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THE HOLDFAST ECOSYSTEM OF LAMINARIA HYPERBOREA
(GUNN.) FOSL. AND ENVIRONMENTAL MONITORING:
AN ECOLOGICAL STUDY

CHARLES R.C. SHEPPARD

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A Thesis presented for the Degree of Doctor of
Philosophy, University of Durham.

March 1976.

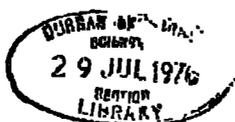


To the memory of my
Father

ABSTRACT

The holdfast fauna ecosystem of Laminaria hyperborea was tested for use as a means of environmental monitoring. Samples of about three litres of holdfast space are desirable sample sizes although one litre is the absolute minimum. Several natural environmental variables, namely fresh water, rock type, depth, exposure and sedimentation were shown to have no significant effects on holdfast fauna composition. In pollution monitoring therefore these can be disregarded as complicating factors. Gradients of heavy metals and water clarity around the U.K. were defined. To these two variables were added those of latitude and longitude, and these four variables have marked effects on holdfast faunas. Changes in holdfast composition at the 35 main sites sampled are interpreted in the light of these variables. Along the North Sea and West coast sewage pollution and heavy metals respectively have a marked effect on the fauna. Along the South coast unidentified variables correlating very closely with longitude are important.

Emphasis in interpretation must be placed on numbers of organisms, species richness and diversity in known sample sizes of holdfasts, and on the community trophic structure. Species presence / absence information has no meaning in holdfast work.



ACKNOWLEDGEMENTS

My thanks are due to Professor D. Boulter of the Department of Botany for the provision of laboratory space and facilities.

My sincerest thanks in particular are due to Dr. David Bellamy who supervised this work and provided considerable advice in all its stages.

I gratefully acknowledge also the financial support given by the British Sub-Aqua Club which enabled several parts of the work to be undertaken, notably the collections from the furthest flung regions of the United Kingdom, in particular the Shetlands. Equal acknowledgement for financial assistance is also due to the E.E.C. (Contract Number 074741-ENV.UK) for supporting this research.

Many people helped in this work, in particular, Anne Cunningham, N. Phillips and Christine Fisher assisted greatly with the collections and preliminary sorting of species.

Acknowledgement of every individual who assisted in the very large diving programme involved in this work would defy description. Over 700 divers from more than 50 diving clubs participated and to all, especially the organisers amongst them, I am most grateful.

In the identification of species help was received from Dr. S. Smith (molluscs), C. Bogdanos (polychaetes) and D. Herdson (nemertines and ascidians) in addition to those who have been acknowledged earlier.

Finally many thanks to Patricia Durkin for typing this manuscript.

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INTRODUCTION

It was the publication of Rachel Carson's Silent Spring in 1963 that engendered widespread concern over pollution of the environments of the world including the sea. One of the manifestations of this concern was a major international and multidisciplinary conference sponsored by the F.A.O. and held at their headquarters in Rome in 1970.

During the conference several conclusions were drawn and recommendations made (Ruivo 1972). One of these was that although the conference recognised the difficulties inherent in marine ecological research it urged that the establishment of useful baselines for the comparative study of marine ecosystems should continue. The need for such studies was emphasised particularly in the light of possible chronic effects of long term exposure to persistent pollutants. Further, it was advised that such studies should not be limited to commercially important species only, since it is in the "unimportant" species, and most specially at the level of whole ecosystems that early recognition of harmful effects might first become apparent.

The F.A.O. conference further proposed that pollution problems could be classed into three broad groups:

(1) Those requiring local action. These are the bulk of occurrences, including as they do pollution of localised coastal areas and estuaries. These usually fall within the jurisdiction of a national or even local government.



(2) Those requiring regional cooperative action. These include the Mediterranean or the North Sea whose welfare is the concern of several nations.

(3) Those requiring global international action. Oil spillages and mid ocean dumping are the best example of this category.

The work reported in this thesis concerns categories (1) and (2), the local effects and regional trends of pollution. However it must be accepted that any major changes in the biology of the North Sea could have global repercussions as well, through for example, both international fishery concerns and migratory birds (Bellamy et al 1973).

In the late 1960's a comprehensive programme of research involving personnel from several Universities and Marine Stations was initiated, centering on the pollution gradients of the East coast of Britain (Croombe 1967). The aim of the programme was to ascertain the impact of a long history of potential pollution of the inshore waters by heavy industry and large concentrations of population.

One aspect of the programme was concerned with the ecology of the invertebrate communities inhabiting the holdfast of the alga Laminaria hyperborea. This thesis reports an extension of this work. However, before describing the research in detail it is relevant to consider (a) the possibility of studying marine pollution and the general methods which are used, and (b) the more specific results of the previous work in this programme.

The Approach

In any investigation of marine pollution, whether of a short term pollution incident or a long term pollution state, the need is to identify both the pollutants and the effects.

Two opposite but complimentary approaches may be found in the literature.

(1) Laboratory based studies, in which the effects of a supposed pollutant or mixture of pollutants are tested using standard L.C. 50 procedures on test organisms, backed by analysis for the levels of the pollutants in the marine environment (e.g. Skidmore 1964; Herbert and Sherben 1964; Herbert and Vandyke 1964; Brown et al 1969; Brown 1971). Such an approach may be useful at least as far as legislation concerning permitted discharges is concerned.

(2) Field based studies, in which either pre- and post- pollution data relating to an organism or ecosystem, or variations in certain attributes of an organism or ecosystem along a supposed pollution gradient are studied (e.g. Bellamy et al 1967a; Bellamy and Whittick 1968; Jones 1970, 1971, 1972, 1973; Moore 1971, 1973a, 1973b; Malachtari 1973; Genakos 1975).

The first approach is limited by the number of organisms which can be tested and the validity of extrapolating the results obtained to the field.

The second approach is limited by the fact that there is enormous variation of the natural environment in the sea over very small distances

which aggravates the problem of assessing cause and effect (Lewis, 1964, 1972).

There seems little doubt that a combination of both approaches might be best in that supposed "sensitive" organisms (indicator organisms) recognised from field studies might then be tested within the laboratory.

Indicator Organisms

Several authors have attempted to identify and make use of indicator species. Henriksson (1969) stated that an indicator species must be a natural component of an animal community, must be abundant, omnivorous, and able to withstand low oxygen tensions. He found that polychaetes such as Nereis diversicolor were most suitable, followed by some Lamellibranchs. In his study the abundance of these organisms correlated with the concentration of Escherichia coli in the water and therefore presumably with pollution by sewage. Wass (1967) using nereids for monitoring thermal pollution came to the conclusion that small organisms of high biotic potential were most suitable. Cairns and Dickson (1971) used a variety of macroinvertebrates, and Howells et al (1970) found the alga Cladophora to be a fair indicator of pollution.

It is of interest that all these are no more than scientific appraisals of the fisherman's concept of "worms and weeds in abundance" means pollution.

Stirn (1970) discusses the unreliability of such indicators, citing several instances where supposed indicators were found with equal abundance in polluted and non-polluted situations. He states that indicator

species are of limited value if considered singly, and even Henriksson (loc cit) stressed that their usefulness comes mainly when they are regarded as part of a community. Stirn further suggests that the use of indices of diversity are of more value in interpreting the condition of a site and proposes that measures of abundance can aid such interpretations, especially if the problems of patch distributions can be overcome.

Diversity

The literature is full of both methods for and attempts to measure diversity.

(1) The simplest measure of diversity is to count the number of species in a given space. The problems with this are the limitations both of time and of adequate taxonomy, especially when dealing with the smaller organisms. In practice an arbitrary size is selected and once the data has been gathered all the classic and new techniques of computer analysis are available for interpretation of the data. John (1968) and Moore (1973b, 1974) have investigated the use of some of these methods in the field of marine ecology. The second major problem with this method of estimating diversity is that it takes no account of abundance, so that a single occurrence of a bacteria would be given as much weight as the presence of a school of whales.

(2) To overcome the latter, Fisher, Corbett and Williams (1943) devised their α index which was derived from the total number of species and the log. of the total number of organisms present. This relationship was formulated because of the common community characteristic that few species are common and many species are scarce, a distribution best fitted by a logarithmic relationship. Despite several modifications (e.g. Preston

1948) and the fact that the log. normal relationship is not a theoretical certainty, the index has continued to be of considerable use.

Later attempts at the description of communities were independent of assumed distribution patterns.

(3) Based on Margalef's (1958) information theory Shannon and Weiner's H value (Shannon and Weaver 1963) is of interest. This was a measure of the uncertainty of predicting which species will be the next to be found in a population. The H value has two components; the number of species, and the evenness of the relative abundance of each. The two components are arranged such that a greater number of species and a greater evenness of their distribution increases H. This today is probably the most widely used index of diversity.

(4) Another approach was that of Simpson (1949). His index D is derived from probability, the probability of two individuals picked at random being the same species. This gives relatively less weight to rare and more weight to common species.

All three approaches were used in the preliminary part of the work (see figure 7). As no important differences were found between the three approaches the α index has been used throughout the bulk of this work.

Biomass

An adjunct to the use of numbers in the above indices is to use biomass, either as a fixed value (standing crop) or as an increment (performance measured against time).

Oglesby (1967) demonstrated that certain organisms increase in size by some function of their distance from a source of pollution containing a high free energy of oxidation (e.g. sewage). In plankton work biomass studies have been a favoured method (e.g. Stirn 1970b; Ghilarov and Timonin 1972; Hopkins 1974). Bellamy et al (1967, 1970) have similarly used various measures of performance of macrophytes to assess water clarity. It must also be remembered that in both aqua- and mariculture fish are often deliberately "polluted" to foster growth (Larkin and Northcote 1969).

It is of relevance that whatever the methods used many of the authors note differences in the trophic structure of polluted communities compared with equivalent, non-polluted ones.

THE HOLDFAST AS A SAMPLING UNIT

The holdfasts of the large brown laminariales have long been recognised as being a rich source of marine animal life. In the early days of taxonomy, and in the nineteenth century in particular, a major part of natural history involved making collections of specimens (some of which earned considerable fame). One very significant source of specimens was the kelp holdfast found on the strand-line which provided animals from regions quite inaccessible to the collector. An appreciation of the possible rewards awaiting naturalists if they could reach the living and growing kelp beds was made by Mrs. Gatty in 1872. Amongst her pages of advice to young ladies - on what to wear when collecting specimens - she looked forward to the day when "diving for seaweeds has become a fashionable amusement and an indispensable part of an algologists education".

Following the advice of the experts, students of marine natural history dissected jetsam holdfasts by the score, extracting their wealth of life. Their importance as a rich habitat is demonstrated in Barrett and Yonge's well known Guide to the Sea Shore where there can be found very many comments to the effect "found also in Laminaria holdfasts". This is particularly true in the polychaete section.

The attraction of the holdfast to the early marine biologists was simple. They were units, or samples, from depths never uncovered by tides, and contained animals presumably representative of those depths. Even today, decades after man first freely entered these regions, the holdfasts still hold an attraction for collectors, taxonomists, and those wanting to compile species lists of special areas (e.g. Colman 1940; Earll 1974).

The only basic difference is that today the researcher can dive into the kelp zone and collect the live holdfast with its fauna intact, rather than rely on those washed up onto the beach which have been subjected to probable loss of fauna.

