence	
C	3H2	Litosiphon laminariae	•
C	3H2	Pilayella littoralis	•
C	3H2	Ectocarpus arctus	•
C	3H2	Urospora penicilliformis	+3
C	3H2	Ectocarpus confervoides	+2
C	3H2	Myriotrichia clavaeformis	•
C	3H2	Polysiphonia brodiaei	+2
C	3H2	Acrochaetium daviesii	•
C	7B1	Chordaria flagelliformis	+1
C	7B2	Halidrys siliquosa	+2

**Subassociation Asparagopsietosum

Differentials of subassociation

(Exp.) **Exposed variant**

Distribution	Aufnahme No.	Species in low presence	
B	26H1	Acrosorium uncinatum	•
C	26H1	Polysiphonia nigrescens	+2
C	26H1	Rhodochorton floridulum	+2
C	26H1	Cystoclonium purpureum	+2
C	23S1 26H1	Cladostephus spongiosus	+2
C	23S1	Codium tomentosum	+2
B	23S1	Polyneura hilliae	+1
C	23S1	Furcellaria fastigiata	+2
C	23S1	Ahnfeltia plicata	+3
C	23S1	Gelidium pulchellum	+2
C	23S1	Callithamnion tetragonum	+2
B	23S2	Acrosiphonia arcta	+2
C	23S2	Polyides rotundus	+2
C	23S2	Sphacelaria caespitula	+2
C	23S2	Chaetomorpha melagonium	+2
C	21P4	Ceramium strictum	+2
C	21P4	Rhizoclonium implexum	•
C	21P4	Polysiphonia denudata	+2
C	22C1	Heterosiphonia plumosa	+2
B	22C1	Ulva rigida	+2
B	22C1	Sphondylothamnion multifidum	+2
B	22C1	Cladostephus verticillatus	+2
C	23S1 22C1	Pterosiphonia parasitica	+2

(Sh.) **Sheltered variant**

Distribution	Aufnahme No.	Species in low presence	
C	28P1	Giffordia secunda	+2
B	28P1	Radicilingua thysanorhizans	+2
B	27P1	Sphacelaria scutellatum	•

Companions

Distribution	Aufnahme No.	Species in low presence	
C	28P1 26H1	Scytosiphon lomentarius	+2
B	28P1 27P1	Callithamnion corymbosum	+2°
C	28P1 23S2	Nitophyllum punctatum	+3°
C	28P2 22C1	Plocamium vulgare	+2
C	28P2 22C1	Ceramium echionotum	+2°

Phytogeographical distribution:-

A Recorded for the East coast of Britain
B Recorded for the South West peninsula of Britain
C Recorded for both regions

TABLE 7

Laminarietum saccharinae (Ass. prov.)

Provisional

Alliance	Laminarion				
Association	Laminarietum saccharinae				
Variant	Dp.		Tp.		
Aufnahme Number	36B3	36B2	28P6	25R5	35S1
Depth (m.-C.D.)	10.1	3.0	4.2	5.1	4.5
Exposure	B	B	C	C	B
Substrate	XV	XV	XVW	XVW	XV
Total cover (%)	10	40	60	60	15
Species Number	16	22	33	16	9
Character species of association					
Laminaria saccharina	13	13	13	34	34
Variant typicum					
Cladestephus verticillatus			+2	+2	+2
Character species of alliance					
Dictyota dichotoma	23		+2	13	+2*
Saccorhiza polyschides		+1	+1	+2	
Giffordia hinksiae		*	*	*	
Cryptopleura ramosa	+3	13	+3*		
(Dp.) Laminaria hyperborea		+1			
(Tp.) Dilsea carnosa			+2		
(Dp.) Callophyllis laciniata		+1*			
(Dp.) Delesseria sanguinea		+2			
(Tp.) Laminaria digitata				+1	
(Tp.) Cystoseira foeniculacea			+3		
(Tp.) Desmarestria aculeata				+3	
(Dp.) Dictyopteris membranacea	+2				
Companions					
Ceramium rubrum	+2*	+2*	+1*	+3	+2*
Plocamium vulgare	+1	+1*	+1	+2	+3
Rhodymenia palmata	+3*	+3*		+3	+3*
Ulva lactuca		+1	+1	13	+1
Enteromorpha compressa	+1	+1*	+1	+2	
Lithophyllum pustulatum	*	*	*		
Lithothamnion spp.	+2	13			+2
Chondrus crispus		+2	+2	+2	
Chorda filum		+2	+3	+2	
Gracilaria verrucoa		+2	+2		13
Furcellaria fastigiata		+2	+2	+2	

(Tp.) Variant typicum

Aufnahme No.	Species with low constancy	
28P6	Scytosiphon lomentarius	+1
28P6	Gigartina teedii	+1
28P6	Spermothamnion repens	*
28P6	Giffordia hincksiae	*
28P6	Bonnemaisonia asparagoides	+1
28P6	Polysiphonia violacea	*
28P6	Sphacelaria pennata	*
28P6	Polysiphonia nigrescens	+1
28P6	Taonia atomaria	+2
28P6	Jania rubens	+2
28P6	Fucus serratus	13
28P6	Ectocarpus fasciculatus	*
28P6	Nitophyllum punctatum	*
25R5	Alaria esculenta	+1
28P6	Cladostephus verticillatus	
(Dp.) Deep water variant		
36B2	Polysiphonia brodiaei	+1
36B3 36B2	Heterosiphonia plumosa	+2
36B3 36B2	Calliblepharis ciliata	+1
36B3 36B2	Halidrys siliquosa	+1
Companions		
36B3 28P6	Polysiphonia elongata	*
36B3 28P6	Cystoclonium purpureum	+2
36B3 28P6	Chondria dasyphylla	*

TABLE 8

Laminarietum ochroleucae (Ass. prov.)

Provisional

Alliance	Laminarion											
Association	Laminarietum ochroleucae											
Subassociation	Typicum					Cystoseiretosum						
Variant	Dp.		Tp.			Ex.				Sh.		
Aufnahme Number	40T6	40T7	39L4	40T4	40T5	40T1	41A6	41A5	41A1	41A4	41A3	44L1
Depth (m.-C.D.)	22.8	18.2	11.5	11.0	13.0	7.0	6.7	3.6	4.5	9.1	6.1	2.4
Exposure	D	D	B	D	D	D	C	C	C	C	C	A
Substrate	XV	XV	XV	XV	XV	XV	XV	XV	XV	XV	XV	XV
Total cover (%)	50	60	65	65	60	45	90	80	70	70	70	90
Species Number	6	18	11	7	12	22	14	14	11	13	12	23
Character species of association												
Laminaria ochroleuca	+1	+1	23	34	34	33	44	23	33	+1	+1	+1
Character species of alliance												
Callophyllis laciniata		+2•	+2	+2	12	13	+1	+1	+?	+1		+2
**Cystoseira foeniculacea												
Cryptopleura ramosa		+1•	+3•		+2	+1•	+1•	+1				+2
Dictyopteris membranacea	+2	+2		+2	+2	+2		+1				
Dictyota dichotoma	13	+1			+1	+2		+2•				+1
Desmarestria aculeata		+1		+1	+1	+2						
**Dilsea carnosa						+2	+2					+2
**Cystoseira tamariscifolia							+1		+1			+1
(Sh.) **Laminaria saccharina										+1	+1	
(Ex.) Desmarestria ligulata				+1				+1				
(Dp.) * Ptilothamnion pluma												
Companions												
Lithothamnion spp.	13	33	13	33	13	35	13		13		+3	13
Chondrus crispus			+2	+2	+2	+2		+2		+2	+2	+2
Corallina officinalis		+1	+2			+3	33		23		12	13
Heterosiphonia plumosa			+2			+2	13	+1		+1	+1	+2
Polyneura hilliae		+1	+1		+1		+1	+1			+1	+1
Pterosiphonia complanata		+1				+2	+2		+2	+2		+2
Plocamium vulgare	+1		+2		+1•	+1		+2			+2	
Stenogramme interruptum	13		+2		+1•	+1						
Enteromorpha ramulosa		+1				+1					+3•	+3•
Gracilaria foliifera			+2			+2		+2			+2	
Gelidium sesquipedale		+2			+2				+1			+1
Asparagopsis armata (diplo.)		+2•					+2•	+2•		+2•		
Asparagopsis armata (tetra.)		+2•					+2•	+2•		+2•		
Phyllophora brodiaei		+1							+2•	+2•		
Ceramium rubrum		+1							+2•			+2•

*Subassociation Typicum

Differentials of subassociation and variants

(Dp.) Deep water variant

Aufnahme No.	Species of low presence	
40T7	Bonnemaisonia asparagoides	+1
40T7	Polysiphonia nigrescens	+1
Companions		
40T1 41A4	Chondria coerulescens	+2
40T1 44L1	Ahnfeldia plicata	+2

**Subassociation Cystoseiretosum foeniculaceae

Differentials of subassociation and variants

(Ex.) Exposed variant

Aufnahme No.	Species of low presence	
41A6	Gigartina teedii	+2
40T1	Scinaia turgida	+1
40T1 41A1	Codium tomentosum	+2
40T1 41A1	Ulva lactuca	+1
40T1 41A1	Liagora viscida	+2
41A1	Calliblepharis ciliata	+2
41A1	Griffithsia flosculosa	+2
41A6	Erythroglossum sandrianum	+1
(Sh.) Sheltered variant		
44L1 L621	Himanthalia elongata	+1
44L1 L621	Chondria dasyphylla	+2
44L1 L621	Jania rubens	+2
44L1 L621	Leathesia difformis	•
44L1 L621	Bifurcaria bifurcata	+2
44L1 L621	Mesophyllum lichenoides	+2
44L1 L621	Ceramium shuttleworthianum	+2
44L1 L621	Gastroclonium ovatum	+1
41A3 LA3	Halopteris scoparia	+2
41A4 41A3	Champia parvula	•
41A4	Bryopsis hypnoides	+1•
41A'	Halidrys siliquosa	+2
Companions		
41A5 L1A3	Plocamium vulgare	+2

TABLE 9

Saccorhizetum polyschides (Ass. prov.)

Provisional	21P2	28P4	22C4	25B4	24L4	24L5	24L1	22C2	23S2	39L1	43M1	41A9	39L2	40T1	40T2
Alliance															
Association	Saccorhizetum polyschides														
Subassociation	Alarietosum									Typicum					
Variant										Ex.	Typicum				
Aufnahme Number	21P2	28P4	22C4	25B4	24L4	24L5	24L1	22C2	23S2	39L1	43M1	41A9	39L2	40T1	40T2
Depth (m.-C.D.)	3.6	3.6	0	2.7	4.2	4.2	3.6	7.0	7.0	2.1	1.2	2.1	7.0	6.0	4.5
Exposure	F/B	C	E	C	E	E	E	E	F/D	E	F/B	C	E	D	D
Substrate	XVW	XVW	XVW	XVW	XVW	XVW	XVW	XVW	XVW	X	X	XV	X	XV	XV
Total cover (%)	80	90	40	70	70	65	60	30	80	65	80	60	60	65	90
Species Number	34	25	24	26	14	27	25	23	19	7	17	17	11	18	18
Character species of association															
Saccorhiza polyschides	34	44	23	34	33	33	23	12	24	23	33	44	33	23	23
Differentials of regional sub-association Typicum															
typical variant															
C. Pterosiphonia complanata										+2	+2	+2	13	+2	+1
C Gelidium sesquipedale										+1	+2	+2	+1		+1
C Codium tomentosum											+1	+1	+2	+1	
Differentials of regional sub-association Alarietosum															
C Membranoptera alata	+2•		+1•	+2•		+1		+1•	13•						
C Polysiphonia aculeata	•	•	•	+1•					•						
C Lithophyllum pustulatum	•	•	•				•	•	•						
C Hypoglossum woodwardii		+1		+1•		•	+2		+1•						
A Alaria esculenta	+2	13	+2	+2											
C Himanthalia elongata	+1		13					+1	+1						
C Cladostephus verticillatus	+2	+2	+2				+3								
C Lomentaria articulata			+1		+3•				+1•						
C Nitophyllum punctatum				+1•		+3•	•	•							
Character species of alliance															
Dilsea carnosa	+2	+2	+2			+2	+2	+2	24	+2					
C** Callophyllis laciniata	+1•	+1•				+1•	+1•		+1•						
C** Cryptopleura ramosa		+2	+1•			+3•	+2•	+2•							
C Desmarestria ligulata	+2	+1	+1			+2						+1	+1	+1	
C Laminaria hyperborea	13			+1	+1	23	23	23	13						
C** Phycodrys rubens	•	+1		+1•	+1•	+3•	•								
C Laminaria ochroleuca				13								+1	+1	+1	33
C** Desmarestria aculeata	+2	+1		+1		+3		+1							
C Dictyota dichotoma	+2					+2								+2	+1•
C** Laminaria saccharina	+1	+1		+1											
C** Delesseria sanguinea	+2		+1			+2									
C** Laminaria digitata	+1	+1						+1							
C** Cystoseira foeniculacea	+1														
C** Ptilothamnion pluma								•							
Companions															
Giffordia hinksiae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Lithothamnion spp.	44	23	44	+3	+3	13	13	34	33	13	23	44	33	13	13
Corallina officinalis	23	+2	33		+3		44	+3	+2	+2	23	33	+3	33	23
Chondrus crispus	+2	+2		+2	+2	+2	+2		+2		+2	13		+2	+2
Ceramium rubrum	+2	+2		+2•	13•	13•	13•	+1•			+1•	+1			+1
Asparagopsis armata (tetra.)	+2•	+2•	+2•		+3•	+2•	+2•	+2•			+2•			+2•	
Cladophora rupestris	+1		+2								+2	+1	+1•	+2	
Heterosiphonia plumosa	+2	+1	23				+3	23	23					+2	33
Plocamium vulgare	+3		+1	+1•			+1	+1				+2			+1
Polyneura hilliae	+2	+2		+1					+1				+1	+1	+1
Ulva lactuca				+1•	23•	13	13		+1		+1			+1	
Asparagopsis armata (diplo.)			+2•		+2•	+2•	+2•	+2•							+2•
Gastroclonium ovatum	+2		+2		+1	+1					+2				
Ectocarpus fasciculatus							•					•		•	•
Halurus equisetifolius			+2				+2	+2	+1			+1			
Laurencia pinnatifida	+2	+1									+2				
Griffithsia floscolosa			+2											+2	+1

