Ecological studies of the fauna inhabiting the Hapteron of the kelp plant Laminaria Hyperborea

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ECOLOGICAL STUDIES OF THE FAUNA INHABITING THE HAPTERON OF THE KELP PLANT *LAMINARIA HYPERBOREA*

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

SUMMARY

This thesis is an account of a study in the sublittoral kelp forests dominated by Laminaria hyperborea, which took place mainly along the North East coast of England.

A quantitative method was developed by which elements of the kelp forest invertebrate fauna can be used in comparative studies between widely separated areas of coastline. The habitat provided by the growth of the hapteron of Laminaria hyperborea was measured using a simple mathematical formula and the rate of habitat increase over the life history of the plant determined. This volume of habitat, called ecospace, was found to vary with depth and geographical location of the sampling station. The size of the shallow water ecospace habitat was not significantly affected by chronic pollution along the middle reaches of the North East coast study area. Thus the ecospace habitat becomes an ideal microcosm for study as it provides a similar habitat for colonisation by invertebrates at widely separated stations in different regional environments.

A comparison of the invertebrate communities reveals that geographical and regional elements in the fauna can be separated and a regional 'NORM' can be determined against which other areas can be compared. This technique was then used for isolating possible effects of pollution on the invertebrate communities.

Spatial and temporal studies reveal that over half the species complement is lost in polluted waters. Biotic variation is reduced and the communities become dominated by suspension feeders. These simple communities become violently unstable and the community undergoes a 'neotenous' development retaining pioneer species in all stages of habitat development.

Preliminary studies of the polluted water communities reveal that some pollution-indifferent species are able to tolerate higher levels of 'toxic' heavy metals than normal and the possibilities that this kind of physiological adaptation may contribute to the success and/or the instability of polluted water communities is discussed.

The usefulness of comparative ecological techniques and the effects that naturally occurring biotic variation may have on the interpretation results is discussed. The consequences of polluting the kelp forest community are briefly considered as one ecological price that is paid for convenient waste disposal.

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SECTION I

PART 1

Introduction

The hydrosphere is the largest transport system on Earth. Driven by solar energy, the circulation of water is the main factor in the process of erosion of the Earth's crust. The oceans must therefore be regarded as systems of accumulation and deposition. The great variety of sediments so formed characterise the benthic marine environment.

Only in the turbulent waters of the shallower parts of the continental shelves, scour by water movement ~~(and wave action)~~ exposes areas of bedrock which can become permanent features of the shallow benthic environment. Such areas, although minute in comparison with the surface area of the sea floor (Hedgpeth 1957) support a characteristic fauna and flora and are an important part of the total marine ecosystem.

A basic classification of this restricted but important marine habitat is given in Table 1.

The splash zone and the eulittoral is characterised by periodic submergence and emergence as a result of daily tidal movements and must represent one of the harshest environments for life on Earth. The biology of these areas is a function of the extremes of abiotic variation to which they are subjected and any interpretation of their ecology is necessarily complex (Lewis 1964). In the sublittoral, abiotic stability increases due to the permanent cover of sea water, the main environmental variables being a decrease with depth of both light intensity and quality and exposure to wave or surf action. The former limits the

TABLE 1

The Classification of Neritic Rocky Facies in Temperate Latitudes

(Modified after Lewis, 1964 and Hedgpeth 1957)

Tide level	Depth	Zone	Biological limit
			Upper Limit of Littorina and Verrucaria
		Littoral Fringe (Lewis) Supra Littoral (Hedgpeth)	
Mean High water mark			Upper Limit of Barnacles
		Eulittoral (Lewis) Intertidal (Hedgpeth)	
Mean Low water mark	OM		Upper Limit of Laminaria sp.
		Sublittoral (Lewis) Inner Sublittoral (Hedgpeth)	
	-50M-		Lower Limit of Laminaria sp.
		Outer Sublittoral (Hedgpeth)	
	-250M-		Edge of Continental Shelf

vertical extent of the Inner Sublittoral which is characterised by a large biomass of photosynthetic organisms. The latter determines the extent of the bare rock habitat in the Outer Sublittoral zone which itself extends to the edge of the Continental Shelf.

Inner Sublittoral Ecosystems around the British Isles are dominated, characterised and delimited by one, (more rarely by two or more) of five species belonging to two genera of the Laminariales.

These are Laminaria hyperborea (Gunn) Fosl., Laminaria digitata (Huds) Lamour, Laminaria ochroleuca (Pyl) and Sacchorhiza polyschides (Lightf) Batt. The geographical distribution of these species is given below.

Northern Forms	Northern Limit	Southern Limit	Other Limits
Laminaria hyperborea	Arctic Circle	Portugal	Iceland
Laminaria digitata	-ditto-	N.W. Spain	N.E.American continent
Laminaria saccharina	-ditto-	Portugal	N.E. and N.W. American Continent
Southern Forms			
Laminaria ochroleuca	S.E. England	N. Africa	Mediterranean
Sacchorhiza polyschides	W. Norway	-ditto-	-ditto-

Detailed descriptions of these species, their distribution and ecology, can be found in many accounts, including Harvey (1851), Batters (1890), Sauvageau (1897, 1918), Borgensen (1905), Hamel (1928) (1931-1939), Felvrov and Karsakoff (1932), Miranda (1937), Feldman (1934), Lami (1943) (1954), Lunde (1947), Parke (1948b), Dangerad (1949), Spooner (1957), Molinier and Picard (1953), Station Biologique de

Roscoff (1954), Fischer-Piette (1955-1958), Ardre (1957) (1967), Taylor (1957), Ardre et al (1958), Crisp and Southward (1958), Gayral (1958), Hure (1958), Den Hartog (1959), Jones (1960), Seoane-C mba (1960-66), Dixon (1961), Davy de Virville (1963), Zenkevitch (1963), Druehl (1968), Norton (1968) and John (1969), all of which indicate that a sublittoral 'kelp forest' (North 1961) characterises the shallow water rocky benthos in temperate regions.

The distribution of these members of the Laminariales varies in relation to depth, aspect, wave action, latitude and longitude (John 1969), the two most important and widespread around the British Isles being *Laminaria hyperborea* and *Laminaria digitata*. *Laminaria digitata* is the dominant plant in a narrow zone extending from MLWM to a maximum of -2 metres, below that depth the kelp forest is dominated by *Laminaria hyperborea*.

In any ecosystem the storage of solar energy by the primary producers is recognised as the first 'sink' in a series of energy exchanges which constitute a food web (Odum, 1965). John (1969) divides the primary producers of the kelp forest into four structural units. Jones and Kain (1967) and John (1969) describe the dependence of populations of herbivores on the energy source of the primary producers.

However, primary production is also of a structural significance. The storage of solar energy as standing crop smooths out environmental fluctuations thereby introducing more 'order' into the abiotic component of the ecosystem (Schrodinger 1945). A more stable habitat is therefore produced. This habitat space termed ecospace below is a direct function of the solar energy present as plant biomass. Thus the amount and type of ecospace created is a direct function of the solar energy present as plant biomass. Figure 1 shows a generalised section of the macrophytes in a kelp forest ecosystem. The size, density, morphology and distribution in space of the primary producers will determine the finite limits of ecospace in the ecosystem. Considering the above factors, it is likely that morphology will be the least subject to variation. For this reason it was decided that the diverse invertebrate fauna found around the morphogenetic unit the hapteron of the kelp plant would be the least subject to abiotic variation and the best habitat in the kelp forest for quantitative and qualitative study.

The hapteron of each kelp plant produces one whorl of branches each year which serves to anchor the plant to the rock (Kain 1964). The series of whorls produced encloses a small volume of the abiotic environment which then forms the holdfast habitat. As *Laminaria hyperborea* remains attached to the rock for at least seven years, the holdfast habitat must also be present for seven years providing a more stable abiotic environment within the kelp forest ecosystem than on the bare rock outside it.

The hapteron and its fauna can easily be collected and is therefore an ideal sample unit for detailed study. If the fauna in hapteron ecospace is simply a detritus feeding unit living in passive relation to the kelp forest it can be considered as a separate ecosystem in its own right. Trophic component analysis (see pages 39-52) of preliminary collections made from several stations around the coast of Britain showed that ecospace communities do feed largely on material carried in suspension in water flowing over the holdfasts. The direct contribution of the living plant as a food source is minimal compared with its indirect contribution as a sheltered habitat.

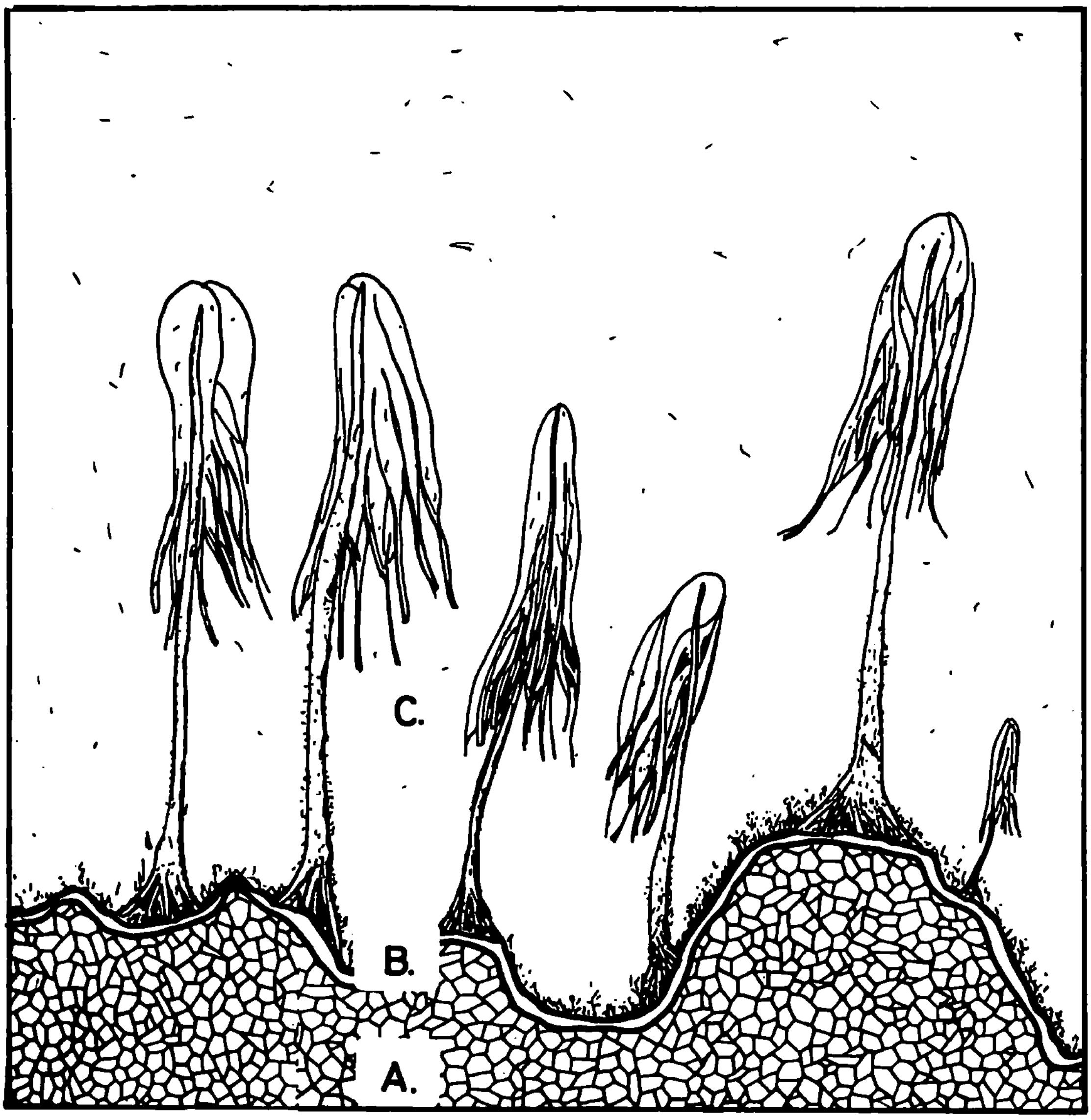

Fig.1
The structured kelp forest

A. The Parent Rock.
B. Crustose Algal Layer.
C. Dominant and Epiphyte Layer

Ecospace communities are thus independent units in the kelp forest ecosystem which can be obtained intact by collecting random samples of the hapteron. Earlier work along the North East coast of England has shown that gross ecological features of the primary producers in the kelp forest could be used in the assessment of certain types of pollution (Bellamy 1968). It, therefore, seemed an obvious extension of this work to ascertain whether this discrete and readily sampled habitat could be used as a more sensitive indicator of the effects of pollution on many invertebrate species present in the kelp forest ecosystem.

The following assumptions seem relevant:

(1) Wherever Laminaria hyperborea grows the hapteron habitat measured as ecospace is produced.

(2) The habitat represents a more uniform environment in a zone where environmental variation and disturbance is the main cause of biotic variation.

(3) Communities developing in ecospace in the main are dependent on detritus as an energy source.

(4) Any change in that energy source (e.g. pollution) should be directly reflected in the structure and function of the ecosystem.

The aim of the project was therefore extended to include a comparative study of the structure and function of holdfast ecospace communities developed in the pollution gradients which exist along the South East Coast of Scotland and the North East Coast of England.

Part 2

The North East Pollution Gradient

One outstanding feature of the east coast of Britain is the concentration of heavy industry and hence a large percentage of the population around the lower reaches of the rivers Forth, Tyne, Wear and Tees.

Industrialisation with its attendant development of large urban populations has gone hand in hand with the production of an increasing amount of waste material which is voided into the sea. Man's activities in this respect may be considered in two categories.

(1) Man as a geomorphological force speeding up the transport of terrigenous material to the sea.

(2) Man as a geochemical force manufacturing substances which do not occur naturally anywhere on Earth and which frequently find their way into the sea.

The result is pollution of the sea which may be defined as the addition of anything to the sea which brings about disruption of the natural balance of the ecosystems present in the vicinity.

Figures 2 to 10 (House. 1969.) shows the distribution of Man and his twentieth century activities along the North East coast of England, indicating that marked areas of pollution must exist.

The pollutants are best considered under four main headings:

1. Toxicoids

Substances whether natural or man made which are toxic to any form of life. These include heavy metals, cyanide, oil, pesticide, herbicides etc.

2. Sediment

Flyash (from coal fired power stations), mine and quarry washings,

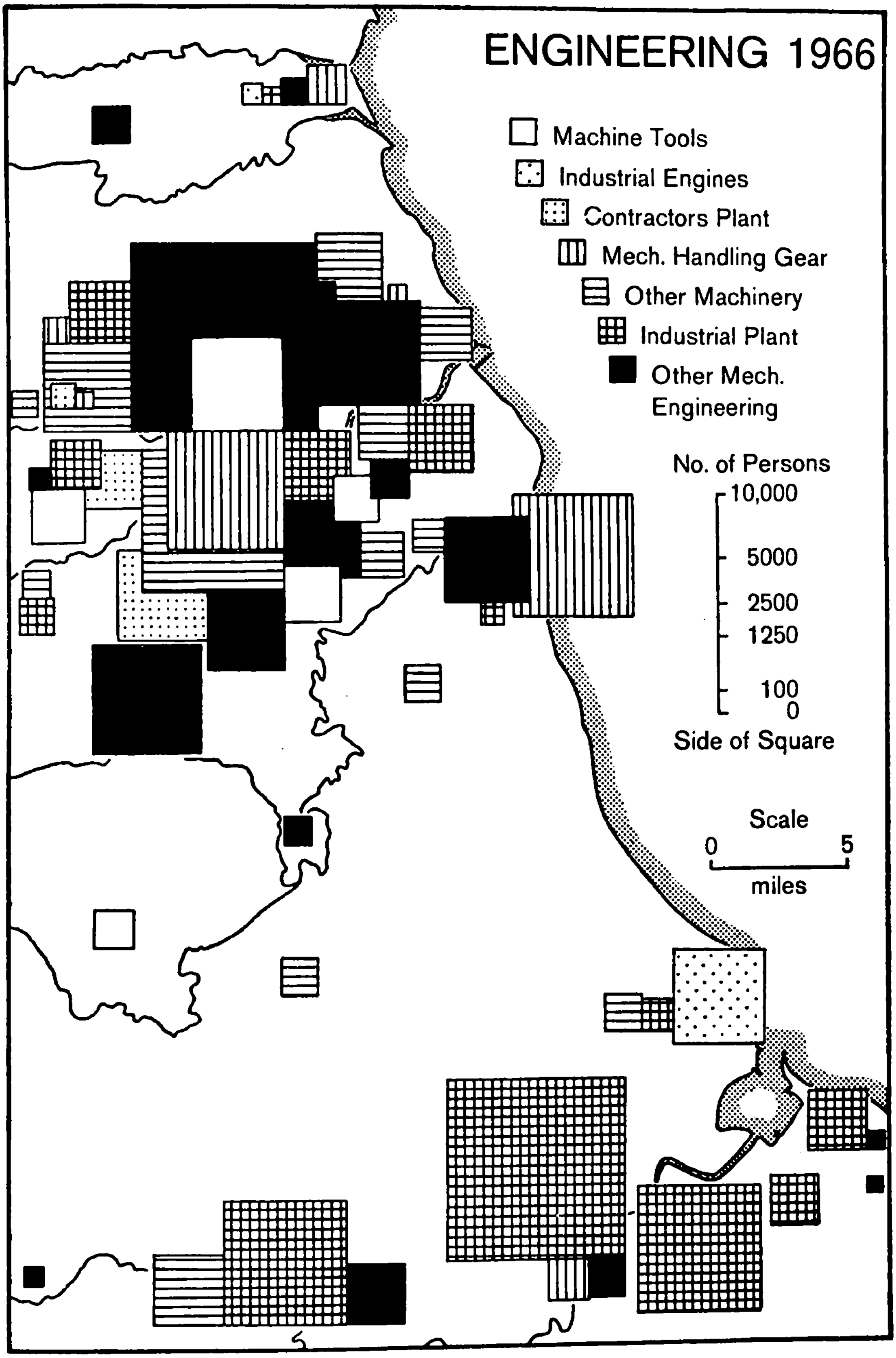
ENGINEERING 1966
Machine Tools
Industrial Engines
Contractors Plant
Mech. Handling Gear
Other Machinery
Industrial Plant
Other Mech. Engineering
No. of Persons
10,000
5000
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.2

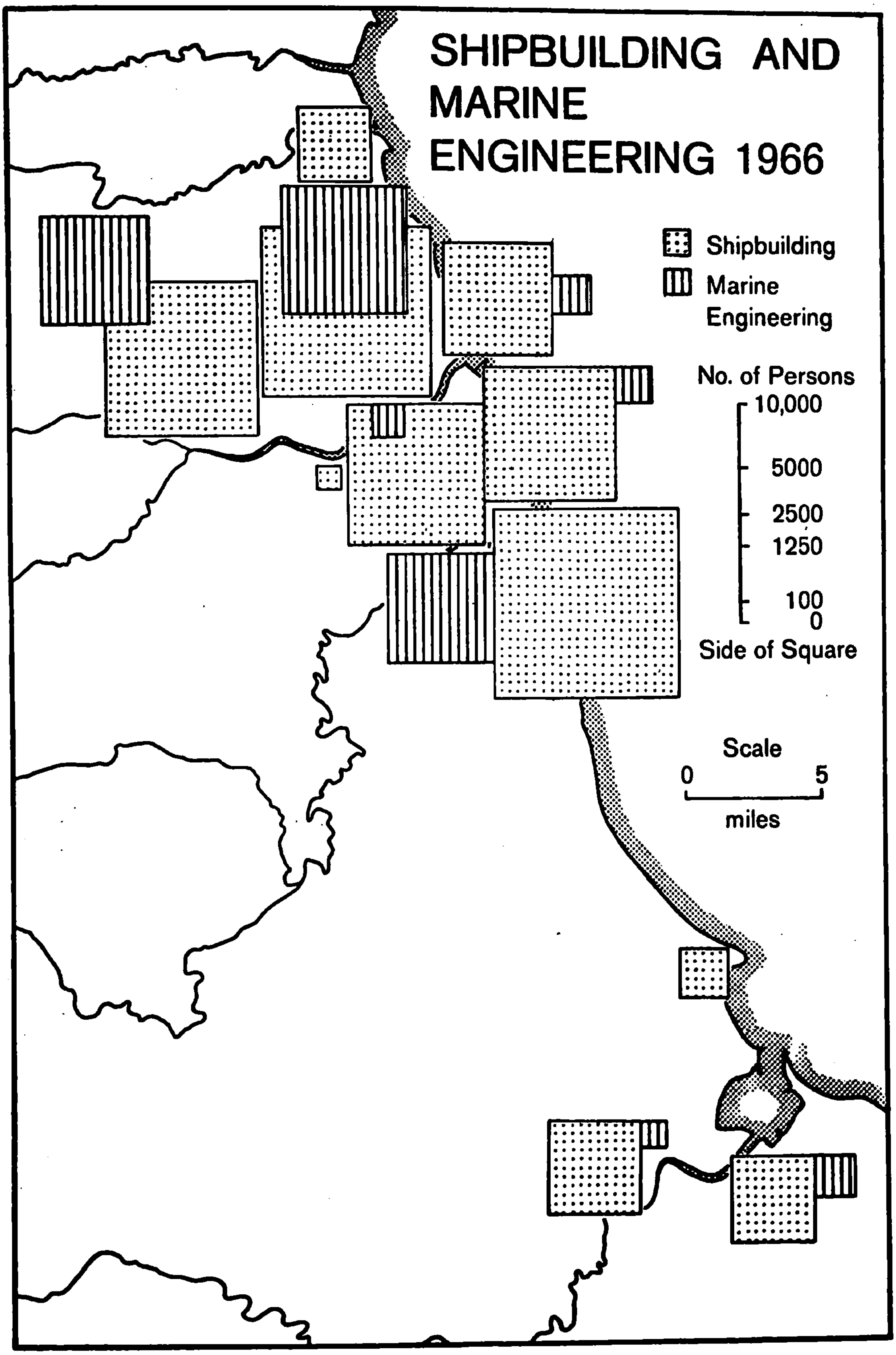
SHIPBUILDING AND MARINE ENGINEERING 1966
Shipbuilding
Marine Engineering
No. of Persons
10,000
5000
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.3

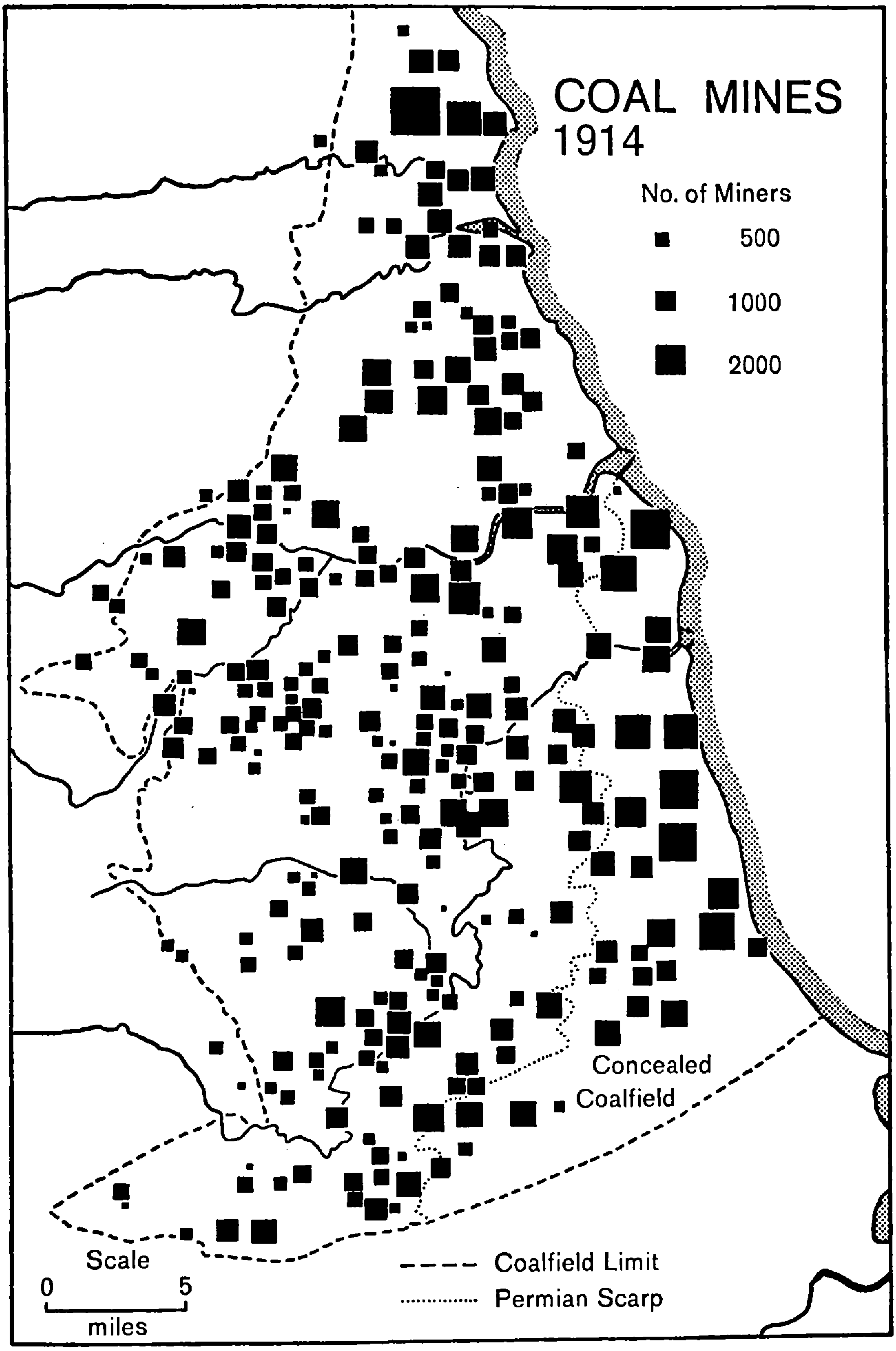
COAL MINES
1914
No. of Miners
500
1000
2000
Concealed
Coalfield
Scale
0
5
miles
Coalfield Limit
Permian Scarp

Fig.4

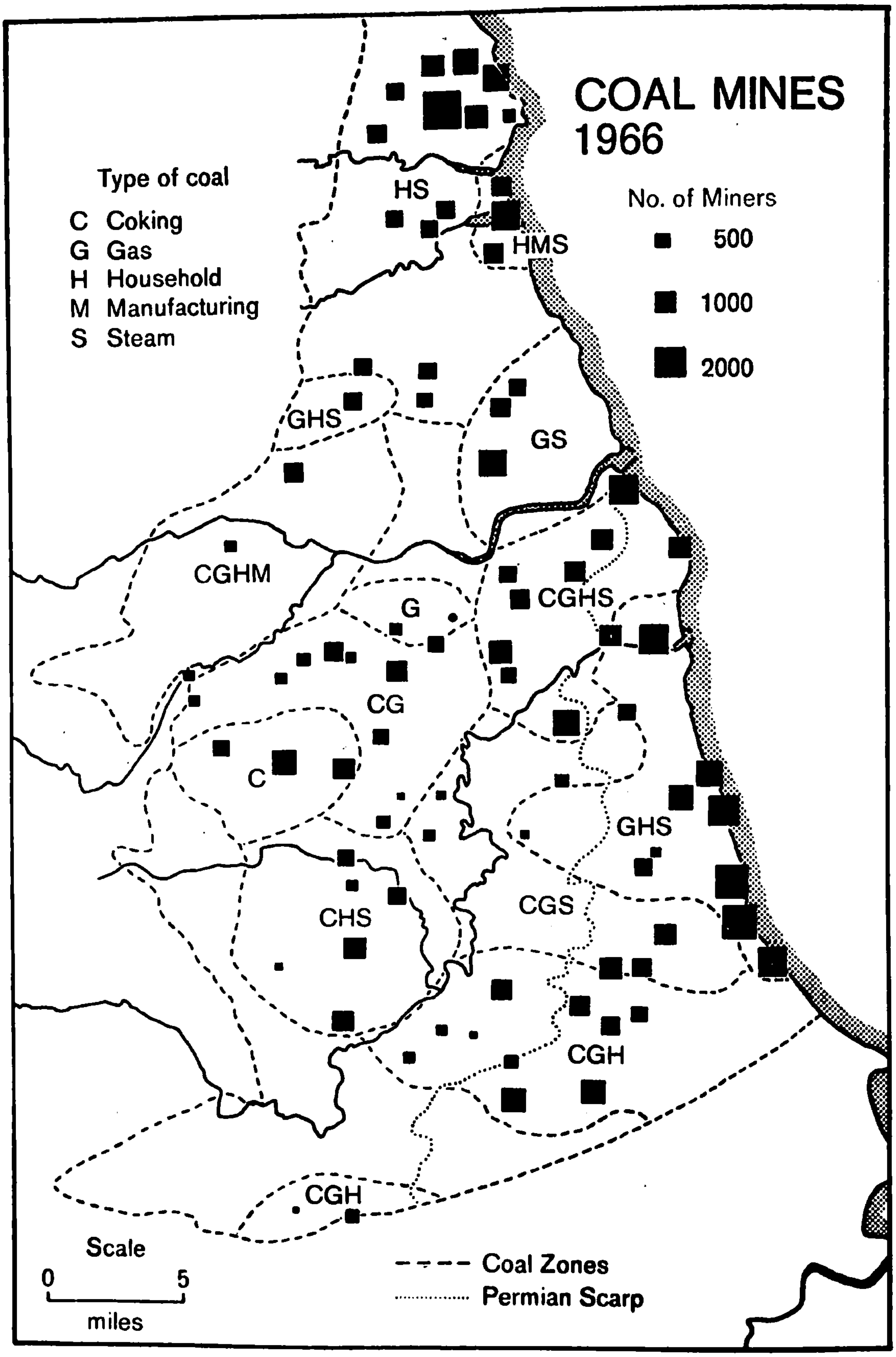
COAL MINES
1966
Type of coal
C Coking
G Gas
H Household
M Manufacturing
S Steam
No. of Miners
500
1000
2000
HS
HMS
GHS
GS
CGHM
G
CGHS
CG
C
GHS
CHS
CGS
CGH
CGH
Scale
0
5
miles
Coal Zones
Permian Scarp

Fig.5

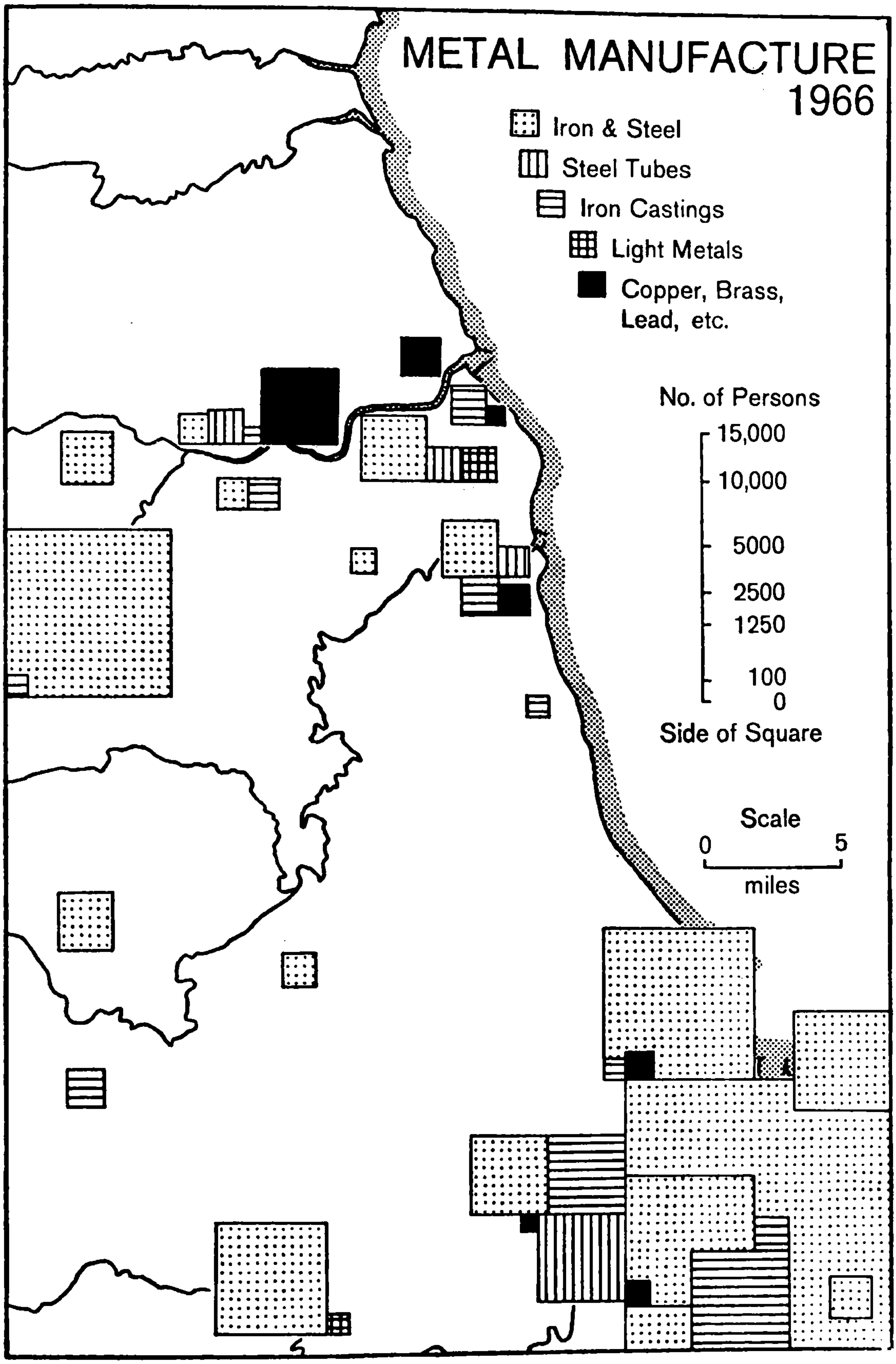
METAL MANUFACTURE
1966
Iron & Steel
Steel Tubes
Iron Castings
Light Metals
Copper, Brass, Lead, etc.
No. of Persons
15,000
10,000
5000
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.6

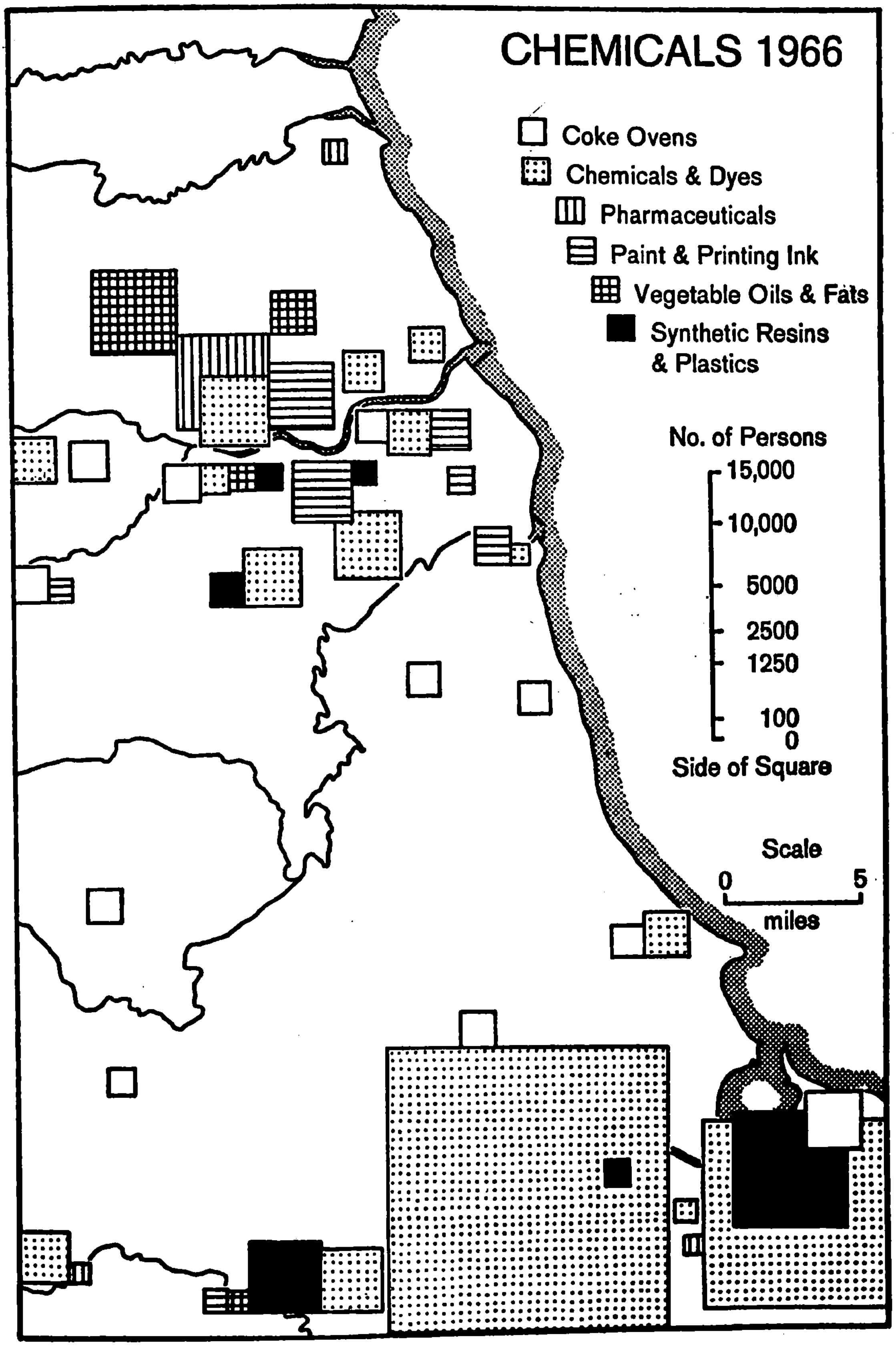
CHEMICALS 1966
Coke Ovens
Chemicals & Dyes
Pharmaceuticals
Paint & Printing Ink
Vegetable Oils & Fats
Synthetic Resins & Plastics
No. of Persons
15,000
10,000
5000
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.7

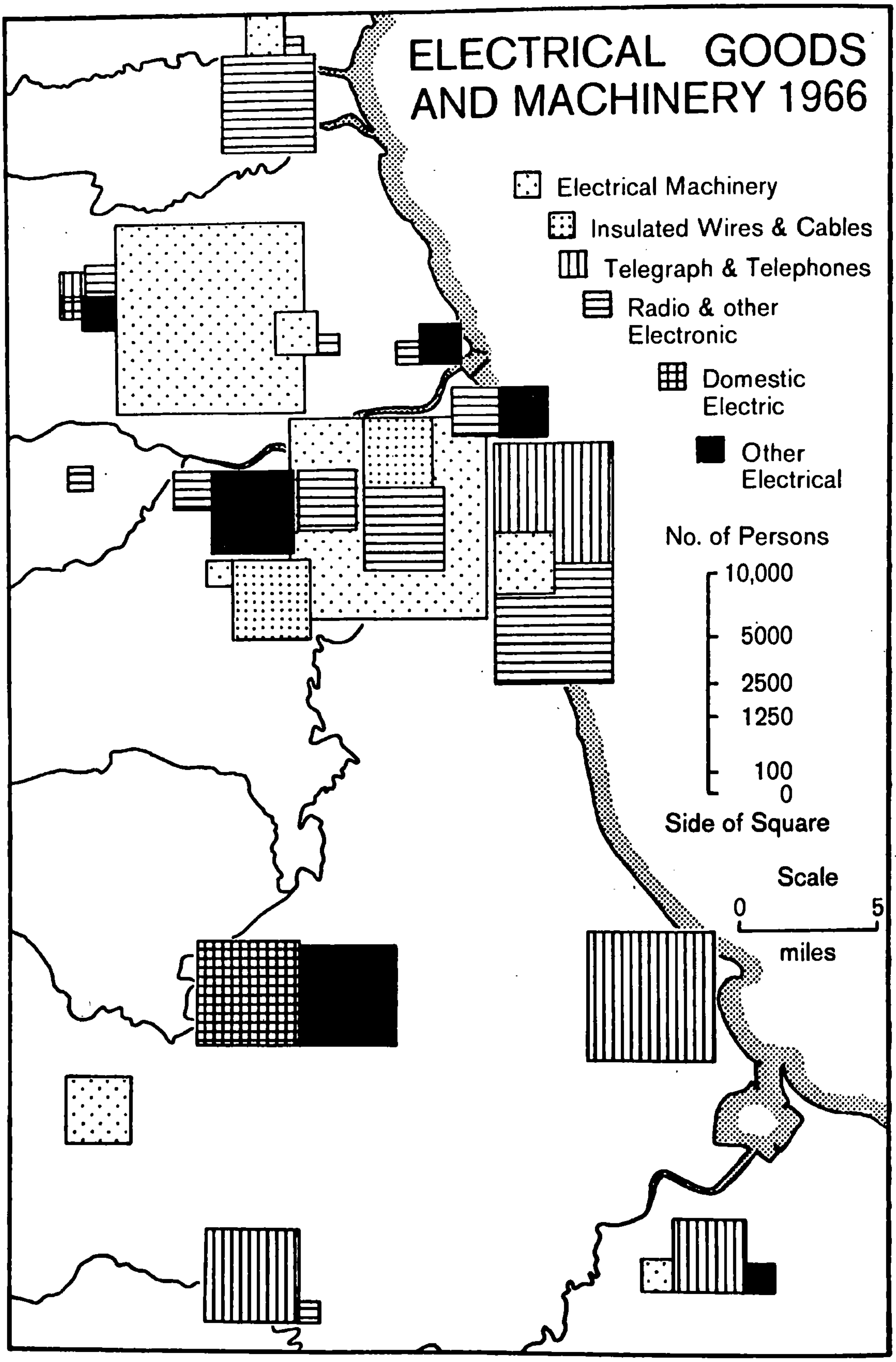
ELECTRICAL GOODS AND MACHINERY 1966
Electrical Machinery
Insulated Wires & Cables
Telegraph & Telephones
Radio & other Electronic
Domestic Electric
Other Electrical
No. of Persons
10,000
5000
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.8

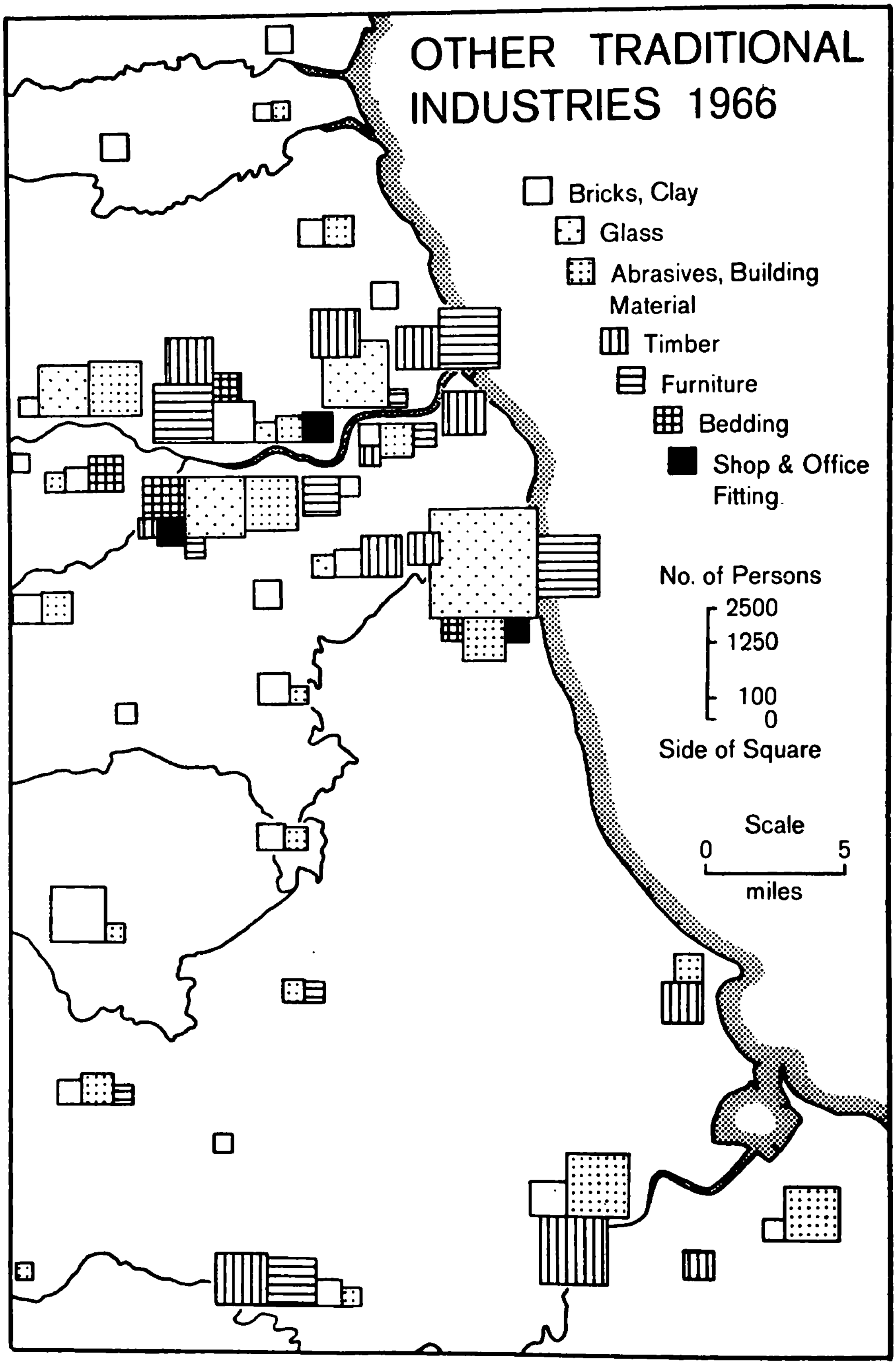
OTHER TRADITIONAL INDUSTRIES 1966
Bricks, Clay
Glass
Abrasives, Building Material
Timber
Furniture
Bedding
Shop & Office Fitting
No. of Persons
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.9

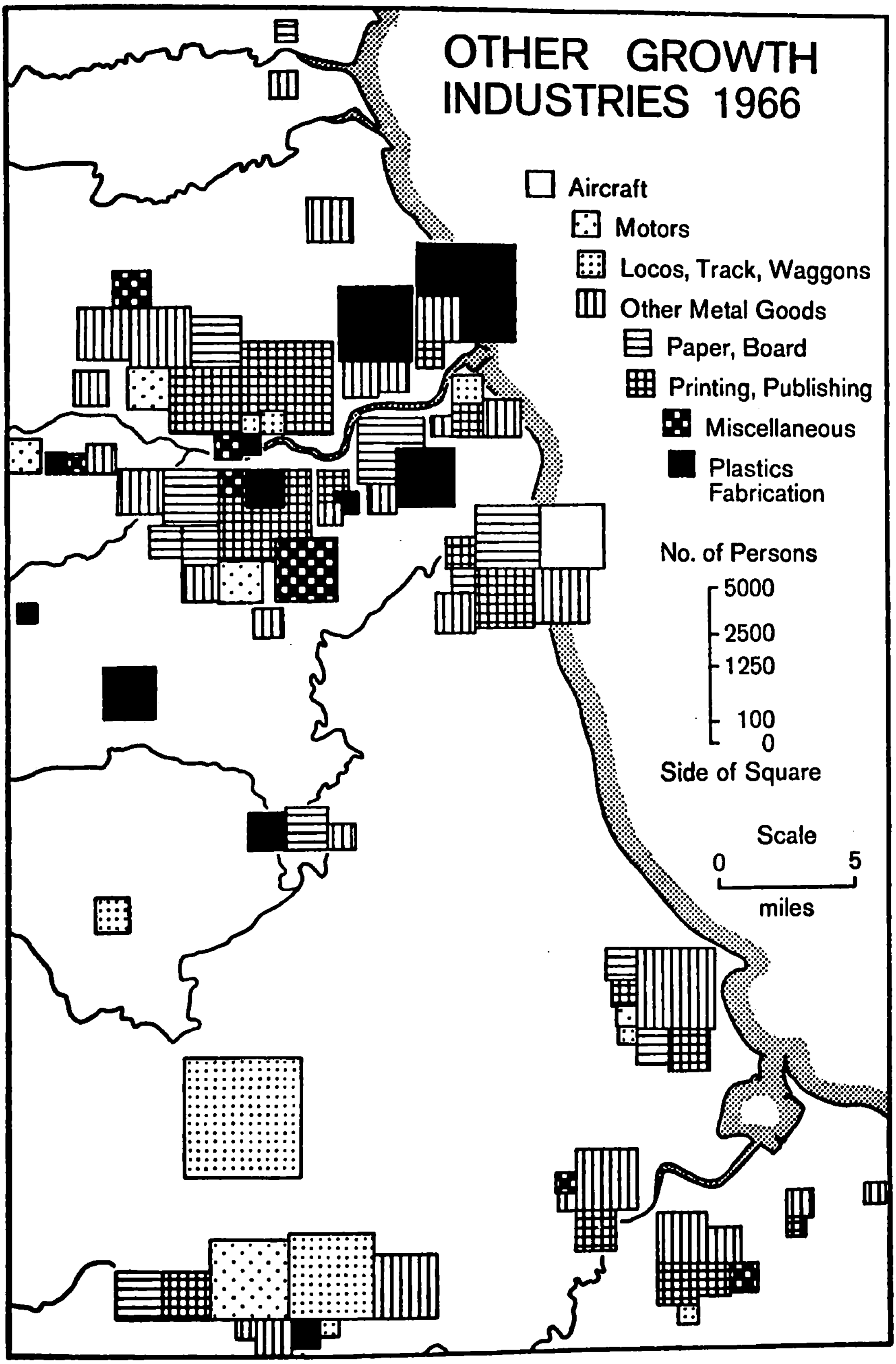
OTHER GROWTH INDUSTRIES 1966
Aircraft
Motors
Locos, Track, Waggons
Other Metal Goods
Paper, Board
Printing, Publishing
Miscellaneous
Plastics Fabrication
No. of Persons
5000
2500
1250
100
0
Side of Square
Scale
0
5
miles

Fig.10

sewage, and other colloids, the products of agricultural and engineering erosion, household and other waste.