The advantages of using holdfasts are obvious to any diver interested enough to cut one open: they contain a far greater concentration of animals than is found on neighbouring patches of bare rock. Also the holdfast is easily collected.

Despite this, only three authors have performed important quantitative and qualitative work on the fauna inhabiting holdfasts. The work of these three are contained in their Ph.D. theses (Scarrett 1960; Jones 1970; and Moore 1971) and in several subsequent papers largely arising from them.

Scarrett (1960) was the first in the field and began his study not long after the potentials of free diving in marine biology became recognised, a point which is reflected by the fact that he goes to some trouble describing and explaining the aqua-lung. His work concerned the holdfast communities of several species of large brown algae; Laminaria digitata, L. hyperborea, L. ochroleuca and Saccorhiza polyschides. The work was carried out along the South and West coasts of Britain and contains some valuable information on the holdfast communities. This was the first treatment of holdfasts as a community rather than as a mere provider of species for a check list.

Jones (1970) and Moore (1971) worked simultaneously but independently (sharing dive time and taxonomic expertise only) along a stretch of the

East coast of Britain, parts of which are polluted by industrial and domestic wastes. They both restricted their work to L. hyperborea.

The original work of Jones was to determine the suitability of using the holdfast as a unit for monitoring pollution. The basic aim was to compare the infaunas of holdfasts collected along the suspected pollution gradient, limiting the species studied to those over approximately 2 mm. in size. Firstly he studied the growth of the holdfast, and appreciating that the sampling unit was changing (growing) with time, he studied the changing composition of the fauna as the habitat enlarged. He concluded that a process akin to succession occurred, with the holdfast community reaching its climax state after four years in unpolluted areas. In polluted areas it was shown that community development was arrested at what he called a neotenus state. The "immature" communities were dominated by suspension feeding species, usually Mytilus or Sabellaria, whose large populations fluctuated violently. Generally the trophic state of the whole fauna seemed adapted to optimum use of the increased organic load in the water. Due largely to these increased numbers but also to a reduction of other species the diversity of the polluted communities fell below that of the unpolluted communities. Jones defined the North East pollution gradient in terms of diversity, and showed that this compared fairly closely to gradients deduced from chemical data. Finally, Jones formulated four components in his gradient from the Firth of Forth to South Yorkshire, which were from North to South: estuarine-polluted, unpolluted, polluted and naturally turbid.

Moore (1971) chose a smaller though equally arbitrary minimum size of organism which encompassed groups such as the nematoda (1971b) and

micro-crustacea (1973c) in addition to all those included by Jones. The increased difficulties of taxonomy and time brought about by this however caused his samples to be quite small; four to six holdfasts per site compared with at least ten in the case of Jones. Moore's data was then subjected to a range of multivariate statistics based on presence/absence information.

The different approaches has led to some controversy (Moore 1974) on the validity of using the holdfast fauna to monitor the marine environment. However it is of interest that even using a wider range of species in smaller sample sizes several of their broad conclusions are similar. Moore also alludes to gradients although one of the primary differences between the two authors concerns whether the causes of the gradients are due to pollution or to natural turbidity. Several of the differences of opinion can be resolved however when an understanding of their different approaches and sampling rationales, and a greater understanding of the statistics used by Moore, are gained. These differences will be discussed in more detail later in the thesis.

The Question of organism size

In any study such as this some arbitrary limit must be set on the size of organism to be included. A total biotic inventory of a single holdfast would take many months and the taxonomic problems relating to even all the eukaryotic organisms would be almost insurmountable without the additional problem of the prokaryotes. In the light of the problems encountered by Moore in taking his study down as far as the free living nematodes and microcrustacea, which severely limited his sample size and his number of samples, it was decided to apply a minimum limit of

approximately 2 mm. All organisms not larger than this in any dimension were excluded from the data treatment. This alleviated many of the more difficult taxonomic problems including the problems of larval identification. Another major difficulty avoided by this size limit is that of parasitic organisms; Moore included the nematode group in his work but excluded the multitude of species within this group that are "parasitic" on almost every living animal. Finally inaccuracies of counting numbers of each species are alleviated by this decision since although the numbers of larger species may all be counted with some accuracy, those of the smallest species cannot. Moore circumvented this problem by claiming that the numbers of each species was not important, but until this was proven or disproven it was decided that data on numbers of each species would be desirable.

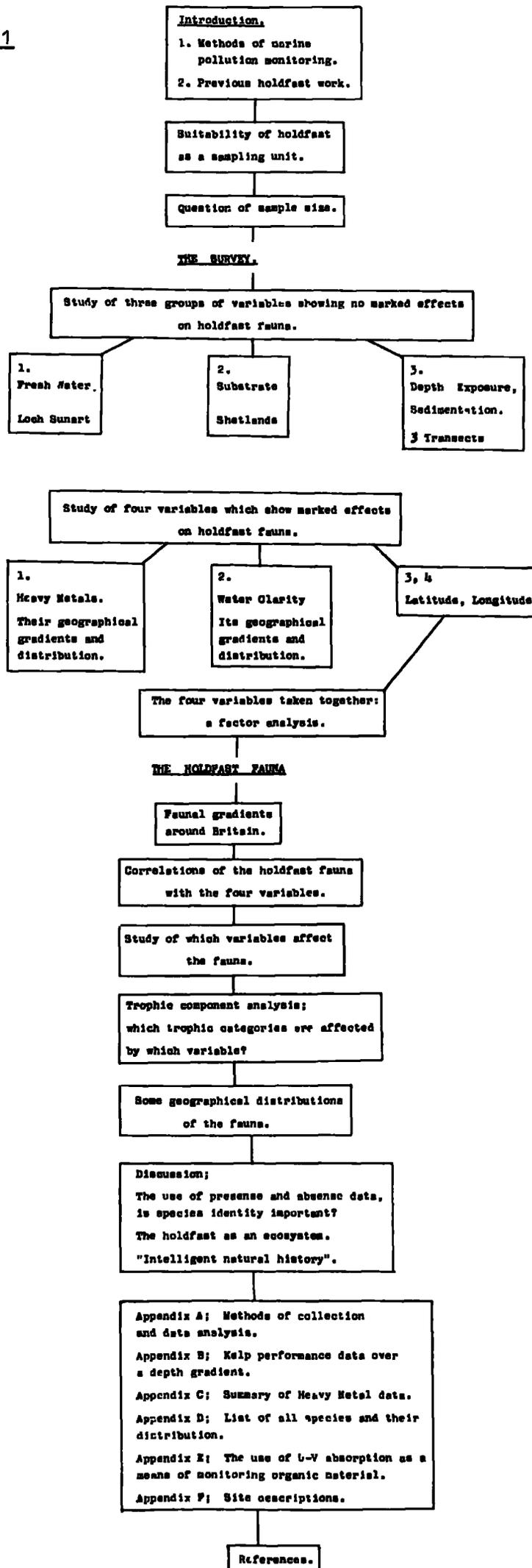
A second arbitrary decision was taken which was to treat colonial ascidians, bryozoans and hydroids as single organisms. Likewise when Spirorbis and Filograna were present they were present in enormous numbers and so these were treated in the same way. To do otherwise would swamp quantitative data treatments and could conceal much information. In terms of biomass none of the groups treated in this way would have contributed more than a very small proportion to the total.

It is emphasised that these decisions were taken in order to allow (1) sample sizes to be adequate and (2) the number of samples to be sufficient.

Outline of research

The design of the research of this thesis is shown pictorially in figure 1. It was decided that an in depth study of the holdfast faunal system, within

Figure 1



the above limitations, around the whole of Britain was required, combining observations of the ecosystem with numerically described levels of pollution arrived at by analyses. The main type of holdfast considered is that of L. hyperborea, with those of L. ochroleuca considered in one section.

With the basis of previous work it was possible to plunge more directly into testing the use of this sampling unit for pollution and environmental monitoring. Before the study could take place however two main questions needed to be answered. The first was whether or not the holdfast itself has an effect on the community which it contains and supports. The second question relates to minimum sample size, something strangely neglected by other workers. The way in which sample size should be measured, and what this size should be were both determined.

INERT SAMPLING SPACE OR BIOTIC UNIT?

The first important question to be answered was; is the holdfast purely an inert sampling unit, providing merely a physical receptacle for its inhabitants, or does it in any way influence the infauna by being itself a living unit with its own chemical and textural characteristics? Would a holdfast made of a different material contain a different fauna?

In places along the South Western tip of Cornwall Laminaria ochroleuca reduces the dominance of L. hyperborea in the photic zone (John 1969). This alga, which in Cornwall is at the northern limit of its geographical range, is very like L. hyperborea, with a holdfast of similar appearance and size. It was therefore decided to make a comparison between the infaunas of the holdfasts of the two species growing in a mixed stand.

A site was selected at a promontory near Falmouth (Grid reference: SW826315) where L. hyperborea alone existed down to about 5 metres depth after which both species co-existed in approximately equal numbers. Twenty mature holdfasts of each species were collected from the lower zone.

The inhabitable volume of the holdfasts were determined by Archimedes' displacement principle, (see Appendix A). The mean volumes of the two species are shown in Table 1, from which it is obvious that there is no significant difference in the internal volumes of the two groups of holdfast:

Table 1

	<u>L. hyperborea</u>	<u>L. ochroleuca</u>
Mean	238 mls.	245 mls.
S.D.	102	149

Moore (1972) has suggested that the degree of openness of the hapteron branches might be important in determining sedimentation and hence the fauna within the holdfast. A measure of the "density" of the branches was therefore obtained by finding the percentage of the total holdfast volume that is filled with plant tissue. The mean percentage of each group was:

Table 2

	<u>L. hyperborea</u>	<u>L. ochroleuca</u>
Mean	37.2%	39.1%
S.D.	8.7	9.9

The values obtained showed a small range. It is assumed from these results that there is a negligible difference in the morphology of the two species.

Differences between the two plants do exist. The stipes and haptera of L. hyperborea have a rough texture which provide a suitable substrate for a large epiphytic growth, while L. ochroleuca is smooth and supports almost no epiphytic growth. Out of the water L. ochroleuca quickly becomes very slippery while L. hyperborea does so much more slowly suggesting that the exudation of extracellular material is much greater in the former. A comparison of the infauna from each group should reveal the effects of holdfast texture on the communities.