Phytogeographical distribution:-

A Recorded for the South West peninsula of Britain
B Recorded for the coast of North West Spain
C Recorded in both regions

Differential species of sub-association Typicum

(Exp.) Exposed variant

Variant typicum

Distribution	Aufnahme No.	Species of low presence	
C	43M1	Stenogramme interruptum	+2
C	43M1	Chondria coerulescens	+1
C	40T1	Mesophyllum lichenoides	+2
C	40T2	Cystoseira tamariscifolia	+2
C	41A9	Litosiphon laminariae	•
**Differential species of subassociation Alarietosum			
C	23S2	Sphaerococcus coronopifolius	+2•
A	21P2	Phyllophora membranifolius	+2
C	21P2	Enteromorpha compressa	+2
A	21P2	Callocolax neglectus	•
C	21P2	Schizymenia dubyi	+1
C	28P4 24L1	Fucus serratus	+2
C	28P4	Halopteris scoparia	+2
C	25B4	Cystoclonium purpureum	+1
A	25B4	Antithamnion sarniense	•
C	25B4	Lomentaria orcadensis	•
A	25B4	Ceramium strictum	•
A	25B4	Brongniartella byssoides	+1
C	25B4	Porphyra umbilicalis	•
C	25B4	Calliblepharis jubata	+1
C	24L4 24L5	Scinaia turgida	•
C	24L1 24L5	Ceramium echionotum	•
C	24L5	Polysiphonia elongata	+2
A	24L5	Polysiphonia fibrillosa	+2
C	24L5	Dumontia incrassata	+1
C	24L1	Rhodicilingua thysanorhizans	+2
C	24L1	Dasya hutchinsiae	•
C	22C2	Plumaria elegans	•
A	22C2 25B4	Phyllophora brodiaei	+2
C	22C4 22C2	Rhodymenia palmata	+2•
Companions			
C	43M1 21P2	Jania rubens	•
C	41A9 24L5	Apoglossum ruscifolium	•

Appendix 5

MODIFICATION OF FIELD METHODS

When cropping in localities other than those along the coast of North East England or South West Scotland, all the material was first weighed and then representative sub-samples were air-dried and brought back to the laboratory for final drying and analysis.

Laminaria ochroleuca and Saccorhiza polyschides, which were cropped on the coast of North West Spain, were air-dried for two days before weighing. Representative sub-samples of this material was then brought back to England for oven drying and analysis. These partly dried sub-samples were used for the convertion of all measurements to values for absolute dry weight and finally to one for organic (ash-free) dry weight.

Appendix 6

THE INDIVIDUAL PERFORMANCE DATA

(Tables 10-53)

TABLES 10-19

The composite mean cropping data and production figures for

Laminaria hyperborea

Table 10 (i)

The composite mean cropping data and production figures

St. Abb's Head - Petico Wick

Depth	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass 1966	Lamina Peak Biomass 1967	Total Biomass 1966	Total Biomass 1967	Total Increment 1966	Total Increment 1967	Stipe length	Stipe Wt./unit	$\int_0^T$ wdt.	
	1	.9 ± .2	.9	1.2 ± .2	1.2	2.4 ± 4.6	1.4 ± .1	4.5	3.5	4.5	3.5	6.0 ± .5	2.0	I.M.P.	85
	2	3.1 ± .6	2.2	3.0 ± .6	1.8	11.2 ± 1.2	8.2 ± .1	17.3	14.3	15.2	12.2	25.0 ± .3	1.2	I.S.P.	154
	3	6.5 ± .6	3.4	10.8 ± .8	8.1	42.0 ± 3.3	37.0 ± 3.1	59.3	54.3	53.5	48.5	57.0 ± 2.7	1.8		
3.0m.	4	12.8 ± .9	6.3	25.0 ± 1.8	14.2	65.0 ± 2.8	49.0 ± 2.5	102.8	86.8	85.5	69.5	78.0 ± 2.2	3.2	I.L.P.	328
	5	22.4 ± 2.4	9.6	37.2 ± 2.1	12.2	88.0 ± 3.4	94.0 ± 6.5	147.6	153.6	109.8	115.8	88.2 ± .7	4.2	I.S.L.	422
	6	24.6 ± 2.7	2.2	45.0 ± 1.8	7.8	81.6 ± 9.7	85.0 ± 5.2	151.2	154.6	91.6	95.0	102.0 ± 1.4	4.4		
	7	25.5 ± 3.3	.9	49.0 ± 1.8	4.6	76.9 ± 2.8	84.0 ± 4.9	151.4	158.5	82.4	89.5	104.0 ± 1.8	4.7	I.W./U.L.	14
	1	.9 ± .2	.9	1.2 ± .2	1.2	2.1 ± .1	2.0 ± .1	4.2	4.1	4.2	4.1	4.0 ± 1.3	3.0	I.H.P.	83
	2	3.4 ± .6	2.5	3.6 ± .6	2.4	12.0 ± 1.2	9.0 ± .9	19.0	16.0	16.9	13.9	23.2 ± 2.4	1.6	I.S.P.	125
	3	7.0 ± .6	3.6	10.8 ± .9	7.2	36.0 ± 4.0	23.0 ± .9	53.8	40.8	46.8	33.8	42.0 ± 3.0	2.6		
7.6m.	4	12.0 ± .9	5.0	21.0 ± 1.5	10.2	36.0 ± 2.8	37.0 ± 2.2	69.0	70.0	51.2	52.2	60.3 ± 2.3	3.5	I.L.P.	255
	5	23.2 ± 2.7	11.2	31.2 ± 2.4	10.2	65.0 ± 5.2	61.0 ± 4.0	119.4	115.4	86.4	82.4	81.0 ± 1.6	3.8	I.S.L.	369
	6	25.3 ± 3.3	2.1	37.2 ± 3.0	6.0	61.0 ± 4.0	71.0 ± 4.0	123.5	133.5	69.1	79.1	97.0 ± 1.0	3.8		
	7	26.1	.8	40.0 ± 2.4	2.8	56.0 ± 4.3	67.0 ± 5.0	122.1	133.1	59.6	70.6	111.0 ± 4.7	3.6	I.W./U.L.	15

Table 10 (ii)

The composite mean cropping data and production figures

Petico Wick

Depth	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
10.6m.	1	.6 ± .3	.6	.1 ± .02	.1	3.4 ± .8	.3	I.H.P.	30
	2	1.2 ± .5	.6	.5 ± .02	.4	13.3 ± .7	.4	I.S.P.	49
	3	1.4 ± .2	.2	1.6 ± .1	1.1	22.3 ± .8	.7	I.S.L.	228
	4	3.6 ± .5	2.2	3.9 ± .2	2.3	30.8 ± 1.1	1.3	I.W./U.L.	7
	5	5.4 ± .6	1.8	6.7 ± .6	2.8	39.8 ± 4.3	1.7		
	6	8.9 ± .9	3.5	14.5 ± 1.5	7.8	56.6 ± 2.2	2.6		
	7	19.9	11.0	38.8	24.3	72.0	5.4		
12.7m.	1	-	-	-	-	-	-		
	2	.1	.5	.1 ± .01	.5	6.3 ± .6	.1	I.H.P.	9
	3	.4 ± .01	.3	.3 ± .02	.2	10.8 ± .5	.3	I.S.P.	8
	4	1.1	.7	.8 ± .02	.5	15.8 ± .7	.5	I.S.L.	110
	5	1.2 ± .2	.1	1.1 ± .6	.3	20.0 ± 1.4	.5	I.W./U.L.	2
	6	2.6	.4	2.6 ± .1	1.5	29.6 ± 1.3	.9		
	7	-	-	-	-	-	-		

Table ii

The composite mean cropping data and production figures

St. Abb's Head - Harbour mouth

Depth	Age	Stipe Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	.2	.2	8.5	.2		
	2	2.1 ± .5	1.9	25.4 ± 2.5	.8		
	3	4.1 ± .6	2.0	35.0 ± 2.9	1.8	I.S.P.	101
3.0m.	4	11.4 ± 1.4	7.3	57.0 ± 3.4	2.0	I.S.L.	192
	5	21.1 ± .8	9.7	71.4 ± 1.6	2.9	I.W./U.L.	10
	6	31.0 ± 1.7	9.9	78.9 ± 3.3	3.9		
	7	52.5 ± 1.1	21.5	108.6 ± 5.7	4.8		

Table 12

The composite mean cropping data and production figures

Beadnell - Lady's Hole (Inlet)

Depth	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
	1	.2	.2	.2	.2	1.5	1.9	1.9	4.5	.4	I.H.P.	70
	2	1.1 ± .1	.9	1.1 ± .08	.9	5.6	7.8	7.4	19.1 ± 1.8	.6	I.S.P.	131
	3	4.6 ± 1.0	3.5	8.3 ± .7	7.2	16.8 ± 1.4	29.7	27.5	46.0 ± 4.8	1.8		
3.0m.	4	9.6 ± 2.0	5.0	24.0 ± 2.5	15.7	31.2 ± 3.4	64.8	51.9	78.0 ± 5.6	3.1	I.L.P.	208
	5	19.0 ± 3.2	9.4	30.0 ± 2.6	6.0	62.0 ± 5.6	111.0	77.4	93.0 ± 4.1	3.2	I.S.L.	446
	6	19.2 ± 3.8	.2	39.8 ± 3.7	9.8	61.0 ± 7.1	120.0	71.0	100.8 ± 4.5	3.9		
	7	29.0 ± 2.9	9.8	47.5 ± 2.7	7.7	62.0 ± 4.3	138.5	79.5	109.0 ± 4.2	4.3	I.W./U.L.	13
	1	.6 ± .1	.6	.2 ± .03	.2				3.0 ± .5	.7	I.H.P.	73
	2	.8 ± .1	.2	2.4 ± .4	2.2	2.7 ± .3	5.9	5.1	14.1 ± 1.0	1.7	I.S.P.	127
	3	2.2 ± .2	.4	5.8 ± 1.9	3.4	8.0 ± .3	16.0	11.8	33.0 ± 5.9	1.7		
7.6m.	4	11.2 ± .5	9.0	21.0 ± 2.3	15.2	22.0 ± 1.5	54.2	46.2	75.0 ± 4.3	2.8	I.L.P.	156
	5	15.0 ± 1.8	3.8	36.0 ± 2.2	15.0	41.0 ± 2.0	92.0	59.8	92.0 ± 5.3	3.9	I.S.L.	412
	6	26.0 ± .6	11.0	44.0 ± 2.6	8.0	49.0 ± 2.8	119.0	68.0	110.0 ± 6.0	4.0		
	7	36.8 ± 3.4	10.8	46.0 ± 7.3	2.0	50.9 ± 5.2	133.7	63.7	107.0 ± 9.0	4.3	I.W./U.L.	12