3. Inorganic Nutrients

Frequently the by product of all the above categories including throughput of agricultural fertilisers in fresh water run off from the land.

4. Hot Water

Effluent from cooling plants. Heat in this case is the main pollutant as the water has been diverted simply for the purpose of cooling.

Table 2 summarises the scant physical, chemical and bacteriological data collected along the pollution gradient during this study.

It must be emphasised that data of this type however comprehensive only indicate that differences in water quality exist. They give no insight into the effects of these differences on the balance of the ecosystems developed in them. They are no more than a record of the alleged pollutants in the seas and there is always present the uncertainty that such measures are not biological parameters influencing the ecology of the benthic biota. (~~living on the benthos.~~)

From this brief description of data available for North East Britain, the following conclusions on the quality of the water can be drawn:

1. The urbanisation and industrial development of land adjacent to the Firth of Forth has certainly lead to pollution in the estuarine waters of the Firth. For instance, the entire City of Edinburgh has no sewage plant and 'disposes' all of its raw sewage into the estuary ("The Times" 24 March 1970). At the Forth River Bridge, faecal bacteria counts in excess of 100,000 bact per litre are frequently recorded

TABLE 2

The North East Pollution Gradients. Physical, Chemical and Biological Parameters

Station	Suspended Solids Mg/litre	Faecal Bacteria per litre	ug/litre PO_4	ug/litre NO_3	ug/litre NO_2	ug/litre NH_4	ug/litre SiO_3	% Laminaria Performance gms.Ash free Dry weight	Species Lost	Flyash	Coal Waste (tons/year)	Urbanisation/ Population
Forth Bridge	3.8	100,000	5.9	-	-	8.2	-		-	0	0	
Isle of May		-	9.0	-	-	1.2	-		-	0	0	
Petticoe Wick	12.1 }	200	0.37	2.10	0.14	1.7	4.5	100.0	13 sp.	0	0	} 6,000
St.Abbs Harbour			2.55	4.27	0.35	5.8	6.9			0	0	
Eyemouth			2.34	35.30	0.23	8.2	10.45			0	0	
Spittal			1.71	132.5	0.63	29.7	58.6			0	0	
Holy Island			1.33	7.8	0.13	1.3	50.0			0	0	
Seahouses			0.99	14.3	0.29	8.0	7.25			0	0	
Beadnell			1.740	10.5	0.21	2.5	5.01	43.0		0	0	
Craster			1.85	4.45	0.30	4.3	5.5			0	0	
Amble			1.84	5.75	0.33	28.8	32.4			0	0	
Newbiggin			2.21	6.05	0.19	2.4	4.85			0	0	
Blyth			1.65	10.05	0.26	1.4	5.35			-	-	}
St. Mary's			1.68	7.85	0.31	4.1	6.75			-	-	}
Tynemouth		160,000	1.08	15.88	0.13	9.8	12.0			400-500,000	1,429,000	} 190,000
Souter	5.8		2.78	19.0	3.25	13.5	14.5	8.0	86 sp	-	-	}
Roker Beach			5.3	22.7	1.36	15.1	19.0			-	-	
Sunderland			-	10.2	1.40	3.5	11.6			-	-	
Seaham			1.95	23.30	1.95	27.2	12.0			-	-	
Seaton Carew			2.06	20.5	4.99	30.0	13.0			-	-	}
Tees Bay		160,000	71.90	140.0	9.5	37.0	19.8	14.0	36 sp	-	-	} 170,000
Redcar			3.3	18.7	1.45	19.0	6.4			-	-	}
Whitby			2.08	38.35	0.28	16.0	34.4			0	0	
Robin Hood's Bay	52.5		2.48	18.8	3.59	20.7	8.7			0	0	
Flambrough Head			2.10	11.65	0.26	5.1	5.9			0	0	

All figures quoted as means for samples collected over 3 year period and suspended solids may reach levels of 38 mgms per litre, (Ouil 1968).

2. The chemical constituents of sea water at Station 6 (St.Abbs Head), Berwickshire compares favourably with the open ocean (P.Head personal communication).

3. Proceeding south from St. Abbs, a gradient of increasing pollution of all kinds can be demonstrated reaching a peak along the shores of County Durham. Thus the coastline from Craster in Northumberland to Redcar in Yorkshire is polluted. This has resulted in a drastic reduction in the common and abundant species of benthic algae (Bellamy 1968). It has also been shown that the productivity of the dominant sublittoral alga, *Laminaria hyperborea* has been reduced by 92% (Bellamy 1968). Faecal bacteria counts in Tynemouth and Teesmouth frequently reach 160,000 organisms per litre. Three million tons of coal waste dumped in seas of County Durham in 1969 (Times, 27 September 1970). Up to five hundred thousand tons of flyash are deposited off Tynemouth per year (Watson and Watson, 1968). The coastline from Redcar to Flambrough Head in Yorkshire is unpolluted but contains high levels of inorganic material in suspension from the fresh water erosion of the boulder clay cliffs characteristic of this region.

To attempt any correlation of benthic ecology with these regional variations in water quality, an extensive survey of the benthos is necessary. Figure 11 presents the site matrix for all sampling during this study. Kelp forest dominated by *Laminaria hyperborea* are a constant feature of sublittoral rocky outcrops along this length of coast. Twenty stations were selected on these areas for study of the hapteron ecospace ecosystem. These are shown in Table but a brief description is given below:

Stations 1 - 4 lie in the Firth of Forth

Stations 5 -12 are located in the unpolluted waters of Berwick and Northumberland.

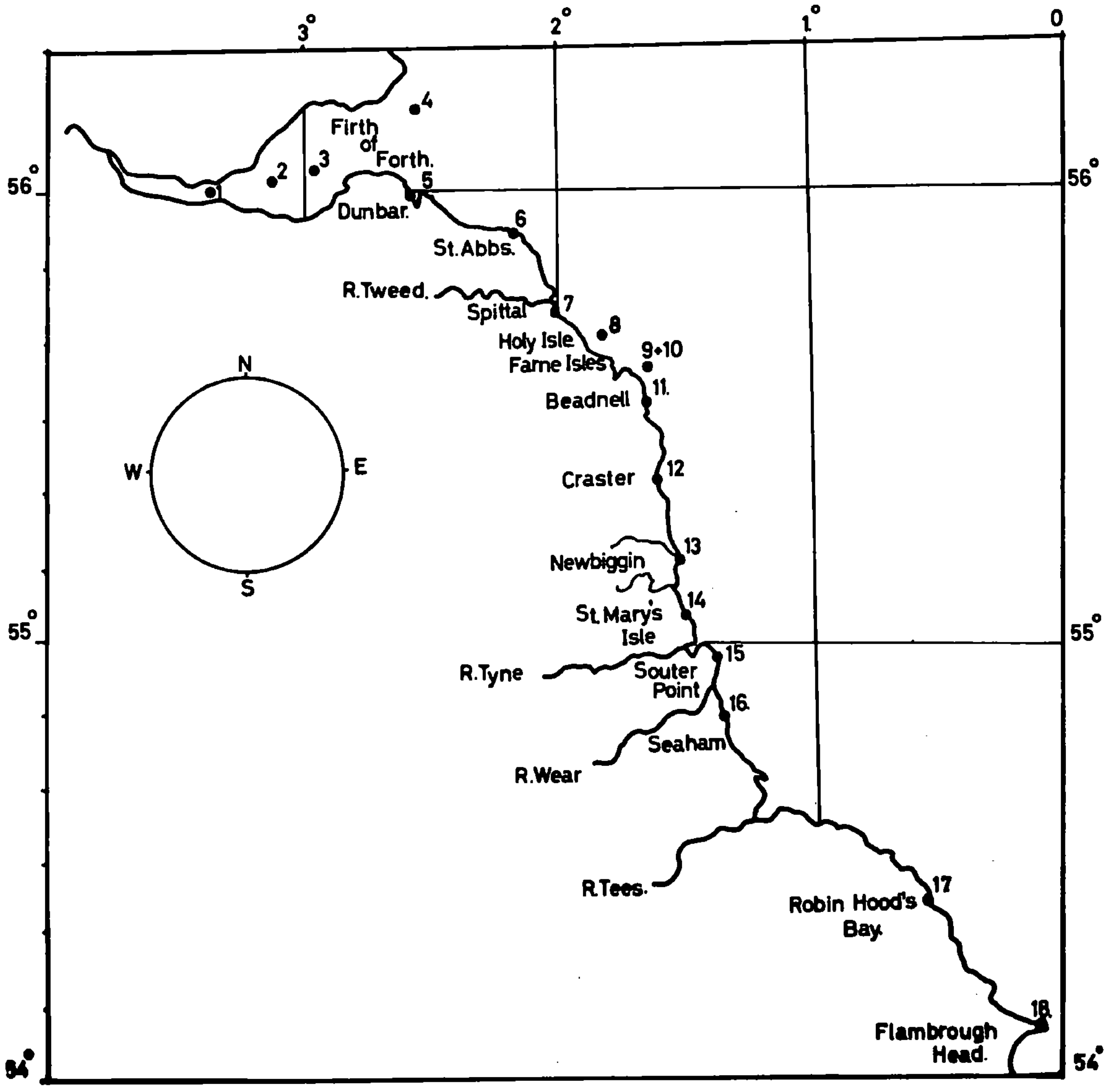

Fig.11

The location of sampling stations along the North East coast of England.

TABLE 3

Geographical Location of Sampling Stations - Extent of Kelp Forest

Station Number	Locality	County	Location Latitude	Location Longitude	Grid Reference	Kelp Depth Range below MLWM	Natural Allochtonous Material	Pollution	Turbidity
1	Forth Bridge	West Lothian	$56^{\circ}3'$	$3^{\circ}30'$	NT.1481	0-1.5	++++	++++	++++
2	Inch Mickery	Mid Lothian	$56^{\circ}5'$	$3^{\circ}20'$	NT.2180	0-3.0	++++	++++	++++
3	Inch Keith	Mid Lothian	$56^{\circ}5'$	$3^{\circ}10'$	NT.2964	0-7.0	++++	+++	++++
4	May Isle	Fife	$56^{\circ}10'$	$2^{\circ}30'$	NT.6593	0-10.0	+++	+++	+++
5	Dunbar	East Lothian	$55^{\circ}59'$	$2^{\circ}30'$	NT.6593	0-10.0	++	+	++
6	St.Abbs Petticoe Wick	Berwickshire	$55^{\circ}55'$	$2^{\circ}9'$	NT.9069	0-15.2	+	-	+
7	Spittal	Berwickshire	$55^{\circ}4'$	$2^{\circ}2'$	NU.0154	0-7.0	++	-	+
8	Holy Isle Castlehead Rocks	Northumberland	$55^{\circ}38'$	$1^{\circ}47'$	NU.1344	0-6.2	++	-	+
9	Farne Isles (a) Inner	Northumberland	$55^{\circ}35'$	$1^{\circ}45'$	NU.2438	0-10.5	+	-	+
10	Farne Isles (b) Outer	Northumberland	$55^{\circ}35'$	$1^{\circ}30'$	NU.2639	0-10.5	+	-	+
11	Beadnell	Northumberland	$55^{\circ}33'$	$1^{\circ}37'$	NU.2428	0-10.7	++	-	+
12	Craster	Northumberland	$55^{\circ}18'$	$1^{\circ}40'$	NU.2719	0-9.0	++	+	++
13	Newbiggin	Northumberland	$55^{\circ}8'$	$1^{\circ}40'$	NZ.3288	0-5.0	+	++	++++
14	St. Mary's Isle	Northumberland	$55^{\circ}4'$	$1^{\circ}42'$	NZ.3576	0-5.0	+	+++	++++
15	Souter Point	County Durham	$54^{\circ}48'$	$1^{\circ}21'$	NZ.6541	0-3.5	+	++++	++++
16	Seaham Harbour	County Durham	$54^{\circ}44'$	$1^{\circ}28'$	NZ.4549	0-3.5	+	++++	++++
17	Robin Hood's Bay	Yorkshire	$54^{\circ}24'$	$0^{\circ}38'$	NZ.9606	0-5.0	++++	++	+++
18	Flambrough Head	Yorkshire	$54^{\circ}8'$	$0^{\circ}10'$	TA.2274	0-6.0	++++	++	+++
19	Loch Ewe	Ross & Cromarty	$56^{\circ}48'$	$4^{\circ}45'$	NG.8585	0-24.0	+	-	+
20	Bantry Bay	County Cork	$10^{\circ}20'$	$9^{\circ}20'$	U.500900	0-10.0	+	-	+

Stations 12 - 16 cover the polluted waters ('chronic pollution' Bellamy, 1968).

Stations 16 - 18 in the unpolluted but naturally turbid waters of Yorkshire

Stations 19 - 20 are Not contiguous with the other stations, but taken as control areas.

Part 3

Ecospace

The rock/water interface on all except the most sheltered shores is a hostile environment for colonisation by the majority of animal species commonly observed in the sublittoral.

Shelter is of prime importance and the fauna will preferentially select areas of sea bed providing it (Kitching, 1934), (Lilley, 1953), (Drach 1952), (Forster 1952) (1958), (Knight-Jones, 1955). The distribution patterns of such animal populations are thus a reflection of the underlying abiotic pattern in an area and the fauna is clumped and aggregated into areas that provide the essential shelter, such as rock crevices and beneath large boulders. (Vectorial pattern, Hutchinson, 1962), The main problem in the study of such ecosystems is that of selecting a uniform sample for detailed study.

The storage of energy by primary producers introduces 'order' into ecosystems, (Schrodinger, 1945), by stabilising environmental fluctuation. Some amelioration of the rock water interface environment is caused by the growth of algae. The algal growth patterns allow much more extensive colonisation by the animals and biotic and sociological pattern begin to play a major role in the spatial and temporal structure of the ecosystem.

Laminaria hyperborea is the dominant perennial algae in the kelp forest ecosystem. It can be aged accurately up to seven years (Kain, 1964) and the growth patterns in different areas can be compared (Bellamy, 1968). Large stands of this plant appear to represent the 'climatic climax' vegetation around much of the rocky coasts of Europe.

Collectively, the dense populations of this dominant provide shelter for the development of an associated fauna. The advantage of such shelter can best be observed in the hapteron or holdfast of Laminaria hyperborea where a diverse community of benthic animals develop. After a study of the growth of two thousand holdfasts, the following basic growth pattern has been determined (see Plate 3).

The base of the holdfast is always roughly elliptical and the maximum area of a holdfast can occupy can be delimited by the eliptical growth pattern. The yearly addition of a whorl of hapteron branches to the holdfast (Kain, 1964) adds not only to the area covered but also to a third dimension, hapteron height.

The maximum possible amount of euclidian space occupied by any one holdfast can be determined using the formula:

$$\frac{1}{12} \pi h \quad {}^{B}/_{L} \left\{ h^2 + ha + a^2 \right\} \quad *$$

where π = 3.14

h = hapteron height

B = Breadth (length of shorter basal axis)

L = Length (length of longer basal axis)

a = Diameter at cut surface (Stipe diameter)

The tissue of the holdfast occupies some of this volume. The exact amount can be found by comparison of the tissue wet weight to a volume. The Specific Gravity of the tissue of Laminaria hyperborea was found to be constant and equal to 1.3.

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* see appendix for derivation of this formula

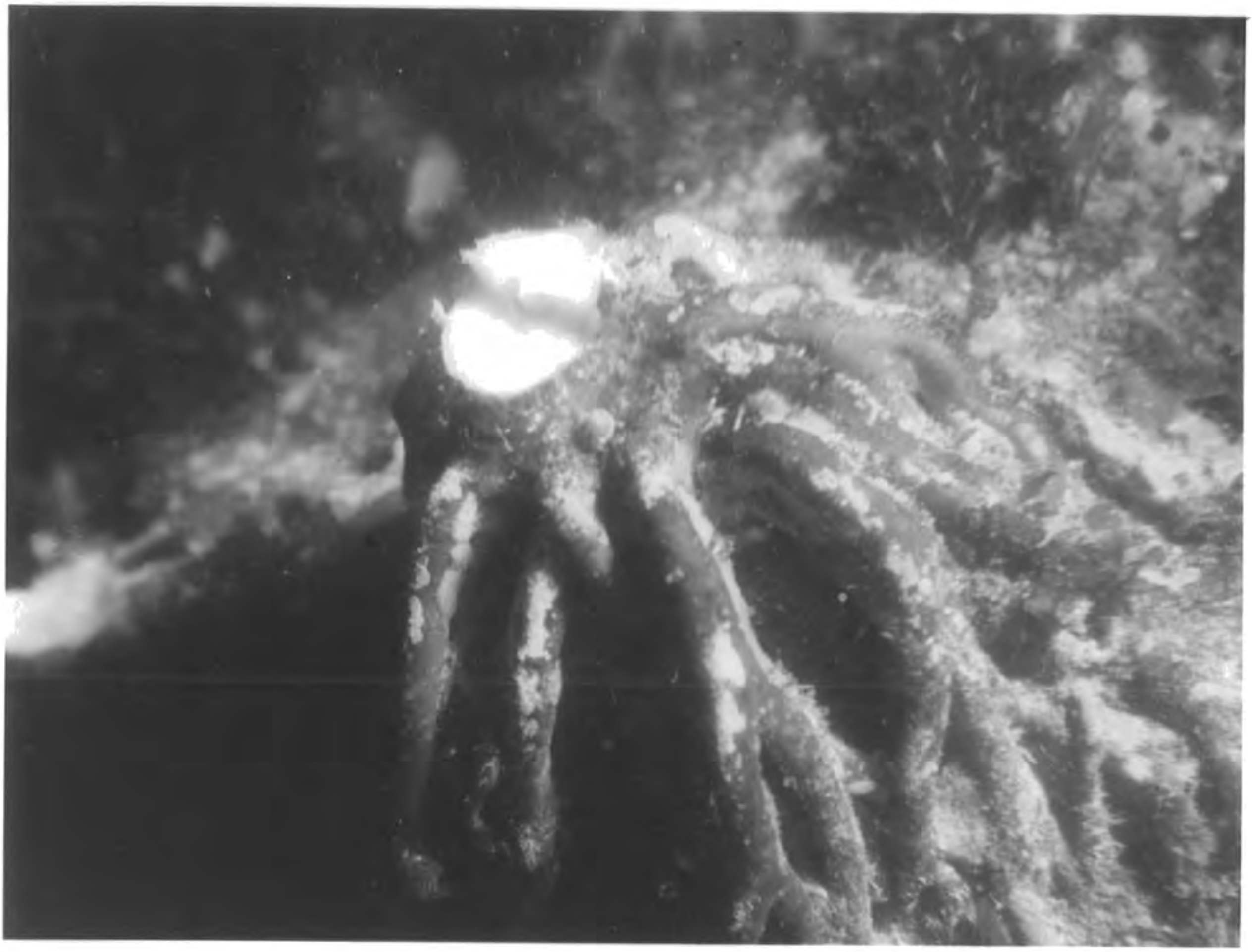


Plate 2

Laminaria hyperborea holdfast with stipe removed in situ on rock water interface.

Station 6 (St. Abbs). Depth 7 metres, May 1970.
Approximately one half of life size.

A few encrusting forms and one small porcellain crab (Porcellana longicornis) are the only species visible to the naked eye, on this holdfast.

Thus, wet weight holdfast tissue xSP.Gr = Tissue Volume CC's. By subtraction of the real tissue volume from the theoretical volume calculated earlier, ecospace can be determined.

Thus,

$$\frac{1}{12}\pi h \frac{B}{L} [h^2 + ha + a^2] - [\text{wet weight} \times \text{Sp.Gr}]$$

$$= \text{Ecospace in CC's}$$

In this way, simple measures of mass and linear dimension can be used to estimate the ecospace available as a sheltered habitat for animal colonisation. Ecospace determined in this way can be defined as a measure of the stabilising influence of plant biomass on the amplitude of physical parameters which create system instability detrimental to faunal components of the ecosystem.

Ecospace computed for fourteen hundred and fifty plants, collected at twenty one sampling stations, in three distinct regions of Britain (see Part II), from mean low water mark to 16.7 metres (Tables 4,5) indicates that,

(1) The size of the holdfast increases with the age of the plant. Size is a function of solar energy accumulated as plant tissue. Thus, in the final analysis the rate of ecospace increase depends upon the rate of a balance between anabolism and catabolism in plants.

(2) Using $\log_n$ transformation of ecospace as the y axis and minimum holdfast age in years as the x axis, the rate of ecospace increase for any population can be determined by simple linear regression analysis (Snedecar and Cochran, 1968 p.140, table 6.3.1) and the growth rates for spatially distinct populations of Laminaria hyperborea can be compared.

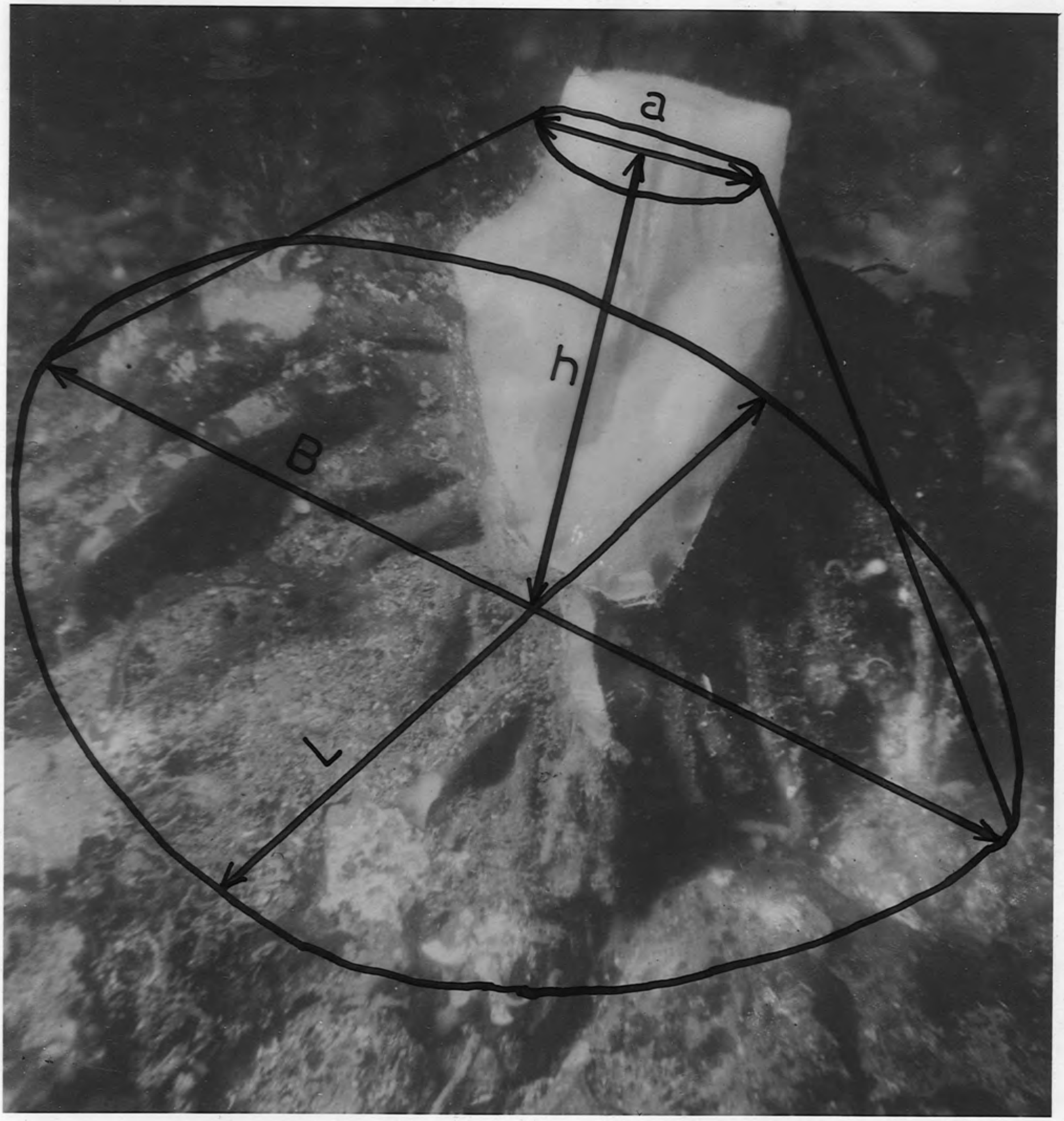


Plate 3

THE ECOSPACE HABITAT

Hapteron Wet Weight = 290 gms.
" Breadth = B = 16.0 cms.
" Length = L = 18.0 cms.
" Height = H = 8.0 cms.
Stipe Diameter = a = 3.6 cms.

ECOSPACE = 351.0 CC's

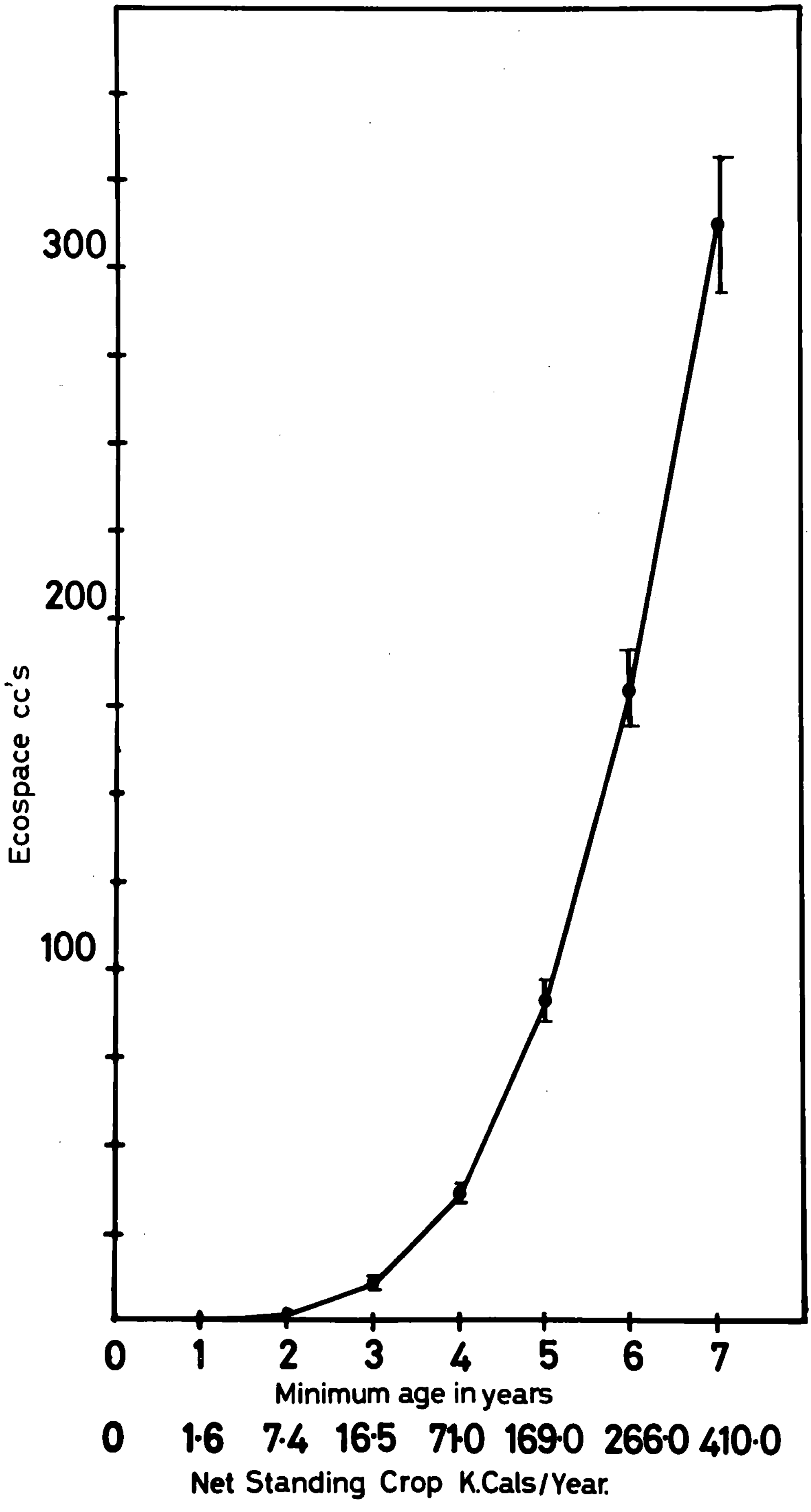


Fig.12

The British Standard Holdfast. Ecospace increase with age of plant for all plants, at all depths from all stations.

TABLE 4

Ecospace

THE BRITISH STANDARD HOLDFAST

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq. cms)	Ecospace (CC's)
1	2.3 ± 0.0	1.5 ± 1.2	0.8 ± 0.1	1.1 ± 1.3	0.5 ± 0.2	10.2 ± 3.8	0.0 ± 0.2
2	4.1 ± 0.2	3.0 ± 0.1	1.9 ± 0.0	5.0 ± 0.0	1.3 ± 0.0	11.1 ± 0.2	2.7 ± 0.1
3	6.9 ± 0.0	5.2 ± 0.0	2.2 ± 0.3	21.0 ± 1.4	1.7 ± 0.0	32.6 ± 2.2	10.2 ± 1.3
4	10.2 ± 0.2	7.5 ± 0.2	3.4 ± 0.0	47.5 ± 2.7	2.5 ± 0.0	64.3 ± 3.2	36.4 ± 3.9
5	14.3 ± 0.3	10.1 ± 0.3	4.9 ± 0.1	113.8 ± 5.3	2.9 ± 0.0	120.6 ± 5.5	92.6 ± 6.7
6	16.5 ± 0.2	12.7 ± 0.2	6.0 ± 0.1	178.0 ± 6.8	3.2 ± 0.0	162.4 ± 5.2	186.2 ± 17.3
7	18.7 ± 0.3	13.9 ± 0.2	7.8 ± 0.1	274.9 ± 12.0	3.8 ± 0.0	207.9 ± 6.9	312.1 ± 19.6

Number of plants measured = 1450 through all the age classes at all stations

THE NORTH EAST (Stations 1-18) 0.0 - 3.5 metres

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq. cms)	Ecospace (CC's)
1	2.5 ± 0.1	1.6 ± 0.3	0.6 ± 0.1	0.8 ± 0.4	0.5 ± 0.1	3.2 ± 0.9	0.0 ± 0.1
2	4.1 ± 0.2	3.2 ± 0.1	1.5 ± 0.0	5.5 ± 0.6	1.2 ± 0.0	10.9 ± 1.3	1.4 ± 0.8
3	7.2 ± 0.2	5.7 ± 0.2	2.2 ± 0.0	18.6 ± 1.2	1.9 ± 0.0	36.6 ± 3.0	11.1 ± 1.4
4	10.9 ± 0.3	8.1 ± 0.2	3.5 ± 0.1	48.6 ± 3.6	2.4 ± 0.1	74.0 ± 4.8	45.1 ± 6.3
5	15.6 ± 0.3	11.6 ± 0.3	6.0 ± 0.8	128.7 ± 4.5	2.9 ± 0.0	142.2 ± 7.0	149.4 ± 20.0
6	16.1 ± 0.3	12.8 ± 0.3	6.0 ± 0.1	188.9 ± 7.9	3.2 ± 0.0	169.3 ± 5.4	186.8 ± 16.2
7	18.9 ± 0.5	14.1 ± 0.3	7.5 ± 0.1	244.3 ± 14.3	3.8 ± 0.0	204.5 ± 20.0	305.4 ± 25.3

Number of plants measured = 190

THE NORTH EAST (Stations 1-18) 3.5 - 6.7 metres

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq. cms)	Ecospace (CC's)
1	2.9 ± 0.4	2.0 ± 0.0	0.8 ± 0.1	1.3 ± 0.5	0.5 ± 0.0	4.3 ± 0.4	-0.1 ± 0.1
2	4.4 ± 0.5	3.1 ± 0.3	1.4 ± 0.2	5.9 ± 1.3	1.0 ± 0.1	11.4 ± 1.8	0.5 ± 1.2
3	7.4 ± 0.2	5.6 ± 0.3	2.3 ± 0.1	21.8 ± 1.9	1.8 ± 0.0	34.4 ± 3.3	9.3 ± 2.3
4	10.9 ± 0.4	7.9 ± 0.3	3.4 ± 0.1	51.8 ± 3.3	2.5 ± 0.1	63.6 ± 5.3	36.9 ± 7.9
5	14.7 ± 0.8	11.5 ± 0.7	4.8 ± 0.1	126.9 ± 10.4	3.0 ± 0.1	134.1 ± 13.1	123.5 ± 19.5
6	15.9 ± 0.4	12.8 ± 0.3	15.1 ± 0.3	186.8 ± 13.9	3.2 ± 0.0	162.2 ± 7.8	140.6 ± 21.7
7	18.7 ± 0.4	14.0 ± 0.5	7.6 ± 0.3	313.8 ± 16.5	3.8 ± 0.1	200.0 ± 18.3	257.2 ± 43.7

Number of plants measured = 200

THE NORTH EAST (Stations 1-18) 6.7 - 11 metres

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq. cms)	Ecospace (CC's)
1	- ± -	- ± -	- ± -	- ± -	- ± -	- ± -	- ± -
2	5.5 ± 0.8	3.8 ± 0.7	1.7 ± 0.1	6.9 ± 1.8	2.2 ± 0.0	17.5 ± 6.8	3.0 ± 1.0
3	7.1 ± 0.3	4.8 ± 0.2	2.3 ± 0.1	18.0 ± 1.9	1.6 ± 0.1	28.0 ± 2.9	5.5 ± 3.1
4	9.6 ± 0.3	7.6 ± 0.3	2.8 ± 0.2	41.3 ± 4.2	2.5 ± 0.0	59.7 ± 6.4	26.2 ± 7.2
5	14.5 ± 1.0	10.5 ± 1.0	4.2 ± 0.2	112.6 ± 26.0	3.0 ± 0.1	138.8 ± 22.6	88.5 ± 25.0
6	17.5 ± 1.1	14.0 ± 1.2	6.4 ± 0.8	211.8 ± 39.9	3.4 ± 0.2	196.7 ± 27.0	296.4 ± 81.8
7	19.1 ± 0.6	14.7 ± 0.7	7.4 ± 0.4	290.3 ± 28.5	3.6 ± 0.7	218.8 ± 17.5	351.2 ± 51.0

Number of plants measured = 190

BANTRY BAY (Station 20) 0.0 - 6.7 metres

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq. cms)	Ecospace (CC's)
1	1.0 ± 0.0	0.5 ± 0.0	0.3 ± 0.0	1.0 ± 0.0	0.5 ± 0.0	0.1 ± 0.1	-1.2 ± 0.0
2	2.9 ± 0.2	2.2 ± 0.1	1.1 ± 0.1	3.6 ± 0.4	2.2 ± 0.0	5.8 ± 0.9	-1.2 ± 0.5
3	4.5 ± 0.2	3.4 ± 0.0	1.7 ± 0.0	11.0 ± 1.2	1.4 ± 0.0	14.6 ± 1.7	-2.1 ± 1.1
4	8.0 ± 0.3	5.6 ± 0.3	2.7 ± 0.1	32.3 ± 2.7	2.2 ± 0.0	38.4 ± 3.2	12.3 ± 3.9
5	9.2 ± 0.3	6.3 ± 0.3	3.3 ± 0.3	51.2 ± 3.6	2.0 ± 0.0	48.8 ± 3.7	7.3 ± 4.2
6	10.9 ± 7.7	7.7 ± 0.3	4.1 ± 0.1	91.0 ± 6.6	2.1 ± 0.0	70.6 ± 13.0	8.1 ± 7.5
7	11.6 ± 0.7	8.4 ± 0.5	5.7 ± 0 2	119.0 ± 21.9	2.3 ± 0.1	82.2 ± 9.7	32.7 ± 23.7

Number of plants measured = 430

TABLE 5

Ecospace

(SHEET 2)

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq.cms)	Ecospace (CC's)
LOCH EWE (Stations 21) 0.0 - 3.5 metres							
1	1.0 ± 0.5	1.2 ± 0.2	1.0 ± 0.0	0.6 ± 0.1	0.5 ± 0.0	1.6 ± 0.5	0.0 ± 1.0
2	3.2 ± 0.3	2.7 ± 0.2	1.3 ± 0.1	2.9 ± 0.7	1.2 ± 0.0	6.3 ± 1.4	0.7 ± 0.5
3	5.1 ± 0.3	0.3 ± 0.3	2.1 ± 0.2	9.7 ± 1.7	1.4 ± 0.1	16.8 ± 2.7	5.7 ± 1.7
4	8.0 ± 0.1	5.4 ± 0.4	3.6 ± 0.2	28.6 ± 3.7	2.7 ± 0.0	34.9 ± 1.4	26.8 ± 8.6
5	11.7 ± 0.3	7.8 ± 0.4	5.3 ± 0.1	67.7 ± 14.3	2.8 ± 0.2	68.9 ± 8.4	86.2 ±16.2
6	19.0 ± 0.5	13.8 ± 0.8	8.0 ± 0.5	224.0 ± 52.0	3.3 ± 0.2	206.8 ±15.2	379.4 ±37.2
7	19.1 ± 0.4	12.9 ± 1.2	9.0 ± 0.1	340.0 ± 71.5	3.8 ± 0.0	290.0 ±15.0	289.0 ±38.3

Number of plants measured = 722

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq.cms)	Ecospace (CC's)
LOCH EWE (Station 21) 3.5 - 10 metres							
1	0.7 ± - -	0.5 ± --	0.3 ± - -	0.4 ± --	0.3 ± --	0.2 ± --	-0.5 ± --
2	2.2 ± 0.0	1.6 ± 0.0	1.0 ± 0.0	1.1 ± 0.2	1.0 ± 0.5	3.0 ± 0.1	0.4 ± 0.1
3	2.1 ± 1.6	2.7 ± 0.2	2.0 ± 0.1	7.5 ± 2.1	1.2 ± 0.2	11.3 ± 3.7	0.7 ± 0.1
4	6.9 ± 0.2	4.5 ± 0.4	3.6 ± 0.1	21.8 ± 0.6	2.1 ± 0.1	24.5 ± 3.5	15.8 ± 2.6
5	13.2 ± 0.6	5.7 ± 1.1	4.9 ± 0.3	80.9 ±20.5	2.9 ± 0.1	78.0 ±10.5	22.9 ±12.6
6	15.1 ± 2.1	11.2 ± 1.0	7.7 ± 0.2	198.5 ±59.5	3.5 ± 0.3	135.4 ±30.4	196.1±10.1
7	12.9 ± 0.5	7.2 ± 0.5	4.8 ± 0.5	109.0 ±33.1	2.8 ± 0.1	138.0 ±24.7	200.0±10.0

Number of plants measured = 189

Age	Length (cms)	Breadth (cms)	Height (cms)	Wet Weight (gms)	Stipe Diameter (cms)	Area (sq.cms)	Ecospace (CC's)
LOCH EWE (Station 21) 10 - 16.7 metres							
1	-- ± --	-- ± --	-- ± --	-- ± --	-- ± --	-- ± --	-- ± --
2	2.1 ± 0.1	1.5 ± 0.1	1.2 ± 0.1	1.8 ± 0.2	0.6 ± 0.1	2.8 ± 0.0	-0.1 ± 1.0
3	3.9 ± 0.7	3.3 ± 0.8	2.5 ± 0.5	5.2 ± 1.0	1.2 ± 0.1	11.2 ± 4.6	9.6 ± 7.4
4	8.1 ± 0.4	5.3 ± 0.7	3.8 ± 0.8	24.8 ± 0.2	2.4 ± 0.1	40.9 ± 0.4	55.2 ±19.2
5	11.7 ± 0.5	6.6 ± 0.3	5.5 ± 0.8	86.7 ±25.5	2.9 ± 0.5	74.8 ± 2.5	43.3 ± 2.5
6	14.5 ± 2.0	9.5 ± 1.0	5.2 ± 1.0	97.2 ±27.6	3.3 ± 0.1	113.0 ±26.3	143.3 ±56.0
7	15.0 ± 1.0	8.0 ± 0.4	6.8 ± 0.7	200.0 ±33.7	3.4 ± 0.1	96.5 ±11.5	18.6 ±34.4

Number of plants measured = 140

TABLE 6

Between-Region variation in ecospace increase in

Laminaria hyperborea

Station	Equation	Coefficient of Correlation	% Annual Rate increase
6 (The North East)	y=1.0286+1.0170X	0.9570	236.5
21 (Loch Ewe)	y=1.2300+0.9600X	0.8581	223.2
20 (Bantry Bay)	y=-4.500+1.1750X	0.7944	273.2

The table presented above, with the regression lines plotted in Fig. clearly indicates that the annual rate of increase at Loch Eweand St. Abbs, are similar, 223.2% and 236.5% respectively, but that more ecospace is present at Stn.6 (St.Abbs) than at Stn.21 (Loch Ewe) as the plants get older. Ecospace at Stn.20 (Bantry Bay) is not as great as at either of the other two study areas but increases more rapidly after a 'slow start'. In all cases the correlation coefficient is above 0.7 indicating a statistically valid fit between the data and the regression line. Some geographical variation in ecospace is thus evident.

(3) Within-Region variation can be detected in the growth rates of the populations. The effect of two variables is analysed in this study.

(a) Depth of Water and its effect on Ecospace

Variation in ecospace is indicated by the tendency for the rate of ecospace increase to slow down with increasing depth over the 16.7 metre depth range of the kelp forest at Loch Ewe (see Table 4, 5). Over the shallow depth range at Stn.6 the deepest and shallowest samples have similar rates of increase, 241.8% and 233.8% respectively. At the intermediate depth 3.5 to 8 metres, the rate of increase is slower, 183.7% per year. Thus over the relatively

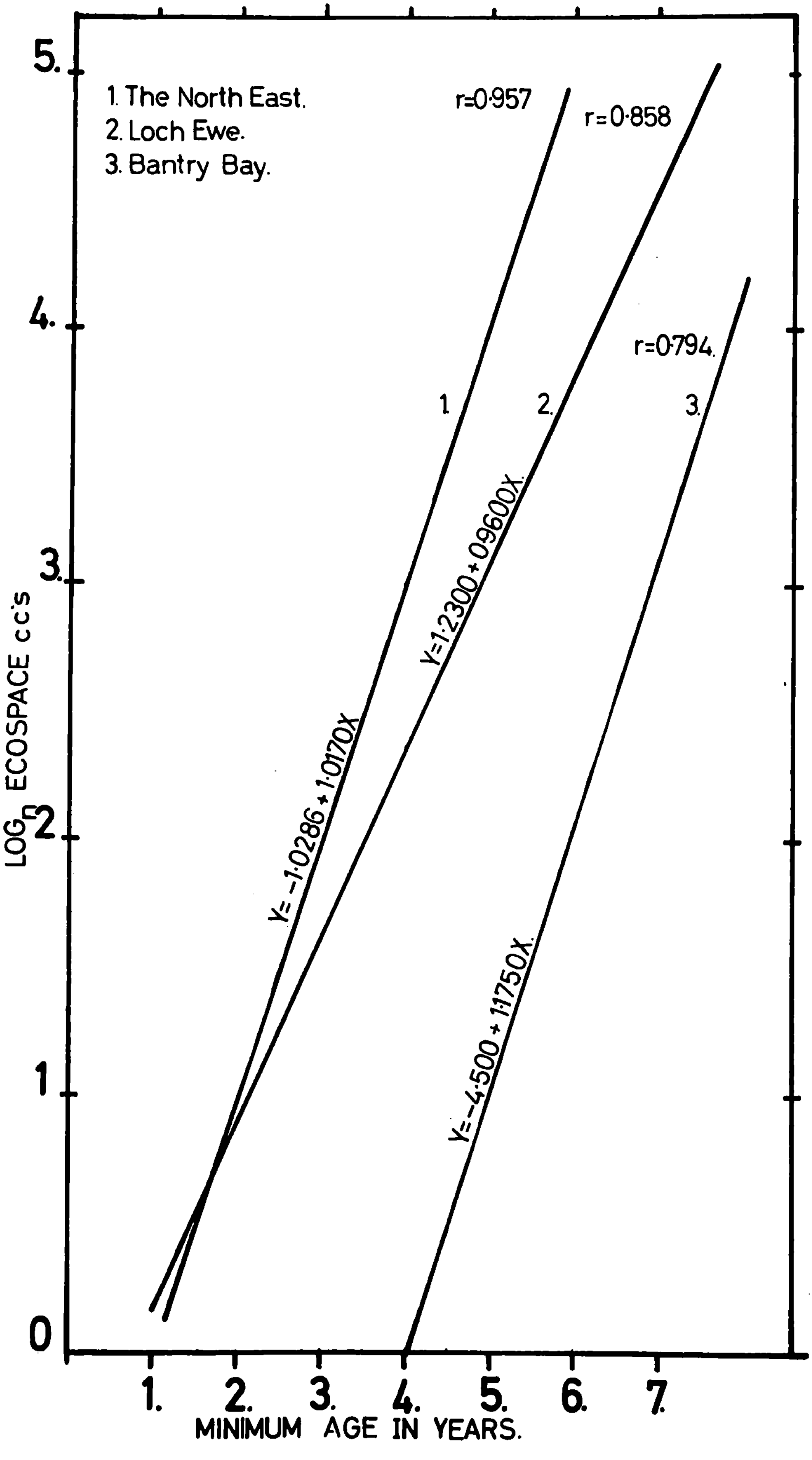


Fig.13

Between Region Variation in Rate of Ecospace Increase

TABLE 7

Within-region variation in ecospace increase with depth

Station	Depth	Equation	$\bar{r}$	% Annual Rate Increase
21	0-3.5	y=1.0586+1.0443X	0.9583	242.8
	3.5-10	y=1.2300+0.9600X	0.8581	223.2
	10-16.7	y=0.0800+0.8100X	0.8145	188.3
6	0-3.5	y=0.9724+1.0457X	0.9030	241.8
	3.5-8.0	y=0.2500+0.7900X	0.9045	183.7
	8.0-13.0	y=1.0027+1.0054X	0.9786	233.8

shallow range at Stn.6 (St. Abbs) it is highly likely that there is no variation in ecospace simply correlated with depth, the variation in the intermediate depth sample being anomalous. Much more detailed work is necessary to clarify this point.