Faunal differences (1) Quantitative

Figures 2(a) and (b) compare the numerical results of the faunal compositions, as related to the accumulated volumes of the holdfasts

FIGURE 2 a

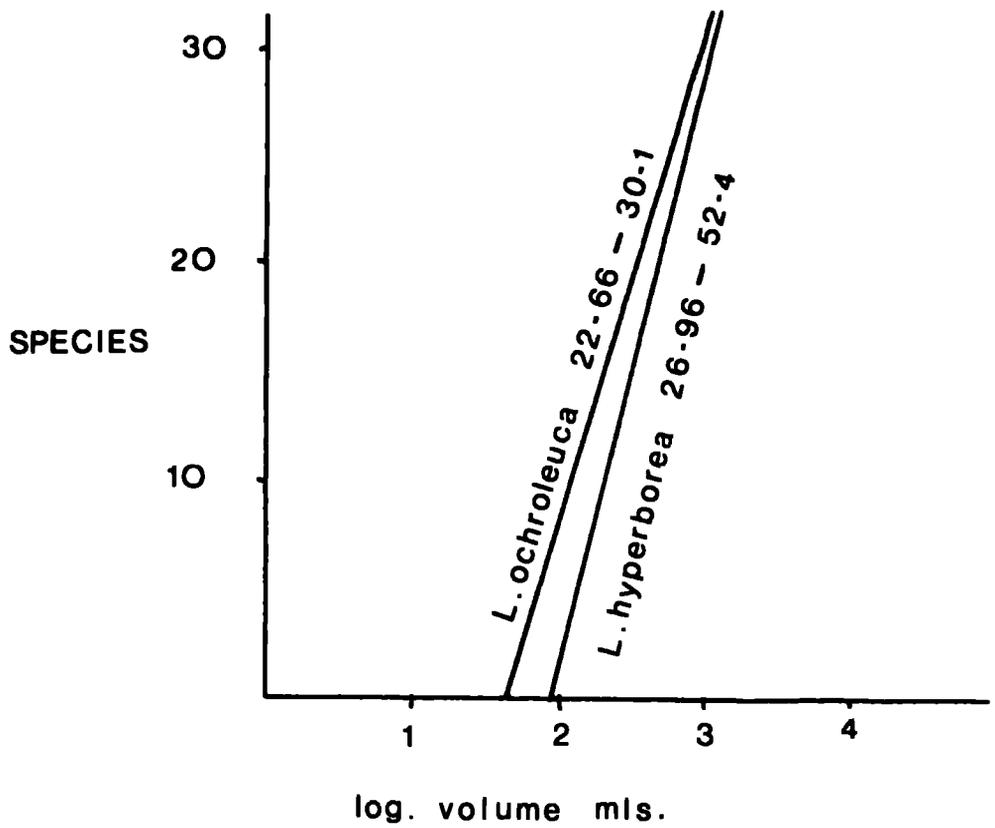
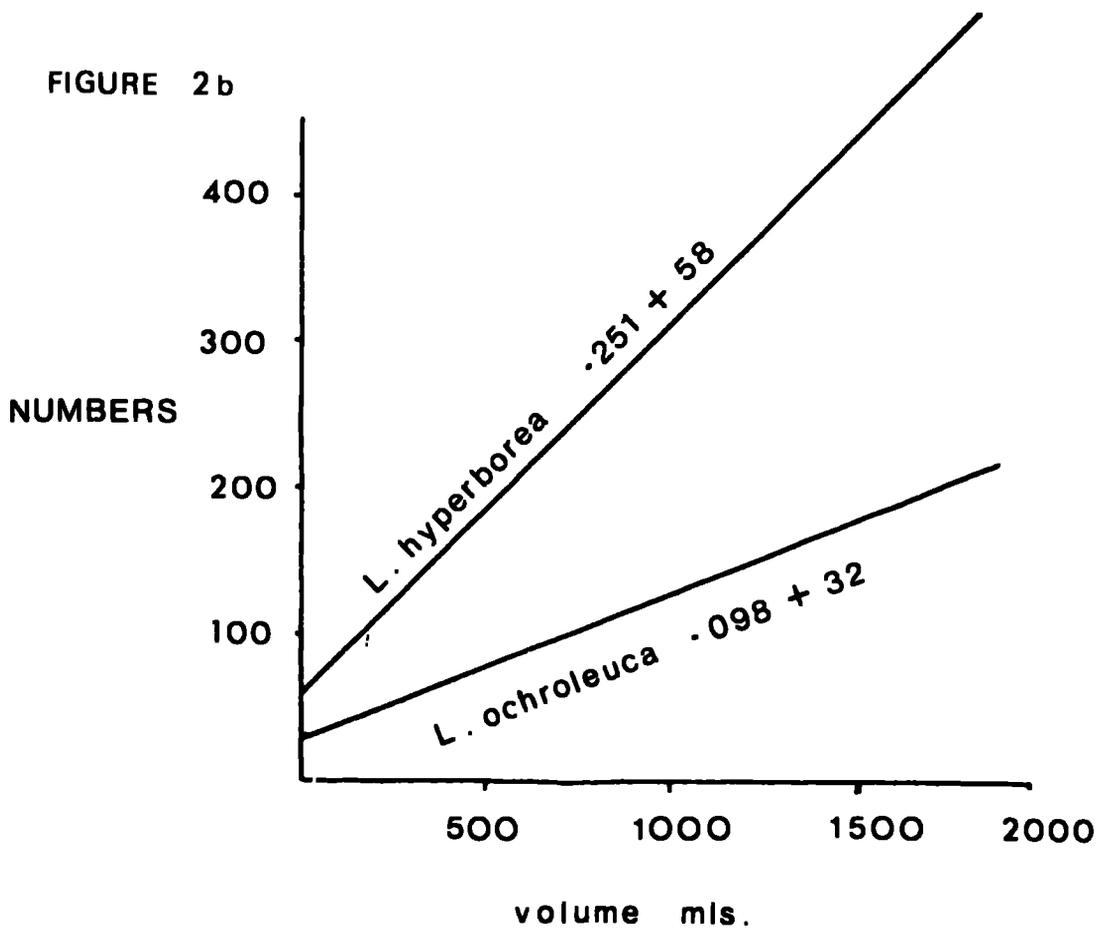


FIGURE 2 b



FAUNISTIC COMPARISON FROM TWO SPECIES OF
LAMINARIA.

sampled. Part (a) shows the regression lines of the number of species plotted against log. volume for both types, and part (b) shows the increase of total numbers of animals with volume. With each line of best fit, analysis of variance showed that the scatter of points about the line was small, each line being significant to .001. (Statistical methods are outlined in Appendix A). Using the regression coefficients and their standard deviations it was found (1) that the two slopes in figure (a) are not significantly different, and (2) the two slopes in figure (b) are very different ($p=.001$). Therefore it can be concluded that the increase in the number of species with log. volume is very similar in the two types of holdfast, while total numbers increase at very different rates. The nature of the difference can be elucidated by examining the species involved.

Faunal Differences (2) Qualitative

(a) Species. Table 3 summarises the data of species found. In terms of species identity little difference is seen between the two types of community, which have the high Sorrensen similarity coefficient of 76% (see Appendix A for formula).

(b) Numbers. It was immediately apparent that large numbers of two species were present in the L. hyperborea holdfasts. This is depicted in figure 3 which includes separately all species contributing 10% or more of the total numbers. Of the 771 animals present in the 20 L. hyperborea holdfasts 377 were the barnacle Chthamalus and another 150 were the saddle oyster Heteranomia.

TABLE 3

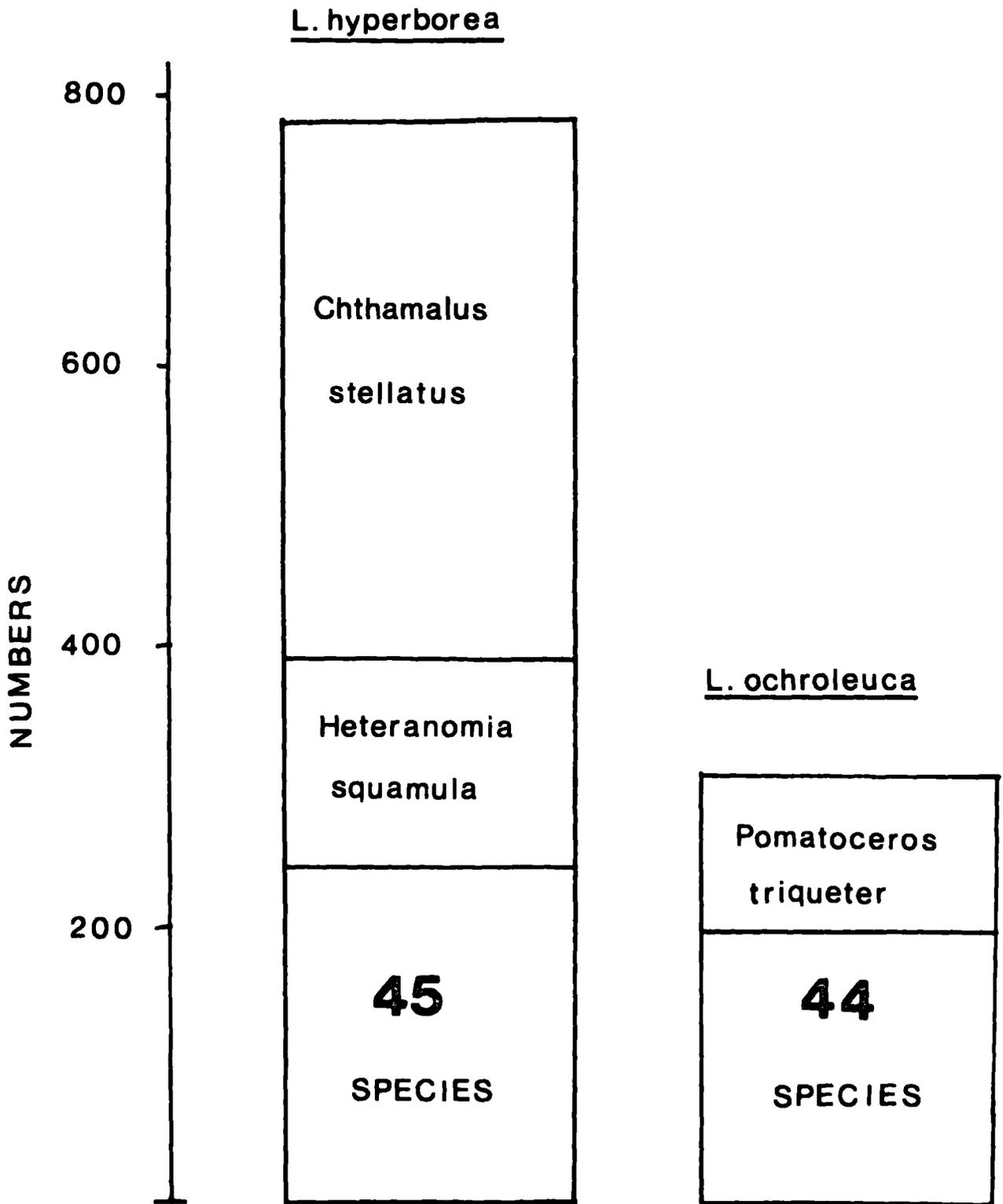
SPECIES LISTS FROM HOLDFASTS OF 2 SPECIES OF

LAMINARIA

	L. hyperborea	L. ochroleuca
Chthamalus stellatus	3	1
Heteranomia squamula	2	1
Hiatella arctica	+	1
Barnea parva	+	1
Nereis pelagica	+	1
pomatoceros triqueter	+	2
Serpula vermicularis	+	1
Amphipholis squamata	-	+
Audouinia tentaculata	+	+
Cancer pagurus	+	+
Corynactis viridis	-	-
Eunice harassii	+	+
Gibbula magus	+	+
Halichondria panicea	+	+
Hydrobidae	-	+
Lepidonotus squamatus	+	+
Lysidice ninetta	+	+
Macoma baltica	+	+
Monia patelliformis	-	-
Mytilus edulis	+	+
Nassarius incrassatus	-	-
Nereis virens	+	+
Orchestia gammarella	-	+
Patina pellucida	-	-
Pinnotheres pisum	+	+
Platynereis dumerilii	+	+
Polynoinae	+	-
Porcellana longicornis	+	+
Spirorbis borealis	+	+
Tellina tenuis	+	-
Rissoa spp.	+	-
Xantho incisus	-	+
Acanthochitona crinitus	-	-
Actinia equina	-	-
Ampithoe rubricata	-	-
Balanus crenatus	+	-
Buccinacea	-	-
Gammarus sp.	-	-
Harmothoe impar	+	-
Lacuna vineta	+	-
Lineus longissimus	-	-
Lineus ruber	-	-
Littorina neritoides	-	-
Musculus discors	-	-
Natica sp.	-	-
Syllis sp.	+	-
Terebellidae	-	-
Acmaea tessulata	-	-
Asterias rubens	-	-
Balanus perforatus	-	+
Cucumaria lactea	-	-
Eunemertes neesii	-	-
Hydroides norvegica	-	+
Modiolus barbatus	-	+
Musculus marmoratus	-	+
Ophiopholis aculeata	-	-
Pholadidea loscombiana	-	+
Protula tubularia	-	-

FIGURE 3

COMMON SPECIES FOUND FROM HOLDFASTS OF TWO SPECIES OF LAMINARIA.