Table 13

The composite mean cropping data and production figures

Beadnell - Ebbe's Snook

Depth	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
	1	-	-	-	-	-	-	-	-	-		
	2	1.0 ± .2	.5	.8 ± .2	.4	2.6	4.4	3.5	15.0 ± 1.4	.5	I.H.P.	35
	3	2.2 ± .4	1.2	2.3 ± .4	1.5	3.7	8.2	6.4	21.2 ± 1.9	1.1	I.S.P.	64
3.0m.	4	4.7 ± .8	2.5	5.4 ± .5	3.1	7.5 ± .6	17.6	13.1	37.6 ± 1.6	1.4	I.L.P.	101
	5	6.1 ± 1.3	1.4	12.1 ± 1.1	6.7	27.0 ± 4.3	45.2	35.1	61.8 ± 4.4	1.9	I.S.L.	251
	6	12.0 ± 1.0	5.9	19.7 ± 1.7	7.6	34.7 ± 2.0	66.4	48.2	72.8 ± 4.9	2.7	I.W./U.L.	7
	7	15.0 ± 2.2	3.0	40.6 ± 3.8	20.9	49.0 ± 3.0	104.6	72.9	100.7 ± 6.6	4.0		
	1	.6	.6	.0	.0				2.5	.2		
	2	.8 ± .4	.2	.6 ± .01	.6				15.2 ± 1.2	.4	I.H.P.	76
	3	2.2 ± 1.5	.4	1.8 ± .2	1.2				28.5 ± 3.0	.6	I.S.P.	48
7.6m.	4	11.2 ± 1.5	9.0	6.6 ± .6	4.8				37.3 ± 2.2	1.8	I.S.L.	266
	5	15.0 ± 5.8	3.8	8.6 ± .8	2.0				55.5 ± 4.2	1.5	I.W./U.L.	9
	6	26.0 ± 2.0	11.0	16.3 ± 1.3	7.7				63.8 ± 3.5	2.5		
	7	36.8 ± 11.2	10.8	25.6 ± 1.7	9.3				84.8 ± 2.4	3.0		

Table 14

The composite mean cropping data and production figures

Marsden - Byer's Hole

Depth	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
	1										I.H.P.	63
	2	1.4 ± .3	.7	3.5 ± .3	1.7	9.7	14.6	12.1	25.0 ± .6	1.4		
	3	4.8 ± .8	3.4	8.7 ± 1.0	5.2	17.0	30.5	25.6	68.0 ± 7.7	1.3	I.S.P.	169
2.0m.	4	8.8 ± .2	4.0	34.0 ± 4.2	25.3	27.0	69.8	56.3	116.0 ± 5.8	3.0	I.L.P.	204
	5	16.3 ± 2.2	7.5	43.0 ± 2.8	9.0	53.0	112.3	69.5	126.0 ± 2.9	3.4		
	6	21.1 ± 2.5	4.8	53.0 ± 3.0	10.0	54.0 ± 3.7	128.1	68.8	132.0 ± 6.8	3.8	I.S.L.	583
	7	25.7 ± 1.3	4.6	59.0 ± 2.6	6.0	60.0 ± 3.1	144.7	71.2	140.0 ± 5.6	4.2	I.W./U.L.	10
	1										I.H.P.	37
	2	.4 ± .08	.2	.2 ± .03	.1	6.0 ± .8	6.6	6.3	8.5 ± .7	.2		
	3	1.3 ± .2	.9	1.1 ± .1	.9	12.9 ± 1.5	15.3	14.7	16.8 ± 1.5	.6	I.S.P.	61
3.7m.	4	2.8 ± .5	1.5	3.0 ± .2	1.9	32.0 ± .9	37.8	35.4	32.0 ± 2.1	.9	I.L.P.	182
	5	8.8 ± .6	6.0	12.8 ± .8	9.8	48.0 ± 1.8	69.6	63.8	69.5 ± 5.8	1.8		
	6	14.2 ± 1.3	5.4	24.2 ± 2.7	11.4	51.0 ± 3.4	89.4	67.8	98.2 ± 5.2	2.5	I.S.L.	301
	7	19.2 ± 1.8	5.0	33.8 ± 3.2	9.6	43.0 ± 1.8	96.0	57.6	127.0 ± 6.0	2.7	I.W./U.L.	6

Table 15

The composite mean cropping data and production figures

Redcar - Salt Scar

Depth	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
	1	-	-	-	-	-	-	-	-	-		
	2	.4	.2	2.9	1.4	3.2	6.5	4.8	24.0	1.2	I.H.P.	64
	3	6.0	5.6	6.6 ± 1.3	3.7	5.6	18.2	14.9	39.0 ± .7	1.7	I.S.P.	167
2.0m.	4	11.8 ± 1.8	5.8	28.8 ± 6.1	22.2	14.5 ± 1.0	55.1	42.5	95.0 ± 10.6	2.9	I.L.P.	126
	5	17.4 ± 1.8	5.6	47.6 ± 5.3	18.8	25.0 ± 2.6	90.0	49.4	165.0 ± 6.4	2.8	I.S.L.	575
	6	17.7 ± 1.6	.3	56.2 ± 5.7	11.5	52.5 ± 5.3	126.4	64.3	158.0 ± 20.4	3.5	I.W./U.L.	14
	7	23.0 ± 4.0	5.3	59.1 ± 6.4	2.9	55.0 ± 5.7	137.1	63.2	162.0 ± 10.6	3.6		
	1	-	-	-	-	-	-	-	-	-		
	2	-	-	-	-	-	-	-	-	-	I.H.P.	30
	3	2.6	.9	3.6	1.2	1.7	7.9	4.3	48.0	.7	I.S.P.	102
4.2m.	4	4.4 ± .5	1.8	12.4 ± 1.9	8.8	5.6 ± .9	22.4	16.2	98.0 ± 8.7	1.2	I.L.P.	36
	5	7.2 ± .6	2.8	17.7 ± 3.3	5.3	7.4 ± .8	32.3	15.5	125.0 ± 13.0	1.4	I.S.L.	571
	6	8.6 ± 3.1	1.4	42.0 ± 3.0	24.0	12.6 ± 3.2	63.2	38.0	172.0 ± 21.3	2.4	I.W./U.L.	7
	7	11.0 ± 2.1	2.4	47.0 ± 4.2	5.0	19.5 ± 5.7	77.5	27.5	180.0 ± 17.9	2.5		

Table 16

The composite mean cropping data and production figures

Inner Hebrides - Soa (Eastside)

Depth	Age	Stipe Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	.05	.05	2.4	.2		
	2	.3	.3	17.3	.2		
	3	-	-	-	-	I.S.P.	94
4.6m.	4	7.2	3.4	52.0	1.4	I.S.L.	434
	5	21.2	14.0	123.5	1.7	I.W./U.L.	8
	6	42.4 ± 3.6	21.2	138.0 ± 17.2	3.0		
	7	47.8 ± 2.7	5.4	157.6 ± 19.3	3.0		
	1	-	-	-	-		
	2	.3 ± .1	.1	17.8 ± 2.1	.2		
	3	2.1	1.8	28.5	.7	I.S.P.	27
18.3m.	4	3.8 ± .1	1.7	43.5 ± 4.4	.8	I.S.L.	241
	5	5.3 ± .3	1.5	49.6 ± 7.1	1.0	I.W./U.L.	5
	6	9.5 ± .6	4.2	61.5 ± 5.3	1.5		
	7	-	-	-	-		

Eilean Iomallach (Westside)

Depth	Age	Stipe Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	.4 ± .03	.4	7.5 ± 1.1	.5		
	2	.5 ± .05	.1	16.7 ± 4.1	.3		
	3	1.2 ± .2	.7	25.6 ± 3.1	.5	I.S.P.	36
4.6m.	4	3.3 ± .2	2.1	38.5 ± 1.4	.8	I.S.L.	261
	5	6.0	2.7	49.5	1.2	I.W./U.L.	6
	6	12.8	16.8	85.0	1.5		
	7	21.7 ± .6	8.9	108.0 ± 7.1	2.0		
	1	.06	.06	9.7	.06		
	2	.4 ± .04	.3	19.0 ± 3.1	.3		
	3	.7 ± .05	.3	19.7 ± 1.7	.3	I.S.P.	15
18.3m.	4	1.7 ± .2	1.0	33.5 ± 3.6	.5	I.S.L.	180
	5	3.3 ± .3	1.6	40.4 ± 6.7	.8	I.W./U.L.	3
	6	4.9 ±	1.6	53.0	.9		
	7	-	-	-	-		

Table 17

The composite mean cropping data and production figures

Inner Hebrides - Coalas Soa

		Stipe		Lamina	Stipe		$\int_0^T$ wdt.	
Depth	Age	Biomass	Annual Increment	Peak Biomass	length	Wt./unit length		
	1	.3	.3	.2	15.7	.2		
	2	.9	.6	4.0	26.5	.3		
	3	3.8	2.9	12.7	42.0	.2	I.S.P.	38
4.6m.	4	5.1 ± .3	1.3	22.9 ± 3.2	51.0	1.0	I.S.L.	309
	5	7.7	2.6	21.3	55.6	1.3	I.W./U.L.	5
	6	10.6 ± 1.1	2.9	38.0 ± 5.6	64.4	1.7		
	7	14.8 ± .6	4.2	38.5 ± 4.4	77.2	1.9		

Table 18

West Scotland - Saddell Bay

Depth	Age	Biomass	Annual Increment	Stipe length	Stipe Wt./unit length	$\int_0^T wdt.$	
	1	.2 ± .02	.2	10.5 ± .6	.2		
	2	.9 ± .2	.7	17.2 ± .6	.5		
	3	2.6	1.7	28.0	.9	I.S.P.	55
3.6m.	4	6.4	3.8	54.0	1.1	I.S.L.	285
	5	10.7 ± 1.1	4.3	49.5 ± 1.8	2.1	I.W./U.L.	7
	6	18.5	7.8	62.0	3.0		
	7	32.8 ± 2.1	14.9	84.6 ± 5.6	3.9		

West Scotland - Rubh'n Amair

Depth	Age	Biomass	Annual Increment	Stipe length	Stipe Wt./unit length	$\int_0^T wdt.$	
	1	-	-	-	-		
	2	.6 ± .2	.3	12.6 ± 1.1	.5		
	3	1.5	.9	17.3	.9	I.S.P.	26
3.6m.	4	2.7 ± .3	1.2	27.2 ± 6.1	1.0	I.S.L.	159
	5	4.1 ± .3	1.4	29.5 ± 5.3	1.4	I.W./U.L.	7
	6	9.8 ± .9	5.7	34.5 ± 6.1	2.8		
	7	-	-	-	-		

West Wales - Cardigan Island

Depth	Age	Biomass	Annual Increment	Stipe length	Stipe Wt./unit length	$\int_0^T wdt.$	
	1	.07 ± .00	.07	3.1	.6		
	2	.2 ± .03	.2	7.3	.5		
	3	.4 ± .02	.2	21.0	.6	I.S.P.	44
3.6m.	4	1.2	.8	45.5	2.4	I.S.L.	275
	5	11.0 ± 1.4	9.8	60.0	1.8	I.W./U.L.	8
	6	-	-	-	-		
	7	25.7	7.3	92.0	2.8		

Table 19

The composite mean cropping data and production figures

Sennen Cove

Depth	Age	Stipe Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	-	-	-	-		
	2	-	-	-	-		
	3	5.0 ± 1.0	1.5	35.0 ± 3.9	1.4	I.S.P.	140
3.0m.	4	12.9 ± 1.4	7.9	63.0 ± 1.5	2.0	I.S.L.	343
	5	26.5 ± 1.5	15.6	86.0 ± 3.1	3.0	I.W./U.L.	11
	6	27.1 ± .1	1.6	71.0 ± 3.3	3.8		
	7	40.7	13.6	83.0	4.9		
	1	-	-	-	-		
	2	2.6	1.3	8.8	2.9		
	3	3.1 ± .5	.5	23.0 ± 4.0	1.0	I.S.P.	124
12.2m.	4	10.2 ± 1.9	7.1	34.0 ± 4.3	3.0	I.S.L.	246
	5	15.9 ± 1.0	5.7	66.0 ± 3.4	2.4	I.W./U.L.	14
	6	13.5 ± 2.3	0.-	62.0 ± 8.1	2.1		
	7	37.7 ± 2.3	24.2	83.0 ± 3.8	4.5		

TABLES 25-32

The composite mean cropping data and production figures for

Laminaria digitata

Table 25

The composite mean cropping data and production figures

St. Abb's Head

		Hapteron		Stipe		Lamina			Stipe		$\int_0^T$ wdt.	
	Age	Biomass	Annual Increment	Biomass	Annual Increment	Peak Biomass	Total Biomass	Total Increment	length	Wt./unit length		
Harbour mouth	1	.1 ± .02	.1	.3 ± .04	.3	2.0 ± .4	2.4	2.4	11.6 ± 1.6	.2	I.H.P.	5
	2	.4 ± .1	.3	.7 ± .3	.4	25.1 ± 4.6	26.2	25.8	28.3 ± 4.0	.2	I.S.P.	21
	3	1.1 ± .3	.7	3.3 ± 1.1	2.6	27.6 ± 4.2	31.0	30.9	46.3 ± 2.2	.7	I.L.P.	149
	4	1.7 ± .3	.6	7.2 ± 1.3	4.9	64.3 ± 11.0	73.2	69.8	62.5 ± 6.1	1.1	I.S.L.	188
	5	4.2 ± .3	2.5	17.6 ± 3.4	10.4	99.3	121.1	112.2	83.4 ± 5.9	2.1	I.W./U.L.	3
Petico Wick	1	.1 ± .02	.1	.1 ± .03	.1	.3	.5	.5	8.3 ± 1.8	.1	I.H.P.	5
	2	.3 ± .02	.2	.4 ± .05	.3	11.2 ± 3.5	11.9	11.7	13.6 ± 2.0	.3	I.S.P.	11
	3	1.2 ± .1	.9	1.6 ± .7	1.2	24.5 ± 4.3	27.3	26.6	29.0 ± 2.9	.5	I.L.P.	110
	4	1.7 ± .2	.5	4.5 ± .7	2.9	46.6 ± 8.4	52.8	50.0	45.3 ± 4.6	.9	I.S.L.	123
	5	3.5 ± 1.6	1.8	8.9 ± 1.6	4.4	56.4 ± 6.4	68.8	62.6	57.0 ± 5.9	1.5	I.W./U.L.	2