(b) Pollution and its effects on ecospace

Within the North East region, two pollution gradients exist (see Part 2).

The kelp forest at Stn. 15 (Souter Point) in County Durham only extends to a depth of 3.5 metres. All comparisons of kelp forests within the North East region are thus confined to the OM to 3.5M depth and any ecospace variation which may be caused by depth of water is thus negated.

TABLE 8

Effects of Pollution on Ecospace increase in the North East Region

(i) The Unpolluted Stations

Station	Equation		% Rate Annual Increase	% Mean Increase
5 (Dunbar)	y=-0.5600+0.9600X	0.9220	223.2	
6 (St.Abbs)	y=-0.9724+1.0457X	0.9030	241.8	
8 (Holy Isle)	y=-0.1505+0.9371X	0.9341	217.9	
11 (Beadnell)	y=-2.2698+1.1977X	0.7913	278.5	220.0±15.1

Station	Equation		% Rate Annual Increase	% Mean Increase
12 (Craster)	y=0.6200+0.7400X	0.9835	172.0	
17 (R.H.B.)	y=0.6400+0.7200X	0.7588	167.4	
18 (Flambrough)	y=-0.6500+1.0300X	0.8086	239.5	
(ii) The Polluted Stations				
15 (Souter)	y=-1.3029+1.0229X	0.9313	237.8	
16 (Seaham)	y=0.9667+0.5500X	0.9356	137.9	197.0±20.9
14 (St.Mary's)	y=-0.6410+0.9943X	0.8593	231.2	
13 (Newbiggin)	y=0.7400+0.7543X	0.8381	175.4	
1-4 (Fth.Forth)	y=-3.3700+1.2300X	0.9329	216.9	

'F' tests on the mean variance of the polluted and unpolluted annual ecospace increase rates show no significant difference at the 5% level. Figure 15 presents the ecospace/age curves for the means of all the polluted and all the unpolluted age classes. Figure 15. presents the regression lines for those curves.

At the 95% confidence limit only the six year old plants appear significantly different when polluted ecospace curves are compared, but regression analysis on these curves indicates no significant difference between unpolluted and polluted growth patterns within the North East region.

It may be concluded that <u>there is no significant difference in the mean value of ecospace increase between polluted and unpolluted waters within the region</u>.

The following conclusions can now be drawn:-

(i) Ecospace exists and can be measured

(ii) Ecospace increases with the age of the holdfast

(iii) There is geographical variation in the amount of ecospace and the rate at which it is produced.

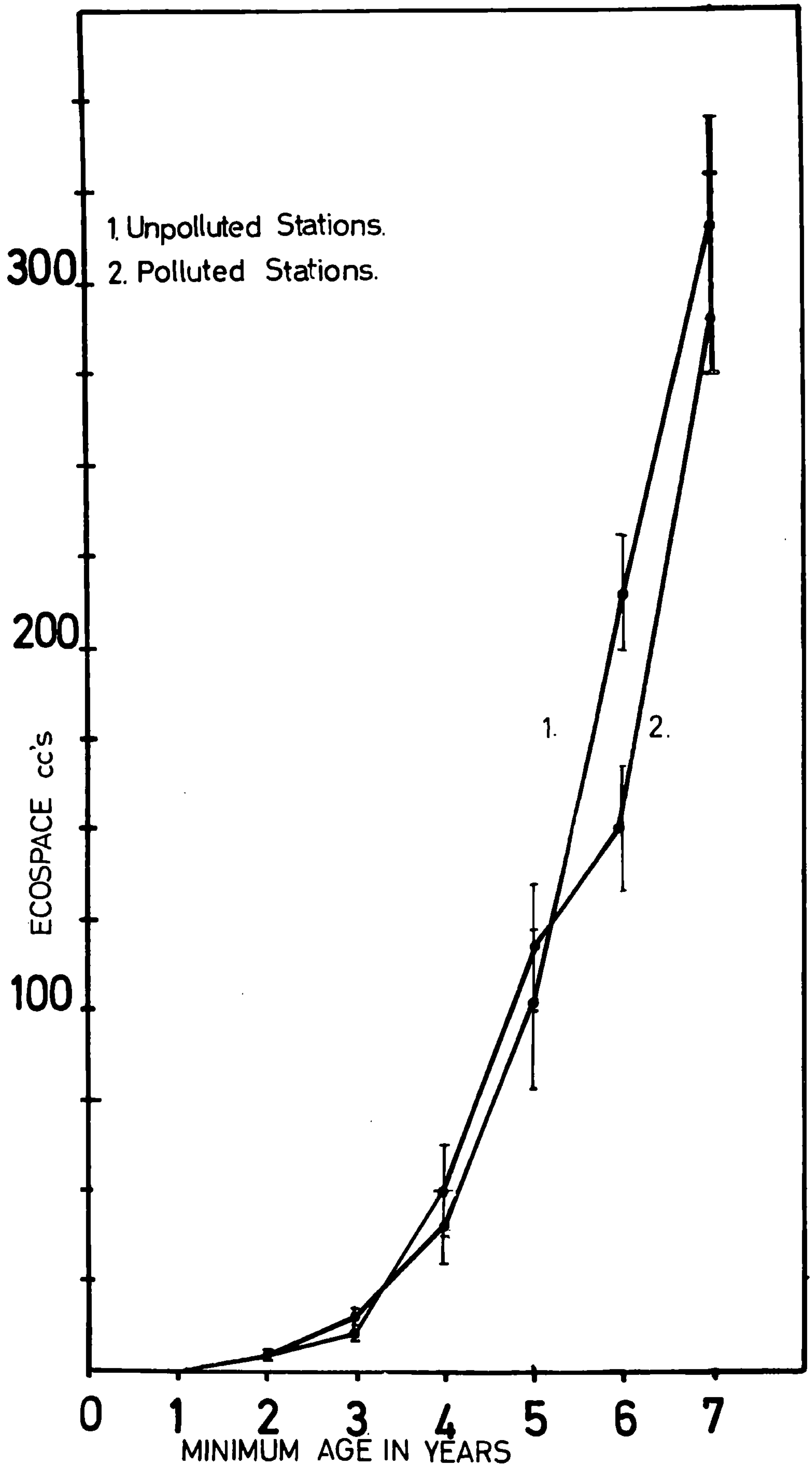


Fig.14
Mean Rate of Ecospace increase with age of plant; Mean values for all North East polluted stations and unpolluted stations.

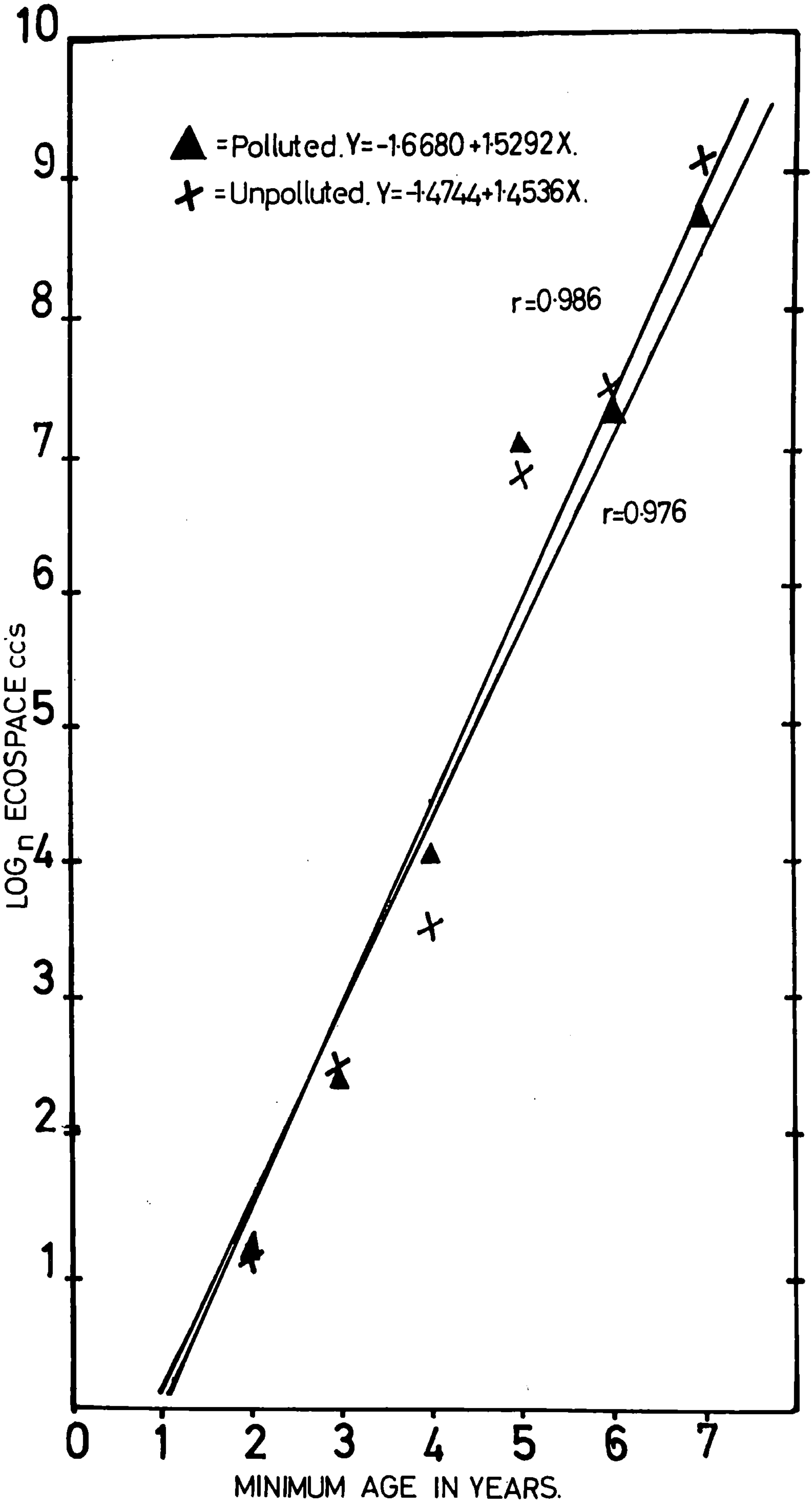


Fig.15

Linear regression analysis on polluted and unpolluted rates of ecospace increase

(iv) Depth tends to reduce ecospace in the holdfast but more research on deeper kelp forests is necessary before drawing firm conclusions.

(v) In the North East Region, pollution does not significantly affect the rate of ecospace production at a depth of 0-3.5M.

The amount of ecospace and the animal communities it contains can now be used for spatial and temporal studies on the fauna on a regional and geographical scale. By sampling plants in all age classes from one to seven years old the accumulation of invertebrate species within the developing habitat measured as ecospace can be determined.

Part 4

Trophic Component Analysis

Many attempts have been made to classify animals by the way in which they feed. These may be divided into two main categories:

(i) Classifications designed on the mechanism of food ingestion (Jordan, 1913), (Blegvad, 1914), (Jordan and Hirch, 1927), (Yonge, 1928).

(ii) Classifications based on the nature of the animals food (Rauschenplat, 1901), (Blegvad, 1914), (Hunt, 1925).

There are well defined correlations between the habitat and the food available for an animal (Yonge, 1928). Thus if an animal species is found to persist in a community, it must have

(i) an available food source

(ii) the mechanism by which to ingest it

(iii) another mechanism by which to digest the ingested food material.

A classification based on the nature of the food substrate must automatically take the mechanism of ingestion and digestion into account. In his work on the food of the bottom fauna at Plymouth, (Hunt, 1925) classified his populations on a modification of Blegvad's scheme (1914) in the following manner:

(A) Carnivores

Animals which feed mainly on other animals either living or as carrion.

(B) Suspension Feeders

Animals which feed by selecting from the surrounding sea water the suspended micro-organisms and detritus.

(C) Deposit Feeders

Animals which feed upon the detritus on the bottom, together with its associated micro-organisms.

This method was never pursued further and (Yonge, 1928) criticised it for dealing 'only with a section of the invertebrates'. Later suggestions by (Wilson, 1935) and (MacGintie, 1939) that a classification on food source might be useful, were ignored.

With the subsequent development of ecological energetics (Lindeman, 1942) and its successful experimental application (Thorson, 1958), (Odum, 1959), (Slobodkin, 1959), (Phillipson, 1966), the 'trophic levels' recognised by the new theory are found to correspond almost exactly to the categories in Hunt's classification system. A consideration of his communities in the light of this new theory indicate that the level bottom communities he was studying were detritus ecosystems, i.e. the majority of species found there were in feeding types B and C obtaining their food supply (energy input) by removing plankton and dead biological material (organic detritus) from the surrounding sea water and substrate interface.

As a preliminary step in the application of ecological energetics it is necessary to establish a tentative food chain relationship upon which quantitative studies of energy flow can then be undertaken.

The marine environment presents three main energy sources which can be used as a food substrate by the fauna. These are:

(i) The Flora (The Primary Producers)

Composed of two main elements, the free floating planktonic algae and the benthic algae and shallow water angiosperms.

(ii) Other parts of the living fauna within the marine ecosystems.

(iii) Organic Detritus

Dead and decaying material of organic origin both from the land and the sea.

These three energy sources can be used in five main ways:

(i) Herbivores

Exclusively plant eating organisms ingesting living plant tissue to the exclusion of all else.

(ii) Carnivores

Flesh eating animals catching and eating other animals as live prey.

(iii) Suspension Feeders

Mainly sessile forms removing material from suspension in the water.

(iv) Deposit Feeders

Bottom feeding species living on detritus and its associated micro-organisms.

(v) Omnivores

Species capable of ingesting most tissues, either living or dead, plant or animal.

Presumably because there was no benthic primary production of any note in his study areas, Hunt (1925), did not have a herbivore section in his community. An extension of Hunt's classification is presented below which includes primary production with its attendant herbivores.

The principal faunistic components of all the communities sampled in this study were established, and a literature search revealed that many of the species had been the subject of autecological studies which provide sufficient data to assign each species to a trophic component. Adaptive radiation within each phylum has been great and the proposed trophic component analysis presented below bears little resemblance to the systematic position of the species in the Animal Kingdom.

When analysing a sample the feeding groups of each species is determined and the number of individuals of each species present in a sample are counted. Each of the five main trophic components which make up the community may then be calculated.

Thus,

$$\frac{\text{Sum of all individuals in a trophic component}}{\text{The sum of all species in a sample}} \times 100$$

The relative importance of the three food sources and the adaptation of the community to the environment which provides them is now determined.

Preliminary results from widely separated stations indicate that by far the largest proportion of the community feeds on organic detritus derived from outside the confines of the habitat (Figure 17). Suspension feeders and omnivores dominate the community and herbivorous forms play only a small role. Thus it can be concluded that the main role of the primary producers is to provide a sheltered habitat within which secondary producers maintain an independant existence worthy of study in its own right.

Details of the feeding habits of the 116 species encountered in this study are given below:-

DEPOSIT FEEDERS

Actaeon tornatilis (Mollusca) see appendix

Bulla sp (Mollusca) see appendix

Nereimyra punctata (Annelida) Moore (personal communication)

Nicolea zostericola (Annelida) Jorgensen, 1966, 'Biology of Suspension Feeding' Academic Press.

Terebella sp. (Annelida) Dales, 1955, J.M.B.A.U.K. 34.

SUSPENSION FEEDERS

Alcyonium digitatum (Coelenterata). Roushdy and Hansen, 1961. 'Nature' *190*. 649-650.

Anemonia sulcata (Coelenterata). Stephenson, 1934, '*British Sea Anemonies*' Ray. Soc.

Anomia ephippium (Mollusca). Atkins, 1936, Quart.Journ.Micro.Sci.*79*: 181-308.

Anthopleura thallia (Coelenterata). Stephenson, 1934, '*British Sea Anemonies*' Ray. Soc.

Balanus balanus (Crustacea). Darwin, 1851-1854 '*Cirripedia*'. Roy.Soc.Lond.

Balanus crenatus (Crustacea). Darwin, 1851-1854 '*Cirripedia*'. Roy.Soc.Lond.

Botryllus schlosseri (Tunicata). Millar, 1970. '*British Ascidians*' Linnean Soc.Lond.

Botrylloides leachi (Tunicata). Millar, 1970. '*British Ascidians*' Linnean Soc.Lond.

Chlamys (tigerina?) (Mollusca). Forbes and Hanley, 1853. '*A History of British Molluscs and their Shells*'. London.

Corella parallelogramma (Tunicata). Millar, 1970. '*British Ascidians*' Linnean Soc. Lond.

Cucumaria saxicola (Echinodermata). Wilson 1951 in '*Life of the Shore and Shallow Sea*'

Dasychone bombyx (Annelida). Parker and Haswell, 1940. '*Textbook of Zoology*'.1.

Dendrodoa grossularia (Tunicata). Millar, 1970 '*British Ascidians*' Linn.Soc.Lond.

Halichondria panicea (Porifera). Wilson, 1951 '*Life of the Shore and Shallow Sea*'

Hiatella arctica (Mollusca). Jeffries, 1862-69. '*British Conchology*' London.

Hydroides norvegica (Annelida). Dales, 1957. J.M.B.A.U.K. *36*.

Hymeniacidon perleve (Porifera). Wilson, 1951 '*Life of the Shore and Shallow Sea*'.

Lanice conchilega (Annelida). Grasse, 1959. *Traite de Zoologie*. Masson.

Membranopora membranacea (Bryozoa). Wilson, 1951 in '*Life of the Shore and Shallow Sea*'. Nicholson and Watson.

Metridium senile (Coelenterata). Stephenson, 1934. '*British Sea Anemonies*' Ray. Soc.

Modiolus barbatatus (Mollusca). Jørgensen, 1966. *Biology of Suspension Feeding*. Pergamon.

Molgula sp. (Tunicata). Millar, 1970 '*British Ascidians*'. Linn.Soc.Lond.

Mya truncata (Mollusca). Yonge, 1923. Brit.Journ.Exper.Biol.1.

Mytilus edulis (Mollusca). Jørgensen, 1966 '*Biology of Suspension Feeding*' Pergamon.

Musculus sp. (Mollusca). Jørgensen, 1966. '*Biology of Suspension Feeding*' Pergamon.

Ophlitaspongia seriata (Porifera). Jørgensen, 1966. '*Biology of Suspension Feeding*'. Pergamon.

Pecten striatus sp. (Mollusca). Jørgensen, 1966. '*Biology of Suspension Feeding*', Pergamon.

Pomatoceros triquiter (Annelida). Dales, 1957. J.M.B.A.U.K. *36*.

Porcellana longicornis (Crustacea). Nicol, 1932. J.M.B.A.U.K. *18*.

Sabellaria spinulosa (Annelida). Wilson, D.P. (personal communication)

Salmacina dysteri (Annelida). Jørgensen, 1966. '*Biology of Suspension Feeding*', Pergamon.

Sagartia (elegans?) (Coelenterata). Gosse, 1860. '*The British Sea Anemonies and Corals*'

Sidnyum turbinatum (Tunicata). Millar, 1970. '*British Ascidians*.'

Taelia felina (Coelenterata). Wilson, 1951. '*Life of the Shore and Shallow Sea*'. Pergamon.

Tubularia larynx (Annelida). Allman, G.T., 1871. '*A Monograph of the Gymnoblastic or Tubularian Hydroids*'. Ray.Soc.Publ.

Umbonula verrucosa (Bryozoa). Yonge, 1949 '*The Sea Shore*'

Venerupis decussata (Mollusca). Jørgensen, 1966. '*Biology of Suspension Feeding*'

Venerupis pullastra (Mollusca). Jørgensen, 1966. '*Biology of Suspension Feeding*'

HERBIVORES

Acanthochitona crinitus (Mollusca). Forbes and Hanley, 1853.
'A History of the British Molluscs and their Shells'
London.

Aplysia punctata (Mollusca). Owen, G. 1966 in 'Physiology of Mollusca'.
Wilbour and Yonge, 11.

Canthaffidus (Trochus) striatus.(Mollusca) Purchon, R.D. 1968,
'The Biology of the Mollusca', Pergamon.

Gibbula cineraria (Mollusca). Fretter and Graham, 1962.
'British Prosobranch Molluscs' Ray. Soc.

Lacuna vincta (Mollusca). Fretter and Graham, 1962.
'British Prosobranch Molluscs' Ray. Soc.

Littorina littorea (Mollusca). Fretter and Graham, 1962.
'British Prosobranch Molluscs' Ray. Soc.

Paracentrotus lividus (Echinoderm). Mortensen, 1927.
'Echinoderms of the British Isles'

Patina pellucida (Mollusca). Purchon, 1968. 'Biology of the Molluscs'
Pergamon.

Rissoa sp. (Mollusca). Pelseneer, 1935. in 'Essai d'ethologie
zoologique d'apres l'etudes'. Des Mollusques.

Tectura (Acmea) testudinalis (Mollusca) Ankel, 1936(a), 'Prosobranchia'
in Die Tierwelt der Nord-Und Ostee. 1X bI.
Grimpe.G. amd Wagler, E. (Ed.). Leipzig
Academische Verlagsgesellschaft.

Velutina velutina (laevigata) (Mollusca). Ankel 1936(a).'Prosobranchia'
in Die Tierwelt der Nord-Und Ostee. IXb(i)
Grimpe,G. and Wagler, E. (Ed.). Leipzig Academische
Verlagsgesellschaft.

CARNIVORES

Aeolidia papilosa (Mollusca). Alder and Hancock, 1845-1855.
'A Monograph of the British Nudibranchiate Mollusca'
Ray.Soc.

Archidoris pseudoargus (Mollusca). Younge, 1949. 'The Sea Shore'. Collins.

Archidoris brittanica (Mollusca). Alder and Hancock, 1845-1855.
'A Monograph of the British Nudibranchiate Mollusca'
Ray.Soc.

Asteria rubens (Echinodermata) Clark, 1962. 'Starfishes'. B.M.Nat.Hist.

Berthella plumula (Mollusca). Eales, 1961. 'The Littoral Fauna of the British Isles'. Cambridge.

Buccinum undatum (Mollusca). Fretter and Graham, 1962. 'British Prosobranch Molluscs'. Ray. Soc.

Diodora apertura (Mollusca). Owen, 1966 in 'Physiology of the Mollusca'.
Wilbour and Yonge (Ed.) Academic Press.

Eulalia viridis (Annelida). Yonge, 1949. 'The Sea Shore'. Collins.

Lamellaria sp. (Mollusca). Fretter and Graham, 1962 'British Prosobranch Molluscs'. Ray. Soc.

Lineus longissimus (Nemertini). Wilson, 1935. 'Life of the Shore and Shallow Sea', Nicholson and Watson.

Lineus ruber (Nemertini). Wilson, 1935. 'Life of the Shore and Shallow Sea'
Nicholson and Watson.

Liparis liparis (Pisces) Moore (personal communication)

Lumbriconereis latreilli (Annelida). Hunt, 1925. J.M.B.A.U.K. 13.

Natica alderi (Mollusca). Fretter and Graham, 1962. 'British Prosobranch Molluscs'. Ray. Soc.

Nereis pelagica (Annelida). Clark, 1959. Animal Behaviour. 7.

Nymphon gracile (Pycnogonida). Eales, 1961. 'The Littoral Fauna of the British Isles'. Cambridge.

Palaemon squilla (Crustacea). Moore (personal communication)

Phyllodoce (sp.) (Annelida). Eales, 1961.'Littoral Fauna of the British Isles'. Cambridge.

Pleurobranchus membranaceus (Mollusca). Jeffries, 1862-69. 'British Conchology', London.

Polycera quadrilineata (Mollusca). Alder and Hancock, 1845-55. 'A Monograph of the British Nudibranchiate Molluscs.' Ray. Soc.

Pycnogonum littorale (Pycnogonidia) Calman (1929). Journ.Quickett Micr.Cl.16. 195.

Rostanga rufescens (Mollusca). Yonge, 1949 'The Sea Shore'

Trivia arctica (Mollusca). Fretter and Graham, 1962 'British Prosobranch Molluscs'. Ray. Soc.

Tubulanus annulatus (Nemertini). Wilson, 1935. 'Life of the Shore and Shallow Sea'. Nicholson and Watson.

OMNIVORES

Amphiopholis squamata (Echinodermata). Mortensen, 1927, 'Echinoderms of the British Isles'.

Amphithoe rubricata (Crustacea). Bate and Westwood, 1863, 'British Sessile-Eyed Crustacea'. 2.

Aoridae (Crustacea) see appendix

Ampherusha jurinei (Crustacea). Moore (personal communication)

Cancer pagurus (Crustacea). Hallback, 1970. Underwater Association Report, 1970 (in press)

Caprella linearis (Crustacea). Harrison (1944) Linn.Soc.Lond. Synop. Brit. Fauna. No.2.

Caprella acanthifera (Crustacea). Bate and Westwood, 1863, 'British Sessile Eyed Crustacea', 2.

Corophium bonellii (Crustacea). Crawford, 1937, J.M.B.A.U.K. 21 (2)

Echinus esculentus (Echinoderm). Clark, 1962, 'Starfishes' B.M.Nat. Hist.

Eupagurus bernhardus (Crustacea). Orton, 1927, J.M.B.A.U.K. 14.

Flabelligera affinis (Annelida). Moore (personal communication) (see also appendix

Galathea squamifera (Crustacea). Nicol, 1932, J.M.B.A.U.K. 18 (1)

Gammarus homari (Crustacea). Moore (personal communication) (see also appendix

Harmanthoe impar (Annelida) see appendix

Henricia sanguinolenta (Echinodemath) see appendix

Hyas araneas (Crustacea) see appendix)

Idotea baltica (Crustacea). Naylor, 1955, J.M.B.A.U.K. 34.

Jassa falcata (Crustacea). Moore (personal communication) (see also appendix

Lepidonotus squamatus (Annelida). Moore (personal communication)

Nassarius reticulatus (Mollusca). Fretter and Graham, 1962. 'British Prosobranch Molluscs'

Ophiothrix fragilis (Echinodermata). Mortensen, 1927.

'Echinoderms of the British Isles'.

Ophiopholis aculeata (Echinodermata). Mortensen, 1927.

'Echinoderms of the British Isles'.

Ophiocomina nigra (Echinodermata). Mortensen, 1927.

'Echinoderms of the British Isles'.

Panoplea minuta (Crustacea) see appendix

Pilumnus hirtellus (Crustacea). Russell and Yonge, 1963.

'The Seas'. Warne.

Primela denticulata (Crustacea). Russell and Yonge, 1963.

'The Seas'. Warne.

Socarnes vahli (Crustacea) see appendix

Species which could not be classified by reference to the literature were placed in a group on information produced by observations of the animals both in the laboratory and in situ on the sea floor.

SECTION II

Ecospace, the Ecoperiod and the Developing Animal Communities

PART 1

Introduction

Once the validity of the concept of ecospace is accepted, its importance in comparative studies of spatial and temporal systems becomes evident.

Community development in this system is a function of the time taken for plant growth to provide a habitat within which an animal community can develop. The time this takes, the finite limits of the habitat, and the composition and abundance of the fauna which colonises that habitat, can all be measured. Each holdfast with its associated fauna can be considered as a distinct ecosystem maintaining a balance between the abiotic and biotic elements in the environment; by so doing itself becoming a persistent and functional unit during the life of the plant. The collective presence of many of these units on the rock water interface are a readily obtainable and meaningful segment of the kelp forest ecosystem.

Thus, the given volume of ecospace developed over a given time, THE ECOPERIOD, permits the study of viable fragments of the kelp forest ecosystem and of the intact miniature ecosystem associated with a single kelp holdfast.

Two major problems in ecological investigation are now, in part overcome

(i) Abiotic variation

This has been 'smoothed' by the stabilising influence of plant biomass.

(ii) Biotic variation

Removal of the holdfast ecosystems intact ensures that all the community elements are sampled. Any spatial or temporal differences observed in the fauna are now likely to be real ones.

PART II

The Ecoperiod as a Sampling Unit

The ecospace habitat is a three dimensional space which is colonised by invertebrate species. Two interpretations can be placed of the accumulation of invertebrates in this space.

(1) The age structure of the holdfasts presents a gradually developing habitat over seven years, which is colonised by invertebrates in a characteristic manner. If this is a true succession, i.e. the presence of one species exerts a biotic influence over the recruitment of the next species, then sets of the seven year ecoperiods sampled at random but at one point in time can be considered as an historical record of the development of ecospace communities.

(2) The presence of other species in the habitat exerts no influence on ecospace and the habitat is colonised by a random series of species, the more space available, the greater the probability of colonisation by large numbers of species.

The alternatives are considered below. Community data obtained from the age range of <u>Laminaria hyperborea</u> at Stn. 6 (St. Abbs) at a depth of two metres in ten replicates of the seven year eco-period is presented (Table 9).

The number of species included in the community increases as eco-space increases over seven years. After the first year when only two species colonise the habitat, there follows a steady accumulation of new species which, by the seventh ecoperiod, amount to 19.0$\pm$1 species composed of 80$\pm$8 individuals. ~~is present~~, (Table 10)

Of the total number of 53 species present, 44 are recruited into the habitat in a distinct series and almost without exception remain in the community, gradually increasing in numbers. The following sequence was observed:

TABLE 9

Invertebrate 'succession' in ecospace at Stn. 6 (St.Abbs) Unpolluted

Ecospace CC's	0	16.0	100.0	360.0	920.0	1810.0	3130.0	Fauna	Per cent of sample
Ecoperiod (years)	1	2	3	4	5	6	7		
Umbonula verrucosa	4	8	10	10	10	10	9	61	3.0
Mucronella coccinea	3	9	10	10	10	10	4	56	2.7
Asterias rubens		3	8	14	18	36	55	134	6.6
Amphithoe rubricata		3	0	5	18	24	46	96	4.7
Lacuna vincta		7	0	0	3	20	20	50	2.4
Ophiopholis aculeata		2	1	3	11	16	83	116	5.7
Ophiothrix fragilis		3	23	42	48	66	139	321	15.8
Acanthochitona crinitus			3	0	9	1	5	18	0.8
Botryllus schlosseri			1	1	2	1	3	8	0.3
Caprella linearis			5	3	7	18	19	33	1.6
Cancer pagurus			1	1	2	1	3	8	0.3
Corophium bonellii			7	18	26	13	50	114	5.6
Echinus esculentus			1	2	4	5	19	31	1.5
Salmacina dysteri			1	4	2	2	5	14	0.6
Henricia sanguinolenta			1	0	1	3	1	6	0.2
Jassa falcata			8	16	29	35	58	146	7.2
Lepidontus squamatus			2	5	14	15	15	51	2.5
Membranipora membranacea			1	0	6	3	2	12	0.0
Mya truncata			2	5	15	17	31	70	3.4
Nereis pelagica			8	15	28	23	68	142	7.0
Porcellana longicornis			1	7	21	24	45	98	4.8
Pomatoceros triqueter			7	15	44	42	44	152	7.5
Alcyonium digitatum				1	1	1	1	4	0.1
Galathea squamifera				1	0	1	2	4	0.1
Hyas araneas				1	3	6	6	16	0.7
Mytilus edulis				1	2	1	1	5	0.2
Monia patelliformis				5	22	22	7	56	2.7
Anomia ephippium				2	23	26	18	70	3.4
Trivia arctica				1	1	4	1	7	0.3
Polycera quadrilineata				1	0	2	1	4	0.1
Archidoris pseudoargus					1	3	4	8	0.3
Balanus balanus					6	16	6	28	1.3
Eupagurus bernhardus					1	2	1	4	0.1
Lineus longissimus					8	0	2	10	0.4
Modiolus barbatus					3	0	2	5	0.2
Tonicella rubra					2	0	1	3	0.1
Halichondia panacea						2	3	5	0.2
Harmothoe impar						1	4	5	0.2
Pycnogonum littorale						3	13	16	0.7
Palaemon squilla						1	2	3	0.1
Taelia felina						1	3	3	0.1
Cacinus maenus							1	1	0.0
Liparis liparis							2	2	0.0
Patina pellucida							2	2	0.0
Buccinum undatum					1			1	0.0
Flabelligera affinis					3	4		7	0.3
Gibbula cineraria					2			2	0.0
Lamellaria sp.					1	1		2	0.0
Molgula sp.					2			2	0.0
Venerupis pullastra					1	1		2	0.0
Tectura testudinalis					1	2		3	0.1
Hydroides norvegica						4		4	0.1
Nymphon gracile						3		3	0.1

'Succession' in ten replicates of the seven year ecoperiod of _Laminaria hyperborea_ ecospace

(i) The Number of species

Age (years)	1	2	3	4	5	6	7
Ecoperiod (years)	1	2	3	4	5	6	7
	0	1	4	12	17	17	17
	0	2	11	16	15	13	20
	0	2	7	7	15	12	23
	0	1	6	10	16	18	18
	1	2	6	8	19	19	16
	0	0	7	11	24	11	16
	2	0	6	7	12	18	21
	0	0	4	11	15	27	15
	0	0	7	8	19	17	25
	0	0	7	6	18	18	19
Mean =	2 ± 0	1.6 ± 0.6	6.5 ± 0.6	9.6 ± 0.9	17.0 ± 1.0	17.0 ± 1.4	19.0 ± 1.0
Corrected to 1.0 =	2.0	2.0 ± 1	7.0 ± 1.0	10.0 ± 1.0	17.0 ± 1.0	17.0 ± 1.0	19.0 ± 1.0

(ii) The number of individuals

	1	2	3	4	5	6	7
	0	1	8	23	46	49	87
	0	4	14	43	25	28	83
	0	2	19	8	31	58	120
	1	1	6	34	53	43	79
	0	1	8	15	62	59	41
	0	0	11	24	68	17	81
	1	0	11	7	28	36	86
	0	0	7	19	28	107	51
	0	0	11	9	56	52	116
	0	0	9	20	50	53	57
	1	2.0 ± 1.0	10.4 ± 1.2	20.2 ± 3.6	44.7 ± 4.9	50.2 ± 7.6	80.1 ± 8.09
Corrected to 1	1	2.0 ± 1.0	10.0 ± 1	20.0 ± 3.0	45.0 ± 5.0	50.0 ± 8.0	80.0 ± 8.0

Year 1

Ecospace = 0.cc's

Umbonula verrucossa and Mucronella coccinea

Year 2

Ecospace = 16.0.cc's

Asterias rubens, Amphithoe rubricata, Lacuna vincta, Ophiopholis aculeata, Ophiothrix fragilis

Year 3

Ecospace = 100.cc's

Acanthochitona crinitus, Botryllus schlosseri, Caprella linearis, Cancer pagurus, Corophium bonelii, Echinus esculentus, Salmacina dysteri, Henrica sanguinolentha, Jassa falcata, Lepidonotus squamatus, Membranopora membranacea, Mya truncata, Nereis pelagica, Porcellana longicornis, and Pomatoceros triqueter.

Year 4

Ecospace = 360.cc's

Alcyonium digitatum, Galathea squamifera, Hyas areneas, Mytilus edulis Monia patelliformis, Anomia epiphium, Trivia arctica, Polycera quadrilineata.

Year 5

Ecospace = 920.cc's

Balanus balanus, Eupagurus bernhardus, Lineus longissimus, Modiolus barbatus, and Tonicella rubra.

Year 6

Ecospace = 1810.cc's

Harmothoë impar, Palaemon squilla, Pycnogonum littorale, Halichondria panicea, Taelia felina.

Year 7

Ecospace = 3130.cc's

Carcinus maenus, Liparis liparis and Patina pellucida.

In years 5 and 6, seven species make a sporadic appearance for a short time but do not become permanent elements within the community.

Thus the overall pattern of development at Stn. 6 (St. Abbs) is one of gradually increasing numbers of species and individuals which develop into an increasingly diverse community. The feeding patterns of the developing community change as the habitat enlarges (Fig. 16). In Year 1, suspension feeders are one hundred per cent dominant. In succeeding years, the dominance of the suspension feeders declines as other feeding groups develop. By Year 5, the suspension feeding element falls to forty per cent, deposit feeders make up two per cent, herbivores 4.2 per cent, carnivores 13.7 per cent and Omnivores forty per cent of the community. All five major trophic groups as distinguished by trophic component analysis are now present. By year 7, suspension feeders have fallen to twenty three per cent, deposit feeders have disappeared, herbivorous forms remain at 1.5 per cent, carnivores increase to 19.1 per cent while fifty four per cent Omnivores dominate the community now.

Thus the developing ecospace habitat is subject to at least two biotic factors which influence the developing community. These are:

(1) The growth patterns of the Laminaria hyperborea plant which makes the habitat.

(2) Invertebrate community development is regulated by the presence of other invertebrate species in the habitat. The result is a distinct sequence of ecospace colonisation by a series of species. This process bears some resemblance to succession. (Tansley, 1953), (Odum, 1962). With little or no knowledge of the life histories of most of the invertebrates involved in this study, ecological evaluation of the sequence

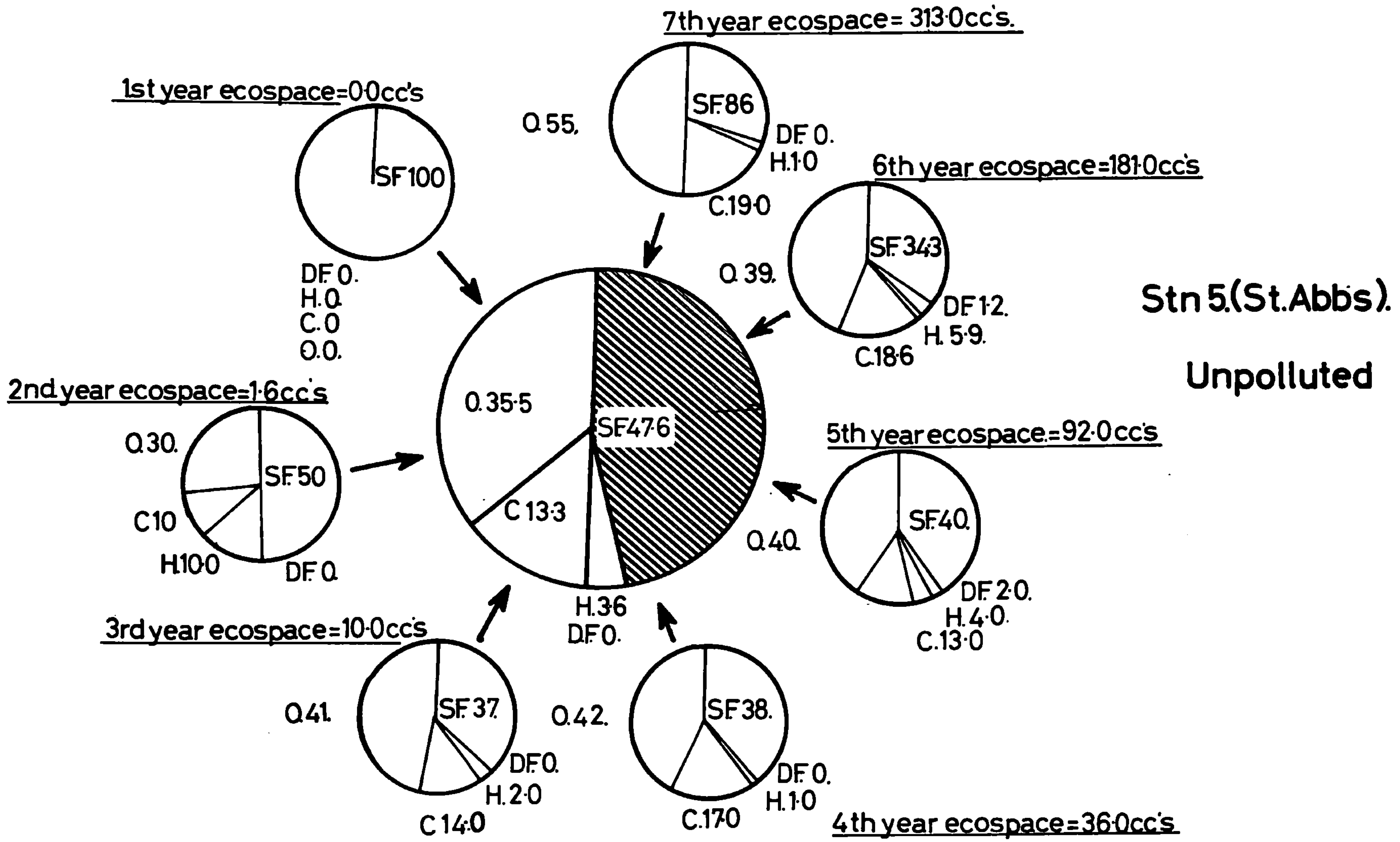


Fig.16
Trophic Component Analysis of seven year ecoperiod.

TABLE 11

Trophic Component Analysis on the annual ecoperiod at Stn. 6 (St.Abbs)
(10 sets of 7 year ecoperiod)

Ecoperiod years	Suspension Feeders	Deposit Feeders	Herbivores	Carnivores	Omnivores
1	100	0	0	0	0
2	50 ± 1.6	0	10 ± 0.0	10 ± 0	30 ± 27
3	37.3 ± 5.6	0	2.4 ± 1.2	14.5 ± 3.8	41.8 ± 8.1
4	38.5 ± 7.0	0	1.3 ± 0.9	17.4 ± 3.5	42.4 ± 4.3
5	40.7 ± 4.3	2.0 ± 1.6	4.2 ± 1.2	13.7 ± 2.2	40.4 ± 4.3
6	34.3 ± 5.5	1.2 ± 0.6	5.9 ± 4.3	18.6 ± 4.1	39.5 ± 4.4
7	23.9 ± 4.1	0.45 ± 0.2	1.5 ± 0.6	19.1 ± 2.2	54.7 ± 5.0
means =	46.3 ± 8.0	0.5 ± 0.25	3.6 ± 1.1	13.3 ± 2.1	35.5 ± 5.5

of habitat colonisation by a series of species, must be approached with caution.

It is unlikely that many of the mobile species remain in one holdfast for six or seven years, whilst the sessile forms will not be uniformly distributed by successive spatfall. More research is necessary to determine how and why these species become accepted into the habitat.

Study of the annual ecoperiod can thus be considered as an historical account of community development. Easily sampled at one point in time, the proportion of the different species accumulated in ecospace, depicts the accommodation of communities to environmental conditions prevailing in the vicinity of the habitat. The sume of ecospace for all seven ecoperiods and the sum of the fauna it contains can now be used with some confidence for compar ative studies with other locations.

In this study the data are subject to several kinds of analysis as no single graphic or mathematical technique was found to be adequate to allow detailed ecological interpretation. The methods used are:-

(i) Species Presence

As an indication of overall species content.

(ii) The Relative Abundance of Species

The presence of a species is expressed as a percentage of all the individuals in a sample.

Thus,

$$\% \text{ species 'x'} = \frac{\text{Number of individuals of Species 'x'}}{\text{Sum of individuals in all species}} \times 100$$

(3) The Species Diversity of the Community

A measurable property of any collection of organisms containing more than one species.

The simplest index of diversity is the total number of species. This index does not take into account the differing abundance of species. Because of this, more sophisticated measures have been proposed which weight the contributions of species according to their relative abundance (Gleason, 1922, 1925), (Fisher, Corbett and Williams, 1948), Developments in Information Theory (Shannon-Werner, 1948), (Baer, 1953), (Barum, 1950), (Goldman, 1953), (Khinchin, 1957) led biologists to adopt another series of formulae based on Information Theory (Shannon-Werner, 1948), (Margalef, 1957), (MacArthur and MacArthur, 1961), (Williams, 1964), (Pielon, 1966), (Monte Lloyd and Ghelardi, 1964), (Hulburt, 1964). The Margalef Diversity Index is used in this study.

Thus, $$I = - \Sigma \, pi . \ln . pi.$$

Where "I" is the diversity index, pi is the number of organisms in a species, i, divided by the total number of organisms in the sample, and $\ln pi$ is the natural logarithm of that function.

The 'equitability' of species (Monte Lloyd and Ghelardi, 1964) is not calculated in this study. The relative abundance of species, is found to be a faster and more convenient calculation which provides as much information on species dominance as the more comples calculations necessary for 'equitability'. Interpretation of the diversity index is as follows:

Low numbers of many species produce a high diversity index. Large numbers of a few species produce a low diversity index. High indices represent diverse stable communities allowing maximal utilisation of all energy input from any source (Odum, 1967). A low diversity index indicates an immature system or one still undergoing succession (Ignatiades, 1969), (Dunbar, 1960).

(4) Trophic Component Analysis
(see Section I Part 4)

By treating the community as one 'superorganism' (c.f. Bodenheimer, 1938) the relative importance of available food substrate, the composition and the trophic accommodation of the community to the physical environment can be demonstrated.

(5) Size Frequency Analysis

Assuming no major differences in growth rates within the region, the size and frequency of individuals of a species within the community ~~will~~ MAY indicate -

(i) The frequency of spatfall recruitments to the community.

(ii) The 'success' of spatfall recruitment, measured as the number of individuals present in any size class (Different size classes = different ages = different spatfalls).

(iii) Predation. The frequency of the largest, therefore, oldest species in a community will indicate how heavily the species is ~~predated.~~ PREYED UPON.

PART III

Spatial Studies

1. Geographical Variation; the establishment of regional reference stations.

The North East coastline known to be unpolluted extends from Dunbar in Midlothian to Craster in Northumberland and all environmental reference areas for pollution monitoring are located here, Stn. 6 (St. Abbs) being the main one studied. The holfast fauna at Stn. 19 (Loch Ewe) and Stn. 20 (Bantry Bay) is compared with Stn. 6 which is located in their unpolluted area, in order to establish the biological equivalence of the North East monitoring stations with other widely separated and unpolluted areas outside the region.