With these deducted from the total some 244 animals are left. If the populations of these two species are deducted from the 304 animals in the 20 L. ochroleuca holdfasts, 266 animals are left. The difference in total numbers between the two groups are explained almost entirely by these two species.

Both Chthamalus and Heteranomia are animals which live firmly attached to a substrate throughout their adult lives, although their mode of attachment is different. It has been remarked upon that L. ochroleuca produces copious amounts of viscous exudate, more so than L. hyperborea. It may therefore be that the slimy nature of the former inhibits attachment by these two species. Direct observation of L. ochroleuca shows that epiphytic macrophytes are unable to attach, and possibly animals are unable to attach in the same way.

One apparent contradiction to this needs explaining. 36% of the animals in L. ochroleuca were the polychaete Pomatoceros triqueter whose calcareous tubes are also cemented to the substrate. However it was very apparent that whereas Pomatoceros on L. hyperborea or on rock were strongly resistant to removal and could seldom be prised away in one piece those on L. ochroleuca came away intact and with little resistance. This observation lends support to the belief that attached animals are less likely to gain a hold on the hapterons of the latter species.

Conclusions.

The dissimilarities observed between the faunas of the two types of holdfast are attributable to differences in the numbers of two attached species. Any differences in the numbers and nature of the bulk of the species would seem to be minimal and well within the range expected by sampling error. It would therefore appear that for the large majority of the animals the holdfast is merely an "inert" and convenient environment in which to live. For a few sedentary species however the textural characteristics of the holdfasts have a governing effect. Bearing this fact in mind it would seem to be a satisfactory sampling unit.

DEFINITION OF THE SAMPLE UNIT

The second question requiring attention before the main study could be undertaken was that of sample size. Sample size is as important a factor in holdfast ecology as it is in any other field of comparative ecology. Samples which are too small do not represent the true situation accurately, and for a similar reason, the use of samples of different sizes in comparative work must be approached with caution.

There are two ways in which sample size in holdfast studies can be regarded. (1) All holdfasts can be regarded as equal, in which case only the number taken is important. Moore took this approach, regarding each holdfast community as an exclusive entity which could be compared to others regardless of size. He felt that "..... the logical sample unit is the kelp holdfast per se" (1973a). (2) The ages or sizes of the holdfasts might be important so that a large one might be "worth" two or more small ones. Jones (1970, 1973) thought that age was important and relevant to the infaunal community; an idea which he elaborated on in his "succession" theory.

From this latter work it would seem that age is important, but since age and holdfast size increase together the possibility exists that size might be the important criteria. Therefore it was decided to examine both with regard to community structure and sample size.

The age and volume of holdfasts

The infauna was studied from 50 holdfasts collected from Loch

Sunart, Argyll (Grid Ref. NM405675). For collection and sorting procedures see Appendix A. The numbers of species from each of the common age groups, 5, 6 and 7 years, were plotted (a) against the number of holdfasts, and (b) their volume (figure 4a, b).

It is clear from the first graph that the increase in species progresses far more rapidly in the older holdfasts than in the younger ones. The second graph shows that when the differences in size are adjusted for by plotting against volume instead of number of holdfasts all three age classes produce very similar curves. This strongly suggests that volume of holdfast space, not just their numbers is important. When volume is taken into consideration the species response is the same regardless of the holdfasts age, at least for the three age classes used.

As the holdfasts in the above study were taken from unpolluted water and because much of the work described in this thesis is concerned with holdfasts from polluted water the investigation was repeated using holdfasts from a supposedly chronically polluted site at Marsden, County Durham (Grid Ref. NZ397658). The results are presented in figure 5a, b. Although fewer species were found here (for the same sample size) exactly the same pattern emerges.

The dangers of ignoring volume should be apparent in a comparison of the curves of 7 year old holdfasts from the polluted site with 5 year old holdfasts from the clear site, both plotted against number of holdfasts. The curves are very similar, not because the species response is the same but because a far larger sample size has in fact been taken from the polluted site.

LOCH SUNART

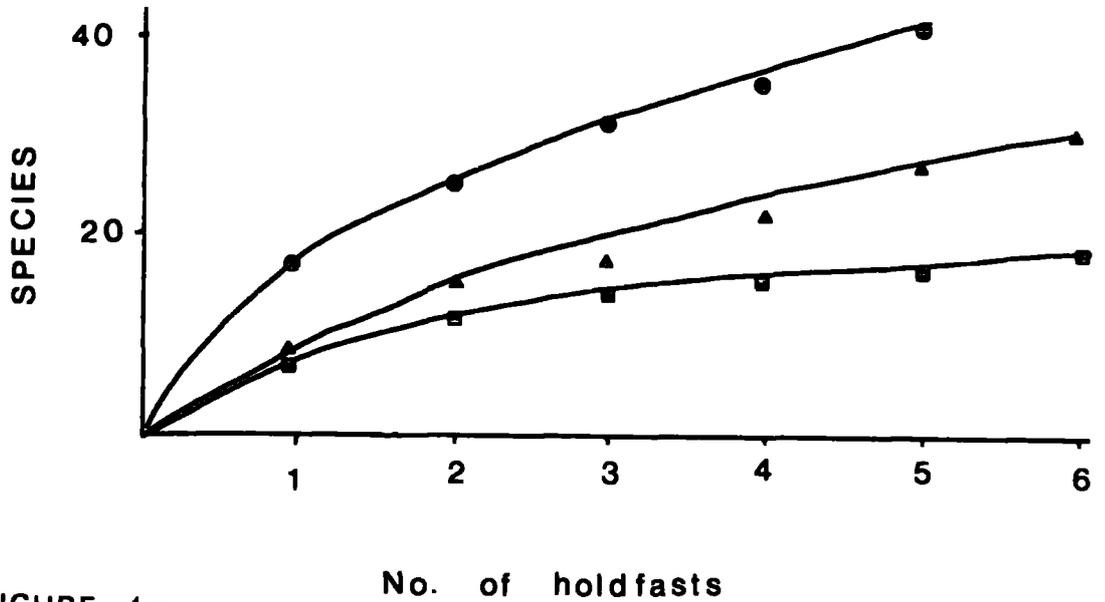


FIGURE 4a

○ 7 yrs

▲ 6 yrs

■ 5 yrs

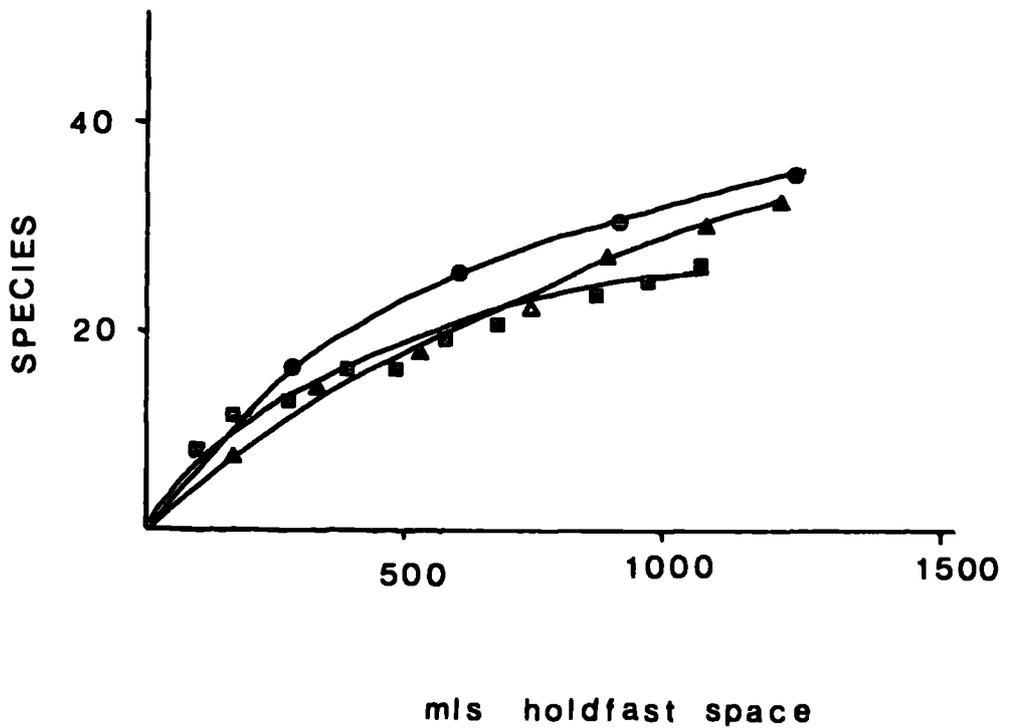


FIGURE 4b

SPECIES / SAMPLE SIZE CURVES (NUMBERS OF HOLDFASTS AND VOLUME OF HOLDFASTS).