Table 26

The composite mean cropping data and production figures

Beadnell - Lady's Hole

	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
	1	.05 ± .01	.05	.1 ± .02	.1	7.2 ± 1.0	7.3	7.3	5.5 ± .9	.1	I.H.P.	5
	2	.4 ± .04	.3	.3 ± .1	.2	18.3 ± 3.2	19.0	18.8	12.2 ± 1.1	.2	I.S.P.	7
Tidepool	3	1.1 ± .2	.7	1.0 ± .1	.7	32.5 ± 5.0	34.6	36.0	20.6 ± 2.0	.4	I.L.P.	125
	4	2.0 ± .3	.9	2.5 ± .2	1.5	47.0 ± 6.8	51.5	49.4	28.7 ± 3.7	.8	I.S.L.	90
	5	4.2 ± .7	2.2	5.0 ± .5	2.5	37.4	46.6	51.3	45.5 ± .8	1.0	I.W./U.L.	2
	1	.08 ± .02	.08	.3 ± .1	.3	3.6 ± .6	3.9	3.9	7.0 ± .2	.4	I.H.P.	7
	2	.5 ± .1	.4	1.2 ± .2	.9	4.1	5.8	5.4	21.3 ± 7.3	.5	I.S.P.	24
Inlet	3	1.3 ± .1	.8	3.3 ± 1.1	2.1	15.7 ± 4.4	20.3	18.6	40.6 ± 4.2	.8	I.L.P.	68
	4	2.5 ± .3	1.2	8.6 ± 1.9	5.3	23.6 ± 2.3	34.7	30.1	63.8 ± 5.9	1.3	I.S.L.	181
	5	4.1 ± .4	1.6	19.5 ± 3.8	10.9	42.3 ± 2.3	65.9	54.8	91.0 ± 12.6	2.1	I.W./U.L.	4

Table 27

The composite mean cropping data and production figures

	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T wdt.$	
Beadnell - Lady's Hole												
	1	.2 ± .03	.2	.2 ± .02	.2	2.1 ± .3	2.5	2.5	9.4 ± 1.2	.2	I.H.P.	8
	2	.5 ± .04	.3	.8 ± .2	.6	5.5 ± .4	6.8	6.4	18.3 ± 1.6	.4	I.S.P.	14
Current surge	3	1.6 ± .3	1.1	2.1 ± .4	1.3	29.9 ± 4.0	33.6	36.0	30.8 ± 3.1	.6	I.L.P.	106
	4	3.5 ± .4	1.9	5.1 ± 1.0	3.0	51.9	60.5	56.8	49.9 ± 2.9	1.0	I.S.L.	142
	5	4.0 ± .5	.5	10.5 ± 2.4	5.4	38.9	53.4	44.8	72.0 ± 5.8	1.4	I.W./U.L.	3
Ebbe's Snook												
	1	.1	.1	.02	.02	.9	1.0	1.0	4.2	.1	I.H.P.	6
	2	.6 ± .1	.5	.6 ± .1	.5	20.2 ± 6.4	21.4	21.2	18.9 ± 1.4	.3	I.S.P.	14
	3	.9 ± .1	.3	2.4 ± .2	1.8	9.1 ± 1.2	12.4	11.2	40.0 ± 3.9	.6	I.L.P.	90
	4	2.2 ± .09	1.3	5.1 ± .8	2.7	27.8 ± 4.0	35.1	51.8	56.0 ± 7.3	.9	I.S.L.	163
	5	4.3 ± .2	2.1	11.8 ± 2.0	6.7	50.6 ± 4.4	66.7	59.4	89.9 ± 10.2	1.3	I.W./U.L.	3

Table 28

The composite mean cropping data and production figures

Marsden

	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T w\,dt.$	
	1	.2 ± .1	.2	.2 ± .03	.2	1.4	1.8	1.8	8.8 ± .7	.2	I.H.P.	7
	2	.8 ± .2	.6	.7 ± .1	.5	5.9	7.4	7.0	18.2 ± 2.5	.4	I.S.P.	14
Byer's Hole	3	1.2 ± .1	.4	2.1 ± .2	1.4	9.8 ± .9	13.1	11.6	30.7 ± 2.4	.6	I.L.P.	65
	4	2.7 ± .3	1.5	4.9 ± .5	2.8	21.0 ± 4.0	28.6	25.3	43.1 ± 2.5	1.1	I.S.L.	127
	5	3.4 ± .2	.7	11.5 ± 2.1	3.6	62.3	77.2	66.6	63.9 ± 3.9	1.7	I.W./U.L.	3

Table 29

The composite mean cropping data and production figures

Inner Hebrides

	Age	Stipe Biomass	Stipe Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	.2	.2	6.0	.3		
	2	.9	.7	9.0	1.0	I.S.P.	28
Soa (Eastside)	3	2.6 ± .9	1.7	30.5 ± 3.7	.8	I.S.L.	132
	4	5.7	3.1	49.0	1.2	I.W./U.L.	4
	5	10.3 ± .7	4.6	72.3 ± 3.4	1.4		
	1	-	-	-	-		
	2	.6	.3	13.5	.4	I.S.P.	13
Coalas Soa	3	1.6 ± .2	1.0	23.6 ± 1.7	.7	I.S.L.	121
	4	-	-	-	-	I.W./U.L.	3
	5	9.7 ± 1.2	5.6	67.0 ± 2.1	1.4		
	1	-	-	-	-		
	2	.7	.4	28.0	.6	I.S.P.	13
Eilean Iomallach (Westside)	3	1.4 ± .2	.7	45.2 ± 1.6	.3	I.S.L.	200
	4	3.4 ± .4	2.0	72.7 ± 6.1	.5	I.W./U.L.	2
	5	14.1 ± 1.2	10.7	92.4 ± 2.5	1.5		

Table 30

The composite mean cropping data and production figures

West Scotland

	Age	Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
Strone Point	1	.1	.1	6.0	.2		
	2	1.1 ± .4	1.0	25.2 ± 3.7	.4	I.S.P.	16
	3	2.5 ± .8	1.4	36.0 ± 6.2	.7	I.S.L.	157
	4	5.0 ± 1.1	2.5	46.8 ± 5.1	1.1	I.W./U.L.	3
	5	14.0 ±	9.0	78.0	1.8		
Rubh'n Amair	1	.1	.1	5.0	.2		
	2	.5 ± .02	.4	9.6 ± 1.2	.5	I.S.P.	5
	3	.6 ± .05	.1	17.2 ± 1.3	.3	I.S.L.	63
	4	1.9 ± .3	1.3	20.3 ± 1.2	.9	I.W./U.L.	3
	5	-	-	-	-		
Sgat Mor	1	-	-	-	-		
	2	.8	.4	18.0	.4	I.S.P.	10
	3	1.7 ± .7	.9	32.0 ± 6.7	.5	I.S.L.	119
	4	4.1 ± .9	2.4	39.0 ± 4.3	1.0	I.W./U.L.	3
	5	-	-	-	-		

Table 31

The composite mean cropping data and production figures

West Wales

	Age	Biomass	Stipe Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
Abereiddy (Quarry)	1	.3	.3	13.3	.2		
	2	.8 ± .1	.5	20.6 ± 1.0	.4	I.S.P.	9
	3	2.0 ± .4	1.2	34.5 ± 2.1	.6	I.S.L.	127
	4	3.2 ± .7	1.2	36.7 ± 1.9	.9	I.W./U.L.	3
	5	5.8	2.6	49.5	1.2		
Abereiddy (Quarry Entrance)	1	.1	.1	10.7	.09		
	2	.8 ± .1	.7	24.2 ± 3.5	.3	I.S.P.	12
	3	2.2 ± .9	1.4	35.3 ± 3.3	.6	I.S.L.	158
	4	4.1 ± .9	1.9	47.2 ± 5.1	.9	I.W./U.L.	2
	5	8.9 ± 1.3	4.8	62.0 ± 7.7	1.4		
Martin's Haven	1	—	—	—	—		
	2	.4 ± .09	.2	18.3 ± 1.6	.2	I.S.P.	14
	3	1.3 ± .2	.9	34.0 ± 3.8	.4	I.S.L.	149
	4	7.1	5.8	51.2	1.4	I.W./U.L.	3
	5	10.8 ± 2.1	3.7	71.2 ± 7.3	1.5		

Table 32

The composite mean cropping data and production figures

South West England

Site	Age	Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	.8	.8	21.0			
	2	1.8 ± .3	1.0	22.0 ± 1.9		I.S.P.	19
Porthmear	3	4.7 ± .6	1.9	41.1 ± 4.9		I.S.L.	152
	4	6.4 ± .9	1.7	49.7 ± 4.2		I.W./U.L.	5
	5	10.8	4.4	56.5			
	1	.5 ± .05	.5	19.1 ± 2.5	.3		
	2	1.8 ± .2	1.3	21.2 ± 1.8	.8	I.S.P.	25
Roskilly	3	3.5 ± .4	1.7	34.8 ± 2.8	1.0	I.S.L.	179
	4	10.4	6.9	43.0	2.4	I.W./U.L.	6
	5	-	-	-	-		
	1	.3 ± .04	.3	11.3 ± 1.7	.3		
	2	.5 ± .08	.2	10.6 ± 1.4	.5	I.S.P.	2
Porthleven	3	.5 ± .1	0	13.9 ± 1.9	.4	I.S.L.	60
	4	-	-	-	-	I.W./U.L.	2
	5	1.0	.2	20.4	.5		

Site	Age	Biomass	Annual Increment	Stipe length	Wt./unit length	$\int_0^T$ wdt.	
	1	.1	.1	11.4	.9		
	2	2.0	1.9	31.7	.6	I.S.P.	25
Lamorna	3	6.3 ± .6	4.3	47.1 ± 2.4	1.3	I.S.L.	179
	4	10.9 ± .8	4.6	57.4 ± 5.4	1.9	I.W./U.L.	6
	5	-	-	-	-		
	1	.9 ± .1	.9	12.1 ± .7	.7		
	2	1.6	.9	24.0	.7	I.S.P.	15
Hoe Point	3	4.9	3.3	40.9	1.2	I.S.L.	199
	4	5.2 ± 1.4	.3	70.8 ± 8.0	.7	I.W./U.L.	3
	5	-	-	-	-		
	1	-	-	-	-		
	2	.7	.3	18.3	.4	I.S.P.	18
Mullion Island	3	2.3	1.6	29.0	.8	I.S.L.	141
	4	5.2 ± .6	2.9	45.2 ± 3.1	1.1	I.W./U.L.	4
	5	20.0 ± 2.7	14.8	83.2 ± 5.7	2.4		

TABLES 36-40

The composite mean cropping data and production figures for

Laminaria saccharina

Table 36

The composite mean cropping data and production figures

St. Abb's Head

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Stipe length	Stipe Wt./unit length
Harbour 2.4m.	1	.3 ± .07	.3	59.5 ± 10.1	9.8 ± 1.4	.3
	2	.9 ± .2	.6	39.1 ± 4.3	23.5 ± 4.5	.4
	3	2.2 ± .4	1.3	-	42.1 ± 4.0	.5
Petico Wick 1.5m.	1	.2	.2	-	12.0	.2
	2	1.2 ± .2	1.0	19.0 ± 2.4	30.3 ± 3.7	.4
	3	1.9 ± .7	.7	-	38.9 ± 4.7	.5
9.1m.	1	.2 ± .04	.2	-	11.7 ± 1.4	.2
	2	1.0 ± .2	.8	18.9 ± 2.6	25.5 ± 3.7	.4
	3	1.7 ± .4	.7	22.9 ± 1.6	39.2 ± 4.5	.4

Inchkeith

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Stipe length	Stipe Wt./unit length
5.0m.	1	-	-	-	-	-
	2	2.2 ± .3	1.1	9.3 ± 1.3	42.7 ± 4.2	.5
	3	5.5 ± 2.6	3.3	17.7 ± 2.1	70.2 ± 2.7	.8

Table 37

The Composite mean cropping data and production figures

Beadnell - Lady's Hole

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Peak Biomass	Stipe length	Stipe Wt./unit length
Tidepool MTL	1	.1 ± .03	.1	19.5 ± 4.2	5.1 ± .9	.2
	2	.3 ± .05	.2	40.0 ± 5.5	11.7 ± 2.2	.3
	3	.7 ± .1	.4	-	17.7 ± 2.5	.4
Inlet 2.0m.	1	.2 ± .09	.2	47.4 ± 6.1	9.6 ± 2.6	.2
	2	.9 ± .2	.7	37.1 ± 9.1	25.6 ± 2.9	.2
	3	1.1 ± .2	.3	-	27.0 ± 2.9	.4