A total of 54 species was obtained at the three stations, (Table 12) of these 30 per cent are common to all three, ten per cent were only found at Stn. 20 (Bantry Bay). These are the species Amphitrite gracilis, Diodora apertura, and the characteristically southern species, Paracentrotus lividus, Anemonia sulcata, and Pilumnus hirtellus. Sixty per cent of the species are common at any one station and 34 per cent at any two stations. The species Mytilus edulis, Membranopora membranacea, Acanthochitona crinitus, Patina pellucida, Lacuna vincta, Pycnogonum littorale, Corophium bonellii, Cancer pagurus, Hyas araneas, and Ophiopholis aculeata were observed at all stations but did not always occur in the samples from each area. This is especially true of Stations 20 and 21 where limited time prevented intensive sampling.

All three communities are dominated by omnivores and suspension feeders (Fig.17). Deposit feeders play no real role in the community. Herbivorous forms are characteristically small species which can therefore be regarded as playing an insignificant role in the kelp

TABLE 12

Species composition and abundance at Stns. 6, 19 and 20. Collected in one seven year ecoperiod at a depth of 5 metres below M.L.W.M.

	Stn. 20 (Bantry Bay)	Stn. 19 (Loch Ewe)	Stn. 6 (St. Abbs)
Anomia Ephippium	172	3	11
Anemonia sulcata	1	0	0
Actinea equina	1	0	0
Balanus balanus	7	37	14
Balanus crenatus	2	0	0
Cucumaria saxicola	1	0	0
Botryllus schlosseri	1	2	0
Hiatella arctica	0	4	0
Hymeniacidon perleve	1	0	0
Halichondria panacea	1	1	0
Mya truncata	32	6	18
Modiolus barbatus	2	1	0
Mytilus edulis	1	0	0
Mucronella coccinea	1	3	6
Membranipora membranacea	0	0	1
Nomia patelliformis	88	4	13
Pomatoceros triqueter	35	40	13
Porcellana longicornis	3	31	16
Sagartia elegans	0	2	0
Taelia felina	11	4	0
Umbonula verrucosa	2	3	6
Amphitrite gracilis	1	0	0
Acanthochitona crinitus	2	0	2
Diodora apertura	2	0	0
Patina pellucida	1	0	2
Lacuna vincta	0	0	2
Trochus striatus	0	2	0
Tectura testudinalis	0	0	1
Trivia arctica			2
Asterias rubens	14	7	17
Lineus longissimus	4	0	1
Nymphon gracile	0	1	2
Palaemon squilla	0	2	2
Pycnogonum littorale	0	2	1
Phyllodoce sp.	0	2	1
Nereis pelagica	10	18	17
Amphithoe rubricata	0	1	10
Caprella linearis	0	0	8
Corophium bonellii	0	0	20
Cancer pagurus	0	3	0
Echinus esculentus	0	4	3
Harmothoe impar	0	4	1
Henrica sanguinolenta	2	0	1
Hyas araneas	0	0	4
Idotea baltica	0	1	0
Jassa falcata	0	2	25
Lepidonotus squamatus	16	8	4
Liparis liparis	0	0	1
Ophiothrix fragilis	20	3	52
Ophiopholis aculeata	0	3	18
Pilumnus hirtellus	3	0	0
Paracentrotus lividus	4	0	0

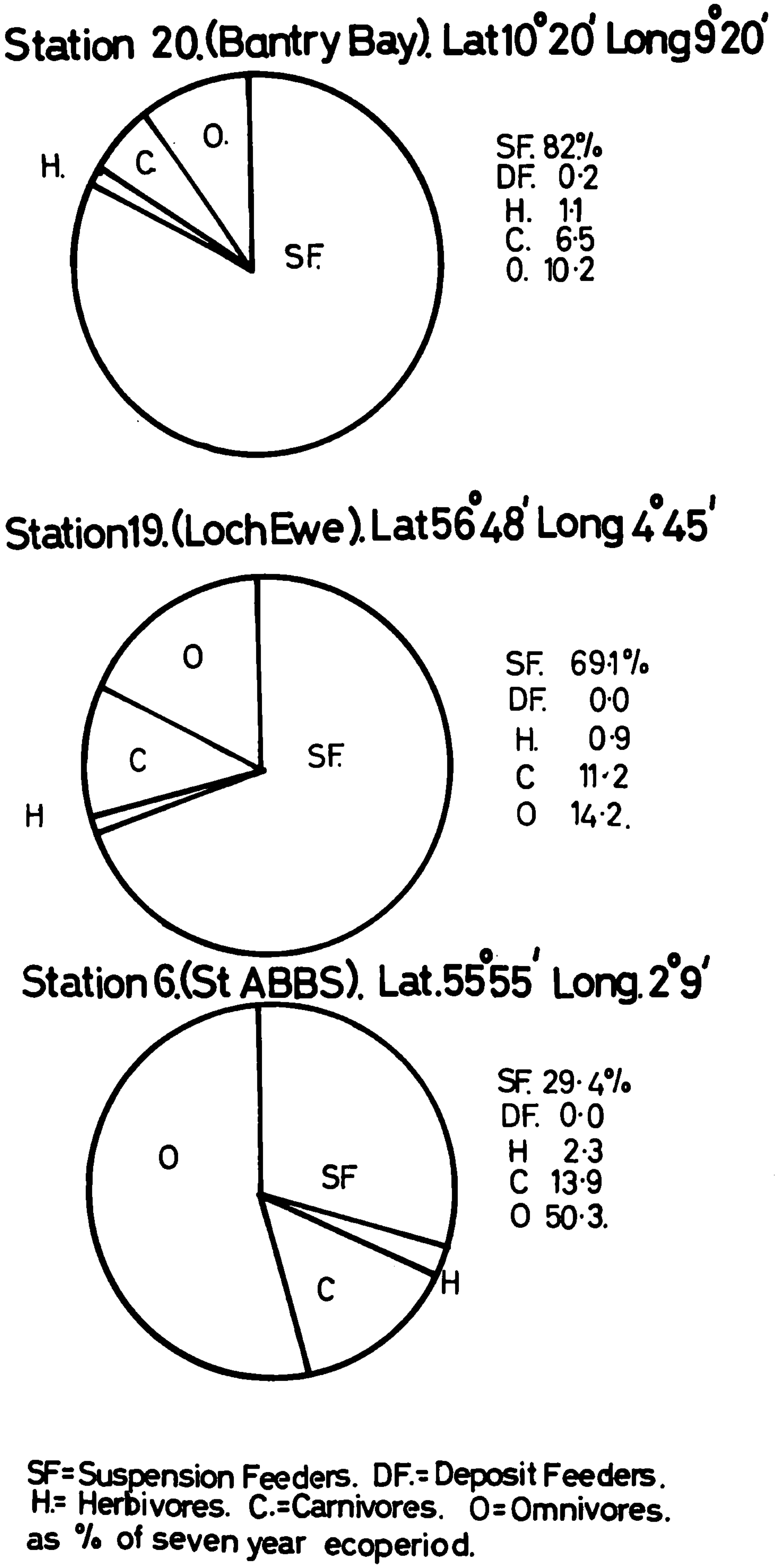


Fig.17

Geographical variation in trophic structure, one 7 year ecoperiod at each station.

forest (carnivores account for ten per cent of the population).

The species diversity at the three stations is high, 3.1 at Bantry Bay and 3.8 at Loch Ewe and St. Abbs. This compares favourably with indices of 3.0 to 4.0 for phytoplankton at climax (Ignatiades, 1969) and 2.4 to 3.2 in the clean water soft bottom ecosystems of San Francisco Bay (Pearson et al 1964). High diversity indices at Stns. 6, 19 and 20 indicate stable climax communities (Margalef, 1957).

Acknowledging that some variation in species composition and abundance is inevitable due to geographical differences in the widely separated areas. The similarity in the structured community systems illustrates the degree of equivalence in the response of the fauna to ecospace in unpolluted kelp forest ecosystems of different regions.

2. Variation with Depth

Only at two stations, Stn. 6 (St. Abbs) and Stn. 21 (Loch Ewe) did the kelp forest extend deep enough to warrant considering the effects of depth on community structure.

Omnivores and suspension feeders dominate the communities at all the depths studied (Fig.18). Species diversity is high at all depths to 15 metres, the limit of the kelp at Stn. 6. Over the 23.0 metre depth range at Stn. 21 there appears a slight but progressive drop in species diversity which however still retains a high value (3.0) at the deepest station studied.

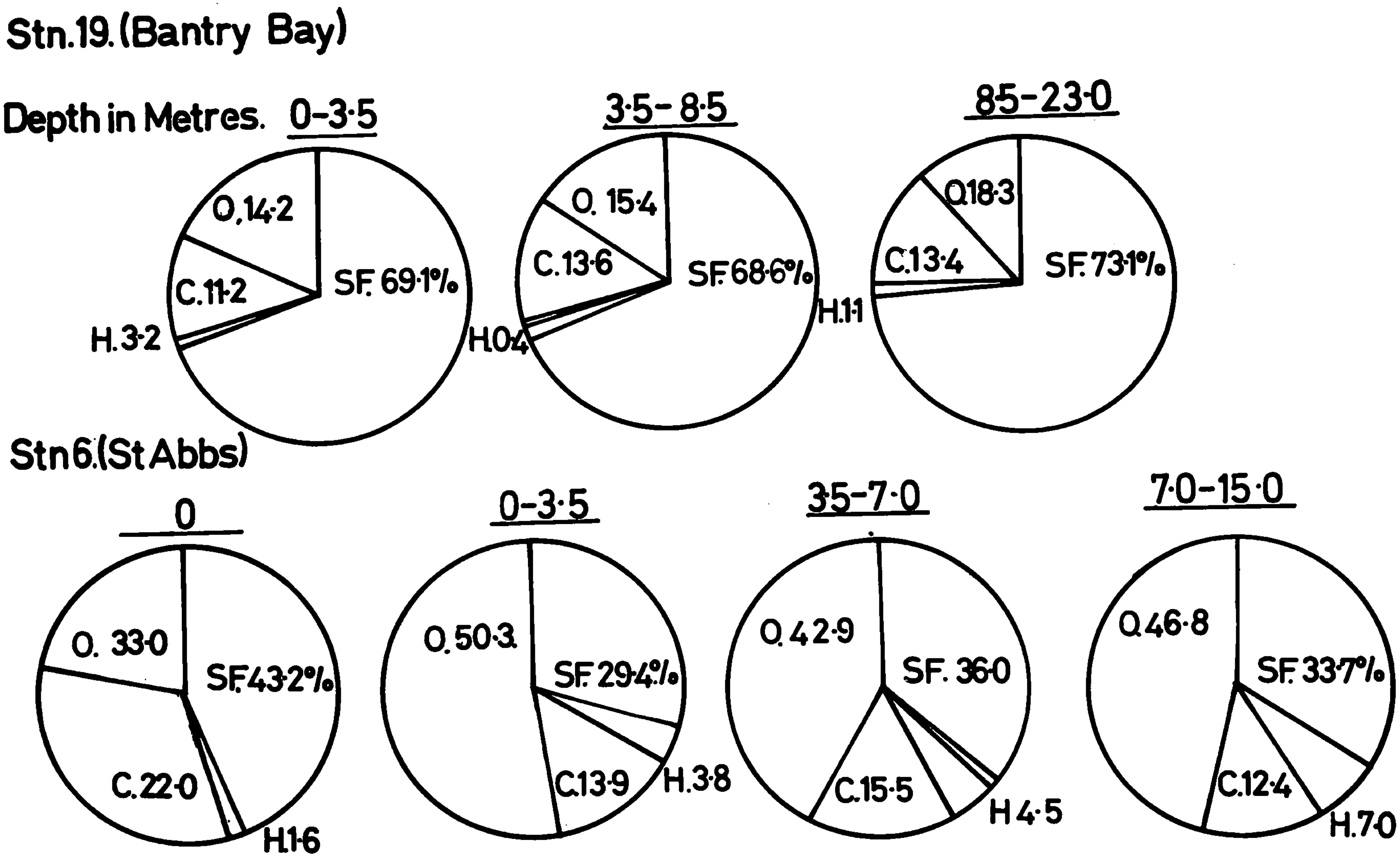


Fig.18
Variation in community structure with increasing depth of water, by Trophic Component Analysis

TABLE 13

Variation in Species Diversity with Depth of Water

Depth (Matres)	0	3.5	6.7	8.3	15.0	23.0
Stn.6 (St.Abbs)	4.1	3.8	4.0	-	3.9	-
Stn.21 (Loch Ewe)	-	3.8	-	3.6	-	3.0

Stn.6 contains larger numbers of omnivores than Stn.21 (Fig.14) They are distributed more or less evenly throughout the shallow depth range of the kelp forest found there. Stn. 21 contains more suspension feeders than Stn. 6 which are distributed evenly across the depth range of the kelp forest found there. The carnivore Nereis pelagica consistently accounts for about 10 per cent of the whole community and is distributed evenly in holdfasts at all depths in the forest. Asterias rubens appears as a consistent predator at all depths studied at Stn. 6. It was commonly observed at Stn. 21 but never found in any samples of holdfasts collected there. (Table 14)

There appears to be little difference in community structure with increasing depth, but more study on deeper kelp forests is necessary before final conclusions on the effect of depth on holdfast community structure can be made.

(3) Regional Studies on pollution gradients

Studies on regional variation were conducted along the shores of North Yorkshire, County Durham, Northumberland, Berwickshire and the Lothian Counties bordering the south bank of the Firth of Forth.

TABLE 14

Species occurring as more than 5% relative abundance with increasing depth

STATION	19 LOCH EWE			6 ST. ABBS			
DEPTH (Metres)	0-3.5	3.5-8.3	8.3-16.7	0	3.5-5.0	5.6	15.0
Species							
Balanus balanus	18.1	7.7	-	-	-	-	-
Pomatoceros triquiter	19.6	15.0	32.0	-	-	10.0	11.0
Porcellana longicornis	15.9	24.5	-	6.7	-	-	-
Sargartia (elegans?)	11.0	-	-	-	-	-	-
Anomia epiphium	-	-	31.0	-	-	-	-
Nomia patelliformis	-	-	11.0	5.0	-	-	-
Mya trunkata	-	-	-	8.4	5.4	-	-
Asterias rubens	-	-	-	6.7	5.1	5.0	7.4
Nereis pelagica	8.8	9.5	9.8	11.8	5.1	9.5	8.0
Caprella linearis	-	-	-	9.3	-	-	-
Lepidontus squamatus	-	-	-	5.0	-	-	9.7
Corophium bonellii	-	-	-	-	6.0	7.0	-
Jassa falcata	-	-	-	-	7.0	11.0	-
Ophiothrix fragilis	-	-	-	-	15.6	9.1	21.0
Ophiopholis aculeata	-	-	-	-	5.4	5.0	-

In this region, two pollution gradients are known to exist (see Section I). Between the two gradients there is a short stretch of coast which has a water quality much like that of the open ocean, and here the holdfast communities at Stn. 6 have been shown to be similar to other widely separated but clean areas of sea water. Stations 6 to 13 are all located in this clean water zone along the North East coast. Comparisons between these stations and other deliberately selected in the polluted waters, Nos. 1 to 5 and 13 to 16 allow the evaluation of some effects of pollutants on holdfast communities.

(i) Species Presence and Absence

Compared with the time scale of evolution, pollution is a recentphenomenon. With the possible exception of some bacteria it is therefore unlikely that any species has yet evolved which is dependent on pollution for its very existence. Absence of species from polluted habitats where they might otherwise have been expected, is likely to give an indication of the effects of pollution although even then, the biology of the species and of the community in which it lives must be taken into account (Hynes, 1960), (McKee, 1967), (Oglesby, 1967), (Wasse, 1967), (Copeland, 1967).

Table 15 presents the occurrence of one hundred and five species of macroinvertebrates, representing eight phyla, at eighteen sampling stations along the North East coast.

There is a distinct variation in the distribution of the fauna reflected in their differential pres ence and absence, from the Northern most site (1) (The Forth Bridge) to the Southern most (17) (Flambrough Head). This distribution has been split into units which correlates with the overall physical parameters of the waters along this length of coast.

Group 1

Estuarine Tolerant : Pollution Indifferent : Only eleven

T.15

TABLE 15

Species Presence abd Absence

ESTUARINE POLLUTED (1–3) · UNPOLLUTED (4–9/10) · POLLUTED (11–16) · TURBID (17–18)

SPECIES	STATION	1 FORTH BRIDGE	2 INCH MICKERY	3 INCH KEITH	4 MAY ISLE	5 DUNBAR	6 ST. ABBS	7 SPITTAL	8 HOLY ISLE	9/10 FARNE ISLES	11 BEADNELL	12 CRASTER	13 NEWBIGGIN	14 MARY ISLE	15 SOUTER POINT	16 SEAHAM	17 ROBIN HOOD'S BAY	18 FLAMBOROUGH HEAD
Porcellana longicornis		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Harmaøthoe impar		+	+	+				+	+	+	+	+	+	+	+	+	+	+
Eupagurus bernhardus		+					+	+	+	+	+	+	+	+			+	+
Asterias rubens		+	+			+	+	+	+	+	+	+	+	+	+	+	+	+
Mytilus edulis		+	+			+	+	+	+	+	+	+	+	+	+	+	+	+
Anomia ephippium			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mya truncata	1		+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Balanus balanus				+			+		+				+			+		+
Terebella sp.				+					+			+	+	+			+	
Nereis diversicolor				+				+			+	+	+			+		+
Ophiothrix fragilis			+	+	+	+	+	+	+	+	+	+	+	+	+*	+*	+	+
Metridium senile		+																
Corella parallelogramma		+		+														
Chlamys (tigerina)?			+															
Ophlithospongia serriata				+	+	+	+											
Hiatella arctica	11			+		+	+											
Pecten sp.				+*														
Dashyone bombyx				+*														
Ophicomina nigra			+	+														
Sagartia elegans					+	+	+	+	+	+	+	+					+	+
Nomia patelliformis					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mucronella coccinea					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Umbonula verrucosa					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Botryllus schlosseri					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Botryllus leachi					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pomatoceros triquiter					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Membranipora membranacea					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cancer pagurus					+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sydnium turbinatum					+	+	+	+	+	+	+	+	+	+*	+	+		+
Patina pellucida					+		+	+	+	+	+	+	+	+	+	+	+	+
Taelia felina						+	+		+	+	+		+	+	+		+	+
Modiolus barbatus						+	+	+	+	+	+	+	+	+	+	+	+	+
Sabellaria spinulosa						+	+	+	+	+	+	+	+	+	+	+	+	+
Neirymyra punctata						+		+	+	+	+	+					+	
Molgula sp.						+	+				+	+		+				+
Acanthochtiona crinitus						+	+	+	+	+	+	+	+	+	+	+	+	+
Tonicella rubra						+	+		+	+		+		+	+			+
Flabelligera affinis	111					+	+	+	+	+	+	+	+	+	+	+	+	+
Amphithoe rubricata						+	+	+	+	+	+	+	+	+	+	+	+	+
Nereis pelagica						+	+	+	+	+	+	+	+	+	+	+	+	+
Lineus longissimus						+		+	+	+		+		+		+	+	+
Lepidonotus squamata						+	+	+	+	+	+	+	+	+	+	+	+	+
Phyllodocidae						+	+	+	+	+	+		+		+			+
Gibbula cineraria						+	+	+	+	+	+	+		+		+		+
Hyas araneas						+	+	+	+	+	+		+	+		+		
Lacuna vincta						+	+	+	+	+	+	+	+	+*	+*	+	+	+
Salmacina dysteri						+	+	+	+	+	+	+	+	+				+
Echinus esculentus						+	+	+	+	+	+	+		+*	+*	+*	+	+
Trivia arctica						+	+	+	+	+	+	+						+
Alcyonium digitatum						+	+	+	+	+	+	+						+
Caprella linearis						+	+	+	+	+								+
Andouinia tentaculata						+	+	+	+	+	+	+	+*		+*	+*	+	+
Ophiopholis aculeata						+	+	+	+	+	+	+	+*		+*	+*	+	+
Nassarius reticulatus							+		+	+	+				+			+
Lineus rubra							+				+	+	+	+	+			
Venerupis pullastra							+					+	+	+	+		+	
Balanus crenatus							+			+		+*	+					+
Hydroides norvegica							+	+	+	+	+	+						
Cantharidus striatus							+	+	+	+	+							
Gammarellus homari								+	+		+		+	+				
Tubularia larynx										+	+	+	+	+	+			
Carcinus maenas							+	+	+	+	+	+	+	+	+	+	+	+
Jassa falcata							+	+	+		+	+		+	+		+	+
Buccinium undatum							+		+			+			+		+	+
Aoridae							+		+			+			+		+	+
Corophium bonelli							+	+	+	+	+	+	+	+	+	+	+	+
Liparis liparis							+		+	+	+	+	+					+
Pycnogonium littorale							+	+	+	+	+	+	+	+	+	+	+	+
Actinea equina							+			+			+			+		+
Idotea baltica							+	+		+	+		+		+	+		+
Lanice conchilega							+				+			+				
Arenicola (clymoides) marina							+		+		+		+	+	+	+		
Halichondria panacea							+	+	+	+	+	+	+	+*	+*	+*	+	+
Henrica sanguinolenta							+	+	+	+	+	+	+	+*	+*	+*	+	+
Amphiopholis squamata							+	+	+	+	+	+		+*	+*		+	
Palaemon squilla							+	+		+	+	+			+*			+
Nymphon gracile							+	+	+	+	+	+			+*			+
Tectura (acmea) testudinalis						+*	+		+					+*	+*			
Velutiana laevegata						+*	+*		+*									
Dendrodota grossularia						+*	+*		+*									
Lamellaria sp.							+*											
Hymeniacidon (perleve) sanguinea							+								+*			
Primela denticulata							+		+					+*				
Tubulanus annulatus							+*		+*									
Doris tuberculata							+								+*			
Rissoa sp.							+*											
Aeolidia papillosa	1V.						+*											
Archidoris pseudoargus							+*											
Aplysia punctata							+*											
Acteon tornatilis							+*											
Bulla sp.							+*											
Eulalia viridis							+											
Amphitrite gracilis							+											
Panoplea minuta							+*											
Cucumaria saxicola							+*								+*			
Rostanga rufescens							+*											
Caprella acanthifera							+		+									
Galathea squamifera							+	+			+							
Berthella plumula							+*			+*	+*							
Littorina littoralis							+				+	+						
Polycera quadrilineata							+*			+*	+*							
Archidoris brittanica										+*								
Eurynome aspere											+*							
Anthopleura thallia															+*			
Nicolea zostericola														+*				

+ Species present

+* Species present but rare

of the species fall into this category.

Group II

Estuarine. Eight species are characteristic of this area. Seven of them are suspension feeders, the eighth Ophicomina nigra is an omnivore. Estuaries always contain much suspended material and the addition of pollutants to this environment makes further interpretation at this level unwise. Knowledge of the fauna in natural estuarine environments is scant (Newell, 1958) and much more information must be obtained before conclusions on estuarine pollution can be drawn.

Group III

Estuarine Intolerant : Pollution Indifferent. Fifty four of the species under study fall into this category. Representing half the fauna studied they characterise the faunistic associations within the North East kelp forest ecosystem.

Group IV

Estuarine Intolerant : Pollution Intolerant. (Pollution Indicator Organisms).

Twenty four species are recorded almost exclusively for the oceanic waters at Stn. 6. Thirteen of these species are rare and were encountered only after intensive searching and sampling on relatively small areas of sea bed. Sample station 6 (St. Abbs) is taken as the 'NORM' for the North East. The absence, or at best, occasional rare occurrance of some of these species in the southern polluted areas would indicate that these differences may be related to pollution.

Tectura testudinalis, Velutiana lovegata, Rissoa sp and Aplysia punctata are herbivorous forms living on the smaller more delicate ephytic algae which are much rarer in the polluted waters (Whittick, 1969 Unpublished).

Cucumaria saxicola, Dendrodota grossularia and Hymeniacidon perleve filter sea water. Their absence from water heavily polluted with inorganic particles in suspension, indicates that even within the suspension feeding group different species select different food substrates. Lamellibranchs, for instance, are well known for their ability to selectively filter sea water (Jørgensen, 1968).

Thus the presence of a large amount of food material made available, e.g. sewage, cannot be considered as a food source without accounting for the effect of inorganic material in suspension with it. This combination of pollutants produces a situation where suspension feeders will survive only if tolerant to an admixture of inorganic silt in the rich food supply. Ingestive mechanisms must account for this factor or the animal will startve and die. The absence of these suspension feeders from polluted water where twenty one other suspension feeders are frequently found would indicate that these species, Cucumaria, Dendrodota and Hymeniacidon are susceptible to high levels of silt and inorganic material in suspension. Cucumaria saxicola is found well north of its normal geographical distribution (Eales, 1961). Ecophysiological experiments on suspension feeding could well provide more subtle interpretations of the impact of the organism on the environment and vice versa.

Of the nine carnivores, Lamellaria sp., Doris tuberculata, Aeolidia papillosa, Archidoris pseudoargus, Rostanga rufescens, Berthella plumula and Polycera quadrilineata browse on the encrusting suspension feeders. Tubulanus annulatus, Acteon tornatilis and Eulalia viridis being more active predators.

Their absence from polluted water indicates a breakdown of the predominantly suspension feeder to carnivore food chain. However, the presence of five pollution indifferent, encrusting suspension feeders in the polluted water, Mucronella coccinea, Umbonula verrucosa, Botryllus schlosseri, Membranipora membranacea and Botryllus leachi, suggests that the carnivore is susceptible to some other factor in polluted water which it cannot tolerate. In this instance, it appears that pollution has destroyed the predator rather than the prey, resulting in a reversal of the normal situation where abundance of the prey determines abundance of the predator (Lack, 1954), (Andrewartha and Birch, 1954) (Wynne-Edwards, 1966).

The feeding biology of the five omnivores, Primela denticulata, Bulla sp., Panoplea minuta and Galathea squamifera, is not well known. Having the ability to select almost any available energy source they should be tolerant of the effects of pollutants on their food supply, but the physiological effects of toxicoids on these animals is unknown and more research on the tolerance of all species must be acquired before even tentative reasons for the disjunct distribution of any species in polluted water can be advanced.

Species which occurred in less than five per cent of the samples were considered rare. Table 16 presents the distribution of rare species on the North East coast. The collection of rare species invariably requires a large sampling effort and the uncertainty that a comprehensive list, including all rarities, has been obtained

TABLE 16

Occurrance of Rare Species

SPECIES	STATION	INCH KEITH 3	DUNBAR 5	ST. ABBS 6	HOLY ISLE 8	FARNE ISLES 9&10	BEADNELL 11	CRASTER 12	NEWBIGGIN 13	ST. MARY'S 14	SOUTER POINT 15	ROBIN HOOD's BAY 17	FLAMBROUGH HEAD 18
Pecten sp.		+											
Dasyone bombyx		+										+	
Ophiocomina nigra		+											
Velutina laevegata			+	+	+								
Tectura testudinalis			+	+									
Dendrodoa grossularia			+	+		+							
Tectura testudinalis			+	+								+	
Tubulanus annulatus			+		+								
Lamellaria sp.				+								+	
Cucumaria saxicola				+								+	
Rissoa sp.				+									
Rostanga rufescens				+									
Aeolidia papillosa				+									
Aplysia punctata				+									
Bulla sp.				+									
Acteon tornatilis				+									
Panoplea minuta				+									
Eurynome aspera				+									
Berthella plumula				+		+	+						
Polycera quadrilineata				+		+	+						
Musculus sp.					+	+							
Archidoris pseudoargus						+							
Ophiothrix fragilis									+	+	+		
Ophiopholis aculeata									+	+			
Amphiopholis squamata									+	+			
Halichondria panicea									+	+	+		
Echinus esculentus									+	+	+		
Henricia sanguinolenta									+	+	+		
Nicolea zostericola									+				
Molgula sp.										+			
Sydnium turbinatum										+			
Nymphon gracile											+		
Anthopleura thallia											+		
Patina pellucida											+		
Palaemon squilla											+		
Hymeniacidon perleve											+		
Archidoris brittanica											+		
Lacuna vincta											+		
Primela denticulata											+		

is always present. However, three distinct groups can be recognised.

A and B
The Estuarine Element

Two suspension feeders and one omnivore are restricted to the Forth Estuary. One of these, *Dashyone bombyx* only occurs elsewhere on the North East coast at Robin Hood's Bay. *Ophicomina nigra* was only found at Stations 3 and 4 in the Firth of Forth.

Of the four rarities present at Robin Hood's Bay, *Dashyone bombyx* and *Cucumaria saxicola* are suspension feeders, suggesting an environment in which suspended material plays an important role. *Tectura testudinalis* and *Lamellaria* sp. are both small browsing forms, freeding on primary producers and suspension feeders respectively.

C
Estuarine Intolerant : Pollution Intolerant (Rare in clean water)

Eighteen species fall into this category which corresponds closely with the pollution indicator organisms mentioned, in figure With the exception of *Cucumaria saxicola*, all these species, regardless of their feeding habits, are small, fragile, browsing forms. Rare even in clean waters, their almost total absence suggests that they are the first casualties amongst the fauna of polluted kelp forests even though their food supply may still persist in some abundance.

D
Rare in Polluted Water

A further nineteen species of rarities are listed for the polluted areas. Except for *Anthopleura thallia* and *Nicolea zostericola*, all these species are abundant and common in the clean waters off Berwickshire. The North/South aspect of the coastline along the gradient and the concentration of pollution in the middle reaches of the study area make the sampling of a site matrix from North to South both desirable and feasible. The justification for this large scale comparative approach is illustrated here for the first time. Abundant species in clean water become rare in dirty water, the first faunistic evidence for a gradient of water quality reflected by corresponding zoological variation. The none appearance of a number of the rare species at Robin Hood's Bay suggests that the waters there are quite different from those of Berwickshire and that pollution is not the only cause of variation in species distribution. The heavy silting and inorganic suspension of boulder clay inshore, must play some ecological role in the waters of North East Yorkshire which is reflected in the biota living there.

The following generalisations can be made from this consideration of the distribution of these species and their feeding habits.

(i) There is a dis tinct estuarine element in the fauna which is confined to the Firth of Forth but Robin Hood's Bay and Flambrough Head with their high levels of silt may have some estuarine qualities.

(ii) Some of the species under study are sensitive to estuarine conditions but tolerant of chronic pollution.

(iii) Over half the species studied are insensitive to pollution, normal, or estuarine conditions.

(iv) Pollution indicator organisms have been distinguished many of which are rare, even under normal circumstances.

(v) Coupled with distribution patterns, trophic component analysis reveals that:

(a) When some primary producers are absent corresponding herbivores are lost.

(b) In polluted waters browsing carnivores are sensitive to some factor other than an absence of prey.

(c) Different suspension feeding species must preferentially select for different food materials from the surrounding water, and the pres ence of a large quantity of potential food substrate need not necessarily provide an ideal food source if other factors are present. The interaction of different pollutants must be considered and wherever possible their different effects isolated.

(d) A biological gradient is apparent which corresponds; to physical and chemical parameters of water composition along the North East coast. Briefly summarised, pollution creates at least three dislocations of the normal marine food web; by removal of parts of the primary producer thus herbivore food chain, suppression of some carnivores and selection on certain suspension feeders.

As a technique for pollution monitoring, recording species presence and absence has its limitations. Providing no more than indications of faunistic variation in areas of sea known to be chemically and physically distinct, no direct correlation can be drawn between biological and environmental variation. The results will depend on the selection of species for study which are representative of the whole environmental spectrum. The omission of apparently insignificant species can easily bias interpretation of results. A large sampling effort is required and the minimum area from which the selected species should be drawn is never known with certainty. The relative abundance of species, seasonal variation and community dynamics are not considered.

At best, the presence and absence of species provides an overall indication of distribution and separates community elements which warrant further study.

(ii) Trophic Component Analysis

Deposit feeders and herbivorous forms remain at low levels throughout the North East region (Figure 19), regardless of the water quality. Carnivores can reach 45 per cent of the community in polluted water (Stn. 13). Omnivores are present in all communities.

There is a natural variation in clean water environments with suspension feeders ranging from 28.4 to 8 per cent of the community, omnivores from 8 to 50 per cent and carnivores from 25 to 6 per cent of the community. The fluctuation in community elements is reduced in polluted water by general specialisation of the community into a suspension feeding unit, e.g. 100 per cent suspension feeders at Stn. 4, 99.9 per cent at Stn. 16.

Small herbivorous forms are lost and there is a general reduction in the number of omnivores present in polluted water. The herbivorous forms seem the most sensitive to pollutants, of the five major community divisions. They range from only 0.8 to 8 per cent in clean water and are absent from the Firth of Forth and the extreme pollution at Stn. 15 and 16 in County Durham.

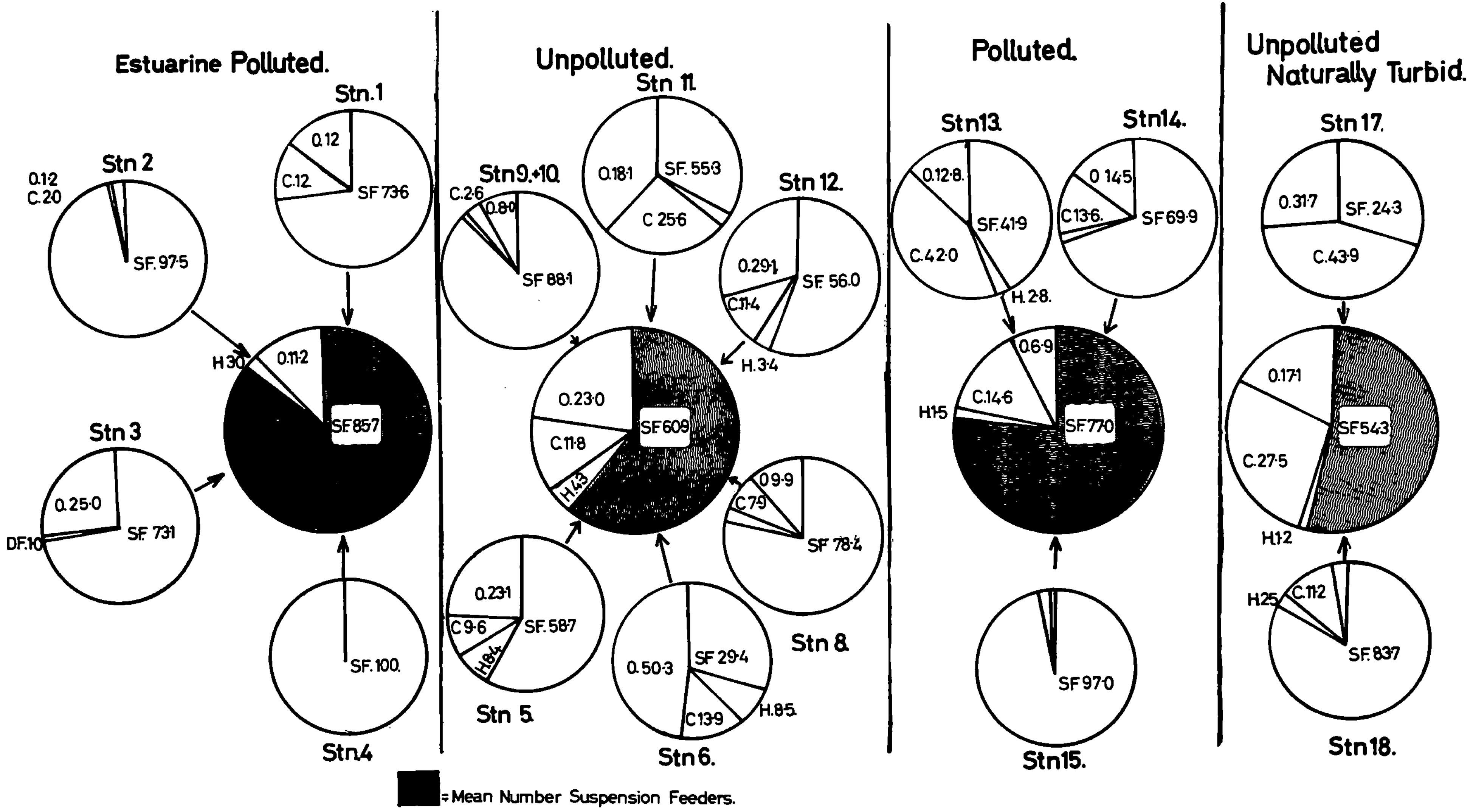


Fig.19

Trophic Component Analysis on Stations through the pollution gradients (Sum of 7 year ecoperiod at each stn.)

In naturally turbid waters at Stn. 18 (Flambrough Head) they make a recovery (up to 2.5 per cent) but their absence at the nearby station 17 (Robin Hood's Bay) suggests again that natural turbidity must have an effect on the community structure.

Omnivores fluctuate from 50 to 0 per cent roughly correlating with the water quality. Pollution tends to reduce their numbers. By definition, this group are all mobile organisms and interpretation of their fluctuating numbers is difficult without more knowledge of their response to available food substrates, their preference for different sorts of food, the effects of pollutants on their food supply and their movements over the sea bed in natural, unpolluted waters.

The carnivores in this study are all highly mobile. One presumes that their distribution and abundance is governed by their prey, but little is known of the prey of most of the species in this study. However, where suspension feeders (which are all sessile and likely to be prey) are found in great abundance, i.e. in polluted waters of Stn. 4, 100 per cent suspension feeders, carnivores are absent.

Considering all the study areas, as the abundance of the suspension feeders goes down, the abundance of the carnivores goes up, i.e. 69.9 per cent suspension feeders to 13.6 per cent carnivores at Stn. 14. Carnivores can be found in excess of suspension feeders at Stn. 17 (Robin Hood's Bay). After an initial lag phase following on a big suspension feeder recruitment to polluted water communities, the indications are that the carnivores 'eat out' this new food supply and themselves increase in numbers.

The absence of a predator in a 100 per cent community of suspension feeders suggests that the large carnivore population must quickly move on, or die, when all the prey species have been eaten. The next suspension feeder spatfall on the remnants of the last community are now almost totally devoid of any trophic elements at all, could well allow the 100 per cent recruitment of a single suspension feeder species in extreme cases. The predator prey relationship alluded to here, follows much the same patterns as other studies on the dynamics of ephemeral plankton communities in the Bristol Channel and North Sea (Raymont, 1963), (Cushing, 1966).

Spatial comparison of the holdfast communities indicates that all the clean water stations are more or less equivalent. Polluted water communities, by the same criterion, are not in an ecologically equivalent state when compared with those in clean waters, nor when compared between themselves. There appears a dynamic relationship between suspension feeders and carnivores, in polluted waters. Herbivores and omnivores are reduced by polluted water. Deposit feeders never play a role of any significance, in any of the holdfast communities studied.

(iii) Species Diversity

The species diversity varies from a value of 1.6 to 4.3 in the North East Region, through the two pollution gradients (Figure 20).

The mean index for the polluted estuary is 2.2 increasing to 3.4 in the clean waters of Berwickshire. It is again reduced in the polluted waters of County Durham to a mean value of 2.7, recovering and reaching a value of 3.3 in the turbid but unpolluted waters off Yorkshire. The diversity of the community is lowered in

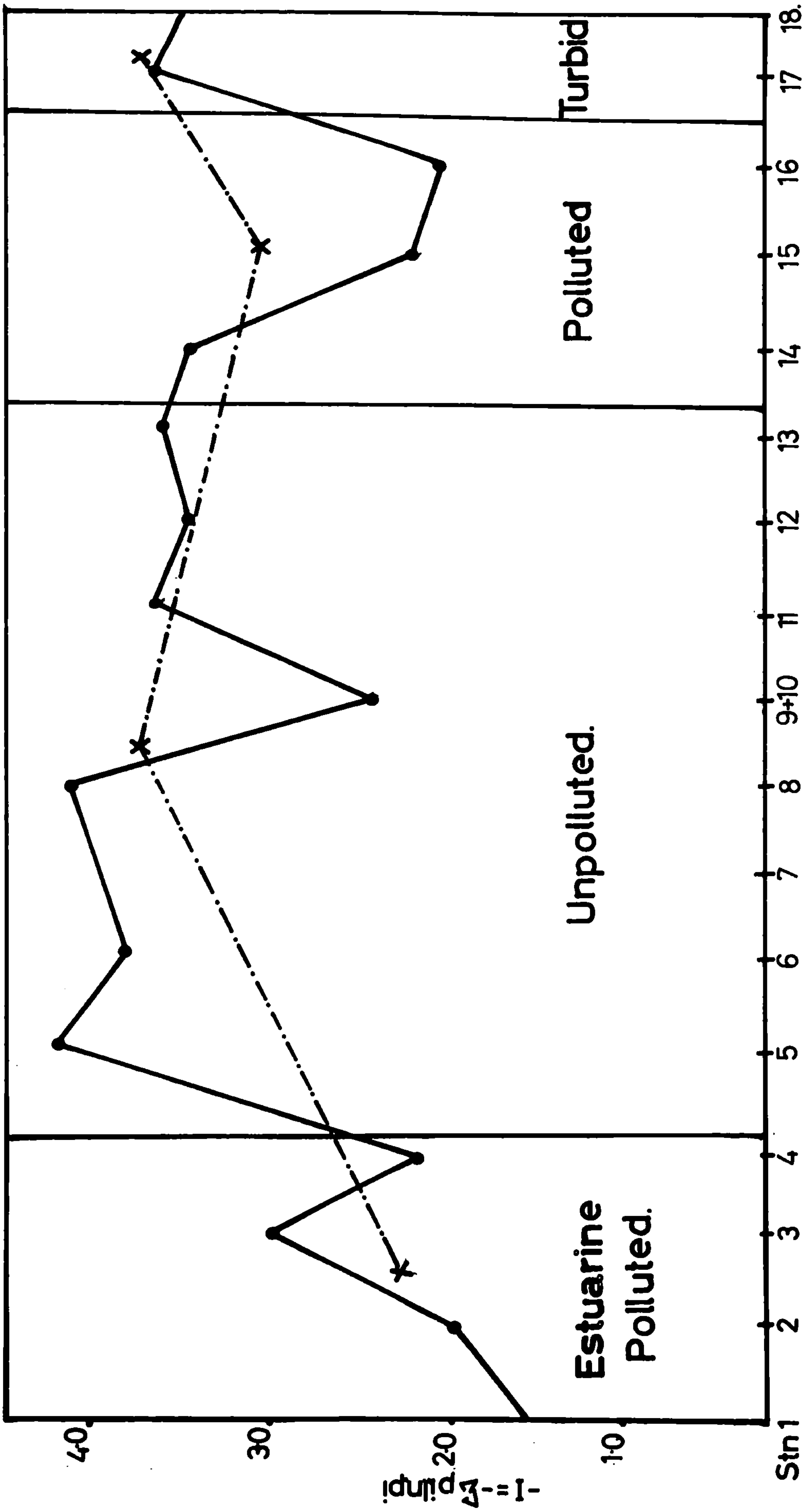


Fig.20.
Species Diversity of ecospace communities through the pollution gradients

the polluted study areas but consistently attains a higher level in the unpolluted study areas. Individual community fluctuations occur in both polluted and unpolluted study areas. There is a natural variation in species diversity in the clean waters of Stns. 5 to 13. The low value of the index at Stn. 10 and 11 (The Farne Isles) can only be attributed to the extreme water movements in this area, often in excess of five knots, even on calm summer days (personal observation). In all the other clean water communities the diversity index rises to a value in excess of 3.0 and the fluctuation between 3.0 and 4.3 must be considered as natural biotic variation.

In the polluted waters of the Firth of Forth the diversity index rises to a value of 3.0 at Stn. 3 located in the middle of the Firth. This value for the index is on a par with that for equivalent clean sea areas. However, water movements in the Firth are known to be erratic and tidal currents are largely restricted to the northern shores of the estuary (personal communication from a Skipper at the Lothian River Authority). Station 3 is not in the path of the pollution 'stream' issuing through the narrow and chronically polluted reaches of the Forth Bridge area and being deflected north eastwards by tidal currents. The index drops sharply to a value of 2.2 at Stn. 4 (Isle of May) in the northern most, seaward end of the Forth. This indicates that perhaps pre-selection of Stn. 3 as a polluted area was a mistake. Tidal movements and the effects of water movements on the transport of pollutants through the Forth should have been considered before the selection of Stn. 3. The indications are that Stn. 4 is located in the pollution stream but Stn. 3 is not.

Stations 13 to 19 are located in polluted water. Proceeding south from Stn. 14 the holdfast community seems able to withstand a degree of pollution, the diversity index remaining high at 3.3 for Stn. 13 and 14. Chronic pollution at Stn. 16 and 17 correlates with a low species diversity index, 2.2 and 2.0. In this study the species diversity index provides the first mathematical measure for a correlation of water chemistry with benthic community structure, a first step in the estimation of the ecological quality of the environment, into which the biota will be recruited.

On a similar pollution study,(Pearson et al 1967) calculated a similar diversity index on the soft bottom faunas in San Francisco Bay, where polluted water communities range from 0.7 ± 0.3 rising to 2.5 ± 1.0 in unpolluted waters, falling again to 0.4 ± 0.3 on encountering yet more pollution at the other end of the bay.

Species diversity indices calculated for the North East indicate that where values range from 0.0 to about 2.5 the environment is adverse, preventing a high level of species diversification in the community. Values of the index above 3.0 and ranging up to as high as 4.3 indicate a diverse community, the 'normal' state in the ecospace habitat.

On the North East coast all the areas subject to chronic pollution have a diversity index below 2.5.

(iv) Relative Abundance

Numbers of species occurring as more than 5 per cent of the community at each station are shown in Table 17.

TABLE 17

Relative Abundance. Species occurring as more than 5% dominant at any Station

	FORTH BRIDGE	INCH MICKERY	INCH KEITH	MAY ISLE	DUNBAR	ST. ABBS	HOLY ISLE	FARNE ISLES	BEADNELL	CRASTER	NEWBIGGIN	MARY ISLE	SOUTER	SEAHAM	ROBIN HOOD'S BAY	FLAMBROUGH HEAD
SPECIES STATION	1	2	3	4	5	6	8	9&10	11	12	13	14	15	16	17	18
Anomia epiphium			17.0	39.2	15.6		10.0	5.8	11.4							27.0
Balanus balanus				5.7					6.4							
Corella parallelogramma			13.0													
Mytilus edulis	6.6	72.6			5.8		31.2	62.4	9.8		32.2	41.4	85.0	97.6		15.0
Mya truncata					5.0	5.4			10.6	10.0	10.2					
Anomia patelliformis			7.0	29.0	24.0		11.2	5.0		14.2					5.4	7.2
Pomatoceros triqueter			13.0	19.8												
Porcellana longicornis																
Sabellaria spinulosa							28.4			29.3	19.3	18.9			5.4	24.0
Venerupis pullastra			5.0													
Asterias rubens	13.2					5.1					12.6					
Nereis pelagica					5.8	5.1	5.6		24.0	9.6	25.2	12.6			23.9	9.0
Amphithoe rubricata									5.6	18.8					7.6	
Harmothoë impar			8.0												5.4	
Ophiothrix fragilis			16.0		9.5	15.6									6.5	
Ophiopholis aculeata						5.4										
Eupagurus bernhardus	9.0					7.5										
Jassa falcata						6.0										
Corophium bonellii																
	ESTURINE POLLUTED			UNPOLLUTED							POLLUTED				TURBID	

Amongst the suspension feeders Mytilus edulis is almost universally common in the communities and is present in very large numbers in chronically polluted waters. The principal carnivores are Asterias rubens and Nereis pelagica.

Anomia ephippium and Nomia patelliformis seem able to withstand some degree of pollution but not the extreme of pollution at Stations 1 and 2, 14, 15 and 16, reappearing at Stn. 18 (Flambrough Head). These two closely related species appear to have almost equivalent ecological prerequisites.