MARSDEN

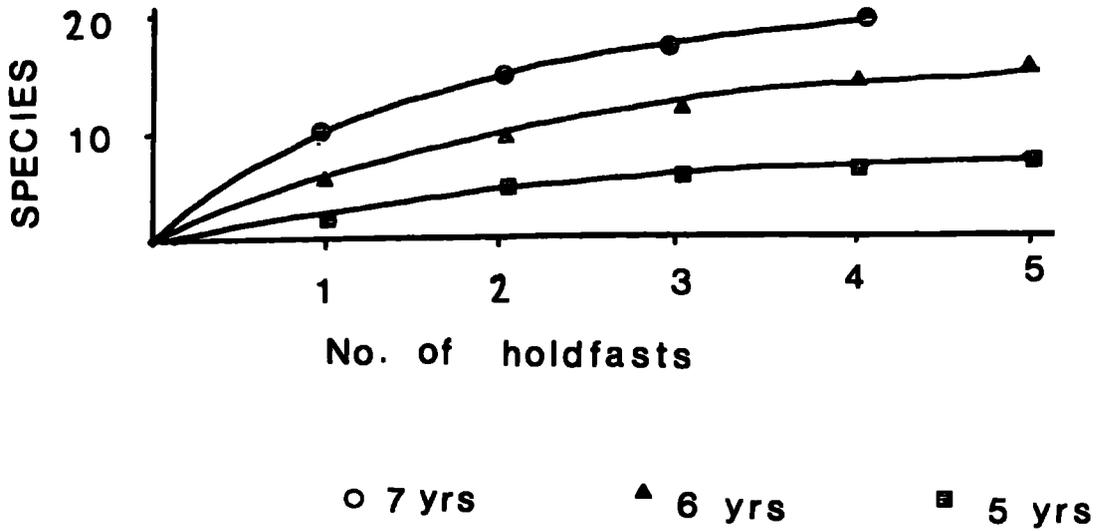


FIGURE 5 a

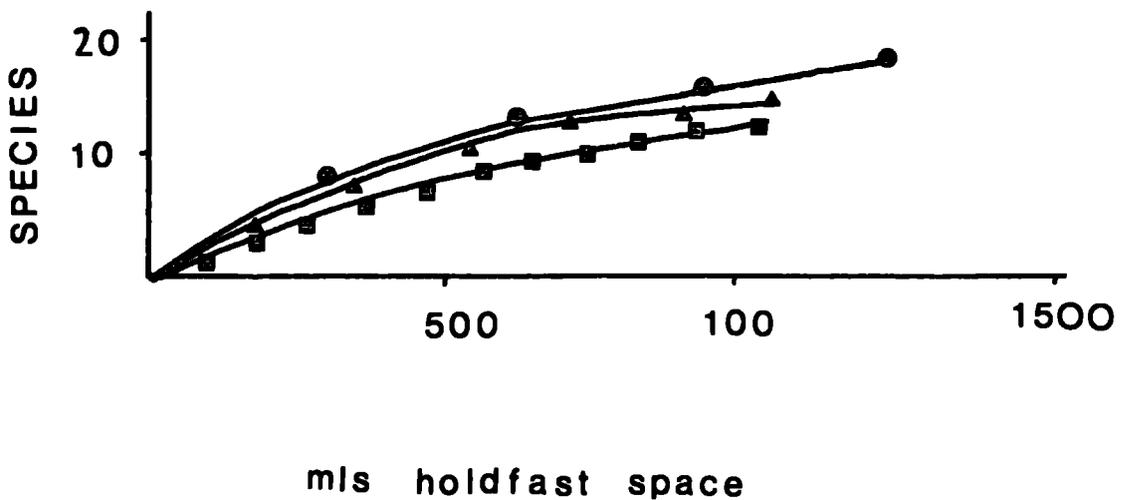


FIGURE 5 b

SPECIES / SAMPLE SIZE CURVES (NUMBERS OF HOLDFASTS AND VOLUME OF HOLDFASTS).

It is concluded that the inhabitable holdfast volume must be the criteria for sample size. It is not satisfactory to take a fixed number of holdfasts of any age. Nor would it seem adequate to regard each holdfast as an individual entity in comparative studies.

Minimal Volume

Having shown that sample size should be measured in terms of volume an attempt was made to determine the size of an adequate sample.

Of the three authors who have been concerned with holdfast ecology to date none have attempted to find out the minimum size of sample that should be taken either in terms of volume or numbers of holdfasts.

Scarrett (1960) did try to determine whether a half or even a quarter of a holdfast was an adequate sample, the intention then being to multiply the results obtained by two or four to produce the expected composition of that holdfast. His investigation showed this to be quite unsatisfactory as too many species were missed in such a small sample. He then arbitrarily decided on three holdfasts as his usual sample size.

The inadequacy of this number is well illustrated by his experiment on diurnal variation in holdfast animals. To illustrate diurnal migration into and from holdfasts he collected three holdfasts during one day and another three from the same spot the following night. A comparison of the faunas from each group revealed differences in the numbers of certain groups, notably some crustacea and polychaetes. The differences were usually threefold or more and he concluded that the reason for this was

due to diurnal migration. However from a brief study of his data exactly the same conclusions can be reached regarding the sponges and barnacles! Since the sedentary organisms presumably do not migrate diurnally the differences must be due to random, within site variation. Clearly three holdfasts are inadequate as a sample.

Scarrett went no further in determining minimum size. Despite this neither Moore nor Jones tried to find this preliminary requirement. Moore chose to take between 4 and 6 holdfasts (usually 5) and Jones took 10 when determining his "succession" process and an undisclosed number for the rest of his work. These sample sizes were more a reflection of what could be collected on one dive, or what could be worked on in the time available for sorting and identification, rather than of what was required to reliably reflect the local holdfast fauna. Also the sample sizes taken by each author often differed substantially in terms of volume from site to site.

The usual way to determine minimal size is to produce a species-area curve and take the point on the graph which shows a marked inflection.

The relevant data from Loch Sunart and Marsden are depicted in Figure 6. At the former site there is no inflection marked enough to indicate a minimal volume. There is however a reduction of the slope around the one litre mark such that the rate of species increase above one litre is only half that below it. In contrast at Marsden there is a marked inflection occurring at approximately one litre resulting in a near horizontal slope. This may be due to the absence of rare or uncommon species, a situation which has been reported to be typical of polluted

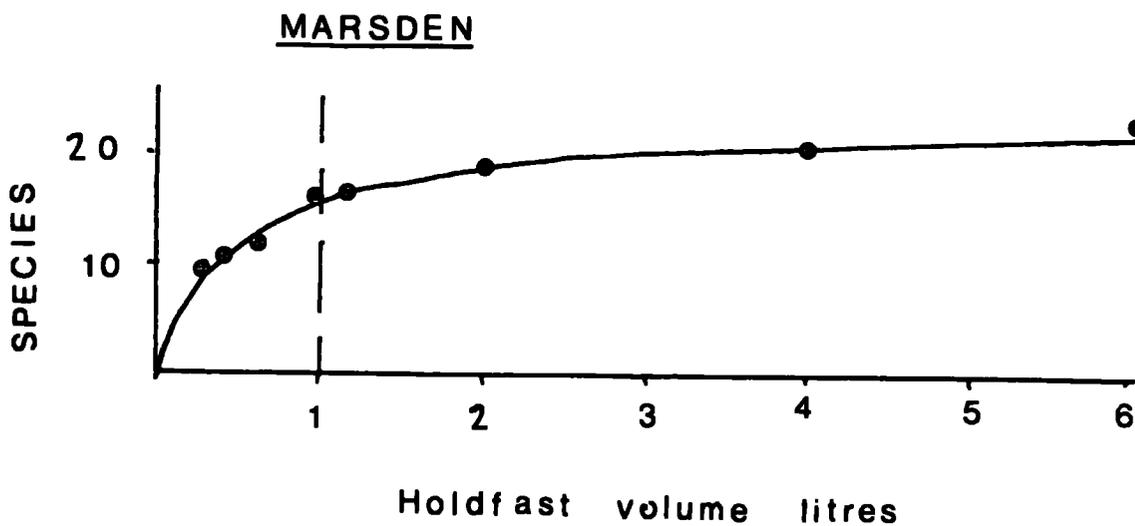
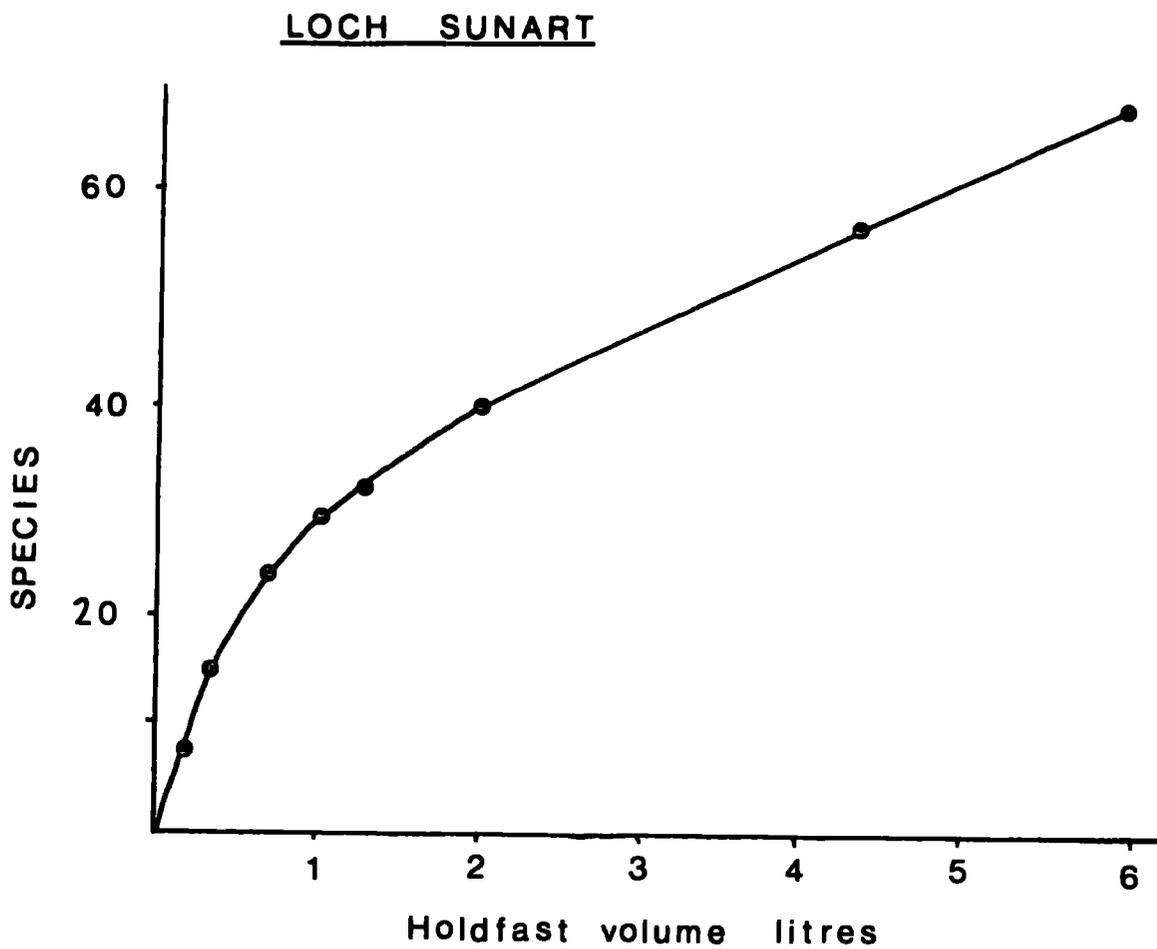