Table 38

The composite mean cropping data and production figures

Inner Hebrides

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Biomass 4.7.67	Stipe length	Stipe Wt./unit length
Soa (Eastside) 6.1m.	1	.2	.2	8.1	18.0	.1
	2	1.5 ± .02	1.3	36.7 ± 10.4	26.6 ± 3.3	.6
	3	4.2	2.7	71.5	52.1	.8
21.4m.	1	-	-	-	-	-
	2	.8 ± .2	.4	13.1 ± 3.1	16.7 ± 2.9	.5
	3	-	-	-	-	-
				7.7.67		
Loch Eatharna 3.0m.	1	-	-	-	-	-
	2	9.5 ± 1.4	4.7	69.5 ± 7.7	71.0 ± 6.7	1.3
	3	-	-	-	-	-

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Biomass 8.7.67	Stipe length	Stipe Wt./unit length
Eilean Iomallach (Westside) 6.1m.	1	.3 ± .06	.3	11.9 ± 2.5	13.0 ± 2.0	.2
	2	1.2 ± .2	.9	24.2 ± 7.6	25.6 ± 5.1	.5
	3	-	-	-	-	-
21.4m.	1	.3	.3	13.9	11.5	.3
	2	1.0 ± .09	.9	16.2	21.0 ± 3.7	.4
	3	-	-	-	-	-

Table 39

The composite mean cropping data and production figures

West Scotland

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Biomass	Stipe length	Stipe Wt./unit length
Strone Point 3.0m.	1	.3	.3	27.8	14.0	.2
	2	.9 ± .1	.6	34.1 ± 6.1	24.0 ± 1.4	.4
	3	2.3 ± .2	1.4	37.1 ± 7.2	40.0 ± 2.0	.6
Sgat Mor 3.6m.	1	.6 ± .09	.6	18.8 ± 2.9	17.6 ± .8	.3
	2	1.6 ± .2	1.0	32.4 ± 6.2	36.8 ± 3.4	.4
	3	4.1	2.5	92.5	56.8	.7
Sannox Bay 3.6m.	1	-	-	-	-	-
	2	.9 ± .2	.4	137.1 ± 33.5	24.4 ± 2.2	.4
	3	2.9	2.0	97.0	49.3	.6

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Biomass	Stipe length	Stipe Wt./unit length
Strone Point 7.6m.	1	-	-	-	-	-
	2	1.4 ± .3	.7	53.0 ± 3.5	26.7 ± 1.6	.5
	3	3.7	2.3	139.5	48.0	.8
Rubh'n Amair 3.6m.	1	.3 ± .02	.3	39.5 ± 7.3	29.8 ± 1.3	.3
	2	.7 ± .04	.4	45.0 ± 3.8	20.5 ± 1.6	.3
	3	-	-	-	-	-
Saddell Bay 3.6m.	1	-	-	-	-	-
	2	1.0 ± .2	.5	34.7 ± 9.1	19.2 ± 2.1	.5
	3	-	-	-	-	-

Table 40

The composite mean cropping data and production figures

West Wales

	Age	Stipe Biomass	Stipe Annual Increment	Lamina Biomass 4.3.67	Lamina Biomass 19.7.67	Stipe length	Stipe Wt./unit length
Abereiddy Quarry 1.5m.	1	.2	.2	.5	17.3	10.8	.2
	2	.5 ± .04	.3	2.4	22.1 ± 3.1	17.9 ± 1.6	.3
	3	1.8	1.3	3.6	-	32.2	.5
Abereiddy Quarry (Entrance) 0m.	1	.2	.2	.6	-	9.0	.2
	2	.8 ± .04	.6	2.8	13.9 ± 2.4	24.2 ± 2.5	.3
	3	-	-	-	-	-	-
				27.7.67			
Martin's Haven 3.0m.	1	.3	.3	39.9		14.0	.2
	2	1.1 ± .3	.8	26.3 ± 3.9		33.3 ± 3.7	.3
	3	-	-	-		-	-
				14.5.67			
Cardigan Island 3.0m.	1	.1 ± .02	.1	.4 ± .05		8.4 ± 1.7	.1
	2	.4 ± .04	.3	.7 ± .09		12.3 ± 1.1	.3
	3	-	-	-		-	-

TABLE 44

The composite mean cropping data and production figures for

Laminaria ochroleuca

Table 44

The composite mean cropping data and production figures

North West Spain

Depth (m.-C.D.)	Age	Hapteron Biomass	Hapteron Annual Increment	Stipe Biomass	Stipe Annual Increment	Lamina Biomass	Total Biomass	Total Increment	Stipe length	Stipe Wt./unit length	$\int_0^T$ wdt.	
	1	.1	.1	.2 ± .02	.2	1.5 ± .4	1.8	1.8	2.1 ± .1	.9		
	2	.2	.1	.4 ± .01	.2	10.6	11.2	10.9	8.7 ± .9	.5	I.H.P.	22
	3	.6	.4	1.2 ± .07	.8	17.8	19.6	19.0	17.1 ± 1.9	.7	I.S.P.	56
1.8-8.4	4	2.0	1.6	3.9 ± .2	2.7	26.9	32.8	31.2	30.3 ± 1.0	1.3	I.L.P.	218
	5	4.1	2.1	9.5 ± .5	6.6	51.7	65.3	60.4	41.0 ± 3.5	2.3	I.S.L.	184
	6	8.2	4.1	21.5 ± 1.8	12.3	90.5	120.2	106.9	52.1 ± 2.0	4.1	I.W./U.L.	20
	7	13.7	5.5	42.6 ± 3.2	20.8	90.1 ± 15.3	146.4	116.4	71.8 ± 2.7	5.9		
South West England												
	1	.2 ± .02	.2	.4 ± .07	.4	2.9 ± .5	3.5	3.5	11.0 ± 1.0	.4		
	2	1.5 ± .4	1.4	.7 ± .1	.3	12.5 ± 1.2	14.7	14.2	21.3 ± 2.3	.3	I.H.P.	40
	3	2.8 ± .6	1.3	1.7 ± .1	1.0	16.6 ± 2.9	21.1	18.9	26.7 ± 2.6	.6	I.S.P.	35
1.8-8.4	4	4.9 ± .7	2.1	3.7 ± .4	2.0	16.8 ± 3.5	25.4	20.9	37.9 ± 2.6	1.0	I.L.P.	163
	5	7.6 ± .3	2.7	8.9 ± .9	5.2	26.0 ± 3.8	42.5	33.9	59.0 ± 2.3	1.5	I.S.L.	275
	6	10.1 ± .6	2.5	12.1 ± .6	3.2	30.6 ± 3.8	52.8	36.3	72.8 ± 4.9	1.7	I.W./U.L.	7
	7	11.5 ± .9	1.4	17.3 ± 1.7	5.2	70.5	99.3	77.1	85.1 ± 7.3	2.0		

TABLE 45-47

The seasonal changes in lamina production in

Laminaria hyperborea

Table 45

The seasonal changes in lamina production

St. Abb's Head - Petico Wick

Depth	Age	24.4.66	30.5.66	15.6.66	7.7.66	17.8.66	25.9.66	19.1.67	9.3.67	19.6.67	26.7.67	7.9.67
	1	- -	-	2.0 ± .4	2.4 ± .5	1.4	1.8	.07	.1	.6	-	1.4
	2	.7	4.2	8.7	11.2 ± 1.0	4.4 ± .9	5.0 ± .8	.7	.5	3.4	8.2	4.4
	3	1.8	8.0 ± .5	13.2 ± 1.5	42.0 ± 3.4	37.0 ± 3.1	38.0 ± 1.5	.1	-	6.0 ± .7	37.0	26.0
3.0m.	4	3.5 ± .8	15.0 ± .9	27.0 ± 2.2	65.0 ± 2.8	43.0	64.0 ± 4.6	.6 ± .1	6.8 ± .6	20.0 ± 2.3	43.0 ± 4.6	49.0 ± 2.6
	5	11.7 ± .5	15.0 ± 1.6	47.0	88.0 ± 3.4	74.0 ± 7.2	77.0 ± 2.1	.8 ± .4	5.2 ± .6	31.0	74.0 ± 6.1	94.0 ± 6.4
	6	11.0 ± 1.8	20.0 ± 2.3	53.0 ± 1.2	81.6 ± 9.5	83.0	63.0 ± 4.3	.8 ± .1	7.0 ± .6	46.0	83.0 ± 4.3	85.0 ± .6
	7	11.0 ± .4	27.0 ± 2.0	46.0 ± 2.9	76.0 ± 2.8	77.0	42.0 ± 3.9	.5 ± .1	7.5 ± .7	51.0 ± 7.1	77.0 ± 4.6	84.0 ± 4.9

Depth	Age	24.4.66	15.6.66	7.7.66	25.9.66	9.3.67	19.6.67	26.7.67	18.8.67
	1	-	-	-	-	-	-	-	-
	2	.4 ± .1	4.9 ± .8	12.0 ± 4.2	8.4 ± 1.1	1.2 ± .1	6.2 ± .8	9.0 ± .9	5.0 ± .3
	3	6.5 ± .4	6.6 ± 1.4	26.0 ± 3.9	29.0 ± 1.2	.9 ± .1	8.2 ± .8	23.0 ± 1.6	18.0 ± 2.2
7.6m.	4	7.8 ± 1.0	7.2 ± .6	36.0 ± 2.7	34.0 ± 1.9	3.8 ± .4	17.0 ± 1.0	34.0 ± 2.5	37.0 ± 2.2
	5	9.6 ± .7	13.0 ± 1.0	65.0 ± 2.3	64.0 ± 3.7	3.6 ± .3	28.0 ± 2.0	60.0 ± 4.3	61.0 ± 3.9
	6	7.5 ± .5	13.0 ± 1.0	54.0 ± 2.0	61.0 ± 4.0	6.8 ± .9	48.0 ± 5.2	71.0 ± 4.0	63.0 ± 2.0
	7	4.5 ± .5	12.0 ± .6	61.0 ± 4.0	46.0 ± 5.2	4.3 ± .09	45.0 ± 2.1	67.0 ± 5.5	67.0 ± 2.7

Mean organic (ash-free) dry weight in grams.

Table 47

The seasonal changes in lamina production

Marsden - Byer's Hole

Depth (m.-C.D.)	Age	22.4.67	15.5.67	2.6.67	17.7.67	13.9.67
	1	-	.3	-	-	1.6
	2	.3	.5	-	6.1 ± 1.0	9.4 ± 1.0
	3	-	.6 ± .1	3.5 ± .7	13.1	16.2 ± 2.0
2.4	4	2.7 ± .3	1.2 ± .4	4.0 ± .6	-	24.0
	5	3.1 ± .3	1.9 ± .3	7.3 ± 1.0	24.0 ± 1.0	51.0 ± 3.1
	6	4.1 ± .2	2.5 ± .3	8.9 ± .4	30.0	49.0 ± 3.7
	7	2.8 ± .2	3.2 ± .1	8.1 ± .8	37.0 ± .8	56.0 ± 3.1

Depth (m.-C.D.)	Age	22.4.67	15.5.67	17.7.67	13.9.67
	1	.02	-	-	-
	2	.04	.1 ± .04	-	6.0 ± .8
	3	.19	.5 ± .09	12.9 ± 1.5	12.0 ± 1.5
3.7	4	.2 ± .09	1.0 ± .1	18.6 ± 2.0	32.0 ± .9
	5	.6 ± .1	2.0 ± .2	21.7 ± 1.6	48.6 ± 2.4
	6	1.5 ± .1	2.8 ± .2	29.7 ± 2.8	51.0 ± 3.4
	7	2.0 ± .2	3.8 ± .4	30.3 ± 3.6	43.0 ± 4.9

Mean organic (ash-free) dry weight in grams

TABLES 48-51

The seasonal changes in lamina production in

Laminaria digitata

Table 48

The seasonal changes in lamina production

St. Abb's Head

Harbour Wick

Age	12.1.67	19.5.67	6.8.67	7.9.67	30.11.67	22.3.68	28.4.68
1	-	-	1.3	1.3 ± .1	-	2.0 ± .4	1.8
2	2.4	-	9.8 ± 1.4	5.7 ± 1.6	9.4 ± 1.3	4.3 ± .8	25.1 ± 4.6
3	3.0	44.3	27.6 ± 4.1	10.0 ± 2.4	10.7	13.1	24.1 ± 1.6
4	5.6 ± 1.0	51.6 ± 10.7	64.3 ± 11.0	33.2 ± 5.5	9.6	14.3 ± 2.9	26.9 ± 3.3
5	15.2 ± 1.9	154.8	99.3	46.9 ± 4.0	17.0 ± 5.6	32.4 ± 5.9	63.0