Balanus balanus does not extend into polluted water but its sporadic occurrence at Stations 11 and 18 make interpretation of the distribution of this organisms doubtful. Corella parallelogramma is abundant only in the estuary at Stations 3 which is not located in the main stream of estuarine pollution. Mya truncata is confined to the clean water reaches of the coastline.

Sabellaria spinulosa can be found in quite high numbers in and out of polluted water. This species was never found in the estuary during this study. With the odd exception of Eupagurus bernhardus none of the omnivores venture into polluted water. The dominant species in the clean waters are Amphithoe rubricata, Harmanthoe impar, Ophiothrix fragilis, Ophiopholis aculeata and Jassa falcata.

In the clean water communities a large number of species are repres ented by small numbers of individuals. This tends to reduce the relative abundance of all the species in these diverse communities. The relative abundance of a single species in

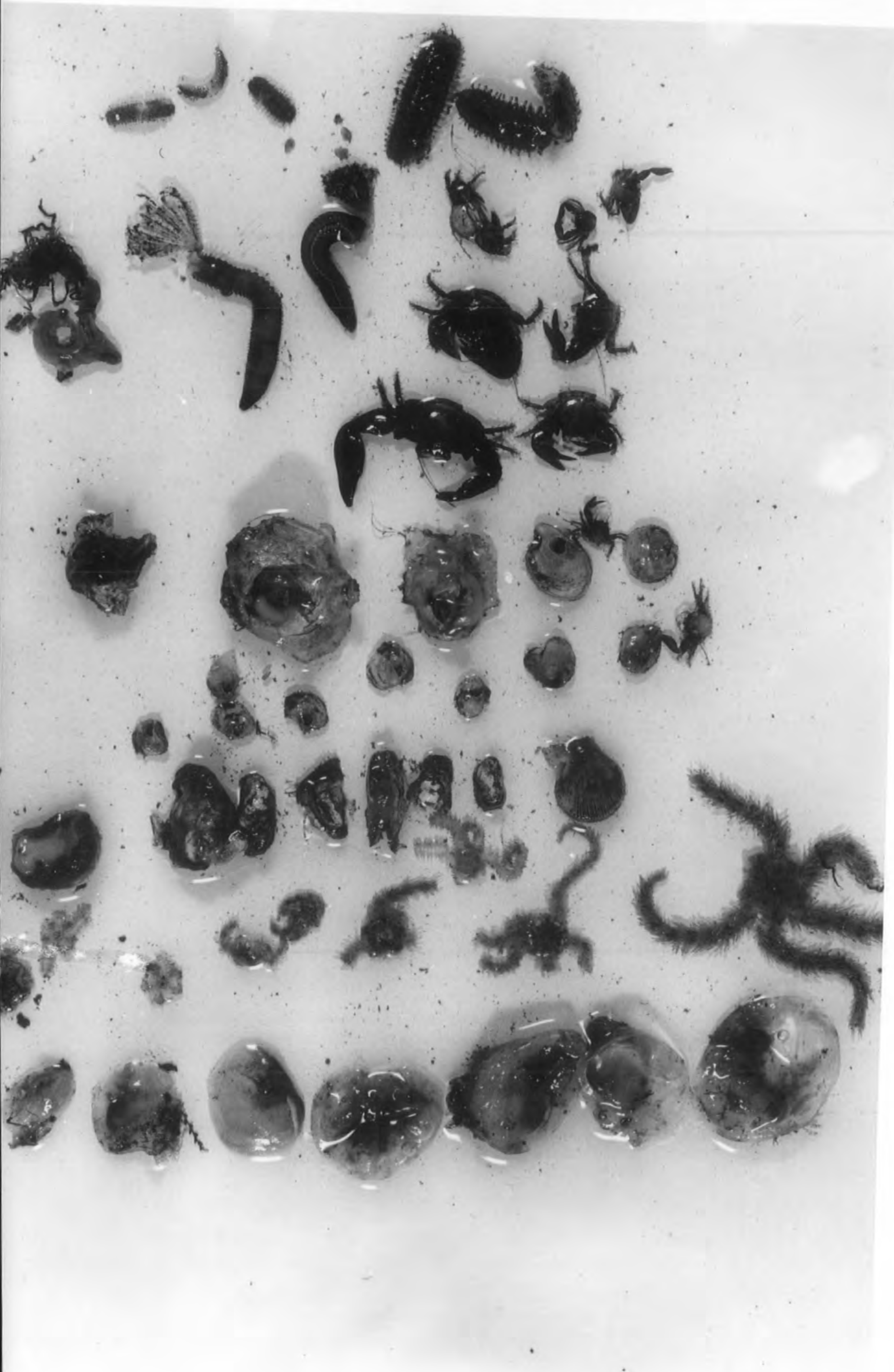


Plate 4
Estuarine Unpolluted Community Stn.3 (Firth of Forth) Depth 3 metres

polluted water can be as high as 97.6 per cent. This is a virtual monoculture of one species in the habitat.

Excessive water movement protects mussels from their predators (Kitching et al 1959). The principal predators Nereis pelagica and Asterias rubens are present in small numbers in the fast moving waters of the Farne Isles (Stn. 9) and Stn. 10. This factor probably allows the persistence of a quite large number of mussels here accounting for the seemingly anomalous situation in the clean water station.

(v) Size Frequency Analysis

Of the principal species observed to vary with pollution six are selected for size frequency analysis. These are:

SPECIES	GROWTH INDEX
Mytilus edulis	Shell length. Cms.
Nereis pelagica	Length. Cms.
Asterias rubens	Arm diameter. Cms.
Ophiothrix fragilis	Disc diameter. Cms.
Ophiopholis aculeata	Disc diameter. Cms.
Porcellana longicornis	Carapace 'Area' (LXB).sq.cms.

With the exception of Mytilus edulis (Seed, 1969), the growth rates of the other species are not known. Mytilus edulis appears as a spatfall in polluted waters reaching numbers in excess of 1,000 in the 5 mm age class at Stn. 15 and 15. At Station 6 in clean water small and regular recruitment of mussels is indicated by the small numbers of specimens spread over all the four size classes up to 3 cms. Mussels over 3 cms in length were never found in any of the holdfasts studied.

The uneven distribution of the size classes when different sites are compared suggests that recruitment to the mussel populations occurs at different times or that the predation rate varies. The absence of many large specimens of Mytilus in polluted waters suggests that the predation rates must be very high, or that some other factor is affecting the population. (Figure 21)

The high species diversity of clean water communities seems to prevent the settlement of very large numbers of any single species. This may be one explanation of the 'ecological resistance to change' suggested by (Elton, 1958) for climax communities.

Porcellain crabs, Porcellana longicornis show a preference for clean water where small numbers of them can be found in most size classes. They do not occur at Stations 13, 14, 15 or 16, but reappear again at Stn. 17 (Robin Hood's Bay). Their absence from Stn. 18 (Flambrough Head) is probably a collecting gap.

Nereis pelagica is present at all stations. Restricted to the smaller size classes in clean water, greater numbers of larger specimens occur in polluted waters. Asterias rubens occurs as a few large specimens or several small ones, the larger specimens seem confined to polluted waters. This is very similar to distribution patterns of Nereis pelagica.

Although in diffe rent size classes, Ophiothrix fragilis and Ophiopholis aculeata are common at all stations as far as Stn. 12 (Craster). They disappear in the polluted waters of Stn. 13, 14, 15 and 16 making a recovery in the turbid waters of Station 17 (Robin Hood's Bay).

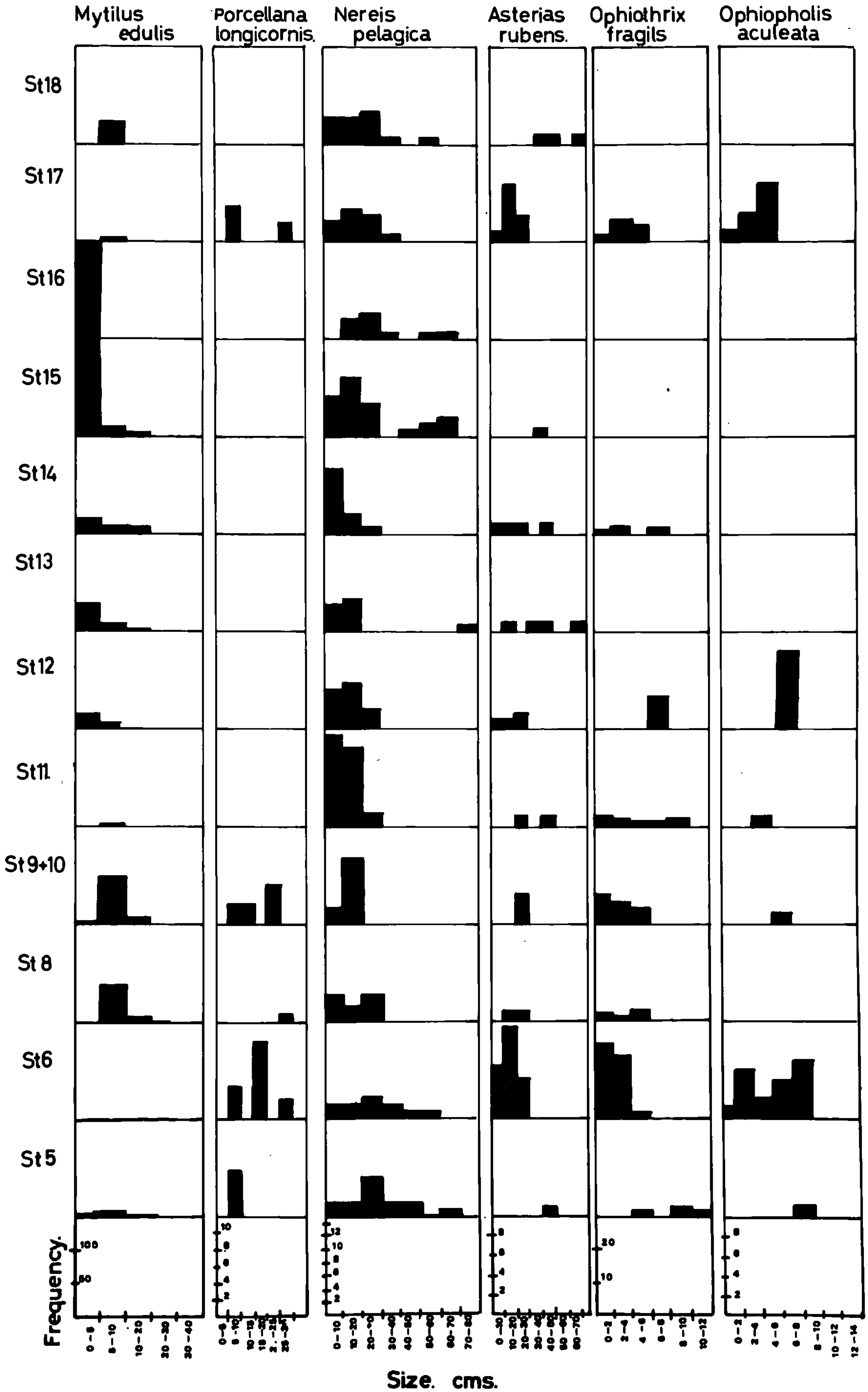


Fig.21

Size Frequency Analysis on selected species

The Annual Ecoperiod as a Unit for Comparative Study

A 'succession' of species colonising developing ecospace habitats has been demonstrated (page 57) which is characterised by the increasing number of species included in the habitat as ecospace increases over seven years. In polluted waters, a similar kind of succession takes place which is markedly different in detail when compared with unpolluted waters. The data used in the interpretation of the ecoperiod (page 57) is compared with statistically similar data obtained from the polluted waters at Stn. 15.

The number of species included in the polluted water habitat is significantly lower than in clean waters. After the second year when both communities contain two species, the rate of accumulation of species in polluted water is halved. By the seventh year there are 19 ± 1 species at Stn. 6 and only 8 ± 1 at Stn. 15 (Fig.22) Though fewer species are present in polluted water many more individuals are present per ecoperiod. The pattern of colonisation by larger numbers of fewer species in polluted waters is also modified when compared with clean waters. Small numbers of species are steadily accumulated in the clean water habitats reaching a maximum of 80 ± 8 in the seventh year. The maximum numbers at Stn. 15 are reached by the 5th year when 203 ± 86 individuals are present. Though the habitat continues to enlarge these numbers fall to 44 ± 2 by the 7th year. The populations thus develop faster in polluted water habitats reaching their peak in the 5th. year ecoperiod then undergoing a rapid decline in numbers.(Figure 23)

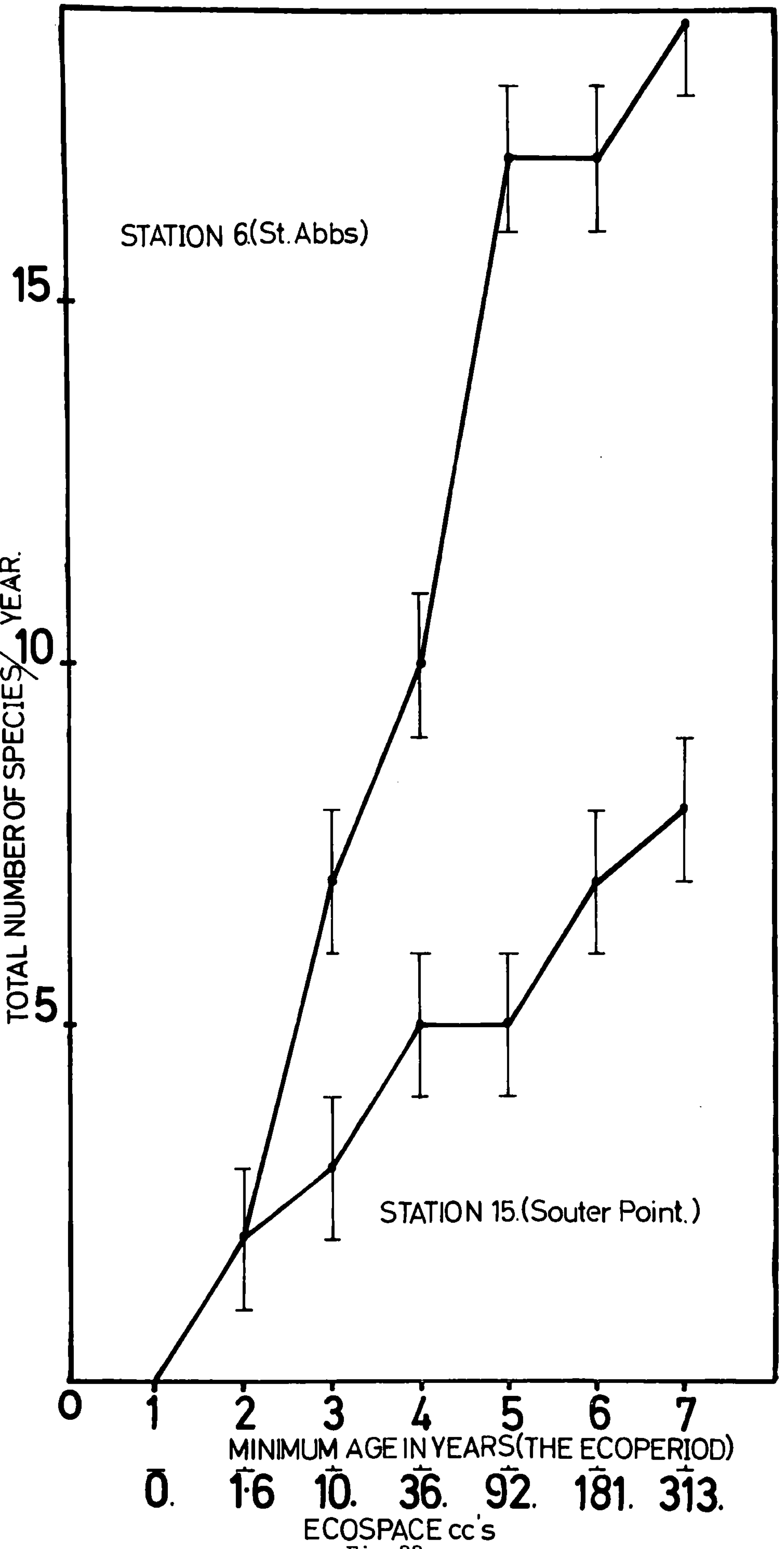


Fig.22
Increase in species numbers with enlarging ecospace habitat

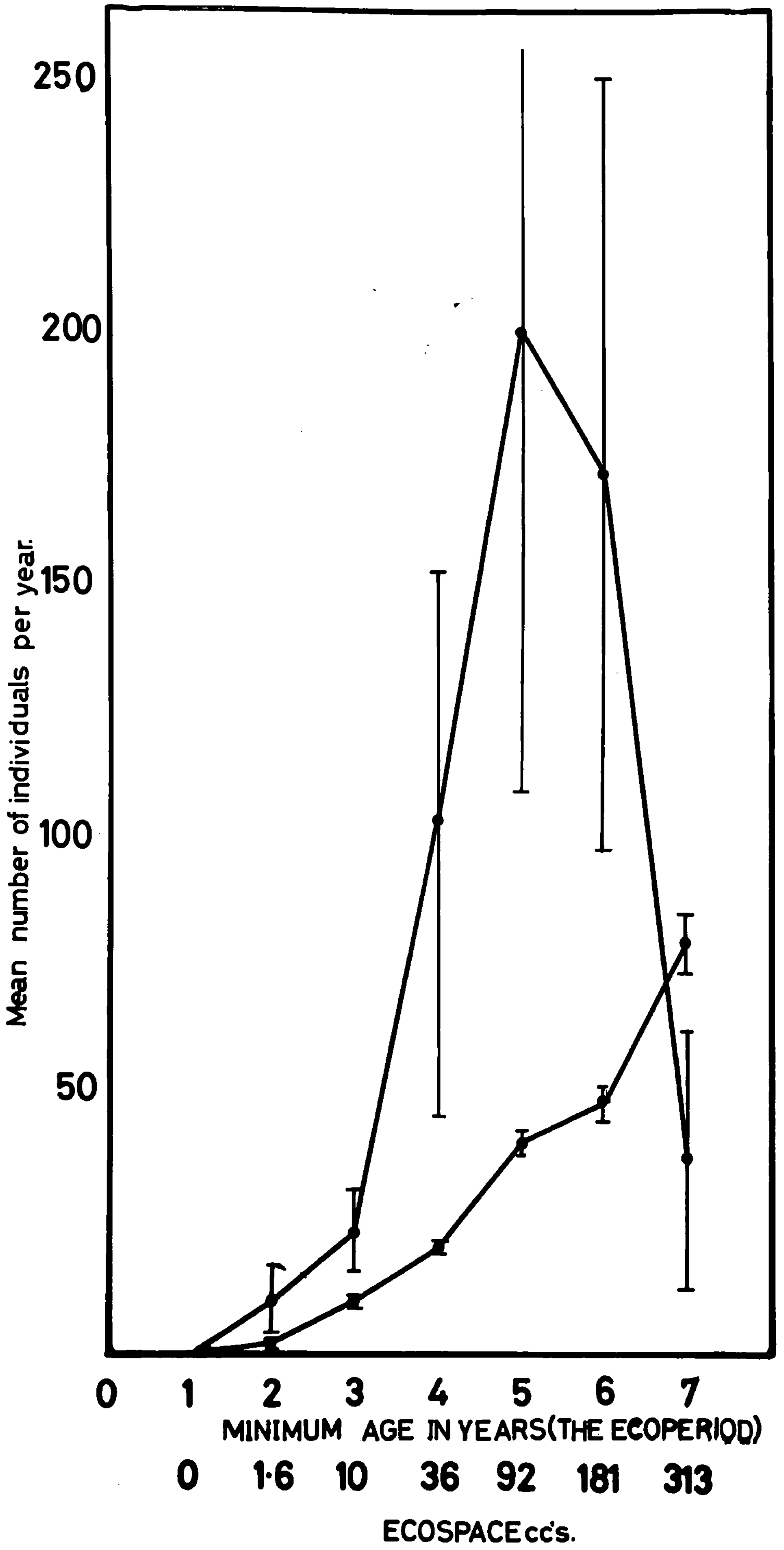


Fig.23
Increase in number of individuals with enlarging ecospace habitat

The large standard error about the mean of the populations developed in the ecoperiod also indicate that much greater variation in the numbers of species present in the developing habitat of polluted waters suggesting greater instability of the species poor community found there. The species composition of polluted communities is also different from those developed at the unpolluted station and the total number of species that colonise the habitat is lowered (fig. 22). A total of 44 species colonise the developing habitat of which only 27 species become progressively and permanently included. This is a 61 per cent reduction in the species complement present in the developing polluted water community. The number of individuals and the kinds of species is also different in polluted water. The following sequence of colonisation was observed in dirty water. (Table 18)

Year 1

Ecopsace = 0.cc's

Mytilus edulis, Halichondria panacea

Year 2

Ecospace = 16.0.cc's

Sabellaria spinulosa, Balanus balanoides, Nereis pelagica, and Asterias rubens appear.

Year 3

Ecospace = 100.cc's

Mya truncata, Flabelligera affinis, Lepidodontus squamatus.

Year 4

Ecospace = 360 cc's

Anomia epiphium, Phyllodoce sp.

TABLE 18

Invertebrate 'succession' in ecospace at Stn. 15 (Souter Point) Polluted

Ecospace CC's	0	16.0	100.0	360.0	920.0	1810.0	3130.0		
Ecoperiod (years)	1	2	3	4	5	6	7	Nos.	Per cent of community
Mytilus edulis	8	60	115	939	923	1515	211	3771	78.1
Halichondria panicea	2	3	2	2	1	2	0	11	0.2
Sabellaria spinulosa		2	10	55	242	50	344	703	14.5
Balanus balanus		2	0	10	1	11	0	24	0.4
Nereis pelagica		1	3	11	17	23	21	76	1.5
Asterias rubens		2	4	9	2	17	31	65	1.3
Mya truncata			6	0	1	2	6	15	0.3
Flabelligera affinis			1	0	2	4	2	9	0.1
Lepidonotus squamatus			1	0	2	5	5	13	0.2
Anomia ephippium				8	8	0	5	21	0.4
Phyllodoce sp.				1	0	3	1	5	0.0
Pomatoceros triqueter					1	2	1	4	0.0
Acanthochitona crinitus					1	1	4	6	0.1
Tonicella rubra					1	0	5	6	0.1
Cancer pagurus					2	1	4	7	0.1
Ophiothrix fragilis					1	1	7	9	0.0
Henricia sanguinolenta					1	0	1	2	0.0
Actinia equina						1	1	2	0.1
Pycnogonum littorale						1	4	5	0.1
Harmanthoe impar						1	9	10	0.2
Botryllus schlosseri							1	1	0.0
Nicolea zostericola							5	5	0.1
Terebella sp.							1	1	0.0
Nymphon gracile							2	2	0.0
Ophiopholus aculeata							1	1	0.0
Echinus esculentus							1	1	0.0
Umbonula verrucosa	2	2						4	0.0
Mucronella coccinea	2	2						4	0.0
Patina pellucida	1	1						2	0.0
Monia patelliformis		1	0	6	5			12	0.2
Hymeniacidon perleve		1	0	2				3	0.0
Idotea baltica			1					1	0.0
Hyas areneas			1			1		2	0.0
Amphithoe rubricata			3		2			5	0.1
Jassa falcata			1					1	0.0
Taelia felina				1		3		4	0.0
Modiolus barbatus				4				4	0.0
Tubularia larynx					1			1	0.0
Sydnium turbinatum					1			1	0.0
Primela denticulata					1			1	0.0
Amphiopholis aculeata						1		1	0.0
Carcinus maenas						1		1	0.0

TABLE 18

'Succession' in ten replicates of the seven year ecoperiod of *Laminaria hyperborea* ecospace habitats Stn. 15 Polluted.

(i) Number of Species

Ecoperiod (years)	1	2	3	4	5	6	7
Species Number	0	2	4	7	6	4	6
	0	2	4	8	3	4	12
	0	2	5	4	77	4	8
	0	5	2	4	4	5	9
	0	2	4	9	4	5	6
	0	0	0	3	6	8	7
	0	4	4	1	2	12	77
	0	0	1	4	3	9	6
	0	0	0	4	5	9	7
	0	0	0	4	7	6	9
Mean No/ecoperiod =	0	2.4 ± 0.61	3.0 ± 0.8	4.8 ± 0.7	5.1 ± 0.83	6.6 ± 0.8	8.1 ± 0.6
Corrected to nearest whole number	0	2 ± 1	3 ± 1	5 ± 1	5 ± 1	7 ± 1	8 ± 1

(ii) Number of individuals

	1	2	3	4	5	6	7
	0	2	83	216	35	605	46
	0	3	42	226	10	5	231
	0	2	31	21	334	8	21
	0	64	4	18	506	17	17
	0	3	5	28	203	35	22
	0	0	0	6	32	41	11
	0	5	4	1	2	31	36
	0	0	10	25	93	549	16
	0	0	0	519	8	123	7
	0	0	0	7	808	319	33
Mean No/ecoperiod	0	11.2 ± 8.9	22.3 ± 10.2	106.7 ± 53	203.1 ± 86.2	173 ± 74	440 ± 21.4
Corrected to nearest whole number	0	11.0 ± 9	22 ± 10	107 ± 53	203 ± 86	173 ± 74	44 ± 21

Year 5

Ecospace = 920 cc's

Pomatoceros triqueter, *Acanthochitona crinitus*, *Tonicella rubra*, *Cancer pagurus*, *Ophiothrix fragilis*, *Henricia sanguinolenta*.

Year 6

Ecospace = 1810 cc's

Actinia equina, *Pycnogonum littorale*, *Harmanthoe impar*.

Year 7

Ecospace = 3130 cc's

Botryllus schlosseri, *Nicolea zostericola*, *Terebella* sp. *Nymphon gracile* *Ophiopholis aculeata*, *Echinus esculentus*.

The species, *Umbonula verrucosa*, *Mucronella coccinea*, *Hymeniacidon perleve*, *Monia patelliformis*, *Patina pellucida*, *Idotea baltica*, *Hyas araneas*, *Amphithoe rubricata*, *Jassa falcata*, *Taelia felina*, *Modiolus barbatus*, *Tubullaria larynx*, *Sydnium turbinatum*, *Primela denticulata*, *Amphiopholis aculeata*, *Carcinus maenas*, *Amphithoë rubricata* make only a sporadic appearance in the community. These seventeen species do not become permanent community elements. This compares favourably with only 7 species in the clean waters after a brief appearance, these species diappear even though the physical dimensions of ecospace are still increasing and other species are colonising the enlarging habitat.

TABLE 19

Relative Abundance of Principal Species at Stn. 6 and Stn. 15.

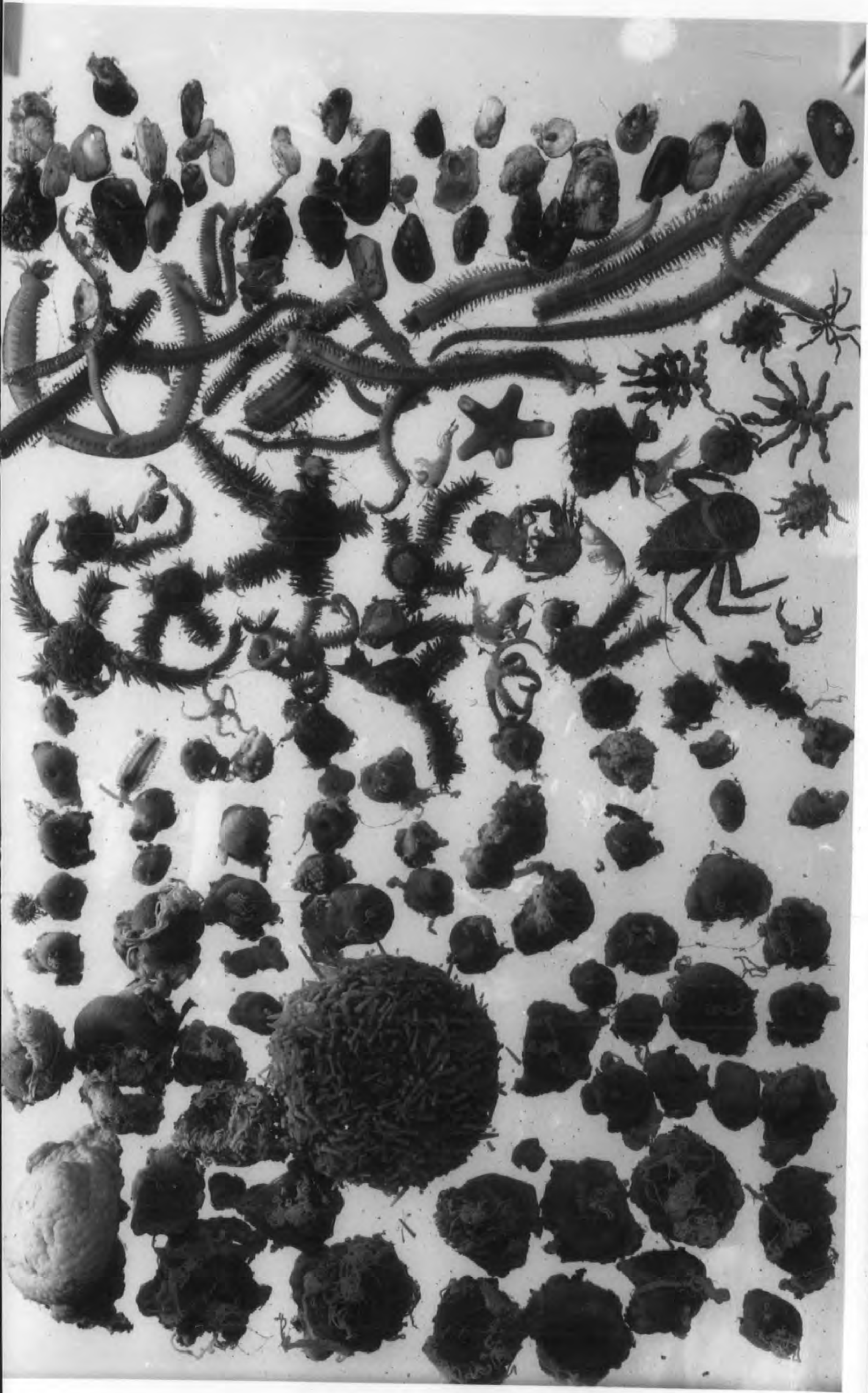
Species	Stn. 6	Stn. 15
Asterias rubens	6.6	
Ophiopholis aculeata	5.7	
Ophiothrix fragilis	15.8	
Corophium bonellii	5.6	
Jassa falcata	7.2	
Nereis pelagica	7.0	
Pomatoceros triquiter	7.5	
Mytilus edulis	-	78.1
Sabellaria spinulosa	-	14.5

Plate 5

Station 6 (St. Abbs) Unpolluted

Open Coast Community Depth

4 metres



By the end of the seventh year ecoperiod, two species, Mytilus edulis and Sabellaria spinulosa dominate the polluted water community accounting for 92.6 per cent of the population. In unpolluted waters, seven species occur as more than 7 per cent abundant but collectively they only account for 55.4 per cent of the community (Table 18). With a larger number of species present in fewer numbers, no single species dominates the clean water community.

The feeding patterns of the polluted water community are distinctly different from those in clean water (fig. 24). Suspension feeders remain dominant throughout the whole of the seven year ecoperiod. As the habitat enlarges filter feeders continue to colonise it in large numbers. Deposit feeders and herbivores form only an insignificant trophic element never exceeding 4 per cent and 5 per cent respectively. The omnivore population reaches its maximum at 14 per cent in year three but falls steadily to 12.1 in year 7. The carnivore population increases steadily to 21 per cent in year 7.

This much simplified community is always dominated by suspension feeders, principally Mytilus edulis and Sabellaria spinulosa and over the 7 year ecoperiod the carnivore population composed mainly of Nereis pelagica and Asterias rubens steadily develops until it becomes the other major component in the community. As the percentage of suspension feeders declines the percentage of carnivores steadily increases. It is probable that any biotic influence of carnivores depleting stocks of suspension feeders is exaggerated in this simplified community. It nonetheless seems to illustrate how biotic factors produced by the presence of other species could affect the structure of the community developed in ecospace.

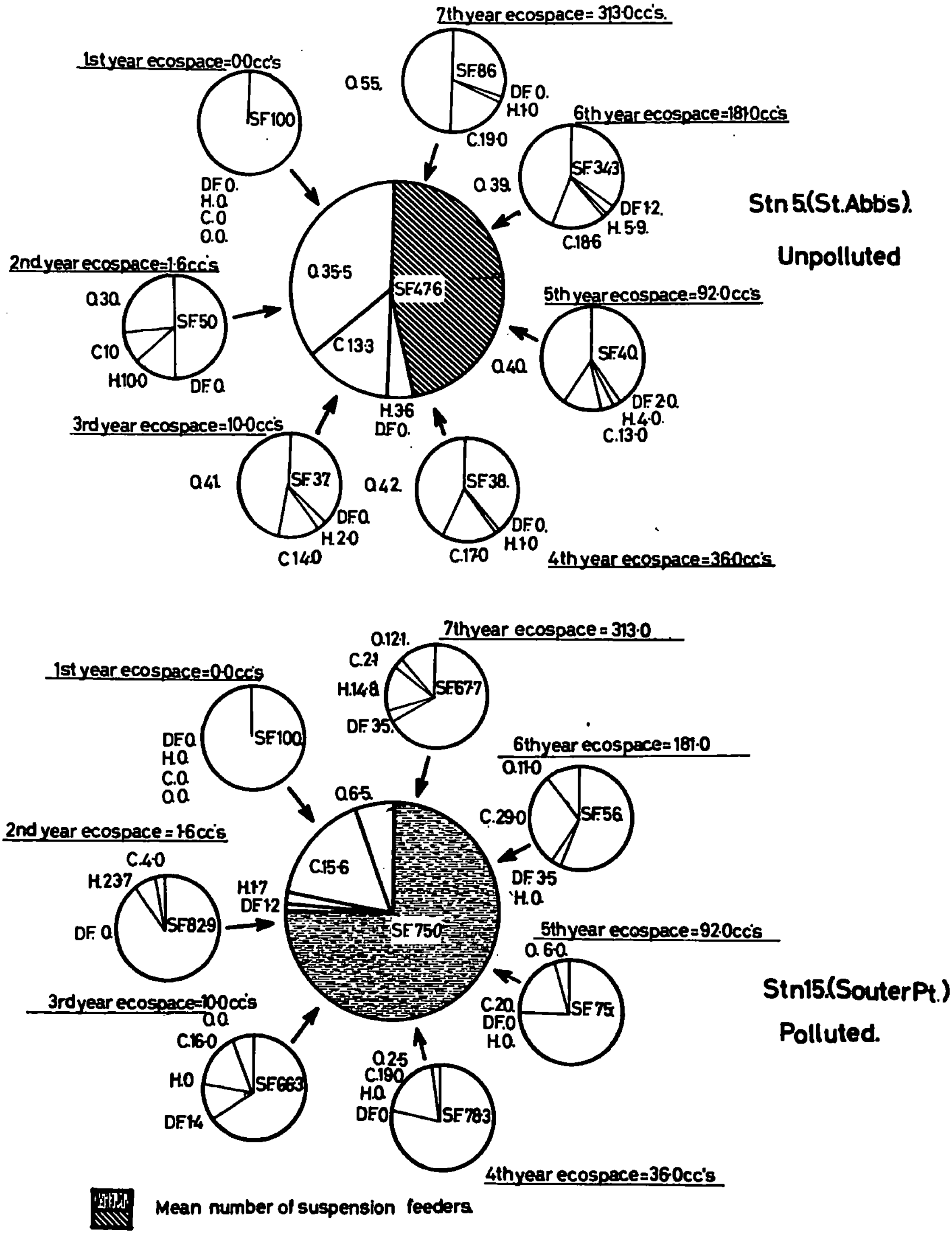


Fig.24

Trophic Component Analysis of Succession in 7 year Ecoperiod. Stn. 6 and 15 compared.

Conclusions from the Spatial Studies

(1) The structured organisation of holdfast communities is remarkably similar and there is little difference between widely separated clean water communities. Species diversity in clean water communities is high.

(2) The main community elements are filter feeders, herbivores, carnivores and omnivores.

(3) No appreciable change in community structure is found with depth.

(4) Two pollution gradients in the North East of Britain affect the holdfast communities in the following way:

There are at least three dislocations of the marine food web and many rare species are lost from the community. Rare species are of little value in this kind of pollution assessment.

Trophic component analysis, Species Diversity, the relative abundance and size frequency analysis reveal that the naturally occurring biotic variation between communities is reduced by specialisation of the community into a filter feeding unit. Erratic spatfalls of large numbers of single species of suspension feeders can occur which do not appear to persist for any great length of time in the ecosystem. Large populations of a few pollution tolerant carnivores can develop which are direct predators of suspension feeders.

There is likely to be no regulatory negative feedback in such a simple system (Odum, 1967). At any given point in time large populations of either suspension feeders or carnivores are present, which utilise quite different and very specific food sources, leaving the remainder to waste. Temporal studies are necessary before more interpretation of this community response to pollutants can be made.

Herbivorous forms are most sensitive to pollution. They could be used to provide a more accurate indication of water quality than pollution sensitive omnivores. Herbivores are always present in low numbers even in clean waters.

In planning surveys of this kind, great care should be exercised in the selection of sampling stations. Adequate sampling over unpolluted areas must be undert aken to evaluate naturally occurring community fluctuations . Naturally occurring abiotic stresses such as high water movement or turbidity can produce an effect on the community reminescent of pollution.

More than one method of ecological interpretation is essential. Considered in isolation, the species dominance of communities within a region would indicate that communities were not equivalent. Trophic component analysis does not reveal which species are dominant. Diversity Indices mathematically define a community in a single numerical expression. The figure is meaningless if the ecological range of that numeral and the reasons for its amplitude are not considered.

Nonetheless, natural variation is not so great that it prevents comparisons. Spatial studies of this kind are thus of value in establishing the range of variation in the structure of the holdfast communities upon which the effects of pollution have been superimposed.

PART IV

Temporal Studies

Temporal studies were undertaken on two stations in the North East region. These were:

Stations 6 St. Abbs, Berwickshire - Unpolluted

Station 15 Souter Point, Co. Durham - Polluted

Sampling commenced in September 1967 and concluded in May 1970. During the thirty one months of the study, rough seas prevented the collection of material on fifteen occasions. The data obtained are analysed in the following ways:

(1) Trophic Component Analysis (see pages

Over the duration of this study the holdfast community developed in ecospace is always different when polluted and unpolluted stations are compared (figs.25, 26). On average the 84 per cent suspension feeding element at Stn. 15 is more than double its counterpart at Stn. 6 where it accounts for only forty per cent of the community.

Omnivorous forms are largely absent from the polluted water station. Herbivorous forms are reduced from 5.9 per cent at Stn. 6 to 1.2 per cent at Stn. 15. Deposits feeders remain at low levels throughout the study never accounting for more than 2 per cent of the community. The polluted water communities consistently show a reduced trophic complexity brought about by specialisation as a suspension feeding unit.

Natural variation in the clean water communities ranged from 31 per cent to 57 per cent for suspension feeders; 0 per cent to 2.6 per cent for deposit feeders; 1.5 per cent to 6.4 per cent for

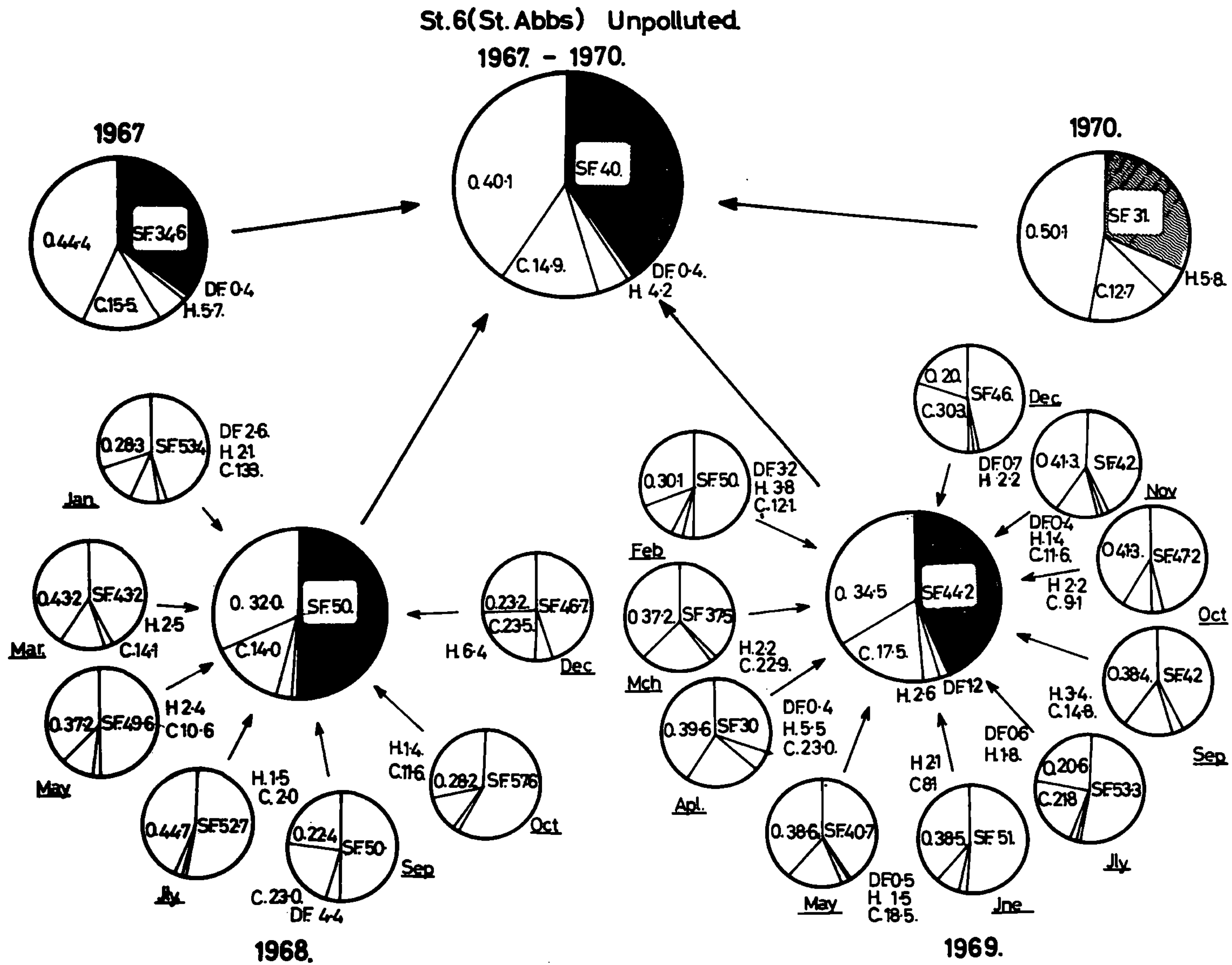


Fig.25
Temporal Studies with Trophic Component Analysis - Stn. 6.

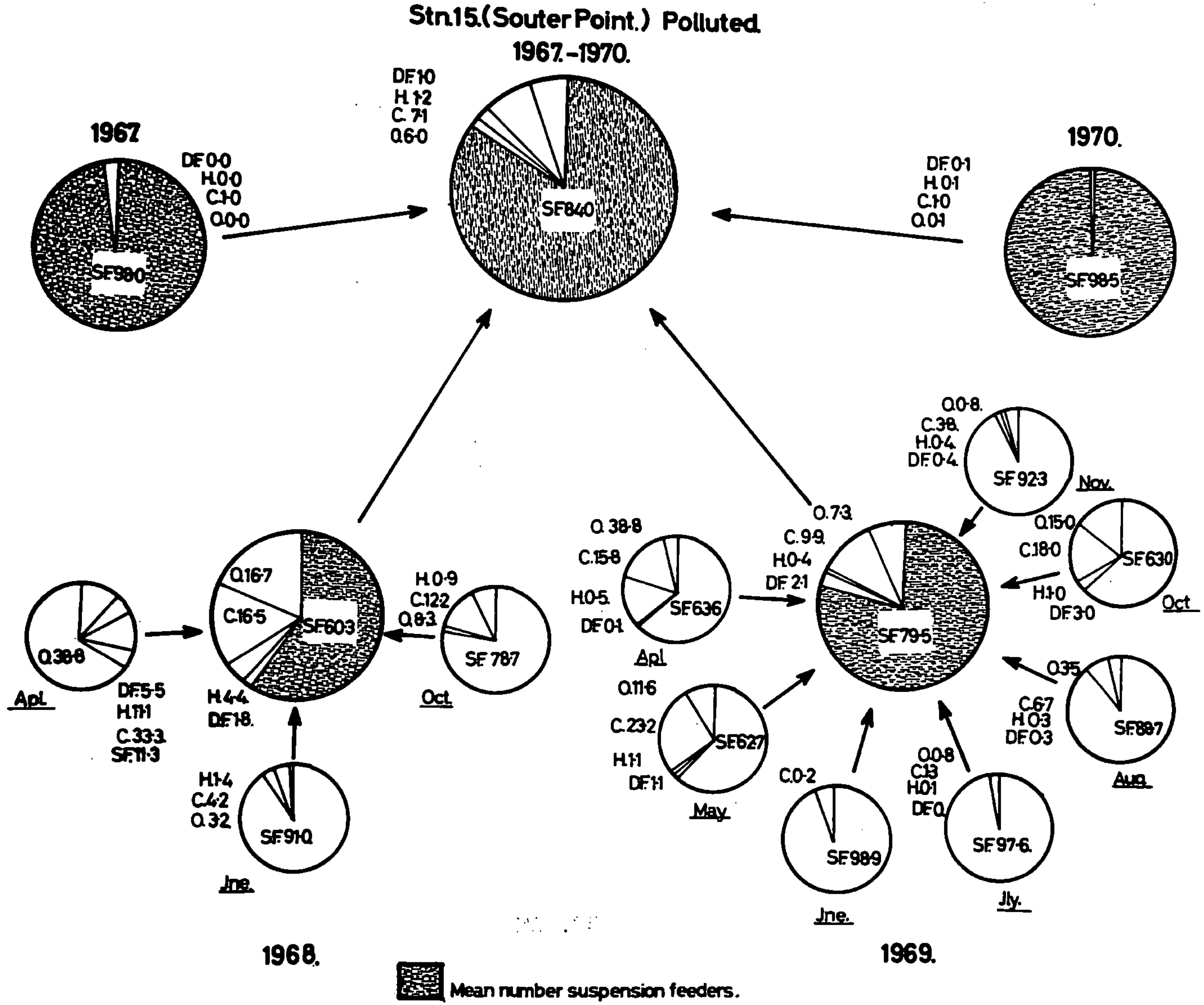


Fig.26
Temporal Studies with Trophic Component Analysis --Stn.15.

herbivores, 2 per cent to 41 per cent of Carnivores and 22 per cent to 50.1 per cent for Omnivores (fig.25)

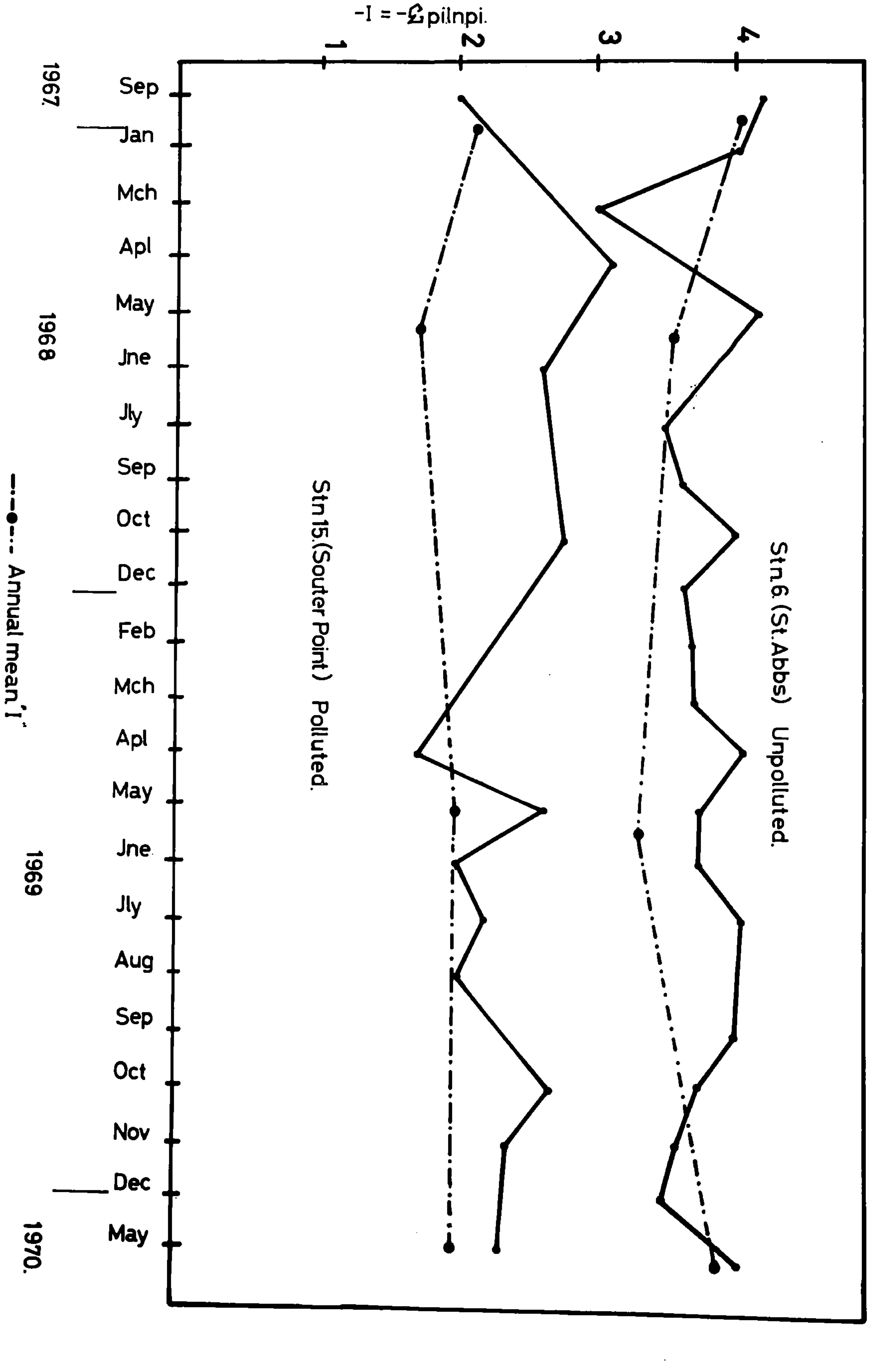
Considering the structure of the whole community as indicated by trophic component analysis, Omnivores and carnivores dominate Stn. 6. Carnivores are always present and can occupy 40 per cent of the community but on average amount to 14 per cent of the community. Deposit feeders and herbivores remain at low levels throughout.