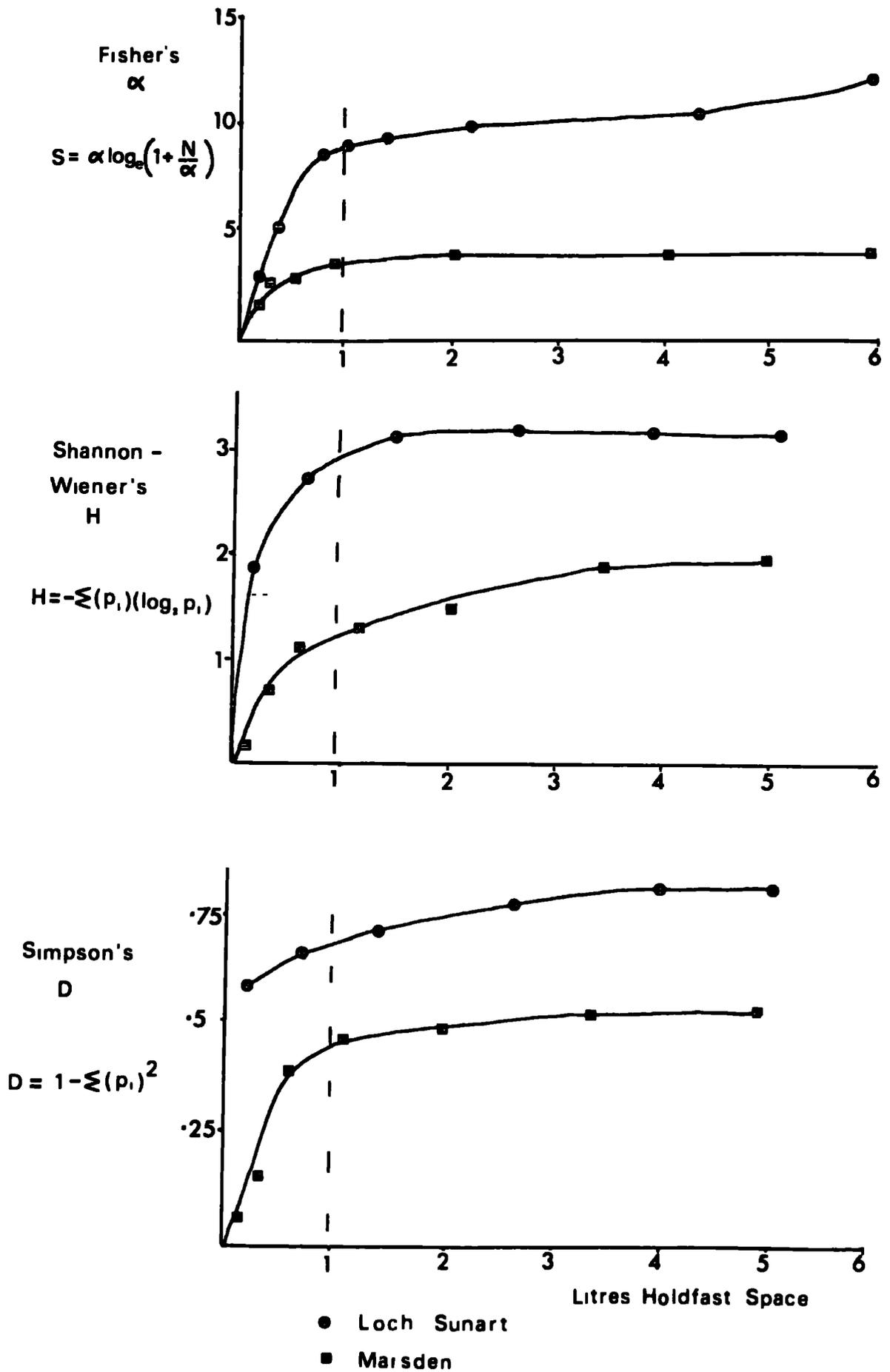
FIGURE 6
SPECIES / VOLUME CURVES FOR AN UNPOLLUTED AND
A POLLUTED SITE.

benthic communities in the Mediterranean (Stirn, 1970). At Marsden 75% of the total species found were present in the first litre. At Loch Sunart only 35% were. Clearly a fast rate of species increase continues for longer in the latter site. This illustrates that the smaller the samples are the more alike will these two obviously different sites appear in terms of species richness and probably in terms of presence/absence information also. In any comparable study sample sizes of less than one litre could certainly give misleading results.

Species number is only one characteristic of the holdfast fauna, and since it was shown to be rather inconclusive in designating a meaningful value for minimal volume an alternative approach appeared to be worthy of investigation. To this end it was decided to calculate three indices of diversity for the Loch Sunart and Marsden data and plot these against volume (figure 7) (see Introductory chapter for an explanation of the indices).

The first index, α , is supposed to be "independent of sample size" (Fisher 1943), but below one litre this is clearly not the case, and with smaller samples this index can have no meaning. The same picture emerges with the other two indices as well. The curves for all three indices flatten out at around one litre, although they may still rise slightly afterwards. This suggests again that one litre of holdfast space should be the absolute minimum that can be used as a sample, although more would be desirable especially in Loch Sunart and similar species rich areas. One litre of volume is usually reached with 6 to 12 holdfasts of mature 5 - 7 year old plants.

FIGURE 7
DIVERSITY / VOLUME CURVES



The data from samples that are smaller than three litres fall on those parts of the curves where the faunal composition is changing most with least change in sample size. The inadequacy of the samples taken by previous workers can thus be seen. It can also be seen that different sized samples, if they are small, must be compared only with great caution. As sample size accumulates the change in faunal composition becomes less with each additional holdfast, so that by the time 20 holdfasts are obtained the addition of one more makes little difference to the total. In a sense the twenty holdfasts should be regarded as one sample, not as 20 samples. In this respect Jones was probably correct in believing that a large holdfast was "worth" two or more smaller ones, but many of his and Moore's conclusions would seem to be invalid due to their sample size. The possibility exists however that Moore's species/sample size curves, had he prepared them, would have been different due to the smaller species he included. Yet as he included the larger organisms recognised in this study his "minimal" sample size could not have been much smaller.

Throughout most of this study 20 holdfasts, all being from plants aged 4, 5, 6 or 7 years, were taken from each site. The volume of the sample was measured and numerical data were corrected to three litre volume as a standard for comparative work.

THE MAIN STUDY

After establishing the suitability of the holdfast as a sampling unit and reaching conclusions on sample size, the sampling rationale for the main study was decided upon.

During the summer period in 1974 and in a few cases in 1975 as well, samples were collected from 35 sites in the United Kingdom (figure 8 and Appendix F). In addition to these, three groups of collections were made from Loch Sunart, the Shetland Islands and the Hebrides. These were used for the study of the responses of holdfast faunas to specific natural environmental variables.

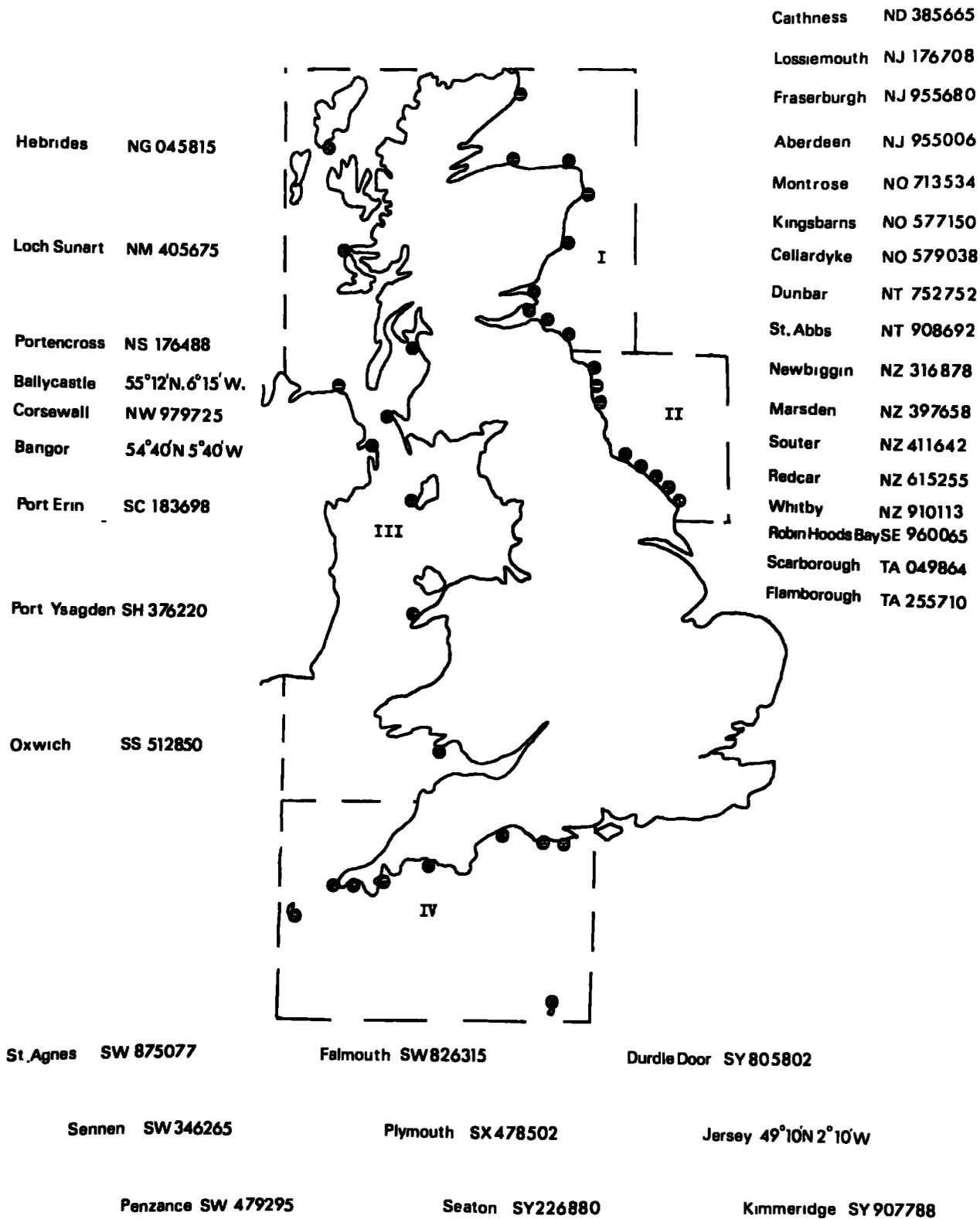
From each site approximately 20 large plants of L. hyperborea were collected from a depth halfway between the surface and the lower limit of the kelp, where light limited growth. (See Appendix B).

The holdfasts of these large mid-point plants were used for faunal analysis, and the bases of the stipes of the 5 year old plants were analysed for heavy metal content.

The sites were divided for convenience into four sectors; North Sea Scotland, North Sea England, West Coast and South Coast, labelled sectors I, II, III and IV respectively (see figure 8).

In the course of the study holdfasts collected from sites as far apart as 1500 km were studied. This represents a considerable proportion of the

FIGURE 8



whole extent of L. hyperborea in Europe (John 1967). Since it has been shown above that sample size should be expressed in terms of volume a preliminary requirement to this study was to ascertain whether the relationship of volume to age varied across the geographical range studied.