Petico Wick

Age	19.1.67	8.3.67	11.5.67	6.8.67	7.9.67	18.3.68	12.4.68	3.5.68
1	.03	.8	-	-	.3 ± .06	.3 ± .06	-	-
2	-	2.0 ± .5	2.8	11.2 ± 3.5	5.3 ± 1.0	.7	.7 ± .09	1.9 ± .3
3	13.3	5.0	26.8 ± 4.8	14.4	24.5 ± 4.3	2.1	1.6	8.3
4	14.3	11.0 ± 1.5	33.8 ± 2.1	32.5 ± 5.0	46.6 ± 8.4	10.7 ± 1.4	4.5 ± 1.3	16.3 ± 1.6
5	16.3	9.7 ± 1.3	45.1	55.2 ± 11.4	56.4 ± 6.4	15.9	32.9 ± 6.0	29.7 ± 1.3

Mean organic (ash-free) dry weight in grams

Table 50

The seasonal changes in lamina production

Beadnell - Lady's Hole

	Age	29.1.67	1.5.67	3.8.67	4.9.67	22.3.68	14.4.68
	1	.8	1.7	2.1 ± .3	2.0 ± .2	1.9 ± .3	-
	2	8.8 ± 1.7	19.1	4.3	5.5 ± .4	5.1	1.4 ± .5
Current surge	3	13.6 ± 2.7	13.7	20.6 ± 6.3	29.9 ± 4.0	8.0 ± 1.7	8.5 ± 2.3
	4	20.2 ± 2.3	24.2 ± 2.6	51.9	24.1 ± 3.3	-	9.9 ± 1.6
	5	24.9 ± 3.7	59.9	38.9	23.9 ± 1.7	-	20.5 ± 3.5

Ebbe's Snook

	1.5.67	3.8.67	4.9.67	1.3.68	14.4.68	6.5.68
1	-	-	-	.9	-	-
2	-	14.5	20.2 ± 6.4	2.4 ± .3	.8 ± .2	2.6
3	17.2	6.7 ± .5	9.1 ± 1.2	5.7 ± 1.3	3.7 ± .7	3.8
4	-	27.7 ± 4.0	27.8 ± 4.0	8.0 ± 1.0	7.9 ± .9	12.1 ± 1.1
5	17.9 ± 2.8	50.6 ± 4.4	48.9 ± 6.2	9.2 ± 1.6	5.9	-

Mean organic (ash-free) dry weight of lamina in grams

Table 51

The seasonal changes in lamina production.

Marsden - Byer's Hole

Age	17.4.67	15.5.67	30.7.67	4.9.67	1.3.68
1	-	-	-	1.4	.4 ± .09
2	1.0 ± .03	4.2	3.4	5.9	.8 ± .1
3	2.0 ± .1	7.5 ± .5	8.4 ± 1.3	9.8 ± .9	.9
4	4.2 ± .3	21.0 ± 4.0	19.4 ± 2.4	19.7 ± 4.7	1.4
5	8.1 ± .4	30.7 ± 2.7	62.3	21.4 ± 3.4	4.7 ± .7

Mean organic (ash-free) dry weight in grams

TABLES 52-53

The seasonal changes in lamina production in

Laminaria saccharina

Table 52

The seasonal changes in lamina production

St. Abb's Head

		Cropping date					
	Age	12.3.67	19.5.67	6.8.67	7.9.67	22.3.68	28.4.68
Harbour 2.4m.	1	.4 ± .08	59.5 ± 10.1	-	29.1	2.5	-
	2	.8 ± .2	-	26.4 ± 7.3	39.1 ± 4.3	6.7 ± 1.4	16.5 ± 1.0
	3	.4 ± .04	8.1 ± 3.3	-	-	3.4	17.0 ± .6
		19.1.67	8.3.67	11.5.67	6.8.67	7.9.67	12.4.68
Petico Wick 3.0m.	1	.03	-	.5	-	-	.1
	2	.3 ± .1	.9 ± .2	4.7 ± .8	19.0 ± 2.4	18.5 ± 2.9	1.3
	3	.3 ± .01	1.0 ± .1	10.2 ± 1.3	-	-	1.7
		19.1.67	8.3.67	6.8.67	7.9.67	12.4.68	
9.1m.	1	.1 ± .02	-	-	-	-	
	2	.1 ± .02	.5 ± .04	16.4 ± 1.8	18.9 ± 2.6	.5	
	3	.2 ± .02	1.0	-	22.9 ± 1.6	.9	

Mean organic (ash-free) dry weight in grams.

Table 53

The composite mean cropping data and production figures

Beadnell - Lady's Hole

		Cropping date						
	Age	29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	18.3.68	19.5.68
Tide pool MTL	1	2.6 ± .4	4.5	-	15.4 ± 1.8	19.5 ± 4.2	2.1	9.4 ± 1.6
	2	-	3.7 ± .5	6.9 ± .9	11.3 ± 1.3	40.0 ± 5.5	2.3	12.6 ± 1.3
	3	.5 ± .1	-	7.1	-	-	1.9	16.0 ± 2.7
		29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	14.4.68	6.5.68
Inlet 2.0m.	1	.5	1.4	2.0 ± .5	11.4 ± 2.4	47.4 ± 6.1	3.1	5.4
	2	-	2.3 ± .4	1.9 ± .3	13.6 ± 1.7	37.1 ± 9.1	2.6 ± .1	5.4 ± .2
	3	.2 ± .04	1.3 ± .2	-	-	-	.3	3.4 ± 1.0

Mean organic (ash-free) dry weight in grams.

Appendix 7

THE ECOSYSTEM PERFORMANCE DATA

(Tables 54-55)

TABLES 54-55

The "raw" stipe and lamina biomass for

Laminaria ochroleuca in North West Spain

Table 54

Mean Organic (ash-free) dry weight of stipe in grams

Locality	Depth (m.-C.D.)	1	2	3	4	5	6	7
Playa de Lago (Lagoon)	1.6	-	.5	2.8	6.2 ± 1.6	16.3 ± 2.1	42.1 ± 2.1	62.1
Punta de Alada	1.6	-	.5	-	-	6.2 ± .6	13.0	-
" " "	5.0	-	.4	1.4	2.5	6.7	12.4 ± 1.2	-
" " "	8.4	-	.3	1.0	3.9	9.0 ± 1.1	14.8	-
" " "	11.8	-	.2	1.0 ± .2	3.1 ± .5	6.2	-	-
Playa de Lago (Inlet)	1.6	-	.3	1.4 ± .1	5.6 ± .6	10.7	32.2	-
" " " "	5.0	.2	.4 ± .03	1.0 ± .2	3.1 ± .4	8.4	16.1 ± 2.1	31.7 ± 3.3
" " " "	8.4	-	-	1.0 ± .1	4.6	-	26.6 ± 1.3	56.0 ± 3.9
Punta Testada	8.4	-	-	1.0 ± .2	3.6 ± .5	-	17.3	35.9
" "	11.8	-	-	-	2.5	14.6	23.5	44.6 ± 3.1
" "	15.2	-	-	-	3.1	9.4	-	-
" "	18.4	.3	.5	-	-	-	-	-
Las Osas (Westside)	8.4	.04 ± .00	-	-	-	-	-	-
" " "	11.8	.08 ± .00	.2 ± .01	1.0 ± .1	2.8	9.9 ± 1.7	26.8	-
Playa de Lago (Lagoon Channel)	1.6	-	-	1.6	-	-	-	-
Isla Onza (Punta Cocinadoiro)	1.6	-	-	.8	-	-	-	-
" " " "	5.0	-	-	1.0	2.0	-	-	-
" " " "	8.4	.2 ± .04	-	-	-	-	-	-
Drake's Island	3.0-7.0	.4 ± .01	.9 ± .2	2.7 ± .2	5.2 ± .4	10.6 ± .7	13.5 ± 1.1	19.4
Dennis Head	3.0-7.0	-	-	-	-	-	15.1 ± .5	23.5
Roskilly	3.0-7.0	-	.6	1.5	-	11.0 ± .6	14.6 ± 1.1	18.5
Porthallow/Porthkerris	3.0-7.0	-	-	1.0	2.3 ± .3	5.3 ± ..3	8.0 ± .4	10.4 ± .5

Table 55

Mean organic (ash-free) dry weight of lamina in grams

	Locality	Depth (m.-C.D.)	1	2	3	4	5	6	7	8
North West Spain	Playa de Lago (Lagoon)	1.6	-	3.3	9.9	5.0	30.9 ± 1.0	60.3 ± 5.7	22.4 ± 8.8	-
	Punta de Alada	1.6	-	10.6	-	-	41.0 ± 9.9	90.5	-	-
	" " "	5.0	-	1.6	13.5	24.5	51.7	55.5 ± 10.4	-	-
	" " "	8.4	-	.8	7.1	40.3	45.2 ± 8.5	89.2	-	-
	" " "	11.8	-	.8	9.4 ± 2.4	21.4 ± 2.7	32.7	-	-	-
	Playa de Lago (Inlet)	1.6	-	.6	6.3 ± 2.0	12.8 ± 2.5	32.7	28.7	-	-
	" " " "	5.0	.6	1.3 ± .1	3.8 ± .8	14.4 ± 3.7	59.8	46.1 ± 8.8	67.4 ± 13.6	55.5
	" " " "	8.4	-	-	6.9 ± 1.1	10.9	-	80.6 ± 14.9	90.1 ± 15.3	76.8
	Punta Testada	8.4	-	-	6.3 ± 2.0	20.3 ± 2.9	-	52.5	75.3	-
	" "	11.8	-	-	-	5.5	20.5	42.8	58.0 ± 6.8	-
	" "	15.2	-	-	-	18.0	24.7	-	-	-
	" "	18.4	.8	4.5	-	-	-	-	-	-
	Las Osas (Westside)	8.4	.3 ± .01	-	-	-	-	-	-	-
	" " "	11.8	1.0 ± .1	.5 ± .1	5.0 ± 2.1	26.9	33.2 ± 3.9	36.0	-	-
	Playa de Lago (Channel)	1.6	-	-	17.8	-	-	-	-	-
	Isla Onza(Punta de Cocinadoiro)	1.6	-	-	7.0	-	-	-	-	-
	" " " " "	5.0	-	-	7.6	12.1	-	-	-	-
	" " " " "	8.4	1.5 ± .4	-	-	-	-	-	-	-
South West England	Drakes Island	3.0-7.0	2.9 ± .5	12.5 ± 1.2	16.6 ± 2.9	16.8 ± 3.5	26.0 ± 3.8	20.9 ± 2.9	70.5	-
	Dennis Head	3.0-7.0	-	-	-	-	-	21.2 ± 2.0	23.3	-
	Roskilly	3.0-7.0	-	2.3	6.3	-	23.2 ± 3.3	30.6 ± 3.8	38.5	41.0
	Porthallow/Porthkerris	3.0-7.0	-	-	.9	7.9	12.1 ± 2.0	19.6 ± 1.9	18.9 ± 1.8	-