In polluted waters at Stn. 15, deposit feeders range from 0 per cent to 5.5.per cent, herbivores from 0 per cent to 5.5 per cent, Carnivores from 0 per cent to 33 per cent and suspension feeders from 11 per cent to 98.9 per cent. These fluctuations are much greater than those for the clean waters at Stn. 6. The reduced trophic complexity of the polluted water communities is accompanied by greater instability which carries larger fluctuations in the proportions of the feeding groups, than occur in clean water.

(2) Species Diversity

The mean species diversity of polluted water is always lower than the same index for clean water (fig. 27). The mean index for unpolluted water equals 3.7 per cent for polluted water 2.9 per cent.

The annual value of the species diversity is reduced by approximately one half in polluted waters indicating a persistent lowering in the species complement of the community developed there.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1967.
1968
1969
1970.
Stn.6 (St.Abbs) Unpolluted.
Stn.15 (Souter Point) Polluted.
Annual mean 'I'

Fig.27

In the early Spring of 1968, the species diversity figure for Stn. 6 and Stn. 15 overlapped. The index at Stn. 6 dropped to a value of 3.0 and at Stn. 15 rose to 3.1. This kind of overlap occurs only once during the study period, at all other times the indices remain quite separate. Thus when spatial comparisons are made using this diversity index, more than one set of spatially distinct stations should be sampled. This will greatly reduce the risk of incorrect interpretation of the diversity index at stations where biotic variation may temporarily produce an unusually low index which will later recover to a higher value.

The advantage of the Margalef index lies in the mathematical combination of the number of species and the number of individuals within one species with the total number of individuals of all species. This produces the single numerical index indicative of the diversity, i.e. species richness of the community, which can then be used for comparison with other communities. One great disadvantage of the calculation is that it obscures much of the information on the kinds of species and their abundance in the habitat. Because ecospace and the ecoperiod remain unchanged at both stations throughout the study, the number of individuals and the number of species present can be separated to become two very simple indices of species diversity.

The number of species that colonise the habitat at Stn. 6 is consistently higher than at Stn. 15. The unpolluted community contains between 25 and 36 species whilst at Stn. 15, a smaller

Plate 6

Station 2. Firth of Forth. Depth 2 metres

Typical Polluted Water Community with Mytilus edulis dominant. Slightly larger than life size.

number, between 8 and 20 are present, this is an average reduction in the species complement of 50 per cent in unpolluted water. The amplitude of the fluctuation in species is roughly the same and equals about 12 species. However, whenever the stations are compared there are always more species present in the clean waters at Stn. 6.(Fig.28)

The total number of individuals of all species in the habitat varies throughout the study period at both Stn. 6 and Stn. 15, (fig. 29), but there is a dramatically greater fluctuation in the numbers of individuals in polluted waters. Between September 1967 and May 1968 the numbers of individuals at Stn. 15, falls from 1,429 individuals to 18, a drop of 1,231 in the total population of all species in the habitat. By June 1968, there is a recovery to 210 followed by a drop to 86 individuals in the Spring of 1969. In all, four violent fluctuations occur in the total numbers of individuals in the community involving a loss or gain of 1000 individuals each time. At Stn. 6 the population fluctuates at the most between 413 individuals and 135, a difference of 278.

(3) Relative Abundance

The number of species occurring as more than 5 per cent of the sample are quite different when polluted and unpolluted stations are compared (Tables 19). The most commonly recurring species at Stn. 6 are the suspension feeders Porcellana longicornis and Pomatoceros triquiter, the carnivores Nereis pelagica and Asterias rubens and the omnivores Ophiothrix fragilis and Ophiopholis aculeata. Over the study period the clean waters are consistently dominated by these species and there is a considerable degree of species diversification in the habitat (Appendix 6)

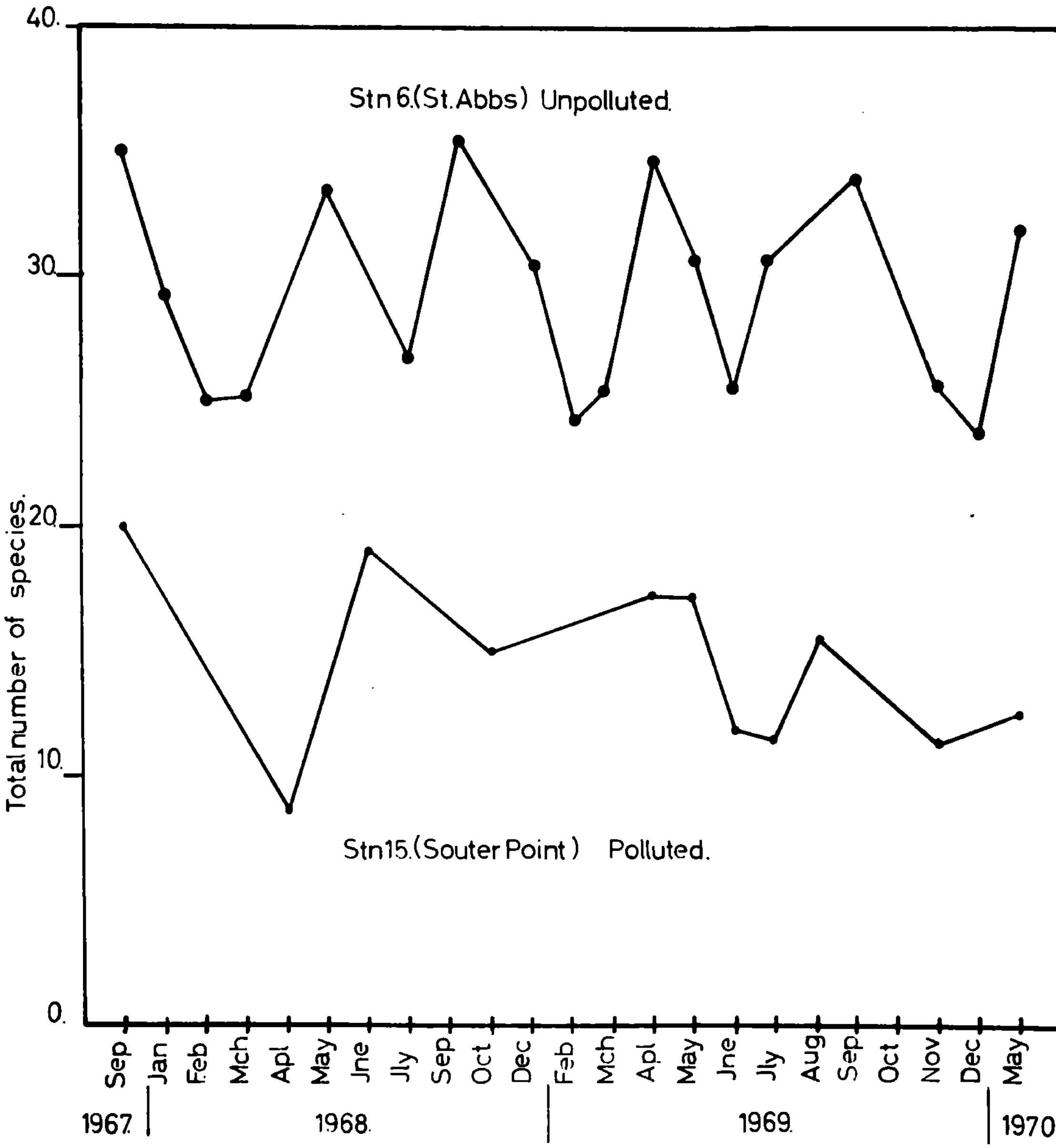


Fig.28
Variation in Species number in polluted and unpolluted waters.

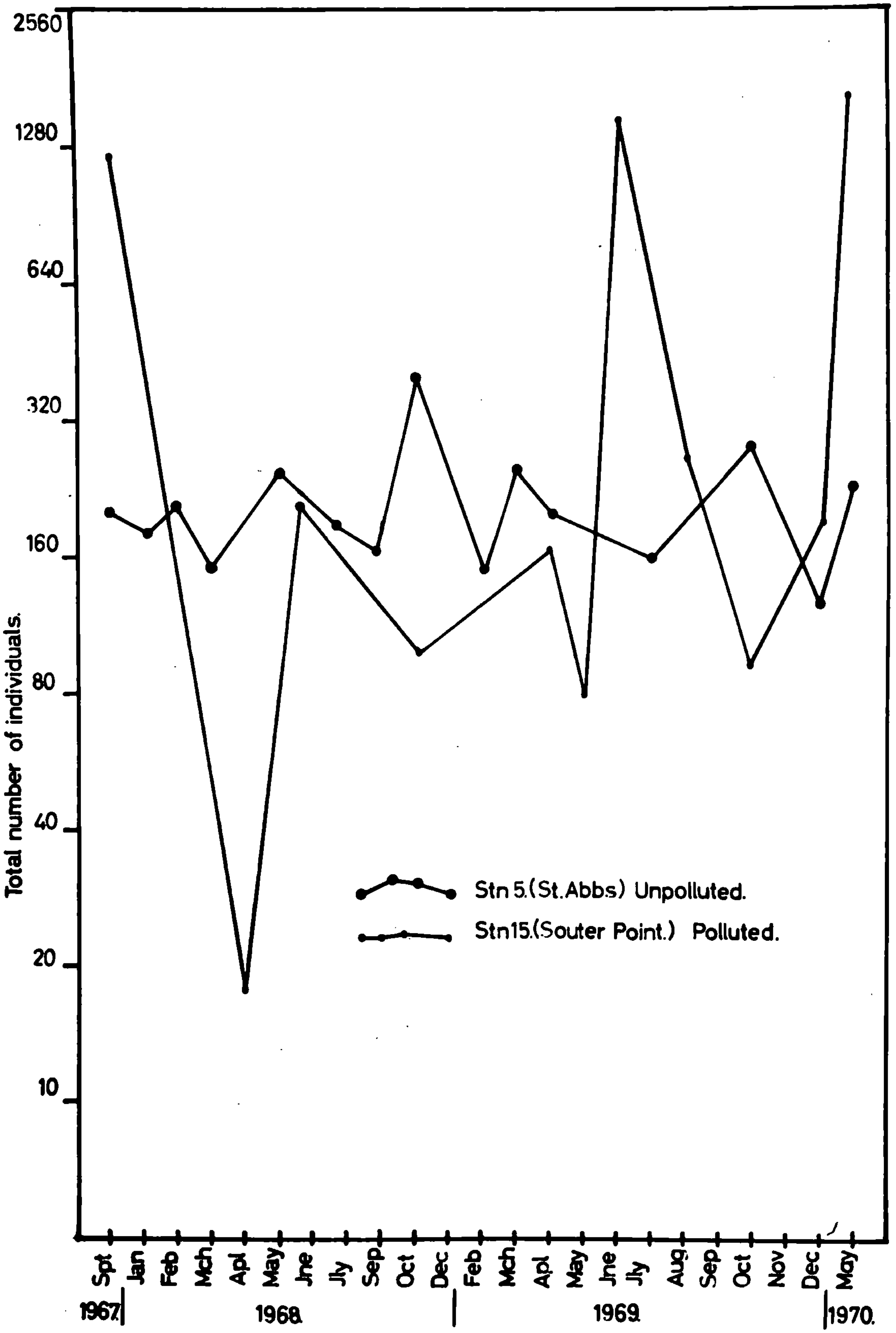


Fig.29
Variation in total population numbers Stn.6 & 15.

The unpolluted station retains a characteristic association of species as described by (Peterson, 1915), (Sparck, 1937), Einarsson, 1941), (Gislen, 1931), and (Jones, 1950). It is a typical epifaunal association known as the 'Modiolus modiolus' or 'Mytilus edulis biome' and can be dominated by these two species accompanied by Ophiothrix fragilis, Ophiopholis aculeata, Porcellana longicornis, Balanus sp, Galathea sp and a range of annelids (Jones, 1950). This species configuration on the shallow water rocky benthos is known for most North West European rocksy shores including those of Iceland, Denmark, Sweden the North Sea and the Baltic.

At Stn. 15 only 100 kms. away from this widespread community, configuration the characteristic ophiouroids and small crustacea like Porcellana longicornis have disappeared and the suspension feeders Mytilus edulis, Sabellaria spinulosa and the carnivores Asterias rubens and Nereis pelagica are the dominant community elements. This indicates a radically different community developed and maintained in polluted water. The two suspension feeders occur in such numbers that they can occupy 90 per cent of the community with the result that the remainder of the species in the habitat can only be considered as residual elements in a much simplified polluted water ecosystem.

When the numbers of Mytilus edulis are high, the numbers of Sabellaria spinulosa are low and the two species do not co-dominate in the habitat (fig. 30), (Table 20).

Colonisation by Mytilus edulis is sporadic and difficult to predict on the littoral shores (Lewis, 1964), (Seed, 1969). During this sublittoral study, large recruitments into the hapteron ecosystem occur in the polluted waters at Stn. 15, but not in the unpolluted waters at Stn. 6.

TABLE 19

Relative Abundance. Species occurring as more than 5 per cent of the habitat
Stn. 6. Unpolluted. Depth 3.OM.

	Sept. 1967	Jan. 1968	Feb. 1968	Mch. 1968	May 1968	June 1968	Sept. 1968	Oct. 1968	Dec. 1968	Feb. 1969	Mch. 1969	Apl. 1969	May 1969	June 1969	July 1969	Sept. 1969	Nov. 1969	Dec. 1969	May 1970
Anomia ephippium		12.8		5.1	6.7			5.3	5.0	12.8							6.0		
Mya truncata		11.7	6.0		5.3	5.2		10.0	6.0	11.5	8.2			10.8	9.6			19.0	
Nomia patelliformis					9.5			9.0						5.4	6.6	6.0	6.9		
Pomatoceros triquiter	16.0	6.4		6.4	8.5	13.7		8.2	6.7	7.6				6.3	13.3	8.3			5.9
Porcellana longicornis	5.7	15.5	14.1	18.0	6.7	8.9	11.7	8.9	21.0	11.5	16.9	22.1	27.3	5.1	8.4	9.5	18.1	14.0	11.1
Venerupis pullastra			8.5																
Nereis pelagica	13.3	10.1	14.5	12.9	5.6	4.7	17.4	8.2	12.8	7.6	10.1	9.2	10.0		9.6	9.5	9.3	17.0	
Nassarius reticulatus			8.0																
Lacuna vincta																			5.2
Asterias rubens						7.4			7.8		10.9	11.9		6.9	10.9			10.3	5.1
Amphithoe rubricata	16.4												8.7						
Corophium bonellii													6.0						
Caprella linearis																		5.5	
Jassa falcata					7.8	6.3							11.4		4.3	5.7			15.1
Harmothoe impar													4.8						
Lepidontus squamatus	5.3								5.0										5.1
Ophiopholis aculeata	7.5					6.3						12.9		8.1		7.9	27.0		5.9
Ophiothrix fragilis		13.8	18.0	20.0	13.4	15.3	6.7	12.3	5.3	17.3	19.5	11.9	11.4	22.2		9.5	26.0	5.1	8.7

TABLE 18

Trophic Component Analysis on the Annual Ecoperiod at Stn. 15 (Souter Point). Polluted.
(Ten sets of 7 year ecoperiod)

Ecoperiod (years)	Suspension feeders	Deposit feeders	Herbivores	Carnivores	Omnivores
1	100 ± 2	0	0	0	0
2	89.2 ± 7.0	0	6.6 ± 1.0	4	0
3	66.3 ± 17.6	1.4 ± 0.0	0.8 ± 0.0	16.3 ± 8.9	14.2 ± 9.3
4	78.3 ± 1.9	0	0	19.0 ± 4.0	2.5 ± 1.8
5	75.5 ± 12.9	0	0	20.0 ± 12.8	6.0 ± 3.0
6	56 ± 13	3.5 ± 2.0	0	29.0 ± 10.0	11.0 ± 3
7	57.7 ± 12.0	3.7 ± 1.6	4.8 ± 2.0	21.0 ± 7.0	12.1 ± 3.5
Mean	77.2 ± 6.3	1.2 ± 0.6	1.7 ± 1.1	15.6 ± 3.8	6.5 ± 2.2

TABLE 20

Relative Abundance. Species occuring as more than 5 per cent of the habitat. Stn. 15. Polluted. Depth 3.OM.

Species	Sept. 1967	April 1968	June 1968	Oct. 1968	April 1969	May 1969	June 1969	July 1969	August 1969	Nov. 1969	May 1970
Actinea equina		11.1									
Modiolus barbatus						10.4					
Mytilus edulis	94.5			15.7	1.1	34.8	96.0	93.0	57.0	14.0	96.3
Nomia patelliformis						5.8					
Sabellaria spinulosa			70.4	58.3	48.0				22.0	5.6	10.0
Flabelligera affinis		5.5									
Terebella sp.					5.0						
Acanthochitona crinitus		11.1									
Asterias rubens		22.2			5.6	5.8					
Nereis pelagica		11.1		5.5	5.6	11.6			6.0		
Phyllodoce sp.						5.8					
Amphithoë rubricata		5.5		15.2							
Jassa falcata		11.1									
Harmothoë impar		22.2									

After a primary settlement of pelagic larvae on a temporary sublittoral substrate (Seed, 1969), the plantigrades later emigrate and some form a permanent colony in ecospace. Spectacular colonisation by Mytilus edulis took place in the Autumn of 1967, the Spring of 1969 and the Spring of 1970. After each spatfall this species accounted for over 90 per cent of the community but soon began to suffer heavy losses which cause a rapid decline in the abundance of the species (Fig.30). In the Spring and early summer of 1968 and the Autumn of 1969, the suspension feeder, Sabellaria spinulosa succeeds the former dominant Mytilus edulis. After a large initial settlement resulting in Sabellaria spinulosa becoming 70.4 per cent dominant in the community, it steadily declined in numbers throughout the summer of 1968 and the early months of 1969. This population of Sabellaria. was replaced in the spring of 1969 by another spatfall of Mytilus edulis which by October 1969 had rapidly declined in numbers to only 14 per cent of the community but re-established itself over winter to become 96 per cent dominant by the late spring of 1970. A smaller sptafall of Sabellaria spinulosa again assumed dominance during the Autumn and winter of 1969.

Extensive research by (Seed [1969a and 1969b]) (Bayne, [1963], (1964, 1964a, 1965) on Mytilus edulis and by (Wilson [1929, 1968a, 1968b, 1970a, 1970b) on Sabellaria spinulosa has shown both species to produce planktonic larval forms which preferentially select their place of final settlement. If a suitable surface is not available, settlement and subsequent metamorphosis can be delayed by some weeks in both species. During this time the larvae can be moved many miles by the sea and the pronounced north to south currents along the

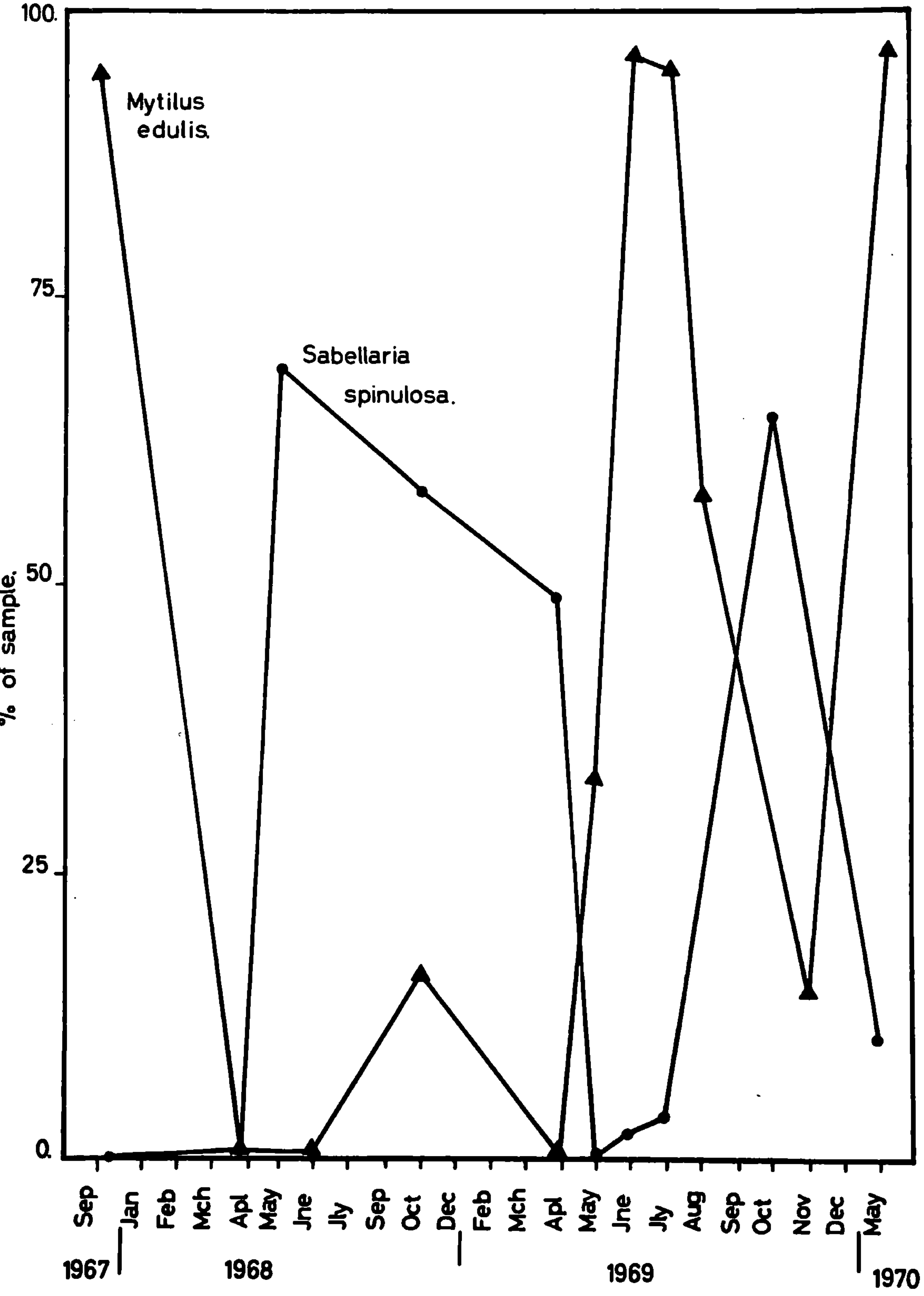


Fig.30

Intra specific competition in polluted waters community dominants at Stn. 15.

North East shores make this highly likely in this case. If these larvae are capable of withstanding immersion in polluted water without being killed then they could delay settlement until carried out of the polluted waters. Characteristically, large numbers of Sabellaria spinulosa and Mytilus edulis in polluted waters indicates that planktonic larvae of these species must actively select polluted waters as a suitable place for settlement. There is no detectable recruitment of a single species on such a scale in the unpolluted waters at Stn. 6.

During the Spring of 1968, the polluted waters are not dominated by suspension feeders for a short time (fig.30) The residual community elements Flabelligera affinis, Acanthochitona crinitus, Amphithoe rubricata, Jassa falcata, and Harmanthoe impar assume a dominant role in the absence of the suspension feeders, but their total numbers in the habitat amount to only 18 individuals. The residual fauna does not remain dominant for more than a few weeks because of the rapid recolonisation of the habitat by another single species population of suspension feeders. By June 1968, the habitat is again occupied by a 70 per cent dominant single species, Sabellaria spinulosa (fig.30). The residual species thus remain subordinate to the two dominant suspension feeders in the polluted water habitat. Any drop in the numbers of the dominant species effectively 'empties' the habitat, leaving it available for the next spatfall of a single species which fills it to capacity once more. Further research is now necessary on the residual species in the habitat to determine if they are suppressed by direct competition with two well adapted polluted water species, or by a direct effect of the polluted waters upon the metabolism of the individual species of the residual polluted water fauna. It is also possible that a combination of direct and indirect pollution effects restricts the abundance of the residual species. This would leave a large part of the habitat free for species better suited to polluted waters. Colonies of Sabellaria spinulosa tubes filled most of the ecospace habitat after settlement but never became the massive structures described by McIntosh (1922) on sublittoral bare rock. When the Sabellid populations had disappeared, large numbers of mussels similarly 'jammed' into the ecospace habitat but were never seen to form the dense colonies on bare rock that can be found on many littoral shores (Lewis 1964).

This is evidence but not proof that sewage enrichment of the water enhances sublittoral ecospace habitats for species able to withstand the other pollutants in the water. The two dominant suspension feeders in this study are sessile forms for whom space on which to settle is of paramount importance. Settlement of planktonic phases of Mytilus and Sabellaria is an elaborate exercise as the larvae of both species have been shown to discriminate between substrates and select optimum conditions before committing themselves to settlement and metamorphosis. The accumulation of large numbers of these species in sewage polluted ecospace habitats therefore seems to indicate a good microenvironment into which Mytilus edulis and Sabellaria spinulosa can settle. Such larvae, having now selected nutrient rich water must compete with large numbers of similar larvae for the optimum ecological conditions required for the survival of each individual. Competition for space must become intense but will be secondary in importance to the selection of a nutrient rich area. Intra specific competition for space is likely to be the biggest single factor determining the success of settling pelagic larvae in the polluted waters at Stn. 15.

Plate 7

Station 15 Souter Point. Depth 2 Metres

Primary and secondary plantigrade settlement of *Mytilus edulis* larvae, on typical species impoverished open coast polluted water community.

Mytilus and *Sabellaria* never co-dominate the polluted waters in this study yet both species are known to produce larvae for most of the year which could colonise the habitat in a series of small larval settlements of both species into the same habitat throughout the year. This does not happen. It would appear that the presence of an already established species excludes the other one. Inter specific competition seems to occur here but the exact mechanism was not determined. When neither species is present in any numbers, as in the Spring of 1968, settlement leading to eventual single species dominance in ecospace communities would appear to be a case of first come, first provided with a habitat.

(4) The annual ecoperiod

The dominant suspension feeders *Mytilus edulis* and *Sabellaria spinulosa* have a similar effect on succession in ecospace (Table 21, 22)

Spatfall of either species fills each ecoperiod and smothers the natural sequence of species accumulation and increase which is a feature of unpolluted systems. The numbers of species and individuals which occupy the habitat in which either *Mytilus* or *Sabellaria* is dominant are reduced to an insignificant level and the succession of these species into the habitat is fragmented and often incomplete.

By comparison with Stn. 6 the retention of suspension feeding domination of the seven annual ecoperiods is a retention of the pioneer stages of succession where suspension feeders are dominant. With succeeding ecoperiods, a larger and more complex community containing omnivores, herbivores, deposit feeders and carnivores

TABLE 22

Succession in 7 Year Ecoperiod. June 1969. Depth 3.5 Metres.
Mytilus edulis dominant in polluted waters.

Station 6
St. Abbs

Ecoperiod years	1	2	3	4	5	6	7	Total species	Per cent of community
Ecospace CC's	0	1.6	10.0	36.0	92.0	181.0	313.0		
Species									
Umbonula verrucosa	1	1	1	1	1	1	1	7	2.1
Mucronella coccinea	1	0	1	1	1	1	1	6	1.8
Ophiopholis aculeata		1	0	1	3	6	2	13	3.9
Asterias rubens		1	0	2	4	10	7	23	6.9
Salmacina dysteri			1	1	1	0	1	4	1.2
Pomatoceros triqueter			2	0	4	10	5	21	6.3
Ophiothrix fragilis			1	9	5	7	16	38	11.4
Amphithoe rubricata				4	3	3	0	10	3.0
Jassa falcata				6	12	10	10	38	11.4
Corophium bonellii				2	8	0	10	20	6.0
Nomia patelliformis				3	0	5	10	18	5.4
Anomia ephippium				5	0	5	2	12	3.6
Balanus balanus				2		8	2	12	3.6
Mya truncata				3	2	1	5	11	3.3
Porcellana longicornis				1	1	8	7	17	5.1
Caprella linearis					2	6	1	9	2.7
Nereis pelagica					5	1	10	16	4.8
Lepidonotus squamatus					4	4	2	10	3.0
Hyas araneas					1	1	1	3	0.9
Pycnogonum littorale						2	13	15	4.5
Cancer pagurus							1	1	0.3
Modiolus barbatus							1	1	0.3
Henricia sanguinolenta							1	1	0.3
Mytilus edulis				1				1	0.3
Acanthocitona crinitus					1		1	2	0.6
Lacuna vincta					3	5		8	2.4
Echinus esculentus					2	3		5	1.5
Botryllus schlosseri					1			1	0.3
Phyllodoce sp.					1	1		2	0.6
Membranopora membranacea					1			1	0.3
Salmacina dysteri						1		1	0.3
Alcyonium digitatum						1		1	0.3
Nymphon gracile						2		2	0.6
Palaemon squilla						1		1	0.3
								332	100.0

Station 15
Souter Point - June 1969

	1	2	3	4	5	6	7	Total species	Per cent of community
Mytilus edulis	4	60	80	200	500	300	200	1344	94.5
Nereis pelagica		1	1	2	4	3	6	17	1.1
Asterias rubens		1		1		4	1	7	0.4
Halichondria panacea		1		1	1	1		4	0.2
Hymeniacidon perleve		1		1				2	0.1
Lepidonotus squamatus				1				1	0.0
Sabellaria spinulosa				10		10	20	40	2.8
Mya truncata					1		3	4	0.2
Flabelligera affinis				1				1	0.0
Cancer pagurus						1		1	0.0
Harmathoe impar							1	1	0.0
								1422	100.0

TABLE 21

Succession in 7 Year Ecoperiod. June 1968. Depth 3.5 Metres
Sabellaria spinulosa dominant in polluted waters.

Station 6
St. Abbs

Ecoperiod years	1	2	3	4	5	6	7	Total species	Per cent of community
Ecospace CC's	0	1.6	10.0	36.0	92.0	181.0	313.0		
Species									
Umbonula verrucosa	1	0	1	1	1	1	1	6	3.1
Pomatoceros triqueter		2	0	5	5	6	8	26	13.7
Nereis pelagica			2	1	2	1	3	9	4.7
Mya truncata			1	1	0	1	6	10	5.2
Ophiothrix fragilis			1	4	3	5	16	29	15.3
Mucronella coccinea			1	1	1	1	1	5	2.6
Lepidonotus squamatus				1	1	2	3	7	3.7
Porcellana longicornis				1	1	2	13	17	8.9
Ophiopholis aculeata					4	2	6	12	6.3
Asterias rubens					2	1	11	14	7.4
Jassa falcata					10	0	1	11	6.3
Eupagurus bernhardus						1	1	2	1.0
Salmacina dysteri							1	1	0.5
Phyllodoce							1	1	0.5
Botryllus schlosseri							1	1	0.5
Henricia sanguinolenta							1	1	0.5
Nymphon gracile							3	3	1.5
Echinus esculentus							6	6	3.1
Palaemon squilla							1	1	0.5
Lacuna vincta		2					1	3	1.5
								2	1.0

TABLE 23

Trophic Component Analysis of Seven Year Ecoperiod

St. Abb's. June 1968. Depth 3.5 Metres.

Ecoperiod (years)	Suspension feeders	Deposit feeders	Herbivores	Carnivores	Omnivores
1	10.0	0	0	0	0
2	33.0	0	0	33.0	33.0
3	75.0	0	0	0	25.0
4	42.8	0	0	4.7	52.3
5	17.9	0	5.4	14.1	62.6
6	41.8	0	5.1	13.2	39.9
7	35.3	0	0	19.8	44.7
	49.4 ± 10.8	0	1.5 ± 0.0	12.1 ± 3.3	36.7 ± 7.8

St. Abbs. June 1969. Depth 3.5 Metres

Ecoperiod (years)	Suspension feeders	Deposit feeders	Herbivores	Carnivores	Omnivores
1	10.0	0	0	0	0
2	10.0	0	0	0	0
3	83.0	0	0	0	16.3
4	63.0	0	0	4.5	31.8
5	34.8	1.3	2.3	9.9	51.3
6	53.0	0	3.3	6.6	36.8
7	36.4	0	1.1	16.4	46.1
	67.1 ± 10.6	0.1 ± 0.0	0.6 ± 0.4	5.3 ± 2.3	26.0 ± 8.0

TABLE 24

Trophic Component Analysis of Seven Year Ecoperiod

Souter Point. June 1968. Depth 3.5 Metres.

Sabellaria spinulosa dominant

Ecoperiod (years)	Suspension feeders	Deposit feeders	Herbivores	Carnivores	Omnivores
1	100.0	0	0	0	0
2	66.0	0	33.0	0	0
3	33.0	0	0	33.3	33.3
4	87.0	0	0	2.5	10.7
5	87.0	0	0	12.9	0
6	86.2	1.9	1.9	7.8	1.9
7	86.8	2.1	0	1.0	8.7
	78.0±21.5	0.8±0.5	4.9±4.7	8.3±4.9	7.8±4.6

Souter Point. June 1969. Depth 3.5 Metres

Mytilus edulis dominant

Ecoperiod (years)	Suspension feeders	Deposit feeders	Herbivores	Carnivores	Omnivores
1	10.0	0	0	0	0
2	96.8	0	0	3.1	0
3	97.5	0	0	1.2	1.2
4	98.1	0.4	0	1.3	0
5	99.2	0	0	0.7	0
6	97.4	0	0	2.1	0
7	96.5	0	0	3.0	0.4
	97.9±0.4	0	0	1.1±0.4	0.2±0.1

is developed in clean water.

Conclusions

Two main ecological parameters are affected in polluted waters. These are:-

(1) The Reduction in Species Diversity

The Species Diversity index remains at a value approximately one half of the value of the clean figure. On the one occasion when the index rose to a value of 3.1 in polluted water, it coincided with the absence of large populations of a single suspension feeder the presence of which always reduces the index of diversity. As a result of the loss of species, two trophic elements assume greater importance and four species are found in considerable abundance in polluted waters. Two of these, Mytilus edulis and Sabellaria spinulosa are suspension feeders the others being the carnivores Nereis pelagica and Asterias rubens. The polluted water community has been reduced to only one possible type of food chain,

Suspended Material → Suspension feeder → Carnivore

(2) The Loss of Stability

Compared with the unpolluted communities at Stn. 6 those of Stn. 15 are violently unstable. The two suspension feeders Mytilus edulis and Sabellaria spinulosa compete with each other for space in the habitat as they were never observed to co-exist as dominants throughout the study. Intra-specific competition is likely as naturally large numbers of suspension feeders select polluted waters as a place for final settlement. The planktonic larvae of the two dominant species settle in polluted waters in a pattern roughly correlating with the arrival of Spring or Autumn when their ultimate success at colonising the habitat seems to depend on the absence of previously settled larvae of the competing suspension feeder species. Competition for space is intense and the natural sequence of community colonisation by a process much like succession is almost destroyed when the larvae colonise all the habitats of the seven year ecoperiod. This results in the development of a permanently retarded community, always dominated by suspension feeders. In clean waters the dominance of suspension feeders is lost after the second or third ecoperiod and a more diverse community, containing larger numbers of more species belonging to all trophic groups is developed.

The unaturally large populations of one species of suspension feeder are violently unstable. Within a few months of successfully colonising the habitat the newly settled juveniles undergo a rapid population decline. This leaves a residual fauna of a small number of species in a habitat which is now well below its carrying capacity of invertebrate numbers. The rapid loss of newly settled juveniles remains unexplained. As far as could be determined no significant change occurred in the rate or the kinds of pollution added to the seas in the vicinity of Stn. 15 during this study. The polluted environment remained so throughout and it is unlikely that any major change in the physical and chemical qualities of the water occurred which would affect the community structure. Disease could spread rapidly through a large population of a single species but no signs of this were observed.

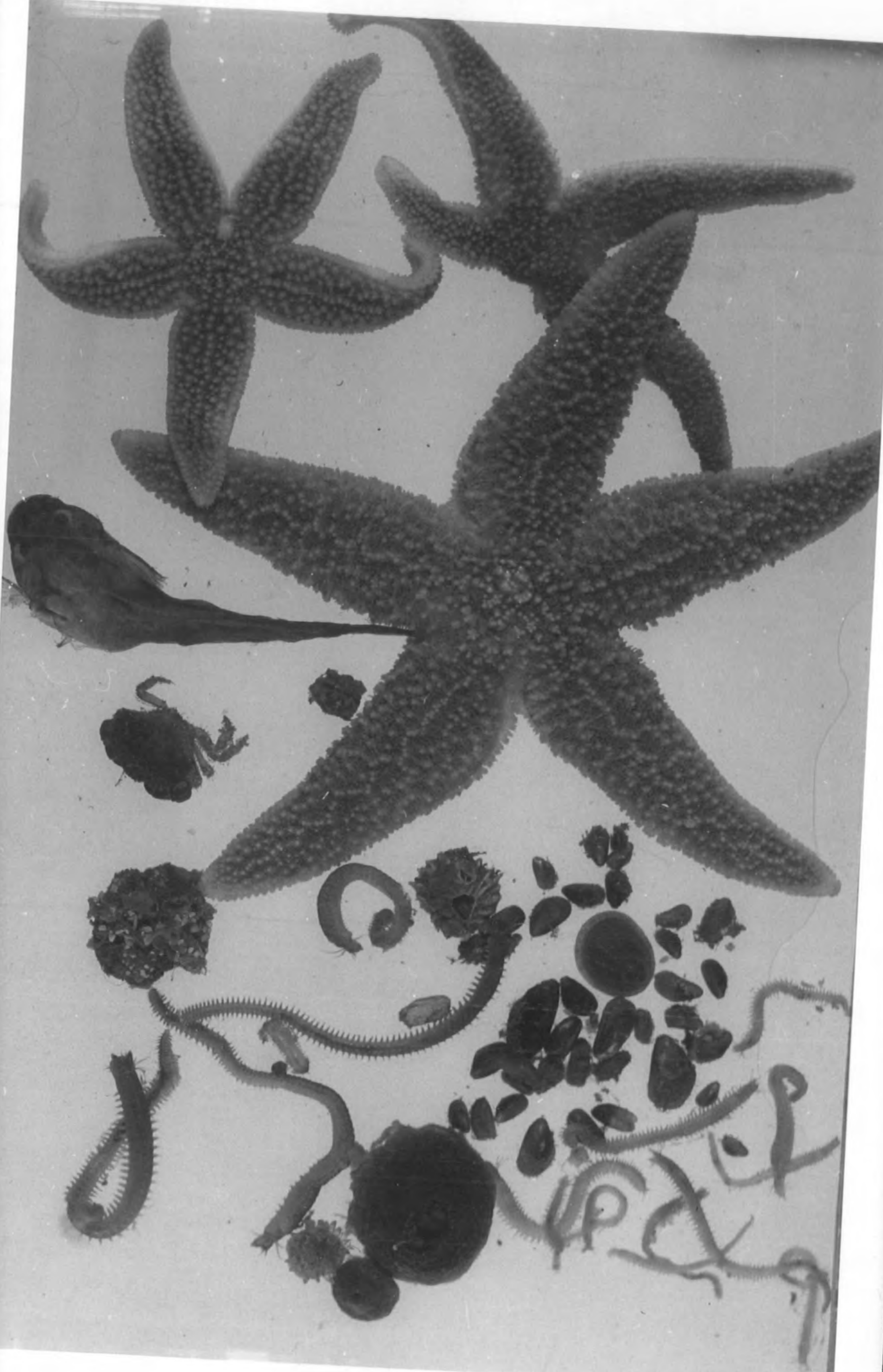
Predation of large numbers of a single species concentrated in one small area can drastically reduce its numbers (Russel & Yonge 1963). The predators <u>Asterias rubens</u> and <u>Nereis pelagica</u>

Plate 8

Station 18. Flamborough Head.

Naturally Turbid. Unpolluted

Typical Community.



are always present in polluted water communities. Mytilus edulis can form a large part of the diet of Asterias rubens. The feeding habits of Nereis pelagica are not known. The carnivore population could increase following the settlement of a large number of suspension feeders some of which are prey species. Seed (1969) describes 'carpets' of Asterias rubens on lower littoral shores in Autumn which decimate populations of Mytilus edulis settled there in Spring. He concludes that predation must be even more significant on the sublittoral populations. However, predators are highly mobile species and no attempts were made in this study to isolate any effects of fluctuations in their abundance. Further experiments on the dynamics of carnivore populations and their impact on the community may provide an explanation for the high mortality apparent in unaturally large, almost single species populations in polluted water. Senility is very unlikely as Mytilus edulis can live for 20 years (Seed, 1969) and Sabellaria spinulosa for up to seven years (Wilson, personal communication). The populations at Stn. 15 change places every nine months. There was no evidence of accelerated metabolism in any of the populations.

The polluted water community can thus be considered as a juvenile stage which has been retained throughout community development. The simple system becomes a virtual monoculture of suspension feeding species which is highly unstable and liable to violent population fluctuations.

More research should now be aimed at explaining -

(1) The reasons why half the available species complement are not found in polluted waters.

(2) The ecological factors subordinating many pollution intolerant species to the dominance of suspension feeders.

(3) The short lived success of large suspension feeder populations.

SECTION III

Some A-biotic data on the polluted environment

Sea Water Analysis

Some analytical data relating to the inshore waters under consideration is given in Table 25. For method of collection and analysis see Appendix 1.

Available inorganic nitrate (NO_3, NO_2 and NH_4), phosphate (PO_4), and silicon (SiO_3) are of extreme importance in sea water, occurring naturally in such low concentrations that they can be rate limiting for plant growth. (Raymount, 1966). Levels of these nutrients at Stn. 6 (St. Abbs) are low and of the same order as the mean annual levels for the more northern oceanic areas of the North Sea (P.Head, personal communication).

Erosion products of the land, can enrich coastal seas adjacent to river estuaries with inorganic nutrients and the decay products of organic material originating on the land mass, (Riley, 1937), (Rees, 1939), (Harvey, 1945) (Kalle, 1953). The addition of industrial and domestic pollutants to river systems can further increase nutrient levels of coastal waters in the vicinity of estuaries (Ren, 1956), (Jeffries, 1962), (Koch, 1959), (Odum, 1961a) (Cronin, 1967).

Scant data exists on the inorganic nutrient levels in the estuaries of the Rivers, Tyne, Wear and Tees. Nitrate (NO_4) levels of 177 μg/100 mls, phosphate (PO_4) at 95 μg/ml and suspended solids in excess of 400 μg/100 ml have been recorded in the mouth of the River Tees (Watson and Watson, 1968). Similar trends in the industrial and urban development along the Rivers Tyne and Wear must inevitably enrich these rivers. It is significant that along the North East coast, the highest levels of nitrate, phosphate and silicon

TABLE 25

Sea Water Analysis

Mean annual phosphate, nitrate and silicon levels along North East pollution gradient

µ gms / litre

Station	PO_4 µgm/litre	NO_3	NO_2	NH_4	SiO_3
6 (St.Abbs)	0.37	2.1	0.14	1.7	4.5
8 (Holy Isle)	1.33	7.8	0.13	1.3	5.0
11 (Beadnell)	1.74	10.5	0.21	2.5	5.0
12 (Craster)	1.85	4.45	0.3	4.3	5.5
13 (Newbiggin)	2.21	6.05	0.19	2.4	4.85
14 (St.Mary's)	1.68	7.85	0.31	4.1	6.75
15 (Souter Point)	2.78	19.0	3.25	13.5	14.5
16 (Seaham)	1.95	23.3	1.95	27.2	12.0
17 (Robin Hood's Bay)	2.48	18.8	3.59	20.7	8.7
18 (Flamborough Head)	2.10	11.65	0.26	5.1	5.9

in solution occur in the polluted coastal seas adjacent to the three polluted rivers of County Durham.

Phosphate levels at 2.78 µgms/litre at Stn. 15 (Souter Point) are over seven times higher than those at Stn. 6 (St. Abbs). Total inorganic nitrates at Stn. 16 (Seaham) reach 52.4 µgms/litre, more than thirteen times higher than at Stn. 6. Similarly, silicon levels are twice as high at Stn. 16 than at Stn. 6.