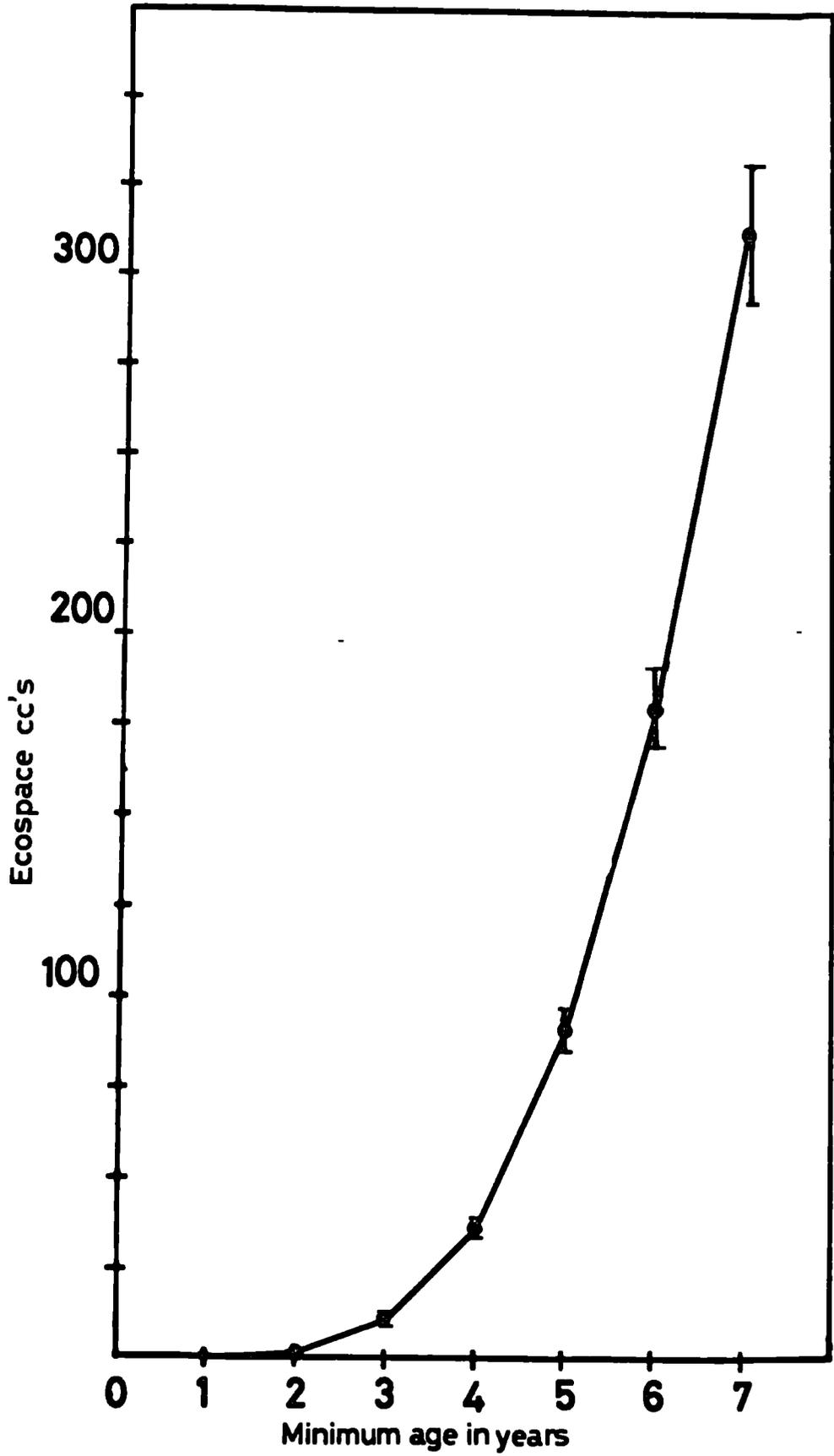
Age: Volume relationship in each Sector

The relationship of age to volume was determined for each of the four sectors (see figure 8). Although Jones did not consider the possibility of standardising sample size he did construct a graph of age against volume, using holdfasts taken from the North Sea (reproduced in figure 9). It was decided (1) to verify this relationship for the North Sea since Jones used a complex method of volume determination - one based on the calculation of the volume of a truncated cone - and (2) to determine whether the relationship in other sectors differed. The comparison is limited to the three age classes 5, 6 and 7 since holdfasts from these groups comprised over 95% of the total sample.

All volumes were determined using the Archimedes displacement principle (see Appendix A). The results obtained for North Sea holdfasts are presented in Table 4 (line a) with the results from Jones' graph (figure 9) presented as line (b).

	<u>Table 4</u>		
	5 years	6 years	7 years
(a)	123 mls.sd=57	192 mls.sd=40	282 mls.sd=144
(b)	107 " " =74	175 " " =41	290 " " =155

FIGURE 9
From JONES 1970



The differences are not significant and the two methods used for estimating volume from age would seem to be interchangeable. Thus the curve in figure 3 is verified for the North Sea.

Regional differences

The verification was then extended to the West and South coast sectors.

The most rapid way of determining whether gross differences exist in holdfasts of different sectors is using weight data alone. Weight data from 40 holdfasts from each group are presented in Table 5.

Table 5

Sector	5 years	6 years	7 years
I	159 g sd=77	209 g sd=88	296 g sd=82
II	164 g sd=55	183 g sd=38	213 g sd=99
III	150 g sd=91	213 g sd=52	293 g sd=97
IV	120 g sd=50	166 g sd=57	225 g sd=67

No differences within each age class are significant.

Examination of their volumes directly gave the following comparison:

Table 6

Sector	5 years	6 years	7 years
I	118 mls sd=27	195 mls sd=33	297 mls sd=107
II	128 " sd=80	203 " sd=51	-
III	100 " sd=27	166 " sd=38	-
IV	129 " sd=44	180 " sd=40	292 mls sd=39

Again no differences are significant. It is judged that the age: volume relationship is very similar for every sector, and the curve in figure 9 is used for all further determinations of volume.

NATURAL ENVIRONMENTAL VARIABLES

The number of environmental variables that could influence the holdfast fauna is large and includes fresh water, different geological substrates, exposure, sedimentation, depth, heavy metals, pesticides, sewage pollution, water clarity and geography. All these with the exception of pesticides are investigated in this study.

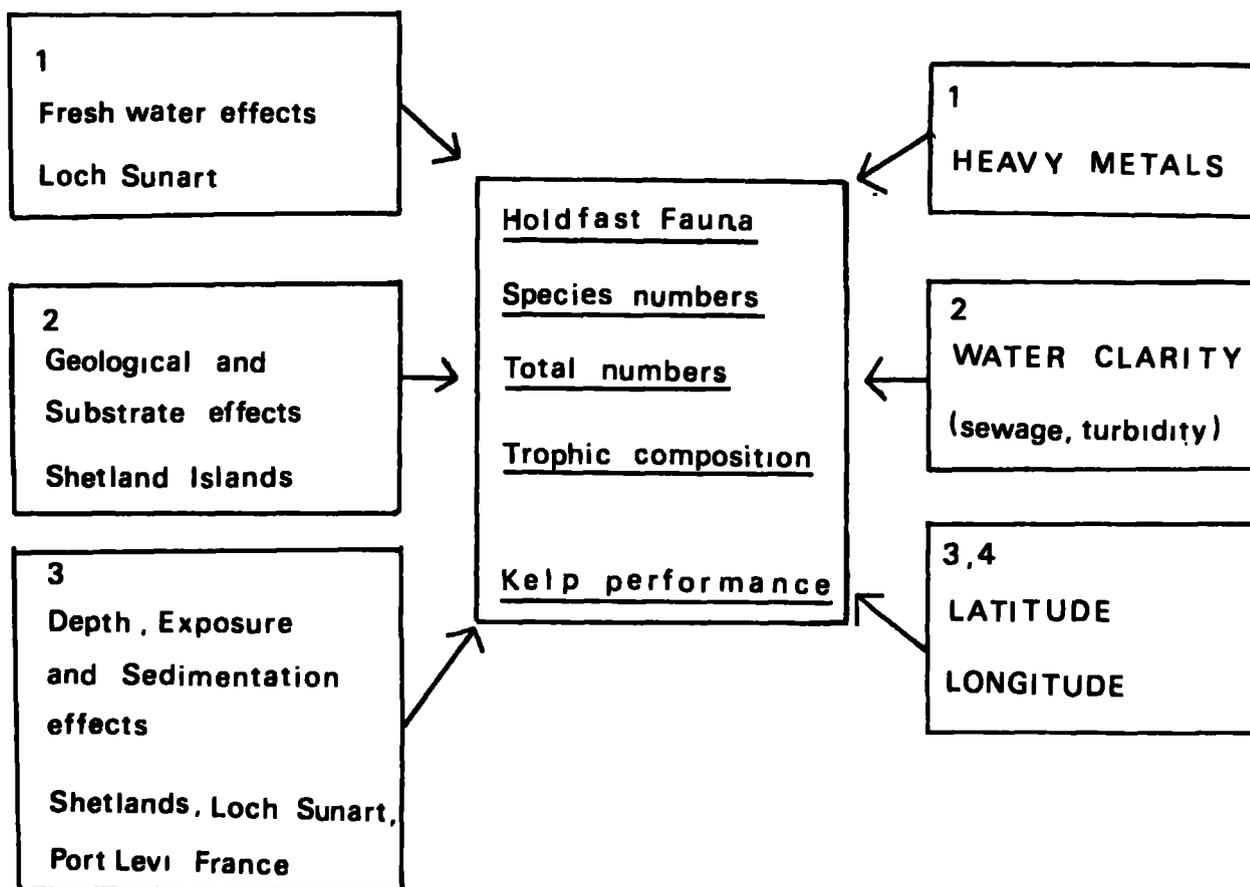
Ideally each of these variables should be examined in isolation. The fact that this is rarely possible has led to controversies, such as that already discussed of whether the gradient recognised by both Jones and Moore along the North Sea coast was attributable to pollution or to natural turbidity. Where several variables act simultaneously it may often be difficult to determine a cause and effect relationship.

In several cases in this study it appeared to be possible to study one environmental variable, or a small group of them, more or less in isolation. The variables considered are depicted in figure 10 where those variables that were found to act to some degree in isolation are written in small print, and those which were completely co-acting are written in large print.

The former group are examined first.

FIGURE 10

DIAGRAMATIC REPRESENTATION OF TWO MAIN GROUPS OF EFFECTS:
small type; no significant effect;
LARGE TYPE; SIGNIFICANT EFFECTS FOUND.



1. FRESH WATER EFFECTS

Loch Sunart in Argyll, Western Scotland (figure 11) is well placed for the elucidation of the possible effects of fresh water in isolation. The loch collects rain water from a part of the wettest region of Britain, and numerous streams flow into it along both banks. The loch is tidal throughout its length and enters the Sound of Mull which is continuous with the Atlantic Ocean. The region has no industry. The population is very sparse causing only a minimum and very localised sewage out-flow. The agriculture is limited to sheep grazing so that no complications arise from artificial fertilizers and pesticides. From West to East there must be an exposure gradient but this is probably small due to the proximity of the islands of Mull and Coll. There has in past years been some lead mining, so the possible existence of a heavy metal gradient was investigated.