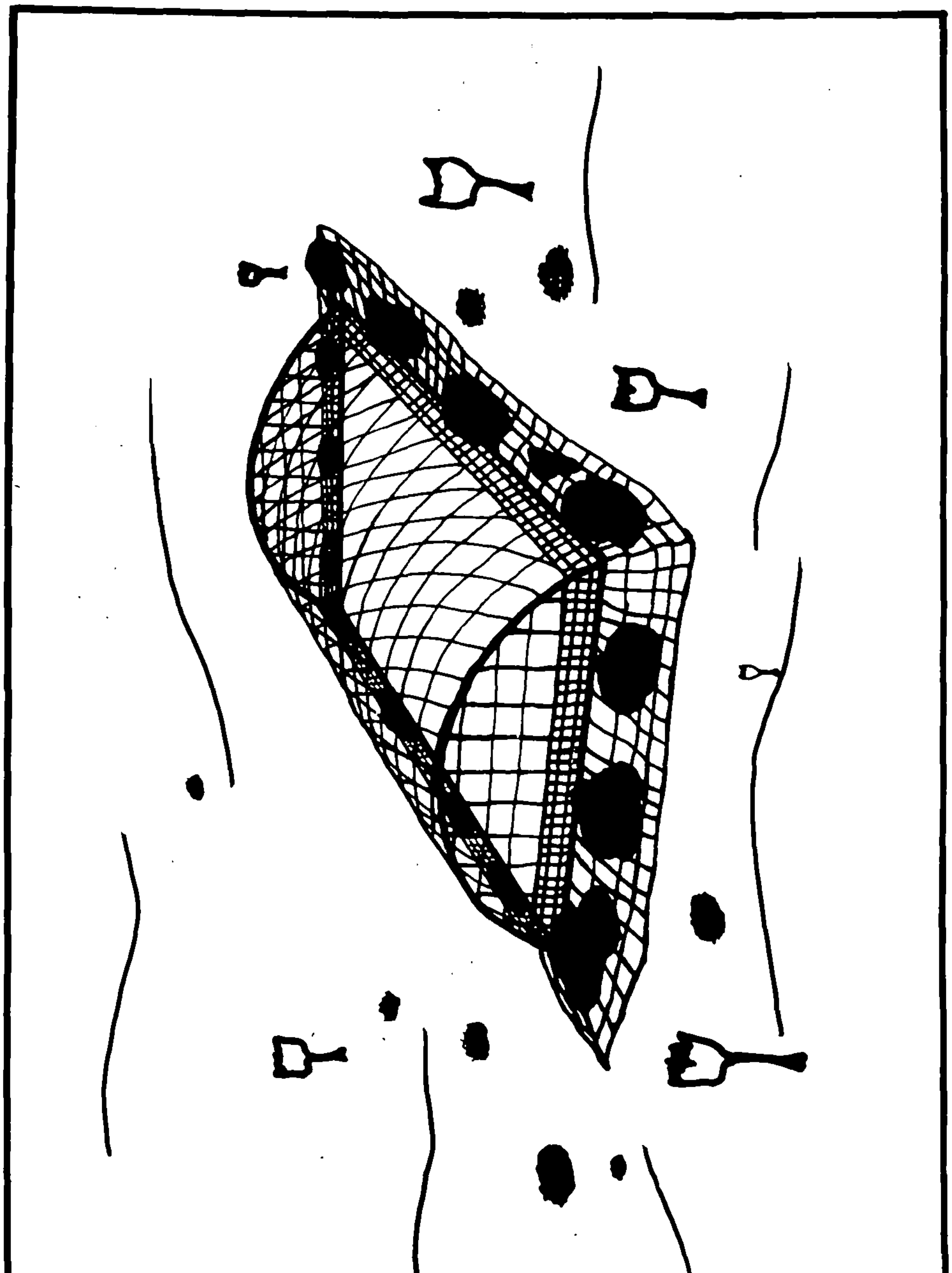
Appendix 8

THE CONSTRUCTION OF THE ENCLOSURES

The base of each enclosure was constructed of heavy gauge "Dexion" of 1 x 3 metres. The enclosures were covered by P.V.C. coated wire with a large mesh (10 cms) covering its upper part and a smaller mesh (5 cms) the lower part. A "skirt" of wire was attached to the framework and this can be moulded so as to fit the bottom contours. The enclosure was anchored by placing large boulders over the surrounding skirt, (Fig. 21).

FIGURE 21

The enclosure in position



Appendix 9

THE CONSTRUCTION OF THE PLATFORMS AND FRAMES

The platforms were constructed of medium gauge "Dexion" bolted together with brass fittings. A corlene rope ran through the centre of each platform and was attached to it by means of P.V.C. coated wire. This rope was anchored to the bottom by means of a wire basket filled with rocks and was also bouyed at the surface. A drag-weight was attached below the lowermost basket so as to allow the platform to rise and fall with the tide and yet still remain in a horizontal position (fig. 22).

The frames consisted of lengths of polythene tubing (one quarter inch) with holes made at regular intervals along its length. The hapteron portion of a young individual was placed in a hole, and then tied in position with corlene string. Each length of polythene tubing was coded by means of a variable number of holes made at one end. Each individual was recognised by recording the number of the hole it occupied from the coded end of the tubing (fig. 23). The frames were then attached to the platforms at the various levels.

FIGURE 22

The transplant platforms

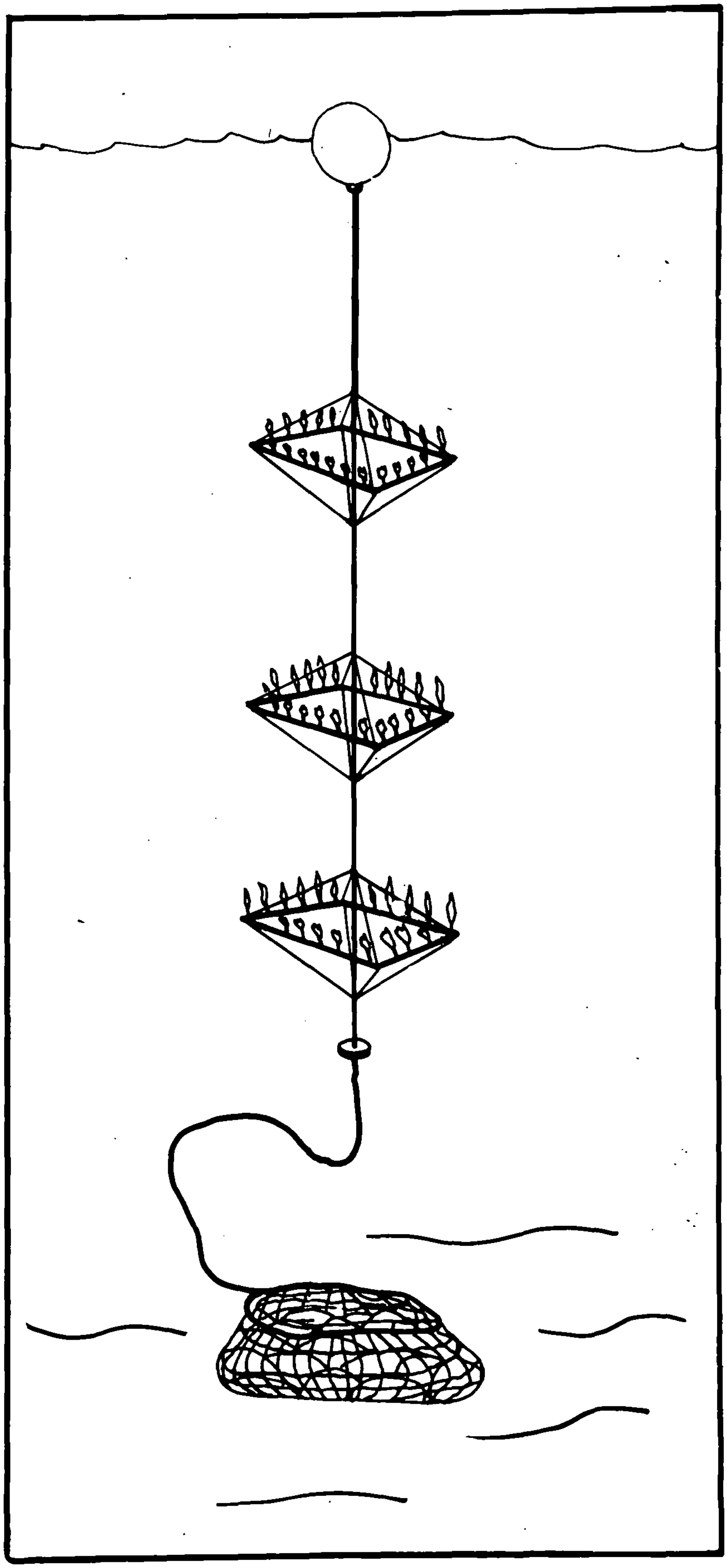
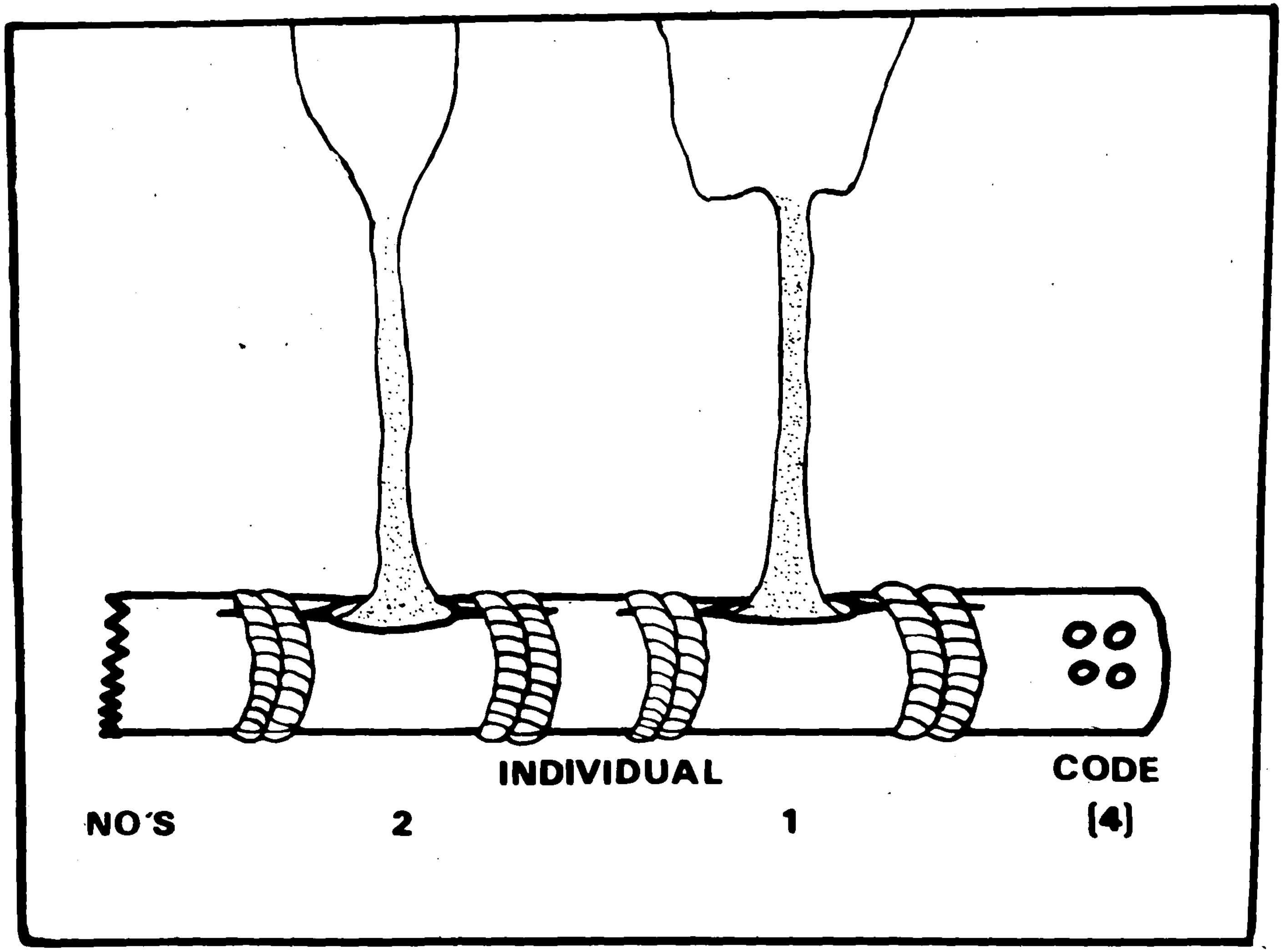


FIGURE 23

The attachment and method of
coding individuals on the frame


INDIVIDUAL
CODE
NO'S
2
1
[4]

Appendix 10

THE COMPOSITE DATA FOR THE TRANSPLANT EXPERIMENTS

(Tables 56-58)

Key

A.	Original	1.	Stipe length (cms)
B.	Final	2.	Lamina length (cms)
C.	Loss	3.	Lamina biomass (grams)
D.	Increment		

Table 56

The composite data for transplants of Laminaria hyperborea at three depths

Depth (m.-C.D.)		1			2			3			4			5			6			7		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	A	7.7	6.0	.2	8.8	8.6	.3	7.6	5.9	.3	6.1	7.0	.1	5.5	6.0	.1	4.5	3.7	.1	5.4	5.7	.2
1.5	B	11.5	57.0	8.2	14.5	57.0	14.1	12.5	43.0	9.4	15.5	58.0	7.0	20.5	74.0	11.0	11.2	54.0	6.4	12.7	44.0	5.9
	C	-	?	-	-	-1.0	-	-	-2^{+}	-	-	?	-	-	3	-	-	?	-	-	-1.0^{+}	-
	D	3.8	51.0	8.0	5.7	48.4	13.8	4.9	37.1	9.1	9.4	51.0	6.9	15.0	68.0	10.9	6.7	50.3	6.3	7.3	38.3	5.7
	A	8.0	6.5	.2	5.4	9.2	.3	7.9	10.0	.4	5.9	11.3	.4	4.3	7.7	.3	6.7	6.1	.1			
7.6	B	12.2	31.0	2.7	9.0	41.5	3.3	11.0	55.0	4.7	13.4	47.0	6.6	7.5	37.0	4.1	7.8	27.0	2.1			
	C	-	-3.5^{+}	-	-	?	-	-	-3.0	-	-	-6.0^{+}	-	-	?	-	-	-3.0^{+}	-			
	D	4.2	24.5	2.5	3.6	32.3	3.0	3.1	45.0	4.3	7.5	35.7	6.2	3.2	29.3	3.9	1.1	20.9	2.0			
	A	3.5	5.1	.1	6.4	10.5	.3	7.9	5.3	.1	3.1	6.4	.2	5.5	8.6	.2						
13.7	B	4.0	19.5	.7	6.4	11.3	.1	8.0	21.5	.7	3.1	12.5	.3	5.6	22.0	.4						
	C	-	?	-	-	0	-	-	?	-	-	?	-	-	?	-						
	D	.5	14.4	.6	0	.8	.2	.1	16.2	.6	0	6.1	.2	.1	13.4	.2						