The inorganic nitrate levels in the naturally turbid waters at Stn. 17 and 18 (Robin Hood's Bay and Flamborough Head) fall between the naturally low figures for Stn. 6 and the unnaturally high figures for Stn. 15 and Stn. 16. The large inorganic suspension load of boulder clay constantly eroding into the sea along the whole of this area of coastline must account for some of the higher than normal levels of inorganic nutrients in the adjacent sea.

No data exists on the exact amount of pollutants carried into the sea along the whole of this area of coastline via the rivers and sewage outfalls. In the absence of contrary evidence, the indications are that sewage pollutants added to the seas off County Durham increase the inorganic nutrient levels found there and effectively enrich the otherwise nutrient poor waters of this coastal region of the North Sea.

Until much more is known about the position of these micronutrients between the sediments, the biota and other extracellular products in suspension any conclusions as to the ecological significance of these values and their effects on the biota must be regarded with caution.

The values of PO_4, NO_3, NO_2, NH_4 and SiO_3 indicate enrichment of the polluted waters. The high values for Stations 17 and 18 could indicate either a southward 'drift' of the enriched water of the Durham coast or the effects of natural erosion stated above. The markedly higher levels of NH_4 at Stn. 17 would indicate the former.

Sediment in Ecospace

Sediments accumulate in ecospace in both polluted and unpolluted waters along the North East coast. Some data is given in Table 26. No sediments accumulate at Stn. 6 in clean waters. Stn 8 and 11 contain large amounts of sediments which increases with the increasing size of the habitat. There is no pollution in this area and the levels of accumulated sediment must be considered normal. Similar levels of sediment are also found in the polluted waters at Stn. 15. and rather lower levels in the unpolluted but turbid waters at Stn. 17.

TABLE 26

Accumulation of sediments in ecospace at Stations along the North East Pollution Gradient. May 1969. GMS. WET WEIGHT.

Ecoperiod (years)	Ecospace CC's	Stn. 6 St.Abbs	Stn. 8 Holy Isle	Stn. 11 Beadnell	Stn. 15 Souter	Stn. 17 R.H.B.
1	0	0	0.0	0.0	0	0.0
2	1.6	0	0.2	0.8	0.2	0.1
3	16.5	0	1.8	2.0	10.0	4.1
4	71.0	0	14.0	13.0	10.7	1.4
5	169.0	0	16.5	17.0	16.0	25.7
6	266.0	0	28.0	15.9	20.0	3.9
7	410.0	0	33.0	36.5	36.5	10.0

The levels of lead, zinc, nickel and copper, iodine, zirconium and barium are higher in polluted water ecospace sediments than those at Stn. 8 and Stn. 11 in unpolluted water (Table 27).

TABLE 27

Mineral Analysis of ecospace sediments at Stn. 8 (Holy Isle), Stn. 11 (Beadnell) and Stn. 15 (Souter Point) in parts per million.

	Pb	Zn	Cu	Ni	Ba	I	Zr	Sr	Br
Stn. 8 Holy Isle	22	55	25	22	250	600	300	450	350
Stn. 11 Beadnell	17	40	15	10	200	450	150	700	550
Stn. 15 Souter Point 1.	55	95	20	20	500	430	600	350	250
2.	55	95	25	20	600	400	650	400	200
3.	80	130	27	30	600	800	600	450	250

High iodine levels indicate oxidising (AEROBIC) conditions at all stations, whilst the higher levels of lead, zinc and copper in polluted water indicate the presence of a greater proportion of organic sludge in polluted water sediments (J.Price, personal communication).

Again the problem of drawing conclusions from data of this kind is a lack of information on the 'NORM'. It is tempting to cite pollution as the cause of higher heavy metal values in the sediments. However, it must be remembered that the Rivers Tyne, Wear and Tees which carry the pollutants also drain areas which have been the centre of much mineral mining, especially for lead.

There is, however, no getting away from the fact that -

(i) ecospace occupied by sediments cannot be occupied by biota,

(ii) the more 'toxic' these sediments, the greater will be their effects on ecospace.

SECTION IV

Further Analysis of Ecosystem Data

1. Heavy Metal Tolerance

There is a large discharge of waste containing heavy metals into the seas off County Durham especially in the vicinity of the Tees estuary (Watson and Watson, 1968), (House, 1969).

It would be tempting to speculate that the instability of suspension feeders in polluted water could be due to accumulation of toxicoids such as heavy metals, in the tissues of the species present in polluted water. Although detailed study of physiological responses to pollution was beyond the scope of the work, the results of a preliminary investigation are reported below:

Levels of iron, lead, copper, zinc and mercury were measured in the tissues of selected species collected from polluted and unpolluted waters in an investigation of the resistance of pollution indifferent species to this pollution stress. (For methods of extraction and analysis see Appendix 1). Three common species which were abundant in all study areas and hence are known to be pollution tolerant were selected. These were,

Laminaria hyperborea

Mytilus edulis

Asterias rubens

Specimens were collected from Stn. 6 (St. Abbs). Unpolluted. Stn. 15 (Souter Point. Chronically polluted, and Stn. 17 (Robin Hood's Bay). Unpolluted but naturally turbid.

It was found that similar species contain different amounts of the same metal at the three stations (Table 28). In all cases, the highest concentration of iron, lead, copper and zinc, efficient • polluted water communities. The situation that exists at present appears to rely on essential species replenishment from outside the affected area. Anything that interferes with this outside source of planktonic larvae could easily destroy the polluted water community which at present seems unable to exist independently of breeding stocks some distance away.

The last remnants of a once diverse and mature community can thus be looked on as a natural adaptation of the community in its efforts to adjust to the 'stress' or opportunity of pollution. The successful community removing some of the pollutants and tending to contain the affected area to the near shore environment. If this system could be stabilised and matured it would further restrict the pollutants to the smallest possible area. The loss of many species from the polluted communities would be the ecological price that is paid for such development. Providing other areas are maintained pollution free which act as reservoirs for pollution affected species this loss need not be as alarming as it would at first appear.

Such a compromise between Man and the ecosystem would appear to provide the only practical answer to the problem of disrupted natural systems occurring in areas polluted by ever increasing amounts of waste products which are poured into the sea.

APPENDIX 1

MATERIALS AND METHODS

1. Fieldwork

Sampling stations are located at convenient access points to the sea where coastal roads lead to harbours, shipways and piers. Divers collected all samples using aqualungs so that coastal installations greatly assist the divers entry into the water by providing firm footing and shelter from rough seas. Swimming out on the surface a diver and his partner submerge when over the kelp forest. Using a wrist depth gauge the vertical extent of the kelp forest is determined by swimming over it. Inaccuracies in the calibration of depth gauges and the changing level of the tide during sampling, invariably leads to an error in all depth estimations of approximately one metre.

At a chosen depth, a holdfast is selected, quickly removed from the rock with a sharp knife and placed in a small hessian sack some 20 x 25 cms square. The sack is quickly drawn closed using nylon draw strings in the neck. The protuding stipe and lamina are cut away. A size range of six holdfasts at each depth is collected in this way, one plant being placed in one bag. With experience, one diving pair can sample eight stations in one day at any depth in the kelp forest. Stations 1,2,3,4 are located in the Firth of Forth Estuary and were sampled from a boat provided by the Lothian River Authority. Samples stations 11 and 12 are located on the Farne Isles which were reached using a PB-16 'Z' boat powered by a 33H.P. outboard engine.

In this largely shore based study, the sampling area is rarely more than 150 yards from the divers point of entry to the water. It has been found that the grid reference is sufficient information for the relocation of a station. Where boats are in operation the latitude and longitude of the station and some description of the physical features which are above water in the vicinity are sufficient for relocation of the study area. The moment a diver submerges his description of the sublittoral terrain becomes of no use to anyone but himself when the relocation of specific areas of the study area is required.

High winds making rough seas are the main factor preventing regular access to the sublittoral. Turbidity is the most important factor controlling the accurate relocation of study areas. In this study divers frequently worked 'by touch' in the total blackness of highly turbid polluted seas.

Cold is not a problem if adequate equipment is available. Continuous sampling throughout the winter months is always hampered and frequently halted by severe storms which commonly occur over winter in the North Sea. Items of steel equipment weighing approximately half a ton, designated for in situ physiological experiments were totally destroyed by rough seas within months of their installation on the sea bed. Five attempts at in situ experiments with this kind of equipment were all destroyed by heavy seas after which this experiment design was abandonded for the remainder of the study.

In all approximately 200 hours 'bottom time' were logged, i.e. submerged and sampling the kelp forest, spread over two and half years. With the assistance of other divers some 500 man-hours submerged are logged in the course of this study.

2. Laboratory sorting of field material

Whenever possible all material is best handled still fresh and alive, but samples placed in a cold room at 5°C remain alive for up to four days. Each holdfast is treated in the following manner:-

(a) Record date, station and depth at which collected.

(b) Measure the length and breadth of the basal part of the holdfast.

(c) Measure the vertical height and maximum stipe diameter.

(d) Weigh the entire holdfast.

(e) With a sharp knife, cut away successive hapteron whorls, stopping at frequent intervals to remove exposed specimens of the fauna. Collect all the fauna within the holdfast in this way.

(f) Age the plant

(g) Wash all detritus and sediment from the cut up holdfast. 'Damp dry' with absorbent tissue and reweigh all the pieces of holdfast together.

(h) Store the detritus and sediment collected from one station.

(i) Identify the fauna

(j) Count each species present

(k) Weigh the individuals from one plant together.

(l) Measure the length of each individual in a species or some indication of growth (see Section II Part 2 - Size Frequency Analysis).

It is now possible to calculate -

(1) The ecospace surrounding one holdfast. The weight of washed and dried holdfast is taken as the true weight of tissue present.

(2) The age of the plant

(3) The species list for an ecospace community about one plant.

(4) The numbers of individuals of one species in an ecospace community. Where encrusting forms are found the colony is considered as one individual, thus

Umbonula verrucosa = 1

(5) The size frequency of the individuals in a species.

(6) The weight of species in ecospace.

Samples of the seven year ecoperiod used in this study are obtained from 21 stations around British coasts over a period of three years. Approximately 2,000 plants were sampled and of these, 1,400 were used for ecospace determinations. The fauna located in 1,000 holdfasts of all ages were studied and documented for 600 plants. One hundred and twelve species from eight phyla are used in the study.

3. Laboratory Analysis

(1) Calculation of Ash free dry weight.

Using weighed crucibles the dry weight and organic weight of a species can be determined in the following manner.

If A gms = Crucible weight

B gms = Wet tissue weight plus Crucible Weight

C gms = Dry tissue weight plus crucible weight

D gms = Ash weight plus crucible weight

Then

(i) Wet tissue weight = (B-A) gms.

(ii) Dry tissue weight = (C-A) gms (Dry to constant weight at 91°C)

(iii) Ash weight = (D-A) gms (Burnt in air at 410°C)

(iv) Ash free (organic) weight = (C-D) gms.

A Fortran IV computer programme converted the raw data to comparisons of one gram wet weight per set of weighings. This allows absolute comparisons of the proportion of water, to ash, to organic weight between similar species collected at different stations and comparisons between different species to be made. The percentage composition per gram wet weight was also calculated to allow some comparison of the relative proportions of ash plus organic content to be made. Most of the species involved in this analysis weigh less than one gram wet weight per individual specimen. All weighings were, therefore, taken to the fourth decimal place as weight changes were frequently only detectable at the third and fourth decimal place.

2. Ash Free Dry Weight in Ecospace

As long as the amount of ecospace and the ecoperiod are equivalent, comparisons of the biomass of ecospace communities remain ecologically sound. Using the ash free dry weights calculated above, simple conversions of the total wet weight of an animal can quickly be made. The sum of the ash free dry weight for animals removed from one plant is the total organic weight in ecospace for that habitat. This is equivalent to the nett secondary productivity of the habitat.

Dry weights and mineral (ash) weights contain varying proportions of shell and other skeletal remains which preclude their use in biomass comparisons. The proportion of tissue composed of mineral material varies greatly from species to species. This makes comparisons of communities containing different species difficult if dry or ash weights are used. Organic weights present no such difficulty and are widely used in the estimation of the productivity of communities.

The wet weight of species in ecospace communities is sometimes so small that conversion to organic weight becomes impossible. For this reason all species containing less than 0.01 gms ash free dry weight per total wet weight of the species in the habitat are not included in the estimation of total ash free dry weight in ecospace. Greater care and extreme patience are necessary to obtain accurate weighings of small amounts of living tissue. Small variations in species wet weight become magnified by conversion to ash free dry weight and this technique is liable to large experimental errors through handling of the living organisms during weighing.

Mineral Analysis of Living Tissue

All specimens were sorted within six hours of their removal from the sea. Wet weighings were of 'damp dried' specimens. After drying to a start weight at 105°C weighed aliquots are made up for analysis as described by Jeffries and Willis (1964).

Iron (Fe^{++}) is analysed on a Hilgar and Watts Atomic Absorption Spectrophotometer using a wavelength of 2483Å giving a theoretical sensitivity for 1 per cent absorption of 0.15 ppm.

Copper (Cu^{++}), Lead (Ph^{++}), Mercury (Mg^{+}) and Zinc (Zn^{++}) are determined in an 'Eel' Atomic Absorption Spectrophotometer using 325 $m\mu$ for copper giving a theoretical sensitivity for 1 per cent absorption of 0.1 ppm.

283 $m\mu$ for lead (this prevents sodium interference) giving a theoretical sensitivity of 0.85 ppm.

Mean concentration in μ gms/gm dry weight of the heavy metals, Iron, Lead, Copper, and Zinc at Stn.s 6,15 and 17.

Species	Station	Fe	Pb	Cu	Zn
Laminaria hyperborea	6	58.1 ± 12.7	26.6 ± 3.4	2.6 ± 0.5	1226.8 ± 341.7
	15	128.0 ± 16.9	78.0 ± 9.9	16.0 ± 2.4	3678.0 ± 426.9
	17	98.0 ± 8.7	22.0 ± 5.0	12.0 ± 2.0	2736.0 ± 300.0
Mytilus edulis	6	182.2 ± 14.5	127.7 ± 7.4	9.8 ± 0.4	1652.2 ± 126.7
	15	1682.0 ± 332.7	302.5 ± 95.6	15.0 ± 2.8	3155.0 ± 196.0
	17	648.0 ± 15.8	131.6 ± 15.6	13.3 ± 10.0	5721.0 ± 155.5
Asterias rubens	6	182.5 ± 37.7	150.0 ± 24.4	10.0 ± 0.0	7277.0 ± 245.6
	15	180.2 ± 13.1	336.6 ± 38.2	27.0 ± 5.9	8848.0 ± 224.5
	17	146.6 ± 13.8	110.3 ± 13.1	15.0 ± 5.0	8637.0 ± 140.3

is found in the polluted water specimens. Mercury occurs at less than 250 μgms/gm dry weight at all stations, this was the upper limit of detection by the method used.

The three selected species appear to use at least two methods accommodating heavy metal stress. These are:

(1) Ionic Regulation

The echinoderm Asterias rubens shows no progressive loss or gain of heavy metals in its tissues with increasing size (age). This species tolerates widely different levels of heavy metals in its tissues which are regulated and maintained at a specific level for all size classes at the three stations. Thus, the level of copper never exceeds 10 μgms/gm dry weight at Stn. 6 but never falls below 20 μgms/gm in the polluted waters at Stn. 15. In the naturally turbid waters at Stn. 17 an intermediate level between 10 μgm/gm dry weight and 15 μ gm/gm is maintained (Table 29).

(2) Ionic Acclimatisation

Mytilus edulis spat contains higher levels of lead, copper, zinc and iron than older individuals at the same station. As the individuals get bigger and older, the amount of heavy metals in the tissues gets smaller. This physiological response to stress is described by Prosser (1961) and termed acclimatisation.

At Stn. 6, Zinc levels drop from 2450 μ gm/gm to 1600 μgm/gm. Copper falls from 20 μgms/gm in spat to 10 μgms/gm in adults. Iron levels drop from 280 μgm/gm to 140 μgm/gm and lead from 150 μgm/gm in spat to 120 μgms/gm in eight year old adults. The levels of all four irons are much higher in spat settling in polluted water.

TABLE 29

Heavy metal levels in μgm/gram dry weight in age classes of Laminaria hyperborea and Mytilus edulis and size classes of Asterias rubens at Stns. 6, 15 and 17.

1. IRON (μgms/gm dry weight

	Stn.6	Stn. 15	Stn. 17
Laminaria hyperborea			
Age			
1	-	-	-
2	70	-	120
3	50	170	110
4	50	150	100
5	50	70	90
6	40	110	70
7	40	140	-
Asterias rubens			
0-5 cms	150	230	120
5-7.5	220	160	165
7.5-10	210	176	155
10-12.5	150	175	-
Mytilus edulis			
Age			
Spat	280	2680	170
1	180	1350	930
2	160	1320	930
3	210	1380	990
4	200	-	690
5	170	-	180
6	150	-	-
7	140	-	-
8	140	-	-

2. LEAD (μ gms/gm dry weight)

	Stn.6	Stn. 15	Stn. 17
Laminaria hyperborea			
Age			
1	-	-	-
2	30	-	30
3	40	110	20
4	20	80	20
5	20	50	20
6	20	50	20
7	30	50	-
Asterias rubens			
0-5 cms	90	470	10
5-7.5	150	260	10
7.5-10.0	210	303	25
10.0-12.5	150	365	-
Mytilus edulis			
Age			
Spat	150	180	200
1	110	150	110
2	120	310	120
3	150	570	140
4	150	-	130
5	150	-	90
6	100	-	-
7	100	-	-
8	120	-	-

3. COPPER (μgm/gm dry weight)

Age	Stn. 6	Stn. 15	Stn. 17
Laminaria hyperborea			
1	0	-	-
2	0	-	20
3	2	10	10
4	2	10	10
5	2	10	10
6	3	20	10
7	3	20	-
Asterias rubens			
0-5 cms	10	50	10
5-7.5	10	25	10
7.5-10.0	10	20	25
10.0-12.5	10	20	-
Mytilus edulis			
Age			
Spat	20	20	20
1	10	20	20
2	10	10	10
3	4	10	10
4	5	-	10
5	10	1	10
6	10	1	1
7	10	-	-
8	10	-	-

4. ZINC (μgm/gm dry weight)

Age	Stn. 6	Stn. 15	Stn. 17
Laminaria hyperborea			
Age			
2	2830	4170	3850
3	1310	3540	2440
4	690	2120	2270
5	730	4520	2300
6	760	4040	2820
7	1040	-	-
Asterias rubens			
0-5 cms	7330	8830	5920
5-7.5	7950	8205	10,393
7.5-10.0	6970	8790	9600
10.0-12.5	6860	8820	-
Mytilus edulis			
Age			
Spat	2450	3570	5850
1	1810	3400	5580
2	1400	2900	5910
3	1670	2750	6060
4	1480	-	5900
5	1370	-	5030
6	1160	-	-
7	1930	-	-
8	1600	-	-

The levels of all four irons are much higher in spat settling in polluted water at Stn. 15, though the levels get lower as the species get older, iron, lead and zinc are always present in higher quantities in polluted water specimens of equivalent age groups.

Copper levels decrease at the same rate to the same level in polluted, unpolluted and naturally turbid waters. Zinc levels are higher in naturally turbid waters at Stn. 17 but the rate of loss and the quantities lost at Stn. 6 and Stn. 17 is roughly equivalent.

At Stn. 16 <u>Laminaria hyperborea</u> regulates lead plus copper to 30μgm/gm and 3μgms/gm respectively. The plant becomes acclimatised to iron and zinc. At Stn. 6 young plants contain 2830μgms/gm zinc; seven year old plants at the same station contain 1040μgms/gm zinc, a loss of 1790μgms/gm dry weight over 6 years. In polluted waters at Stn. 15, copper levels increase slightly in <u>Laminaria hyperborea</u>, but iron, zinc and lead decrease as the plants get older. At Stn. 17 levels of iron are acclimatised; two year old plants contain 120μgm/gm falling to 70μgms/gm in 6 year old plants. Copper is regulated to 10μgms/gm; zinc to approximately 2,300μgms/gm and lead to 20μgms/gm. The algae <u>Laminaria hyperborea</u> seems able to acclimatise and regulate the levels of heavy metals in its tissues. Iron is 'acclimatised', copper is regulated while lead and zinc can be both regulated and acclimatised.

These pollution resistant species use at least two mechanisms which can accommodate the organism to varying levels of heavy metals. The active carnivore Asterias rubens regulates ionic levels of heavy metals. The sessile filter feeder Mytilus edulis becomes acclimatised whilst the algae Laminaria hyperborea can use both mechanisms.

All three species maintain higher levels of heavy metals in polluted water. The following points must be made.

(1) The levels of zinc are all much higher than the values recorded by other workers (Black & Mitchell, 1952) (Bryan, 1969), (Young and Langille, 1958). The accuracy of the methods used is thus suspect, but the comparative values of the results between stations is not. There are undoubtably more heavy metals present in the organisms collected from the polluted waters. Great care was taken in cleaning the tissues of adhering matter before extraction but there is still the possibility that particles of sediment or other contaminating material could act as a source of error.

(2) Mussels take at least one year to reach sexual maturity (Seed, 1969). It has been shown that unstable mussel populations crash to virtual extinction within a period of approximately nine months leaving only a very small residual population to grow older and reach sexual maturity. Before the polluted water community can again become dominated by Mytilus edulis, a new population of suspension feeders must first be recruited which can only come in such large numbers from adult populations of mussels, the majority of which must be located outside the polluted area.

Each time a new population arrives in the polluted area it has to establish itself against a high background level of toxicoids present in the polluted water. This is a process which only Mytilus edulis and Sabellaria spinulosa seem capable of, with spectacular if somewhat short lived success.

The logical extension of this work is to seek a more precise correlation of heavy metal levels in the environment and in the organism and to establish if there is a toxicoid build-up in the suspension feeders before a population crash. In this way more accurate measurements can be obtained of the ecological effects of toxicity stresses on populations of suspension feeders. The possible contribution that heavy metal pollution may make to the instability of polluted water populations can then be determined.

(2) Ash Free Dry Weight Analysis

The logical extension of the description of the dynamics of 'succession' and the ecosystem part of the study would be to qualify the processes by measuring the productivity of the ecosystem and its components in polluted, unpolluted and naturally turbid waters.

The first step in the estimation of the productivity of a species or community is the determination of nett biomass in unit area. Water, mineral content (measured as ash weight) and organic weight (measured as ash free dry weight) are the three properties of the biomass of species which can be easily determined by analysis. Ash free dry weight analysis was therefore undertaken on the species in ecospace communities to produce the comparative figures for use in the calculation of the productivity and performance of ecospace communities. The results are given in Appendix 5. Each species contains a characteristic proportion of organic material per gram wet weight of tissue. In all the species sampled, the mean value for the organic content is approximately one tenth of the wet weight of fresh tissue. This ratio remains roughly constant for species belonging to different phyla and different trophic components. It remains constant at all the geographical locations from which a species was collected and the ratio remains unaffected in species collected from polluted water.(Table 30)

Some differences do occur in the proportions of wet tissue weight to ash free dry weight, between 0.001 and 0.01 gms ash free dry weight. However, many of the species which are numerically abundant at a station are only present in very small amounts by weight, e.g. Anomia ephippium, Sabellaria spinulosa, Mytilus edulis and provide only a small biomass for analysis even after extensive searching and sampling.

Inevitable experimental errors introduced by handling such small amounts during analysis must effectively mask small variations in the ratio of wet to organic (ash free dry weight) and prevent the detection of any natural variation which occurs at these low orders of magnitude.

A disjunct distribution of pollution intolerant species has been shown along the North East coast during this study. The investigation of the possible effects of pollution on the ratio of organic weight to tissue weight is therefore not possible on species which are restricted to clean waters.

The biomass of invertebrates present in ecospace habitats is so low that accurate determinations of secondary productivity in a 7 year ecoperiod are liable to considerable experimental error, a result of analysing such small amounts of material and this variation could significantly affect the final productivity figures.

This is especially true of the first three of the seven year ecoperiods when total biomass figures only begin to be detectable at the second decimal place. Furthermore, many rare species and the commoner encrusting forms frequently cannot be collected in sufficient quantity for analysis as they are almost always present in very small amounts by weight.

Spatial and temporal studies of the secondary productivity in ecospace were, therefore, discontinued as they were considered to be an impractical technique for use in this study.

DISCUSSION

DISCUSSION

Kelp forests dominated by Laminaria hyperborea characterise the rocky inner sublittoral of the British coasts. Along certain stretches of the east coast of Britain, this ecosystem bears the brunt of the pollutants voided into the sea from the coastal conurbations. The aim of this work was to determine the effects of this pollution on the structure and function of the ecosystem.

As the areas under consideration have been subject to chronic pollution for more than 100 years prior to the study, comparison with prepollution data was impossible. It was, therefore, decided to base the work on comparative studies between polluted and unpolluted ecosystems. The main problem with this kind of approach is the equivalency of the units of comparison being used in the study.

A. Selection of the Comparative Unit

The unit selected for comparative study was the invertebrate fauna developed within the hapteron of the dominant primary producer, the kelp, Laminaria hyperborea. The reasons for making this choice were as follows:-

(1) Growth of the kelp holdfast provides a sheltered habitat, ecospace, which gradually increases in volume over the life span of the plant. The rate of increase, size attained, and the time scale of habitat development is a direct function of the growth of the kelp which is itself a function of the environment in toto (Bellamy, et al. 1969).

(2) The holdfast and its contained fauna can be rapidly and easily collected for study.

(3) Study showed that the development of the fauna follows a definite pattern with time, a pattern of the successive recruitment and development of populations of different species. Some of these species, having once become established remain as constant members of the community others only remaining for a given period of development. The process would thus appear to represent a true biotic succession. This 'succession' processes from a juvenile stage characterised by a simple suspension feeding system containing only a few individuals to a mature system containing omnivore, carnivore, herbivore and deposit feeding elements in a more complex and diverse community. This biotic succession is unique in that it has a finite life span which along the east coast is usually seven years, the maximum life span of the plant.

(4) Study also showed that the community developed in ecospace was a biotic unit in its own right being a detritus 'baind' ecosystem dependent on the primary producer only for shelter.

(5) Regression analysis of ecospace volume with plant age from 20 stations around the coast of Britain showed that the growth statistic of ecospace varies with depth and geographical location. However, within the North East region under study, this variation is negligible.

B. Selection of Sampling Stations

Three unpolluted reference stations were selected simply by consideration of their location in relation to centres of population and industry. Each was characterised by clear, non turbid waters in which a kelp forest rich in species of macrophytic algae extended to considerable depths. Using one of these stations, St. Abbs, as the centre, other stations were selected both to the North and to the South, each station being progressively nearer to industrialised areas. The study was continued further to the south into waters which, although unpolluted, are characterised by natural turbidity. The whole stretch of 250 kms of coast constituted the pollution gradient for the study.

C. Establishment of the 'NORM'

UNDOUBTEDLY ~~Undoubtably~~, the most difficult problem in comparative studies is to establish exactly what a normal ecosystem consists of and how it varies with variation in the natural physical environment. This was attempted here using spatial and temporal studies of holdfast communities in order to identify variation in space and time.

Investigation of the community developed over the 1-7 year ecoperiod at three widely separated unpolluted reference stations, indicated a basic underlying structure common to all three stations. Each community is rich in species and has a high index of diversity (3.1 at Bantry Bay, 3.8 at Loch Ewe and St. Abbs) being co-dominated by omnivores and suspension feeders. Herbivorous forms occur only in low numbers, detritus feeders are rare while carnivores on average account for about one tenth of the ecospace community. Comparisons with accounts of the Arctic Boreal Epifauna described by Petersen (1915), Spark (1937), Einarsson (1941), Gislen (1931), Jones (1950) shows this to be a widespread feature of North European waters.

The species Paracentrotus lividus, Amphitrile gracilis, Diodora apertura, Anemonia sulcata, Pilumnus hirtellus were confined to Bantry Bay, a station located in the Mediterranean Atlantic region, mean annual sea temperature, 15°C (Ekman 1953). The major zoogeographical variation is thus eliminated as the main study was carried out in the Arctic Boreal region, mean annual temperature 10°C (Ekman, 1953), of the North Sea.

However, detailed consideration of the selected pollution gradients showed that they encompassed three distinct natural sub environments, the clear water open coasts, the naturally turbid open coast and estuarine waters.

(1) The Clear Water Open Coast

Stations 5 to 12 are all situated in areas which on the grounds of their position, water clarity and vertical extent of the kelp forest would be classified as unpolluted. All stations except 9 and 10 have typical Arctical Boreal communities with a high species diversity, Margalef Indices ranging from 3.0 to 4.2. Simplification of the community structure is only found at Stations 9 and 10 which are both situated on the Farne Islands at least 2 kilometres from the mainland in areas of very high water movement. All other sites were, therefore, selected in close proximity to the mainland and in situations where there was not excessive water movement.

(2) The Estuary of the Firth of Forth

Fifty four species, all of which were commonly occurring at the above stations, were absent from Stations 1 to 4 which are situated within the Firth of Forth. Five species, Metridium senile, Corella parallelogramma, Chlamys (tigerina?), Pecten sp and Ophiocomina nigra were only found in the estuary.

Unfortunately, Station 3 is the only estuarine study area which is situated outside the main pollution stream passing through the estuary. Here the diversity index reaches a value of which is as high as the value recorded at some of the clear water open coastal stations. The community is trophically simplified here forming a diverse but predominantly suspension feeding unit in which 73.1 per cent of the community is composed of suspension feeders.

(3) Naturally Turbid Waters

The ecospace communities developed in the naturally turbid waters of Stn. 17 and 18. on the Yorkshire coast at first sight appear very similar to those from the clean water open coast stations. A balanced trophic structure (Suspension feeders 54.3 Herbivores 1.2 per cent,
Carnivores 27.5 per cent and Omnivores 17.1 per cent) is backed by a diversity index of 3.1 and 3.2 both of which, though low, are within the range of the clear unpolluted stations. However, closer examination shows that some similarities between Stations 17 and 18 and those in the Firth of Forth exist. The suspension feeding species Dasychone bombyx is found only st Stn. 17 and within the estuary and the following species were found only in the clear, clean waters.

Velutiana lovegata, Tectura testudinalis, Dendrodota grossularia Tubulanus annulatus, Rissoa sp., Rostanga rufescens, Aeolidia papillosa, Aplysia punctata, Bulla sp. Actaeon tornatilis, Panoplea minuta, Eurynome aspera, Berthella plumula, Polycera quadrilineata, Musculus sp. Archidoris pseudoargus. These species are all of rare occurrance even at the clean water stations and it must be accepted that conclusions based on rare species in a situation where the adequacy of sampling could be in doubt, must be viewed with caution. However, it is probably safe to conclude that some similarities exist between the estuarine environment and the naturally turbid waters at Stations 17 and 18.

Temporal studies at Station 6 over the 31 months of the study bear out the above findings and show that the gross features of the 'norm' for unpolluted open coast communities changed very little. Throughout the study the 0-2 year ecoperiod remains a simple suspension feeding unit which gradually develops into a more complex unit containing elements of the other trophic groups. Although the populations of individuals species in the mature community fluctuates over the year, the diverse trophic structure is maintained. A basis for comparative work was thus established.

Using exactly similar methods, study of the ecospace communities at the polluted stations, 1,2, 4, 13, 14 and 15 showed the following differences. The characteristic fauna of the three natural regional subenvironments has been replaced by one much simplified system. Rare species are missing and species which are 'normally' common and abundant become rare and insignificant elements in the polluted water ecosystem. These include:-

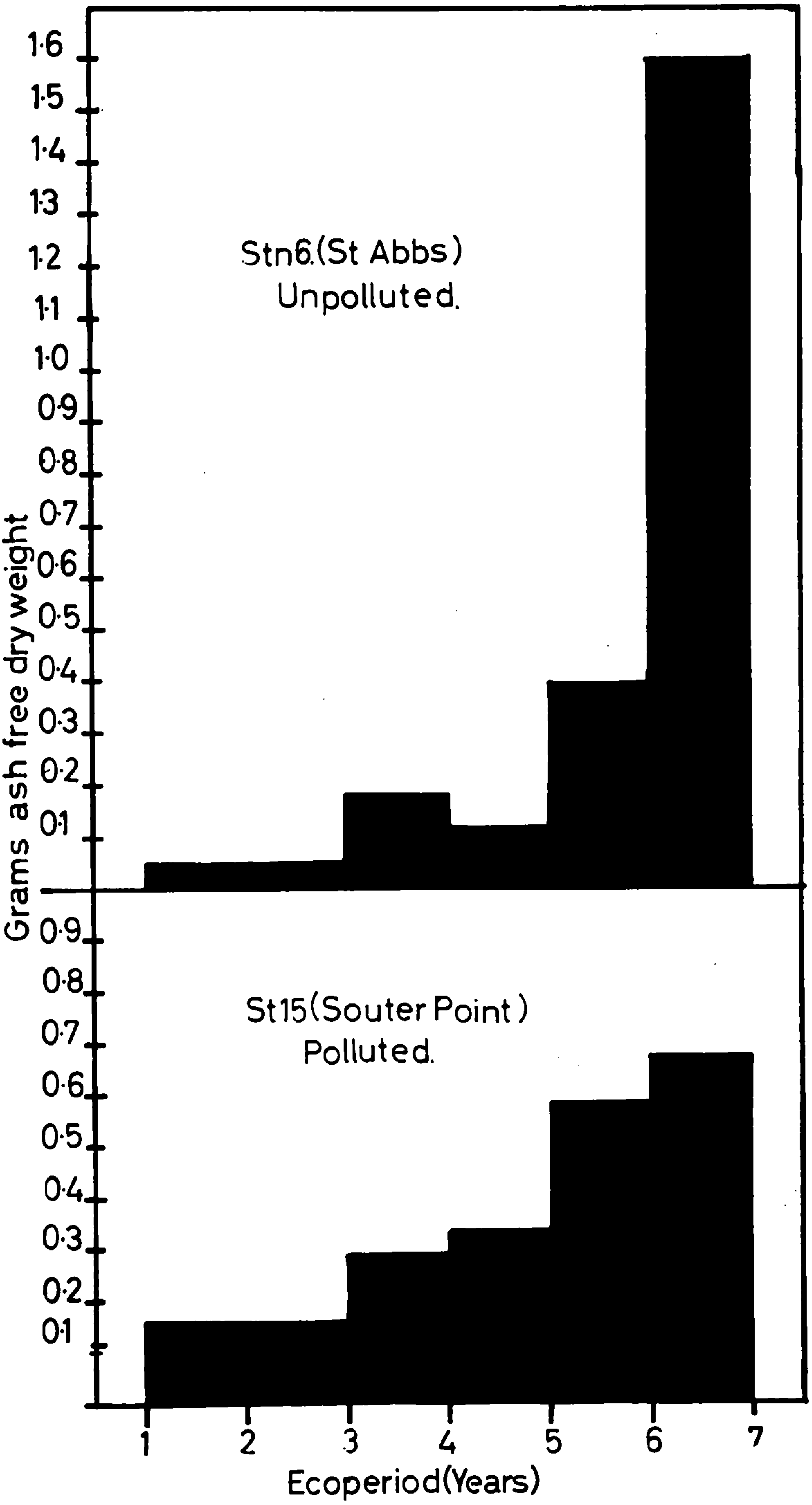


Fig.31

Mean standing crop of secondary producers in Ecospace over seven year ecoperiod.

TABLE 30

Grams Ash Free Dry Weight per Gram Wet Weight

SPECIES	Stn. 5	Stn. 6	Stn. 8	Stn. 9 & 10	Stn. 11 & 12	Stn. 13 & 14	Stn. 15	Stn. 17 & 18	Stn. 19	Stn. 21	Mean Organi Weight
Acanthochitona crinitus	0.153=	0.135	0.125	0.129	0.155	0.121	0.092	0.180	-	-	0.136±0.09
Alcyonium digitatum	-	0.074	-	-	-	-	-	-	-	0.080	0.077±0.00
Amphithoe rubricata	-	0.166	0.110	-	0.122	0.112	0.135	0.218	-	-	0.143±0.0
Anomia ephippium	-	0.1957	-	-	-	-	-	-	-	-	0.195
Asterias rubens	0.120	0.1024	0.111	0.119	0.089	0.100	0.108	0.107	0.089	0.115	0.106±0.003
Cancer pagurus	0.108	0.125	-	0.125	0.166	0.087	0.137	0.150	-	0.084	0.122±0.008
Echinus esculentus	0.062	0.082	-	-	-	-	0.0719	-	-	0.036	0.063±0.010
Eupagurus bernhardus	-	0.1880	0.1667	-	0.140	-	-	0.101	-	-	0.148±0.018
Flabelligera affinis	-	0.0968	-	-	-	-	0.1066	-	-	-	0.101±0.005
Gibbula cineraria	0.0566	0.0968	-	0.0562	0.0122	-	-	-	0.1756	-	0.101±0.028
Harmothoe impar	0.1492	0.153	-	-	-	-	0.275	-	-	-	0.192±0.054
Henricia sanguinolenta	0.130	0.135	0.131	-	0.130	-	0.134	0.096	0.131	0.147	0.129±0.017
Hyas araneas	-	0.158	0.125	0.065	0.136	-	0.132	-	-	-	0.123±0.015
Lepidonotus squamatus	-	0.178	0.216	0.190	-	0.179	0.146	0.135	0.187	0.253	0.185±0.013
Lineus longissimus	-	0.128	-	-	-	0.149	0.127	-	0.131	0.158	0.139±0.006
Liparis liparis	-	0.149	-	0.157	-	-	-	0.117	-	0.341	0.116±0.025
Mytilus edulis	0.066	0.448	0.084	0.145	-	0.062	0.081	-	-	-	0.148±0.068
Ophiothrix fragilis	0.133	0.107	0.106	0.442	0.135	0.098	0.104	0.086	0.098	0.114	0.142±0.024
Ophiopholis aculeata	0.146	0.152	-	-	0.095	0.115	-	0.0229	0.101	-	0.084±0.026
Patina pellucida	-	0.151	0.123	-	-	-	0.205	0.142	-	-	0.155±0.037
Porcellana longicornis	0.138	0.146	0.100	-	-	0.157	-	-	-	0.087	0.125±0.013
Pycnogonum littorale	0.236	-	0.287	-	-	0.070	0.237	-	-	0.189	0.204±0.034
Sabellaria spinulosa	-	0.108	-	-	0.170	-	0.260	-	-	-	0.179±0.006
Tealia felina	0.157	0.140	0.137	-	0.177	0.116	0.143	0.156	0.127	-	0.154±0.006
Terebella sp.	0.140	0.236	-	-	-	-	0.149	-	-	0.381	0.226±0.078
Trivia arctica	0.177	0.137	-	-	-	-	-	-	0.101	-	0.118±0.071

(3) Biomass in Ecospace

Over a seven year ecoperiod, the habitat provided by a single Laminaria hyperborea holdfast enlarges from 0'CC's to 313±19 CC's. A total of 275±1.2 gms wet weight of tissue equal to 55.8±6.0 gms ash free dry weight provide the habitat. This is equivalent to 410±15 K.cals of stored solar energy, the net primary production of the holdfast over seven years.

TABLE 31

Mean Standing Crop of Second Producers in Ecospace over one seven year period

Ecoperiod (years)		2	3	4	5	6	7
Stn.6 (St.Abbs)	0	0.05±0	0.05±0.0	0.18±0.0	0.14±0.13	0.4±0.13	1.6±0.3
Stn.15 (Souter Point)	0	0.26±0.1	0.26±0.1	0.29±0.0	0.34±0.1	0.58±0.1	0.67±0.2

The initial rate of biomass increase is much faster in polluted water, but falls sharply in the seventh ecoperiod. In clean waters there is a slow accumulation of biomass reaching its maximum in the seventh ecoperiod. Over the whole seven year ecoperiod a total of 947.5 K.cals, equal to 127.9 gms ash free dry weight of plant tissue provides 633 CC's ecospace. This is colonised by 2.40 gms ash free dry weight in both polluted and unpolluted waters. As Stn. 6 has been used as the 'NORM' in this study, then the 2.4 gms ash free dry weight is likely to be the total biomass of secondary producers that the habitat can maintain. Thus, even though the rate of accumulation of biomass may initially be speeded up in polluted water (see Table 31) the total biomass of secondary producers maintained in the habitat is unaffected by pollutedwater and remains very low. (Figure 31)

Metridium senile, Corella parallelogramma, Chlamys (tigerina?) Pecten sp and Ophiocomina nigra in the estuary, and Ophiothrix fragilis, Ophiopholis aculeata, Halichondria panicea, Echinus esculentus, Henricia sanguinolenta, Molgula sp., Sydnium turbinatum, Nymphon gracile, Patina pellucida, Palaemon squilla, Hymeniacidon perleve, Archidoris britannica, Doris tuberculata, Lacuna vincta, Tectura testudinalis, and Primela denticulata on the open coast.

The species diversity of the polluted waters shows a corresponding reduction to a value below 2.5 reflecting both the paucity of species and the great increase in the numbers of a few pollution tolerant species. Only once did species diversity rise above 2.5 in the polluted waters. The species diversity of 3.1 corresponded with a severe disturbance in the community at Souter Point in April of 19 68, when the total numbers sampled in the population amounted to only 18 individuals of 6 species.

Only four species are found in any numbers in polluted waters where they can occur in much greater abundance than is normal. These are the suspension feeders Mytilus edulis, and Sabellaria spinulosa, and the carnivores, Nereis pelagica and Asterias rubens which co-fominate the simple system. The bulk of energy flow through the system is thus restricted to two trophic links:

Suspended Material → Suspension Feeders → Carnivore

Mytilus edulis Sabellaria spinulosa	→	Asterias rubens Nereis pelagica

These four species made up 99 per cent of the biomass present at any one time.

Furthermore, this simple system is violently unstable. The population of the dominant filter feeder shows four complete overturns in 31 months of the study. The natural succession of species into the enlarging habitat which is a feature of the stable and diverse communities in unpolluted communities is smothered and almost destroyed by the abundance of suspension feeders which colonise all stages of the developing habitat. The juvenile suspension feeding community is thus retained throughout, in polluted waters. The ecosystem can therefore be regarded as undergoing a neotenous community development characterised by little or no complexity in space nor in time.

The following features may be recognised as neotenous characteristics of polluted water ecosystems, developed at Stn. 15.

(i) There is an unusually large potential energy source available in the form of sewage pollution. The ecosystem response to this increased energy source is a reduction in species diversity and community complexity (c.f. Margalef, 1968).

(ii) Suspension feeding is an unspecialised mechanism compared with the more specific methods used by omnivores and carnivores and as such can be considered a more juvenile method of feeding (Margalef, 1967a).

(iii) The pioneer species Mytilus edulis and Sabellaria spinulosa have a high level of fecundity (Seed, 1969), (Wilson, 1968c), which is necessary for the repeated colonisation of new habitats.

(iv) Both species have planktonic larvae which can remain free floating for many weeks (Seed, 1968) (Wilson, 1968c). This ensures wide dispersal of the species and further increases the chances of successful colonisation of new habitats.

(v) Colonisation of polluted habitats by the two dominant suspension feeders is rapid and efficient occuring as a spectacular spatfall involving large numbers of larvae.

(vi) The great fluctuations in the abundance of the dominant species, once established in the habitat indicate both inter and intra specific competition between species. This is a characteristic feature of immature ecosystems. (Levins, 1962, 1963), (Margalef, 1967).

(vii) Immature stages of succession are invariably simple and there is likely to be no regularity feedback mechanism preventing great instability in the populations (Odum, 1967).

Briefly summarised, polluted water communities are:-

1. Very Unstable
2. Species poor
3. Contain a characteristic association of species which is similar even when developed in two distinctly regional sub-environments.
4. Community development is retarded and neotenous communities are developed.

The addition of industrial waste as well as sewage, however, could well be a contributory factor in producing a polluted water community. Preliminary investigations of pollution tolerant species reveals some resistance to toxic substances.

Pollution resistant species can withstand high levels of heavy metals ions in their tissues and two methods have been shown by which these levels can be regulated by different species. It is probable that pollution tolerant species possess many other physiological mechanisms which contribute to their success in polluted waters. Further investigations are now necessary to determine the nature of stress inducing mechanisms which exclude other species from polluted water. Only when the threshold values for pollution induced stresses have been determined can precise causal relationships be established between pollutants and the polluted.

In polluted waters the diversity of species and the complexity of the community have been replaced by the extreme simplicity of pioneer communities. Sewage pollution of the sea can thus be considered as the nutrient enrichment of an otherwise nutrient deficient system. Somewhat predictably the ecosystem response is a modification of the old system 'designed' for nutrient poor conditions, to produce a new system better adapted to the abundant new energy source. This has been achieved by a recombination of existing species formerly present only in small numbers in the old communities. Some species have been lost in this process and the new polluted water communities can be thought of as utility systems, stripped bare of many surplus energy pathways, concentrating on species which make best use of the new food source The potential energy of sewage pollution is presented as a suspension in the surrounding water. The community response is the development of large suspension feeding populations.

It is hard to imagine a simpler food chain than one possessing only two possible energy exchanges. The suspension feeders remove the sewage suspension from the environment and are themselves removed by carnivores. If this system could be maintained in balance the natural ecosystem response to enrichment may well be sufficient to contain the pollutants in a localised inshore area. Unfortunately, one major disadvantage of the reduction in community complexity is the instability of the few remaining populations which it produces. Two suspension feeder species compete for ecospace and after spatfall each produce an almost single species population. At a time when the suspension feeding population is at its greatest maximal amounts of pollutants are removed from the water. At all other times the populations are either rapidly gaining or losing numbers and for short periods may be absent from the area. During all of this time, energy rich sewage suspensions continue to pour over the communities. As the unstable suspension feeding populations are not permanently available to remove the pollutants, they must spread to affect a much larger area, until a sufficiently large zone becomes modified to remove the pollutants through all the phases of the fluctuating suspension feeder population development. If large permanent populations of suspension feeders could be maintained it would ensure the most rapid removal of pollutants by the smallest area of pollution modified ecosystem and the spread of pollutants would be contained. The rapid turnover of suspension feeder populations prevents this from happening. Instability must therefore be considered as the most serious ecological consequence of the reduction in community complexity which occurs in polluted water.

The suspension feeders are certainly the most important link in any food chain as they are the species which remove to pollutants. Anything detrimental to these populations could destroy what is potentially a very useful waste disposal system.

Thus, any change in the existing environment which speeds up the turnover of the community must make the system more inefficient.

If additional substances are added to this system which prove to be toxic to the suspension feeders the system will completely break-down.

Anything that retards or inhibits rapid recolonisation by suspension feeders will reduce the efficiency of waste removal from the water.

Excessive predation by pollution tolerant carnivores may well be a contributory factor in the rapid declines of suspension feeding species, but little direct evidence was found for this during the study.

More research is now needed on the mechanisms of community instability. Simplified communities are known to be naturally unstable but the possibilities of imbalance introduced as a direct effect of adding toxic substances to the environment cannot be ignored and should be further investigated. Stabilisation of neotenous community development would result in the development of a polluted water plagioclimax containing mature individuals of the suspension feeding species. The breeding stock necessary for the maintenance of the community would then be permanently located in the affected area. This would produce an ~~autonous~~ autonomous, self replicating biological control system restricting pollutants to the smallest possible area. In the event of very long term pollution over an area, physiological adaptation of mature breeding stock may well provide even more pollution resistance, therefore, permanent and more

254 mμ for mercury (this prevents sodium interference) giving a theoretical sensitivity of 4.75 ppm.