Table 57

The composite data for transplants of Laminaria digitata at three depths

Depth (m.-C.D.)		1			2			3			4			5			6			7			8			9		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	A	1.5	16.5	.1	2.0	15.6	.07	4.1	25.0	.07	1.9	13.4	.05	4.6	10.5	.04	1.5	9.0	.02	3.8	24.5	.1	3.0	24.6	.07	4.4	18.1	.05
1.5	B	3.2	54.0	3.7	2.0	60.0	3.4	4.1	52.0	3.4	2.3	61.0	3.6	4.6	47.0	1.7	2.6	55.0	2.6	4.3	47.0	4.0	3.0	36.0	3.1	5.6	98.5	11.0
	C	-	0	-	-	0	-	-	-6^+	-	-	0	-	-	0	-	-	0	-	-	-8	-	-	-7^+	-	-	?	-
	D	1.7	41.5	3.6	0	44.4	3.3	0	27.0	3.3	.4	47.6	3.6	0	36.5	1.7	1.1	46.0	2.6	.5	22.5	3.9	0	11.4	3.0	1.2	80.4	11.0
	A	2.1	16.2	.04	1.9	10.0	.02	6.5	16.0	.07	2.8	19.5	.09	7.2	15.6	.09	6.0	9.5	.06	3.0	15.5	.04	1.5	15.0	.06			
7.6	B	3.1	76.0	1.0	2.5	38.0	.9	6.5	55.2	2.6	2.8	63.5	3.2	7.2	55.0	2.8	6.0	35.2	1.5	3.4	62.0	1.1	1.9	43.0	1.9			
	C	-	0	-	-	?	-	-	0	-	-	?	-	-	0	-	-	?	-	-	0	-	-	?	-			
	D	1.0	59.8	1.0	.6	28.0	.9	0	39.2	2.5	0	44.0	3.1	0	39.4	2.7	0	25.7	1.4	.4	46.5	1.1	.4	28.0	1.8			
	A	2.9	11.5	.04	2.8	7.0	.01																					
13.7	B	3.0	25.0	.2	2.8	19.0	.1																					
	C	-	?	-	-	?	-																					
	D	.1	13.5	.2	0	12.0	.1																					

Table 58

The composite data for transplants of <u>Laminaria saccharina</u> at two depths

Depth (m.-C.D.)		1			2			3			4			5		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	A	6.0	4.4	.05	3.2	3.3	.03	11.3	4.5	.06	4.7	7.0	.01	8.6	15.2	.4
1.5	B	12.5	191.0	13.8	8.0	130.0	9.3	21.0	169.0	17.1	9.4	196.0	17.7	11.2	165.0	18.3
	C	-	?	-	-	?	-	-	?	-	-	?	-	-	-9+	-
	D	6.5	186.6	13.7	4.8	126.7	9.3	9.7	164.5	17.1	4.7	189.0	17.7	2.6	149.8	17.9
	A	4.4	4.1	.03	2.6	6.1	.06	8.5	7.1	.04	5.3	5.2	.05	5.7	8.5	.03
13.7	B	4.4	30.0	.5	3.0	25.0	.6	8.5	42.0	.1	7.0	54.0	.2	5.7	27.0	.04
	C	-	0	-	-	?	-	-	?	-	-	?	-	-	0	-
	D	0	25.9	.5	.4	23.9	.6	0	34.9	.1	1.7	48.8	.2	0	19.5	0.0

Appendix 11

THE ORGANIC (ASH-FREE) DRY WEIGHT

(Tables 60-67)

TABLES 60-62

The seasonal variations in the

lamina values

Table 60

Mean organic (ash-free) dry weight of lamina as a percentage of the dry weight
N.L. = New Lamina, O.L. = Old Lamina

Laminaria digitata

Locality									
Beadnell - Lady's Hole Tidepool		13.1.67	20.4.67	1.5.67	3.8.67	4.9.67	22.3.68	14.4.68	15.5.68
	N.L.	73.3	68.6	68.9	75.6	88.1	68.8	66.6	67.5
	O.L.	?	?	?	-	-	64.2	62.9	61.5
Inlet		29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	18.3.67	14.4.68	6.5.68
	N.L.	68.6	69.3	68.1	73.4	81.3	67.2	68.2	66.8
	O.L.	?	?	?	-	-	65.1	70.3	62.7
Current surge		29.1.67	1.5.67	3.8.67	4.9.67	22.3.68	14.4.68		
	N.L.	68.5	64.7	68.3	73.5	64.5	66.4		
	O.L.	?	?	-	-	64.1	64.1		
Ebb's Snook		1.5.67	3.8.67	4.9.67	1.3.68	14.4.68	6.5.68		
	N.L.	69.4	66.8	78.5	56.6	65.9	66.1		
	O.L.	?	-	-	-	65.7	62.7		
St. Abb's Head Habour		12.1.67	19.5.67	6.8.67	7.9.67	30.11.67	22.3.68	28.4.68	
	N.L.	68.6	73.3	69.2	68.4	62.6	63.3	66.0	
	O.L.	?	?	-	-	-	-	58.3	
Petico Wick		19.1.67	8.3.67	11.5.67	6.8.67	7.9.67	18.3.68	12.4.68	3.5.68
	N.L.	77.0	56.8	56.5	57.8	72.9	67.1	66.3	65.7
	O.L.	?	?	-	-	-	64.6	64.3	63.0
Marsden Byer's Hole		17.4.67	15.5.67	30.7.67	4.9.67	1.3.68			
	N.L.	68.9	69.0	79.4	79.8	63.4			
	O.L.	?	?	-	-	52.1			

Table 61

Mean organic (ash-free) dry weight as a percentage of the dry matter
N.L. = New Lamina, O.L. = Old Lamina
Laminaria hyperborea

Locality	Depth (m.-C.D.)										Mean Stipe
Beadnell			I	III	IV	V	VI	VII	IX	XI	
Lady's Hole (Inlet)	3.0	N.L.	81.5	62.6	66.0	63.8	65.5	75.0	80.1	78.4	63.7
		O.L.	78.3	75.5	73.7	72.0	-	-	-	-	
	7.6		IV	V	VI	VII	IX				
		N.L.	66.7	63.2	66.5	72.0	81.1				65.6
		O.L.	68.2	68.1	-	-	-				
St. Abb's Head			I	III	IV	V	VI	VII	VIII	IX	
Petico Wick	3.0-7.6	N.L.	72.7	66.7	59.7	66.0	69.0	74.4	77.0	84.5	60.0
		O.L.	61.2	60.0	59.7	-	-	-	-	-	
Harbour	3.0		I	III	IV	VIII	IX	VII			
		N.L.	72.1	71.2	63.4	73.2	76.8	72.7			66.4
		O.L.	71.7	64.4	53.7	-	-	-			
Marsden			IV	V	VI	VII	IX				
Byer's Hole	2.0-3.7	N.L.	67.2	66.2	70.2	74.0	81.4				61.9
		O.L.	67.0	-	-	-	-				

Table 62

Mean organic (ash-free) dry weight of lamina as a percentage of the dry weight
N.L. = New Lamina, O.L. = Old Lamina
<u>*Laminaria saccharina*</u>

Locality	Depth (m.-C.D.)									
Beadnell - Lady's Hole			29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	18.3.68	19.5.68	
Tidepool	MTL	N.L.	64.6	63.3	57.8	84.8	85.1	62.6	67.7	
		O.L.	72.3	64.1	-	-	-	68.0	63.0	
									14.4.68	6.5.68
Inlet	3.0m.	N.L.	71.1	61.5	59.7	75.2	83.2	58.3	58.3	62.0
		O.L.	80.5	64.7	61.2	60.1	-	63.0	63.0	56.8
St. Abb's Head			12.3.67	19.5.67	6.8.67	7.9.67	22.3.68	28.4.68		
Harbour	2.4m.	N.L.	63.7	74.5	79.1	80.5	63.1	63.6		
		O.L.	63.2	-	-	-	64.8	-		
Petico Wick			19.1.67	8.3.67		6.8.67	7.9.67	12.4.68		
	3.0-9.1m.	N.L.	68.9	59.7		75.5	66.9	58.6		
		O.L.	65.9	61.2		-	-	59.7		

TABLES 63-64

The seasonal variations in the

stipe values

Table 63

Mean organic (ash-free) dry weight of stipe as a percentage of the dry weight

Laminaria digitata

Locality									Mean
St. Abb's Head	12.1.67	19.5.67	6.8.67	7.9.67	30.11.67	22.3.68	28.4.68		
Harbour	68.0	68.5	69.2	71.2	67.6	59.2	61.4		66.4
	19.1.67	8.3.67	11.5.67	6.8.67	7.9.67	18.3.68	12.4.68	3.5.68	
Petico Wick	64.0	69.0	62.5	65.0	63.6	63.1	65.2	61.6	64.2
Beadnell - Lady's Hole	13.1.67	20.4.67	1.5.67	3.8.67	4.9.67	22.3.68	14.4.68	15.5.68	
Tidepool	70.6	67.6	68.2	69.1	63.6	72.1	67.7	61.1	67.5
	29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	18.3.67	14.4.68	6.5.68	
Inlet	65.8	60.8	71.8	60.0	64.3	64.7	77.0	65.7	66.2
	29.1.67	1.5.67	3.8.67	4.9.67	22.3.68	14.4.68			
Current surge	69.1	66.3	66.4	65.4	66.2	70.3			67.2
	1.5.67	5.8.67	4.9.67	1.3.68	14.4.68	6.5.68			
Ebbe's Snook	63.3	67.4	61.1	56.4	64.6	63.0			62.6
Byer's Hole	17.4.67	15.5.67	30.7.67	4.9.67	1.3.68				
	61.7	65.0	67.7	72.9	66.8				66.8

Table 64

Mean organic (ash-free) dry weight of stipe as a percentage of the dry weight

<u>*Laminaria saccharina*</u>

Locality	Depth (m.-C.D.)									Mean
St. Abb's Head	2.4m.	12.3.67	19.5.67	6.8.67	7.9.67	22.3.68	28.4.68			
Harbour		63.9	78.3	62.8	64.1	64.6	69.8			67.2
		19.1.67	8.3.67		6.8.67	7.9.67	12.4.68			
Petico Wick	3.0-9.1m.	71.0	61.1		72.7	71.3	62.4			67.7
Beadnell - Lady's Hole		29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	18.3.68	19.5.68		
Tidepool	MTL	71.3	69.7	64.1	61.0	60.7	70.4	72.9		67.1
		29.1.67	20.4.67	1.5.67	3.8.67	4.9.67	18.3.68	14.4.68	6.5.68	
Inlet	3.0m	70.7	67.2	76.6	59.2	72.1	67.7	66.7	70.9	68.8

TABLES 65-67

The stipe values in the various regions

Table 65

Mean organic (ash-free) dry weight as a percentage of the dry weight of stipe

Locality	Date	Locality	Date	
Inner Hebrides	4/10.7.67	West Wales		
All sites	70.9	Abereiddy	1.4.67	19.7.67
West Scotland	16.9.67	Quarry	67.8	66.1
Strone Point	68.6	Entrance	66.2	
	15 & 20.9.67	South West England	17/24.8.67	
Sgat Mor/ Rubh'n Amair	68.6	All sites	69.3	

Laminaria digitata

Table 66

Mean organic (ash-free) dry weight as a percentage of the dry weight of stipe

Locality	Depth (m.-C.D.)	Date	Locality	Depth (m.-C.D.)	Date
Inner Hebrides		4.7.67	West Scotland		15.9.67
Soa (Eastside)	4.6	56.3	Saddell Bay	3.6	69.1
	18.3	50.9	Rubh'n Amair	3.6	69.2
		8.7.67	West Wales		27.7.67
Eilean Iomallach (Westside)	4.6	61.5	Cardigan Island	3.6	65.9
	18.3	57.9	South West England		20.8.67
		9.7.67	Sennen Cove	3.0-12.2	61.7
Coalas Soa	3.0	68.0			

Laminaria hyperborea

Table 67

Mean organic (ash-free) dry weight as a percentage of the dry weight of the stipe

Locality	Depth (m.-C.D.)	Date	Locality	Depth (m.-C.D.)	Date	Locality	Depth (m.-C.D.)	Date	
Inner Hebrides		4.7.67	West Scotland		16.9.67	West Wales		4.3.67	19.7.67
Soa (Eastside)	6.1	72.2	Strone Point	3.0-7.6	77.0	Abereiddy (Quarry)	1.5	65.8	64.8
	21.4	71.2			15/20.9.67	(Entrance)	0	67.2	61.0
		8.7.67	Rubh'n Amair/ Saddell Bay/ Sgat Mor	3.6	75.1			27.7.67	
Eilean Iomallach (Westside)	6.1	70.1			14.9.67	Martin's Haven	3.0	66.6	
	21.4	69.1	Sannox Bay	3.6	73.2			14.5.67	
		10.7.67	South East Scotland		17.5.68	Cardigan Island	5.3	67.6	
Loch Eatharna	3.0	72.3	Inchkeith	5.0	66.7				

Laminaria saccharina

Part IX

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