214 mμ for zinc (this prevents sodium interference) giving a theoretical sensitivity of 0.05 ppm.

Sea Water Analysis

Sea watersamples were collected in 250 ml. polythene bottles and stored in dry ice until returned to the laboratory. There the bottles were transferred to a deep freeze at $-32^{o}C$. When sufficient numbers of samples were collected they were transferred to the Department of Civil Engineering, University of Newcastle Upon Tyne, for analysis.

Each sample is analysed for phosphate (PO_4), Nitrate (NO_3), Nitrite (NO_2), Ammonium (NH_4) and Silicon (SiO_3). High phosphate and available nitrate levels are good evidence of sewage pollution. Silicon levels are low in the sea except near fresh water infalls (P.Head, personal communication).

TROPHIC COMPONENT ANALYSIS

APPENDIX

Actaeon tornatilis: Mollusca

Rare on North East England coastline, only one shell with the partly eaten remains of its occupant was found at Stn. 6 (St. Abbs) Berwickshire. Normal habitat for this species is sand.

Aoridae (Crustacea)

No satisfactory key has yet been established for the accurate identification of these animals. Found occasionally in samples from Berwickshire, Northumberland, Durham and Yorkshire.

Amphitrite gracilis (Annelida)

Tube dwelling annelid with large crown of tentacles; observed sweeping the surrounding water and substrate. Of uncertain feeding habits, tentatively called a deposit feeder here.

Bulla sp.

Collected once at Berwickshire, normal habitat sand.

Flabelligera affinis (Annelida)

Common along North East coast of England. Always found in association with mud and detritus. A sedentary polychaete so a 'debris feeder' (Eales, 1961).

Harmathoe impar (Annelida)

Small and slow usually found deep inside holdfast or in abandoned tubes of other animals. Gut contents observed as an amorphous mass composed largely of detritus.

Henricia sanguinolenta (Echinodermata)

'Food unknown' (Mortensen, 1927). Since observed by divers holding fresh living algae (enteromorpha.sp) and mussels, in its jaws at different times. When disturbed in collecting, the food material is quickly released.

Hyas araneas (Crustacea)

Very common on the North East coast of England sublittoral ecosystem. Frequently found covered in cryptopleura sp and other red algae. Observed when diving, holding mussels, and sometimes red algae such as Delesseria in its jaws.

Jassa falcata (Crustacaea)

Commonly found at most stations. Typical crustacean feeding mechanisms with no special modifications for ingesting particular food material.

Liparis liparis (Pisces)

The only fish regularly caught using this sampling method. Very slow swimming and not likely to be an active carnivore. Small teeth present in the upper and lower jaw, but no special modifications for hunting or trapping very active prey.

Panoplea minuta (Crustacea)

Only recorded once for Berwickshire. Rare

Socarnes vahli (Crustacea)

Found only at Bantry Bay in this survey, where they form only an insignificant part of the fauna. No reference to feeding habits could be found. The animal appeared to have no outstanding modifications or adaptations for feeding.

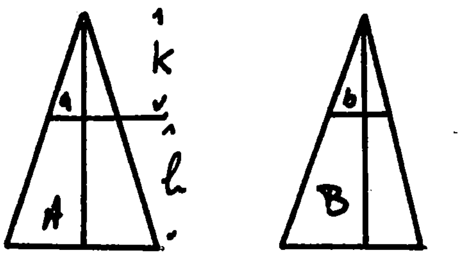
APPENDIX 3

Derivation of Formula for Maximum Euclidian Space containing one *Laminaria hyperborea* holdfast.

Area of an elipse $= \frac{1}{3} \pi$ Rab where 2a = major axis

2b = minor axis

Volume of cone height L eliptical base $= \frac{1}{3} \pi$ Lab



Volume of height h

$= \frac{1}{3} \pi [(AB(h+k)-ab(K)]$

$\frac{a}{A} = \frac{b}{B}$ is necessary condition

$\therefore \frac{K}{K+h} = ak + ah$

$\therefore K(A-a) = ah$

$\therefore K = \frac{aL}{A-a}$

Volume of l $= \frac{1}{3} \pi [AB(h+\frac{ah}{A-a}) - \frac{a^2bh}{A-a}]$

$= \frac{1}{3} \pi h [AB(\frac{A}{A-a}) - \frac{a^2b}{A-a}]$

$= \frac{1}{3} \pi h \frac{1}{A-a} [A^2B - a^2b]$

Substitute for b $= \frac{aB}{A} = \frac{1}{3} \pi h \frac{1}{A-a} (A^2B - \frac{a^3B}{A})$

$= \frac{1}{3} \pi h \frac{B}{A-a} [\frac{A^3 - a^3}{A}]$

$= \frac{1}{3} \pi \frac{B}{A} (A^2 + aA + a^2)$

Volume $= \frac{1}{3} \pi \frac{hB}{A} [A^2 + aH + a^2]$

Substitute following:

$L = 2A$ $\qquad\qquad\qquad a = 2A$

$B = 2B$

$$\therefore \quad \text{Volume} = \frac{1}{3}\pi\, h\, \frac{B}{L} \quad \left[\frac{L^2}{4} + \frac{La}{4} + \frac{a^2}{4} \right]$$

$$\text{Volume} = \frac{1}{12}\pi h\, \frac{B}{L} \quad \left[L^2 + La + a^2 \right]$$

This assumes measured a = length of major axis.

Where π = 3.24

h = Vertical height of holdfast

B = Breadth of holdfast base

L = Length of holdfast base

a = Greatest diameter of cut upper surface of holfast called stipe diameter.

With practice this formula can be calculated on an electric calculator. In this study a simple Fortran IV programme was used throughout. Table 4 presents the ecospace data grouped according to geographical location, and depth of water, with the holdfast characteristics from which the ecospace was calculated.

APPENDIX 4

Mean Ecospace increase with Age of Holdfast
(Unpolluted Stations, 5,6,11,12,17,18)

Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
0.49	7.8	6.3	48.9	114.1	200.0	348.6
-0.19	-0.7	16.1	85.0	144.0	241.0	421.1
0.20	7.0	14.9	61.0	245.5	328.5	459.9
0.29	3.6	20.2	29.6	37.7	378.0	772.0
0.17	3.1	15.0	33.3	38.8	257.4	254.4
0.10	3.0	2.3	18.0	16.3	212.2	216.5
	2.6	38.0	23.0	254.0	226.4	313.2
	3.0	1.8	28.8	23.0	202.0	194.0
	-1.2	12.1	37.4	113.3	183.5	275.4
	3.5	0.7	27.5	106.1	217.3	216.5
	2.3	23.5	72.3	35.8	81.2	244.0
	0.7	13.1	40.5	96.7	279.0	102.8
		4.5	13.1	102.1	143.0	154.6
		12.1	19.7		277.1	273.9
		28.3	44.7		82.2	99.0
		8.0	28.4		151.0	165.1
		5.0	68.0		199.5	396.0
		13.0	29.9		179.3	490.0
		10.1	59.1		213.2	295.0
		2.4	40.4		75.7	246.7
			20.1		18.0	196.3
			4.6			503.0
						317.5
						119.6
						25.8

APPENDIX 4

Mean Ecospace increase with age of Holdfast
(Polluted Stations 13,14,15,16)

Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
3.0	1.2	13.9	15.7	49.3	146.7	179.2
0.2	0.5	10.3	-12.6	113.7	144.4	172.9
0.0	3.0	15.8	21.0	130.4	175.0	187.0
0.2	1.4	11.7	196.0	49.5	204.5	205.8
0.8	2.7	17.9	13.4	91.0	149.8	358.5
1.4	-0.3	8.6	61.8	340.0	5.8	86.5
0.8	9.8	4.4	95.7	106.7	186.4	341.5
	7.1	2.3	38.9	66.1	165.4	319.6
	9.1	11.6	75.7	178.2	237.1	556.7
	1.9	8.2	46.0	187.8	125.6	246.9
	5.7	8.9	68.4	135.7	200.0	226.9
	-1.2	24.5	29.8	45.8	110.0	369.7
	3.6	-0.4	8.8	13.4	64.2	151.8
	3.3	6.3	16.3	134.5	65.2	295.8
	0.9	6.4	50.0	106.6	194.3	149.0
		1.1	50.1	85.0	324.8	156.0
		9.5	13.5	127.3	113.7	463.4
		6.4		80.0	153.6	757.9
		1.6		123.1	73.4	290.2
				56.6	17.9	168.5
				119.3		40.1
				231.0		
				116.8		
				71.3		
				15.5		

Appendix 5

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Mineral Composition and Organic Weight
per Gram Wet Weight Tissue

Station 5
(Dunbar)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochitona crinitus	0.4841	0.3248	0.1513	51.5945	48.4055	32.4801	15.9254
Asterias rubens	0.4030±0.0389	0.2821±0.0411	0.1209±0.002	0.1209±0.002	59.6956±3.8905	28.2098±4.1151	12.0941±0.2241
Cancer pagurus	0.3199	0.2133	0.1086	68.0054	31.9946	21.1348	10.8598
Echinus esculentus	0.5861±0.0307	0.5223±0.0298	0.0627±0.0008	41.3925±3.0695	58.6075±3.0695	52.3333±2.9823	6.2740±0.0870
Gibbula cineraria	0.8341	0.7776	0.0566	16.5858	83.4142	77.7557	5.6585
Harmathoe impar	0.2556±0.0048	0.1064±0.0395	0.1492±0.0444	74.4312±0.4857	25.5687±0.4857	10.6488±3.9554	14.9199±4.4411
Henrica sanguinolenta	0.4044±0.0863	0.2743±0.0936	0.1300±0.0073	51.1210±0.1937	48.8787±0.1934	36.3835±0.4205	12.4952±0.2271
Mya truncata	0.5942	0.1560	0.4382	40.5797	59.4203	15.6008	43.8195
Mytilus edulis	0.4754	0.4089	0.0663	52.4263	47.5737	40.8916	6.6822
Nereis pelagica	0.2220±0.0028	0.1428±0.0397	0.0292±0.0425	77.7999±0.2799	22.1995±0.2784	14.2777±3.9698	7.9224±4.2482
Ophiothrix fragilis	0.4803±0.400	0.3780±0.0347	0.1333±0.0373	51.7172±3.8487	48.0328±3.9987	37.8451±3.4222	10.1841±0.5800
Ophiopholis aculeata	0.5457	0.3993	0.1464	45.4355	54.5655	39.9296	14.6359
Porcellana longicornis	0.4043	0.2658	0.1385	59.5720	40.4280	26.5750	13.8529
Tealia felina	0.2197	0.0621	0.1576	78.0344	21.9656	6.2071	15.7585
Terebella sp.	0.2367	0.0965	0.1403	76.3266	23.6734	9.6456	14.0278
Trivia arctica	0.8105	0.6930	0.1175	18.9484	81.0516	69.3005	11.7511

Mineral Composition and Organic Weight
Per Gram Wet Weight (Stn.6)
St. Abbs.

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochitona crinitus	0.4024±0.0996	0.3107±0.0132	0.1355±0.0085	55.4200±1.3354	44.900±0.1316	31.8659±1.5801	13.3558±0.8290
Aeolidia papillosa	0.1703	0.0261	0.1442	82.9703	17.0297	2.6502	14.4245
Alcyonium digitatum (white)	0.2511±0.0234	0.1767±0.0247	0.0744±0.0027	74.8840±2.3419	25.1250±2.3355	21.5406±4.179	6.9090±0.7442
-ditto- (orange)	0.2833±0.0430	0.2104±0.0407	0.0691±0.0074	71.6702±4.3062	25.1250±2.3355	17.6722±2.4758	7.4404±0.2740
Amphithoe rubricata	0.2243±0.0343	0.0577±0.0071	0.1665±0.0335	78.7402±3.3562	21.2595±3.3562	5.7738±0.7050	16.6570±3.3040
Anomia ephippium	0.2180	0.0221	0.1957	78.1956	21.8044	2.2105	19.5938
Anthopleura thallia	0.1958	0.0908	0.1051	80.4161	19.5839	9.0788	10.5051
Archidoris pseudoargus	0.1933±0.091	0.0704±0.0051	0.1229±0.0119	81.3066±0.9273	18.7021±0.9363	7.5063±0.3056	11.5203±0.9528
Archidoris brittanica	0.1956±0.081	0.0793±0.0051	0.1159±0.0061	80.1833±0.7230	19.8163±0.7236	7.5509±0.6172	12.4475±0.9817
Asterias rubens	0.3588±0.0070	0.2604±0.0076	0.1024±0.0028	62.7691±1.8090	36.1430±0.6353	23.3290±0.7083	10.2477±0.3108
Balanus balanus	0.7344	0.6724	0.0620	26.5568	73.4432	67.2391	6.2041
Balanus crenatus	0.6243	0.5799	0.0440	37.5523	62.4477	57.9886	61.4591
Buccinum undatum	0.3469	0.1546	0.1923	65.3063	34.6937	15.4631	19.2306
Cancer pagurus	0.3300±0.0207	0.2041±0.0157	0.1250±0.0084	67.2592±2.1801	32.6954±2.1913	20.6536±1.5184	11.3314±1.1170
Carcinus maeneus	0.3100±0.0210	0.2139±0.0154	0.1249±0.0079	66.2484	32.6754	19.9874	12.3314±1.1180
Doris tuberculata	0.3274	0.2521	0.0753	67.2576	32.7424	25.2146	7.5278
Echinus esculentus	0.4927±0.0210	0.4422±0.0186	0.0824±0.0228	50.2742±1.5731	49.5984±1.6452	45.0445±2.1671	5.9097±0.3326
Eupagurus bernhardus	0.2658±0.0154	0.1372±0.0114	0.1880±0.0114	72.5824±2.1373	27.2506±2.1604	13.2362±2.1880	13.0871±0.9290
Flabelligera affinis	0.3516±0.1544	0.2548±0.1604	0.0968±0.006	64.8356±15.4488	35.1645±15.4488	34.1744±23.3639	9.6808±0.5999
Galathea squamifera	0.1963±0.0425	0.1119	0.1269	76.1203	23.8789	11.1926	12.2871
Gibbula cineraria	0.6840±0.1055	0.6022±0.1247	0.0968±0.0060	31.5987±10.5514	68.5237±10.5941	60.2191±12.4707	8.1812±1.935
Harmothoe impar	0.2457±0.0211	0.0925±0.0242	0.0510±0.0064	73.1153±2.6726	33.3752±2.3067	7.5887±1.9845	15.2917±0.6512
Halichondria panacea	0.1986	0.1422	0.0559	80.1447	19.8553	14.2662	5.5889
Henricia sanguinolenta	0.4224±0.0174	0.1709±0.0260	0.1357±0.0070	58.9965±2.0670	40.2168±3.1272	29.8480±3.2820	13.8260±1.3205
Hyas araneas	0.4111±0.1245	0.2806±0.0350	0.1582±0.0240	58.8885±3.4570	40.2618±3.1272	29.8484±3.2820	13.8260±1.3205
Idotea baltica	0.2464±0.0025	0.0814±0.004	0.1650±0.0023	75.3590±0.2495	24.6422±0.2520	8.1421±0.0477	16.4981±0.2269
Jassa falcata	0.1377±0.0291	0.0417	0.1353±0.0060	86.2385±3.3240	13.7691±3.3241	4.1708	13.5278±0.6045
Lamellaria	0.2324	0.0924	0.1382	76.7602	23.2397	9.4214	13.8184
Lepidontus squamatus	0.2362±0.0178	0.0572±0.0108	0.1789±0.0092	76.3445±1.9574	27.7002±4.4035	5.8476±1.0647	17.4340±0.8644
Lineus longissimus	0.1759±0.0074	0.0492±0.0020	0.1282±0.0079	82.1003±1.200	17.1773±0.6235	4.7204±0.0856	12.8266±0.7966
Lineus ruber	0.1495±0.0096	0.0361±0.0027	0.1135±0.006	84.0582±0.9588	14.9517±0.9588	3.6147±0.2747	14.8185±0.7522
Modiolus barbaratus	0.6263±0.0362	0.5494±0.0489	0.0565±0.0202	37.3633±3.6308	62.7356±3.5674	55.9465±5.2887	12.7646±0.5571
Molgulia sp.	0.1162	0.0896	0.0267	88.3753	11.6467	8.9588	2.6659
Mya truncata	0.5670±0.0070	0.4437±0.0064	0.1233±0.0081	43.4045±0.0346	56.5945±0.6747	44.3878±0.5833	12.1239±1.0281
Mytilus edulis	0.5297±0.2164	0.5819±0.1315	0.4489±0.1703	42.4253±5.2370	57.5736±5.2348	49.7556±6.1400	7.8188±1.0281
Musculus sp.	0.4689±0.0297	0.4069±0.0280	0.0260±0.0047	53.0439±2.9363	46.8986±2.9721	39.3531±0.2410	6.2026±0.4667
Nereis pelagica	0.2060±0.0021	0.0770±0.0312	0.1650±0.0216	77.8425±2.3067	22.4212±2.3681	5.5939±1.0131	16.6403±2.0575
Nereis diversicolor	0.3298	0.0931	0.2367	67.0213	32.9787	9.3058	23.6702
Ophiothrix fragilis	0.4835±0.0091	0.3570±0.0080	0.1077±0.0073	54.1467±0.9631	43.3168±1.1179	35.1443±0.7788	10.9595±0.7062
Ophiopholis aculeata	0.4829±0.0191	0.3523±0.0168	0.1520±0.0140	49.2835±1.3712	51.6845±1.4477	35.1546±1.9386	15.0494±1.6410
Patina pellucida	0.4005±0.2429	0.2786±0.2382	0.1518±0.0253	59.9479±24.2944	40.0920±24.2944	12.1868±0.4696	12.1853±0.4681
Palaemon squilla	0.1711±0.0480	0.1083±0.0658	0.0727±0.0262	81.9278±4.5624	13.0726±4.5624	10.8327±6.5868	8.9061±1.4334
Porcellana longicornis	0.3085±0.0083	0.1631±0.0071	0.1468±0.0046	69.3033±0.8192	30.7721±0.8919	16.1356±0.7702	14.6472±0.4846
Primela denticulata	0.4258±0.1598	0.3395±0.1318	0.0864±0.0278	57.4120±15.9842	42.5879±15.9842	33.9493±13.1936	8.6386±2.7905
Pycnogonium littorale	0.3434±0.0185	0.1066±0.0156	0.2367±0.0271	48.5162±13.8393	48.5163±13.8393	8.6804±1.3926	39.8358±14.7335
Sabellaria spinulosa	0.1722	0.0636	0.1086	82.7789	17.2211	6.3564	10.8647
Sagartia elegans	0.2397	0.0809	0.1588	72.0286	23.9714	8.0927	15.8787
Taelia felina	0.1777±0.0111	0.1469±0.1089	0.1403±0.0122	82.2210±1.1161	17.7790±1.1161	3.7456±0.2392	15.1892±1.4419
Terebella sp.	0.2491±0.0362	0.1066±0.0152	0.2367±0.0271	73.9722±4.4572	25.0302±4.4568	11.2807±2.8347	[illegible]
Tonicella rubra	0.4565±0.0362	0.1060±0.0152	0.2367±0.0220	[illegible]	[illegible]	[illegible]	[illegible]
Trivia arctica	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Mineral Composition and Organic Weight
per Gram Weight of Tissue

Farne Isles (Northumberland)
Stations 9 and 10

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochitona crinitus	0.4406	0.3115	0.1291	55.9403	44.0597	31.1467	12.9130
Archidoris pseudoargus	0.2177	0.0690	0.1488	78.2253	21.7747	6.8996	14.8751
Asterias rubens	0.3269±0.0103	0.2069±0.0092	0.1199±0.0010	67.3109±1.0271	20.6962±0.9231	32.6895±1.0276	11.9933±0.1045
Cancer pagurus	0.3194±0.0151	0.1939±0.0101	0.1256±0.0051	68.0534±1.5155	31.9466±1.5155	19.3878±1.009	12.5488±0.4964
Gibbula cineraria	0.7812	0.7250	0.0562	21.8815	78.1185	72.4976	5.6210
Hyas araneas	0.1229	0.0572	0.0657	87.7085	12.2915	5.7222	6.5269
Lepidontus squamatus	0.2462	0.0553	0.1908	75.3802	24.6158	5.5336	19.0823
Liparis liparis	0.2444	0.0886	0.1574	75.6037	24.3963	8.6954	15.7369
Mya truncata	0.5370	0.2798	0.2527	42.2597	53.7043	27.9795	25.7247
Mytilus edulis	0.4953±0.0016	0.1408±0.0054	0.0846±0.007	50.4640±0.1633	51.7016±2.0027	41.0756±0.5403	8.4599±0.7036
Nereis pelagica	0.2114±0.0052	0.2583±0.2037	0.1610±0.009	78.8553±0.5227	21.1444±0.5229	5.0404±0.4235	16.1043±0.0992
Ophiothrix fragilis	0.4471	0.0049	0.4422	55.2934	44.7066	0.4876	44.2190
Pomatoceros triqueter	0.2206	0.0666	0.1540	77.9373	22.0647	6.0667	15.4041

Mineral Composition and Organic Weight
per Gram Wet Weight

Holy Isle (Northumberland)
Station 8

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochitona crinitus	0.4128	0.2874	0.1254	58.7194	41.2806	28.7395	12.5411
Amphithoe rubricata	0.2180	0.1071	0.1109	78.2021	21.7980	10.7119	11.0862
Asterias rubens	0.3922±0.0327	0.2812±0.0315	0.1110±0.001	60.7773±3.280	39.2222±3.2800	28.1203±3.1600	11.1000±0.1181
Eupagurus bernhardus	0.3601	0.1934	0.1667	63.9913	36.0087	19.3359	16.6728
Henrica sanguinolenta	0.4299	0.2989	0.1311	57.005	42.9945	29.8856	13.1089
Hyas areneas	0.3387	0.2132	0.1255	78.2020	21.7980	10.7119	11.0862
Lepidodontus squamatus	0.3124	0.1053	0.2162	67.8551	32.1449	10.5256	21.6193
Mya truncata	0.5628	0.4932	0.0696	43.7138	56.2832	49.3187	6.9645
Nereis pelagica	0.2128	0.0922	0.1205	73.7242	21.2758	9.2211	12.0547
Ophiothrix fragilis	0.4155	0.3095	0.1061	58.4492	41.5508	30.9451	10.6057
Patina pellucida	0.6832	0.5602	0.1231	31.6752	68.3248	56.0169	12.3079
Porcellana longicornis	0.2988	0.1981	0.1007	70.1199	29.8801	19.8128	10.0673
Pycnogonum littorale	0.3485	0.0614	0.2871	65.1483	34.8517	6.1375	28.7174
Tealia felina	0.2146	0.0772	0.1374	78.5418	21.4582	7.7217	13.7365

Mineral Composition and Organic Weight
per Gram Wet Weight of Tissue

Beadnell and Craster
(Stations 11 & 12)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthocitona crinitus	0.3571	0.2020	0.1551	64.2875	35.7143	20.2041	15.5102
Amphithoe rubricata	0.1918	0.0689	0.1222	80.8159	19.1841	6.8999	12.2942
Asterias rubens	0.3057	0.2158	0.0899	69.4350	30.5650	21.5753	8.9897
Balanus balanus	0.6176	0.5887	0.0289	38.2392	61.7608	58.8698	2.8910
Botryllus schlosseri	0.1156	0.0618	0.0358	88.4399	11.5601	6.1842	5.3759
Cancer pagurus	0.3506 $\pm$ 0.0169	0.184 $\pm$ 0.0327	0.1667 $\pm$ 0.0330	64.9303 $\pm$ 1.6993	35.0697 $\pm$ 1.6993	18.3992 $\pm$ 3.2707	16.6704 $\pm$ 3.3107
Eupagurus bernhardus	0.2819	0.1419	0.1400	71.8130	28.1870	14.1877	13.9992
Gibbula cineraria	0.5694 $\pm$ 0.1704	0.1429 $\pm$ 0.0771	0.1224 $\pm$ 0.0566	43.0592 $\pm$ 17.0404	56.9408 $\pm$ 17.0400	44.8094 $\pm$ 22.5887	12.2404 $\pm$ 5.673
Henrica sanguinolenta	0.4288	0.2976	0.1308	57.1634	42.8366	29.7596	13.0769
Hyas araneas	0.3970	0.2603	0.1367	60.3037	36.6963	26.0304	13.6659
Mya truncata	0.5324	0.4190	0.1134	46.7620	52.2380	41.8985	11.3394
Mytilus edulis	0.4956	0.3501	0.1455	50.5404	49.5596	35.0082	14.5514
Nereis pelagica	0.1715 $\pm$ 0.0175	0.0355 $\pm$ 0.0051	0.1359 $\pm$ 0.0123	82.8502 $\pm$ 17.465	17.1428 $\pm$ 17.1215	3.5555 $\pm$ 0.5169	13.5942 $\pm$ 1.2295
Ophiothrix fragilis	0.3737	0.2783	0.0954	63.6259	37.3741	27.8337	9.5403
Sabellaria spinulosa	0.1914	0.0213	0.1701	80.8631	19.1369	2.1305	17.0064
Tealia felina	0.1987	0.0215	0.1771	80.1345	19.8655	2.1524	17.7130
Vanerupis pullastra	0.4712 $\pm$ 0.0612	0.3582 $\pm$ 0.0607	0.1251 $\pm$ 0.0126	67.5065 $\pm$ 8.5064	32.4935 $\pm$ 8.5067	19.9802 $\pm$ 9.7696	12.5132 $\pm$ 1.2632

Mineral Composition and Organic Weight
per Gram Wet Weight Tissue

Newbiggin and St. Mary's Isle
(Stations 13 and 14)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochitona crinitus	0.4127±0.0257	0.2915±0.0246	0.1212±0.0099	58.7231±2.5765	41.3101±2.5703	29.1570±2.4590	12.1198±0.9890
Amphithoë rubricata	0.1396	0.0273	0.1123	86.0384	13.9613	2.7321	11.2294
Asterias rubens	0.3122±0.0288	0.2118±0.0258	0.1004±0.0039	68.7756±2.8845	31.1565±2.8971	16.6847±5.4369	10.0377±0.3995
Cancer pagurus	0.2544	0.1673	0.0871	74.5608	25.4392	76.7277	8.7115
Gibbula cineraria	0.8303	0.8106	0.0198	16.9674	83.0326	81.0568	1.9758
Lepidodontus squamatus	0.2386±0.0378	0.0589±0.0063	0.1797±0.0315	76.1622±0.3766	23.8598±3.7806	5.8907±0.6310	17.9690±3.1496
Lineus longissimus	0.1783	0.0292	0.1492	82.1655	17.8345	2.9160	14.9185
Mya truncata	0.3624	0.2713	0.0912	63.7571	36.2429	27.1264	8.7115
Mytilus edulis	0.4456±0.0471	0.3816±0.0406	0.3816±0.0406	55.4312±4.7124	44.5987±4.7200	38.1661±4.0659	6.3993±0.7696
Nereis pelagica	0.1776±0.0027	0.4726±0.0064	0.1298±0.0043	82.0534±0.4291	17.6025±0.4178	4.7293±0.6489	12.2174±0.2293
Ophiothrix fragilis	0.4525±0.0494	0.3545±0.0483	0.0982±0.0012	54.7424±4.9446	45.2573±0.4944	30.4390±0.1732	9.8182±0.1178
Ophiopholis aculeata	0.4523	0.3372	0.1151	54.7734	45.2266	33.7151	11.5115
Porcellana longicornis	0.3552	0.1980	0.1572	64.4806	35.5194	19.7999	15.7195
Pycnogonum littorale	0.1836	0.1133	0.0703	81.6441	18.3586	11.3288	7.0298
Tealia felina	0.1492	0.0324	0.1169	86.0756	14.9244	3.2382	11.6862

Mineral Composition and Organic Weight
per Gram Wet Weight

Souter Point
(Station 15)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochitona crinitus	0.3580±0.0431	0.2904±0.0521	0.0926	58.1928±1.1325	41.8068±1.3350	31.2684±4.2049	10.5384±3.2359
Actinea equina	0.1797	0.0415	0.1382	82.0324	17.9677	4.1475	13.8200
Amphithoe rubricata	0.1377±0.0332	0.0417	0.1352±0.0060	86.2385±3.3240	13.7691±3.3241	4.1708	13.5278±0.6045
Anthopleura thallia	0.1741	0.0465	0.1276	82.5898	17.4102	4.6467	12.7635
Asterias rubens	0.3365±0.0206	0.2687±0.0452	0.1088±0.0077	66.4133±1.9363	33.5562±1.9392	22.8435±2.1433	10.6755±0.6702
Balanus crenatus	0.6245	0.5799	0.0446	37.5523	62.4477	57.9886	61.4591
Cancer pagurus	0.3197±0.0418	0.1886±0.0251	0.1311±0.0173	68.0342±4.1834	39.9711±4.1841	18.8607±2.5112	13.1220±1.7295
Echinus esculentus	0.4553	0.3834	0.0719	54.4684	45.5316	38.3419	7.1897
Flabelligera affinis	0.2341±0.0296	0.2386±0.0995	0.1066±0.0163	75.2698±3.5818	35.9301±11.4120	13.6705±3.2723	10.6597±1.6316
Harmathoe impar	0.3096	0.0337	0.2759	69.0441	30.9559	3.3668	27.5891
Henricia sanguinolenta	0.4304±0.0508	0.2960±0.0239	0.1344±0.0269	56.9562±5.0829	43.0437±5.0829	29.6002±2.3882	13.4435±2.6000
Hyas arenaas	0.2407±0.0137	0.1880±0.0172	0.1327±0.0035	75.9285±1.3732	24.0714±1.3732	10.8038±1.7245	13.2676±0.3512
Lepidontus squamatus	0.2051±0.0221	0.0599±0.0149	0.1462±0.0186	79.4560±3.3769	20.5554±3.5099	5.9543±1.7001	14.4870±2.1097
Lineus longissimus	0.1612	0.0341	0.1271	83.8791	16.1209	3.4127	12.7087
Mya truncata	0.4562±0.0180	0.3927±0.0016	0.0626±0.0155	62.1460±8.8103	37.8559±8.8109	28.5225±11.0143	9.2525±2.8623
Mytilus edulis	0.4689±0.0297	0.4069±0.0280	0.0620±0.0047	53.0439±2.9363	46.8896±2.9721	39.3531±0.2410	6.2026±0.4776
Nereis pelagica	0.1914±0.0133	0.0515±0.0118	0.1495±0.0135	72.0152±7.3010	20.8068±1.4202	5.6347±1.0604	15.4636±1.3528
Nereis diversicolor	0.2247	0.0306	0.1941	77.5281	22.4719	3.0643	19.4076
Ophiothrix fragilis	0.4235	0.3189	0.1045	57.6549	42.3451	31.8924	10.4527
Patina pellucida	0.2276	0.0224	0.2051	77.2433	22.7567	2.2436	20.5131
Palaemon squilla	0.1744	0.0767	0.0977	82.5996	17.4404	7.6656	9.7767
Phyllodocidae	0.1771	0.5005	0.1714	82.2857	17.7143	0.5711	17.1432
Primela denticulata	0.3047	0.1761	6.1286	69.5275	30.4725	17.6[illegible]79	12.8646
Pycnogonum littorale	0.3019±0.0308	0.0659±0.0296	0.2370±0.0187	68.4658±5.007	30.4078±4.0393	10.5946±5.0703	19.8131±3.3207
Sabellaria spinulosa	0.2999±0.0841	0.0391±0.0175	0.2607±0.0665	70.0093±8.4074	29.9906±8.4074	3.9095±1.7577	26.0778±6.6530
Taelia felina	0.1877±0.0122	0.0513±0.0060	0.1438±0.005	79.6241±0.8605	20.3758±0.8605	5.2649±0.6988	15.1118±0.2307
Terebella sp.	0.2315	0.0827	0.1490	76.8546	23.1454	8.2413	14.9040
Tonicella rubra	0.4541	0.3216	0.1299	54.8480	45.1520	32.1597	12.9922
Tubularia larynx	0.2223	0.0642	0.1581	77.7731	22.2265	6.4209	15.8060

Mineral Composition and Organic Weight
per Gram Wet Weight

Robin Hood's Bay and Flambrough Head
(Stations 17 and 18)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Acanthochtona crinitus	0.4371	0.2565	0.1807	52.2866	43.7134	25.6452	18.0682
Amphithoe rubricata	0.2447	0.0264	0.2184	75.5274	24.4726	2.6367	21.8359
Asterias rubens	0.3075±0.0015	0.1987±0.0128	0.1075±0.0124	68.0772±2.9020	31.5670±3.1299	17.6791±2.7651	10.8908±2.1159
Balanus balanus	0.7011	0.6588	0.0423	29.8893	70.1107	65.8830	4.2277
Buccinum undatum	0.1759	0.0416	0.1344	82.4059	17.5941	4.1578	13.4363
Cancer pagurus	0.1306±0.0257	0.2054±0.0024	0.1509±0.0218	64.3616±2.4243	35.6383±2.4243	20.5483±0.2442	15.0934±2.1835
Eupagurus	0.1443	0.0433	0.1011	85.5653	14.4346	4.3274	10.1073
Henricia sanguinolenta	0.3741	0.2828	0.0963	62.5917	37.4083	28.2797	9.1286
Hyas araneas	0.1967	0.1048	0.0920	80.3269	19.6731	10.4774	9.1957
Lepidontus squamatus	0.1691	0.0340	0.1351	83.0896	16.9104	12.4039	3.5605
Liparis liparis	0.2049	0.0915	0.1179	79.0595	20.9405	9.1492	11.7914
Mytilus edulis	0.5598	0.4786	0.0812	44.0213	55.9787	47.8636	8.1151
Nereis pelagica	0.2996±0.08786	0.08886±0.0660	0.1606±0.0567	77.7171±8.4439	22.2833±8.4439	9.5012±3.1960	16.0610±5.6784
Ophiothrix fragilis	0.4198	0.3334	0.0864	51.0183	41.9817	33.3373	8.6444
Ophiopholis aculeata	0.3659	0.3431	0.0229	63.4054	36.5946	34.3080	2.2866
Patina pellucida	0.6287	0.4858	0.1429	37.1334	62.8666	48.5777	14.2889
Taelia felina	0.1893±0.0031	±0.0158	0.1561±0.0456	52.3931±9.8535	40.0010±0.0013	5.6168±1.6857	15.6078±4.5634

Mineral Content and Organic Weight
per Gram of Tissue Wet Weight

Station 21
(Loch Ewe)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Alcyonium digitatum (white)	0.1724±0.0256	0.1884±0.1657	0.0804±0.0392	66.5653±13.7917	33.6342±13.9942	25.4357±9.9182	19.9577±2.6148
Asterias rubens	0.2580±0.2938	0.3479±0.0658	0.1155±0.0209	35.2088±14.2863	46.3412±8.6804	34,7886±6.5846	11.5526± 2.0957
Balanus balanus	0.6609	0.6227	0.0382	33.9119	66.0881	62.2718	3.8163
Cancer pagurus	0.2568±0.0484	0.1726±0.0309	0.0842±0.0178	74.4015±4.8788	51.5654±4.8788	68.6267±3.0965	8.4210±1.7821
Echinus esculentus	0.4181	0.3816	0.0365	77.6149	22.3851	3.9710	18.4140
Henricia sanguinolenta	0.4793	0.3317	0.1476	52.0707	47.9293	33.1654	14.7639
Lepidonotus squamatus	0.3293	0.0763	0.2530	67.0659	32.9341	7.6342	25.2999
Lineus longissimus	0.2390	0.0792	0.1598	76.1013	23.8987	7.9233	15.9754
Liparis liparis	0.4405	0.0987	0.3418	74.5639	25.4361	16.7196	34.1770
Mya truncata	0.5583±0.0072	0.4490±0.0124	0.1091±0.0198	44.1655±0.7207	55.8344±0.7207	44.9172±1.2868	10.9172±1.9824
Nereis pelagica	0.2323±0.0072	0.0592±0.0092	0.1731±0.0020	76.7662±0.7193	23.2338±0.7193	5.9181±0.9277	17.3157±0.2083
Ophiothrix fragilis	0.8890±0.1410	0.3476±0.0906	0.1148±0.1050	53.7576±10.1162	42.2499±10.1163	34.7313±9.1037	11.4820±1.0492
Porcellana longicornis	0.2399±0.0146	0.1527±0.0146	0.0872±0.0000	67.8252±9.7294	32.1741±9.7294	25.9896±12.2949	6.1849±2.5656
Pycnogonum littorale	0.3296	0.1403	0.1893	67.0384	32.9616	14.0308	18.9308
Sagartia elegans	0.2251	0.0639	0.1612	77.4905	22.5095	6.3920	16.1175
Terebella sp.	0.5681	0.1871	0.3810	43.1861	56.8139	18.7137	38.1002

Mineral Content and Organic Weight per Gram
Wet Weight of Tissue

Bantry Bay
(Station 19)

Species	Dry Weight	Ash Weight	Organic Weight	% Water	% Dry Weight	% Ash Weight	% Organic Weight
Archidoris pseudoargus	0.1369	0.0373	0.0996	86.3081	13.6919	3.7288	9.9631
Asterias rubens	0.4180±0.0360	0.1718±0.0396	0.0896±0.0031	70.9363±3.6054	31.0434±1.6055	20.0941±3.9235	8.9695±0.3180
Cantharidus striatus	0.3073	0.1051	0.2022	69.2690	30.7310	10.5071	20.2238
Gibbula cineraria	0.2629	0.0873	0.1756	73.7062	26.2968	8.7323	17.5616
Henrica sanguinolenta	0.3861	0.2547	0.1314	61.3900	38.6100	25.4750	12.1351
Lepidonotus squamatus	0.2261	0.0384	0.1877	77.3865	22.6135	3.8434	18.7701
Lineus longissimus	0.1619	0.0306	0.1312	83.8123	16.7959	3.1691	13.6268
Molgula sp.	0.0668	0.0215	0.0453	93.3220	6.6779	2.1521	4.5258
Nereis pelagica	0.1680	0.0317	0.1363	83.2041	16.7959	3.1691	13.6268
Ophiothrix fragilis	0.3970±0.0220	0.1645±0.1662	0.0983±0.0086	64.9207±2.4712	35.0748±2.4757	25.4065±1.4427	9.6727±1.0284
Ophiopholis aculeata	0.3844	0.2827	0.1017	61.5567	38.4433	28.2742	10.1692
Pilumnus hirtellus	0.3137±0.0164	0.1666±0.0138	0.1470±0.0025	68.6275±1.6486	31.3724±1.6485	16.6655±1.3895	14.6865±1.8820
Tealia felina	0.1519	0.0241	0.1277	84.8145	15.1855	2.4128	12.7727
Trivia arctica	0.7401	0.6383	0.1018	25.9907	74.0093	63.8316	10.1777

APPENDIX

Temporal Studies - Station 6 - St. Abbs.

Raw Data

SPECIES	S 67	J 68	F 68	M 68	M 68	JLY 68	S 68	O 68	D 68	F 69	M 69	A 69	M 69	J 69	J 69	S 69	O 69	N 69	D 69	M 70
Acanthochitona crinitus	3	1	2	3	2	1	2	5	3	1	2	3	1	2	1	3	6	2		
Actinia equina		1																		
Alcyonium digitatum					7		1	1								2			1	
Amphiopholis squamatus						6	1	4	2		4		1						1	
Amphithoe rubricata	37				3			7	12				17			8	5	7		8
Anomia ephippium	8	24	3	8	19	4	3	22	14	20	4	5	4	9	22	12	30	13	4	8
Aoridae																				
Archidoris pseudoargus	1				2			1									2			6
Asterias rubens	2	3	1	2	9		5	10	22	4	29	26	12	2	18	11	8	6	14	43
tentaculata	1																			
Balanus balanus	2	3		3	11	2	2	20	4	2	6	2	1	3	2	5	6	1	3	
Botryllus schlosseri	1			1		1	2	1						1	3	4	2			
Botrylloides leachi						1	3	1												
Cancer pagurus	1	1	3	1	1	1	2		1			5	2	1	1					
Cantharidus striatus																				
Caprella acanthifera								12	12		2					7		12	4	3
Caprella linearis	6				10		3								1					
Carcinus maenus	2	4	2	1		1		1	1		1	1					1		1	
Corophium bonellii											10		10	10	14	10	14			10
Cucumaria saxicola																				1
Echinus esculentus	1	2	4	7	1	4			1	2	2	1	2	1	5	2	8	2	1	11
Eupagurus bernhardus	2	2	1	2			2			2		2			2					
Flabelligera affinis		5	1			2	1			5			1		1	2	1	1	1	1
Galthea squamifera				1								2								3
Gibbula cineraria		1	2		1					1		2				1				
Harmathoe impar	3	9		3		1	2			7	13	3	2	4		4				2
Halichondria panicea	1			1	2	1	1		1			2	1		1					
Henricia sanguinolenta	1		5	3		4			1		7	4	3				1	2	1	
Hiatella arctica					2															
Hyas araneas	1		1				3	2		1	1	1	4	1		1				2
Hymeniacidon perleve (sanguina)															1					
Idotea baltica	1														1					
Jassa falcata	8				22		8	5	2			6	2	8	6	15	8	4	4	38
Lacuna vincta	9		3				5		11	2		1				4			1	13
Lamellaria sp.								3												
Lepidonotus squamatus	12				9	7		16	14		4	5	5		4	7	11	9	7	11
Lineus longissimus	1	1			3		1				5	1	1		1		2	1	2	1
Liparis liparis		1							1	1						1				1
Littorina littorea	1	1	2				1													
Membranipora membranacea				2			6	2								3	1			
Modiolus barbatus	1		2	1	2	3	1	5			1	1		2		2	1	1	1	1
Molgula sp.													1				2			
Mya truncata	3	22	14	1	15	17	37	45	17	18	22	4	7	20	16	6	30	3	26	5
Mytilus edulis	1	1		1			1	8	2	3	2	1		2	6		1		2	2
Mucronella coccinea	4	2		1	2	2	1	6	3	1	1	1	3	2	1	5	6	5		4
Nassarius reticulatus		1	19				1			3		1			1	2		4		1
Nomia patelliformis	4	4	8	3	27	4	3	40	9	5	4		1	4	11	16	29	15	6	6
Nereis pelagica	30	19	34	20	16		31	34	26	12	27	20	20	12	16	25	16	20	24	9
Nymphon gracile			1				3												1	
Ophiothrix fragilis	8	25	42	39	35	42	12	51	15	27	52	28	16	41	10	25	50	26	7	22
Ophiopholis aculeata	17	8	11	4	13	23	7	8	4	6	13	26	10	15	4	21	28	27	1	15
Ophlitospongia serriata														1						
Patina pelucida			1	1	1	1	1			1										
Palaemon squilla												1								
Phyllodocidae.									7					1						
Polycera quadrilineata																				2
Pomatoceros triqueter	36	12	33	10	24	11	2	34	19	12	13		7	16	8	22	6	4	3	15
Porcellana longicornis	13	29	10	28	19	52	21	37	59	18	45	48	53	11	14	25	17	39	20	28
Primela denticulata													1							
Pycnogonum littorale	1		3						1			2	3							
Rissoa sp.					3				1											
Rostanga rufescens																		1		
Sabellaria spinulosa			5									2								
Salmacina dysteri					2	3		5						8	3	4	5	3		4
Sydnium turbinatum															1					1
Tealia felina								3	1				1		1	1	2	2		
Tectura testudinalis															2		1			
Terebella sp.						1		1				2								
Tonicella rubra						2	1	1	3	2	2	1	1	2					2	
Tubulanus annulatus																1				
Tubularia larynx												5								
Trivia arctica		1								1			1			1				1
Umbonula verrucosa	4	2	4	4	5	2	1	6	1			1			1	5	6	5		
Velutiana laevegata														1						
Venerupis pullustra		1	20	3			2	1	1		2			4			1			

APPENDIX

Temporal Studies Station 15 (Souter Point)
Raw Data.

	Sept. 1967	April 1968	June 1968	Oct. 1968	April 1969	May 1969	June 1969	July 1969	Aug. 1969	Nov. 1969	May 1970
Mytilus edulis	1200	0	1	17	2	30	1504	635	180	140	1720
Sabellaria spinulosa	4	0	550	63	85	0	32	24	70	75	24
Actinea equina	1	2	1	-	1	-	-	-	-	-	-
Anomia Ephippium	-	-	2	-	-	4	4	-	-	-	4
Anthopleura thallia	-	-	-	-	3	-	-	-	-	-	-
Balanus balanus	1	-	1	-	-	-	4	-	-	-	-
Botryllus schlosseri	-	-	-	1	-	-	-	1	2	-	-
Botrylloides leachi	-	-	-	-	-	-	-	-	1	-	-
Hymeniacidon perleve	-	-	-	-	-	-	-	-	-	-	2
Halichondria panacea	-	-	-	1	-	-	1	-	-	-	4
Lanice conchelega.	-	-	-	-	-	-	-	-	-	1	-
Membranopora membranacea.	-	-	-	-	-	-	-	-	-	-	-
Nomia patelliformis	-	-	-	-	-	5	-	-	-	-	5
Modiolus barbaratus	1	-	2	-	-	9	-	-	-	-	-
Mya truncata	3	-	2	1	2	3	-	-	-	2	-
Pomatoceros triqueter	3	-	1	-	2	-	-	-	3	-	-
Phyllograna implexa	4	-	-	-	-	-	-	-	-	-	-
Taelia felina	-	-	-	2	-	3	1	1	1	-	-
Umbonula verrucosa	4	-	-	-	-	-	-	-	-	-	-
Flabelligera affinis	1	1	-	-	1	1	1	1	1	1	2
Terebella sp.	1	-	-	-	9	-	-	-	-	-	-
Nicolea zostericola	-	-	-	-	8	-	-	-	-	-	-
Acanthochitona crinitus	1	2	4	-	1	-	-	1	1	1	-
Lacuna vincta	-	-	-	1	-	-	-	-	-	-	-
Patina pellucida	-	-	1	-	-	1	1	-	-	-	1
Tonicella rubra	-	-	4	-	-	-	1	-	-	-	-
Tectura (Acmea) testudinalis	-	-	-	-	-	-	-	-	-	-	1
Asterias rubens	4	4	19	5	10	5	8	7	3	5	3
Lamellaria sp.	-	-	-	1	-	-	-	-	-	-	-
Nereis pelagica	8	2	7	6	10	10	2	2	19	6	15
Nymphon gracile	-	-	-	-	-	-	-	-	-	1	-
Phyllodoce sp	-	-	-	-	5	5	-	-	-	-	-
Pycnogonum littorale	1	-	-	1	3	-	-	-	-	2	1
Amphiopholis aculeata	-	-	-	-	-	2	-	-	-	-	-
Amphithoe rubricata	-	1	-	3	27	2	2	1	2	1	1
Cancer pagurus	-	-	2	1	3	1	-	-	-	-	-
Echinus esculentus	-	-	-	-	-	-	-	-	1	-	-
Harmathoe impar	3	4	6	-	-	3	-	2	3	-	-
Henriqa sanguinolenta	-	-	-	3	1	-	-	-	1	-	-
Hyas areneas	-	-	-	-	-	1	-	-	-	-	-
Jassa falcata	4	2	-	-	-	-	-	-	2	-	-
Lepidodontus squamatus	-	-	4	2	4	1	2	2	2	1	2
Ophiothrix fragilis	-	-	7	-	-	-	-	1	-	-	-
Palaemon squilla	-	-	1	-	-	-	-	-	-	-	-