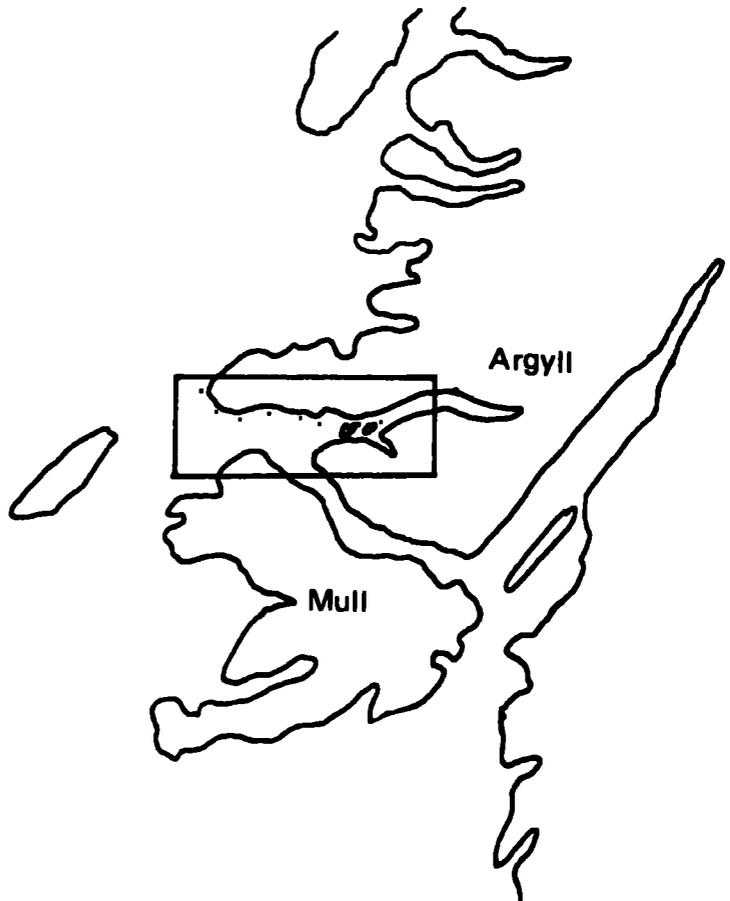
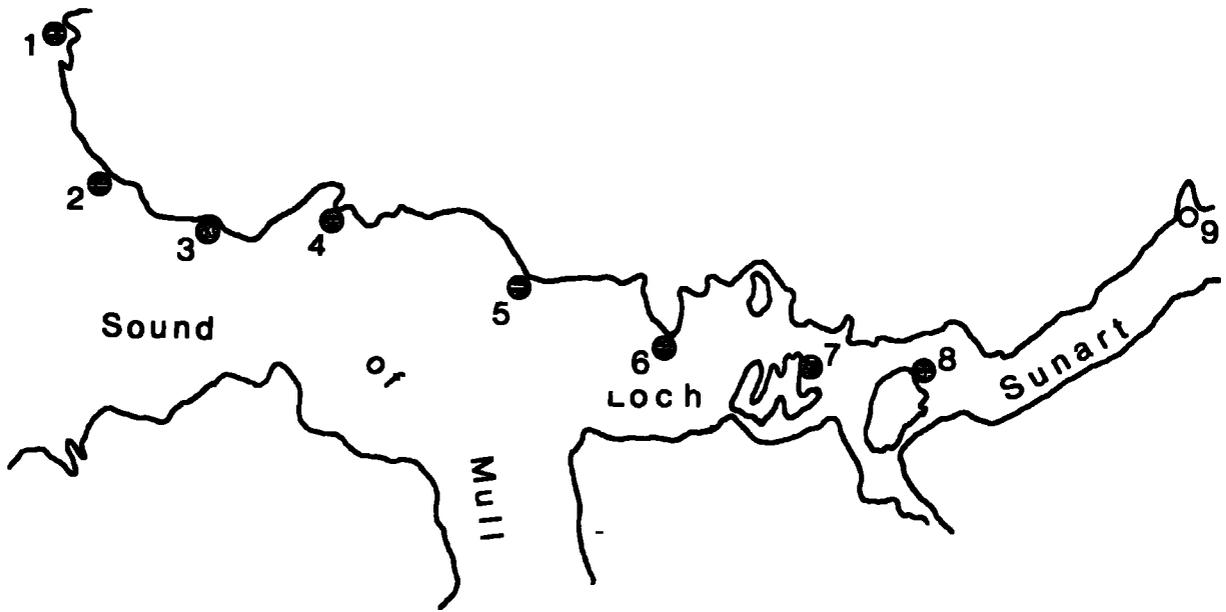
From each of eight sites two to four kilometres apart (figure 11) twelve large individuals of L. hyperborea were taken from a depth of 10 metres below Mean Low Water (M.L.W.) except at sites 6 and 8 where only three and one plants respectively were found. Sampling was carried out in September 1973 which corresponds to the time of peak biomass of laminaria in Britain (Whittick 1969).

Heavy Metal gradient

The possible existence of a heavy metal gradient, in view of the limited lead mining at the eastern end of the loch, was ascertained by

FIGURE 11

LOCH SUNART



analysis of five Patella vulgata from each of the eight sites. Each was between 3 and 4 cms in its longest diameter and collected from mean low water. This organism was selected here and in other regions partly because of its abundance and partly because its extensive use in the literature makes wider comparisons possible (e.g. Nickless et al 1972 ; Peden et al 1973 ; Malachtari 1973 ; Boyden 1974 ; Genakos 1975).

Table 7 summarises the data for each element assayed.

Values are parts per million (p.p.m.) \pm standard error.

Table 7

Site	Pb	Cd	Cu	Ni	Zn	Mn
1	2.9 \pm .6	0.2 \pm .01	6.3 \pm .3	2.7 \pm .6	66 \pm .0	6.0 \pm .05
2	5.0 \pm .1	0.15 \pm .01	5.7 \pm .0	2.2 \pm .4	80 \pm .0	5.9 \pm .6
4	3.0 \pm .7	0.2 \pm .01	6.2 \pm .1	5.4 \pm .1	75 \pm .0	6.8 \pm 1.0
5	9.2 \pm .1	0.25 \pm .01	4.7 \pm .2	9.7 \pm .1	70 \pm 1.0	6.5 \pm .9
6	2.0 \pm .1	0.2 \pm .02	5.2 \pm .2	1.0 \pm .2	80 \pm .7	5.9 \pm .8
7	6.4 \pm .2	0.15 \pm .01	7.1 \pm .1	1.6 \pm .3	89 \pm .8	6.1 \pm .1
8	3.3 \pm .1	0.2 \pm .02	9.3 \pm .3	0.7 \pm .3	84 \pm .3	5.8 \pm .7

No gradient is shown for any element. The levels from these sites are as low as and often substantially lower than any found in the literature and are probably representative of a truly "clean" site.

Salinity Gradient

Two series of samples of sea water were taken for salinity measurements. At each site samples were taken from (1) 12 metres depth and (2) the

surface, within one hour of low water. Assay was by standard silver nitrate titration (Strickland and Parsons 1969). The results (figure 12) show a fall in salinity of the surface water of 4.3‰ from open sea into the loch. No fall was seen in the deep samples. This pattern is what might be expected as fresh water flows over denser sea water (Hair and Bassett 1973). A wedge of sea water thus penetrates the loch below the layer of fresh water, up to and beyond the final sample station.

The wedge effect is reflected in the vertical distribution of the kelp (figure 13). At sites 1-4 the laminaria fronds were exposed at low water, but further inland its upper limit of distribution was progressively deeper. At all sites where the lower limit was reached (all except 1 and 4 where rock gave way to sand at about 16 m) the lower limit of L. hyperborea was around 21 metres below M.L.W. The points on figure 13 for sites 6 and 8 represent the depths at which the few plants were found.

The horizontal distribution of kelp was also of interest (figure 14). L. hyperborea disappeared from the mainland shores of the loch before disappearing from the shores of the islands situated within it. Thus at mainland site 6 only three plants were found during four hours of searching while further inland on the island site 7, this species was abundant, and penetrated as far as site 8 on the islands. This V shaped pattern was also observed for L. digitata several kilometres eastwards (figure 14).

The fall in surface salinity began after site 4, as did the depression of the upper limit of L. hyperborea. This correlation, together with the V shaped horizontal pattern after site 5 strongly suggests that reduced

FIGURE 12 SALINITY MEASUREMENTS.

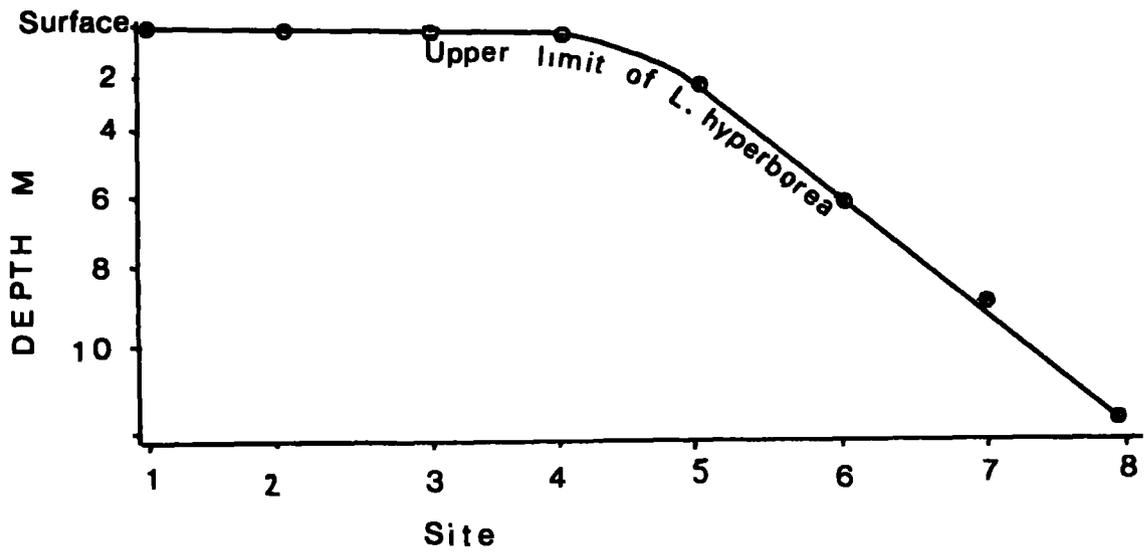
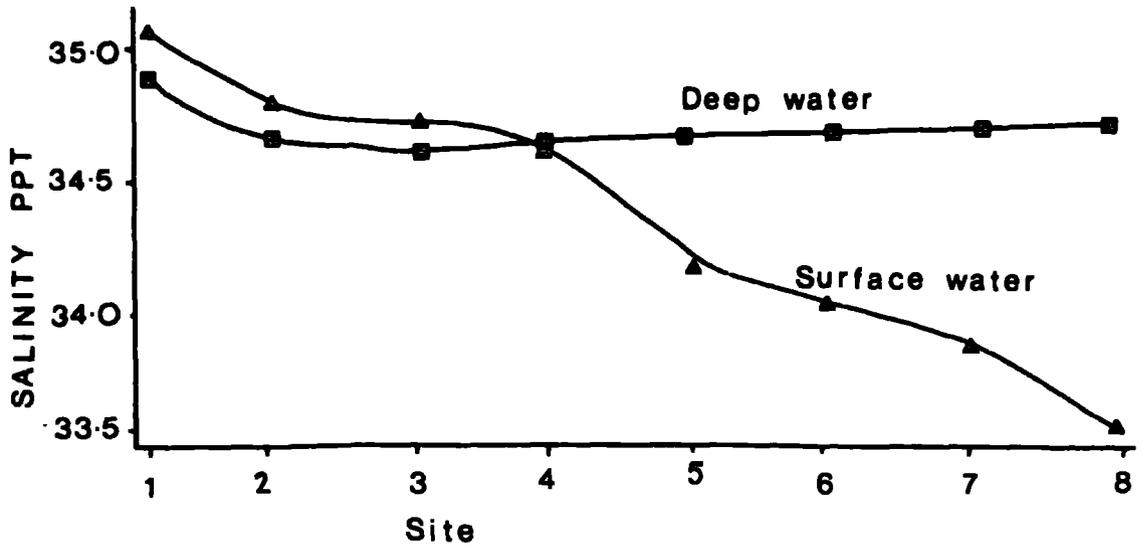


FIGURE 13 KELP DISTRIBUTION (VERTICAL) IN LOCH SUNART.

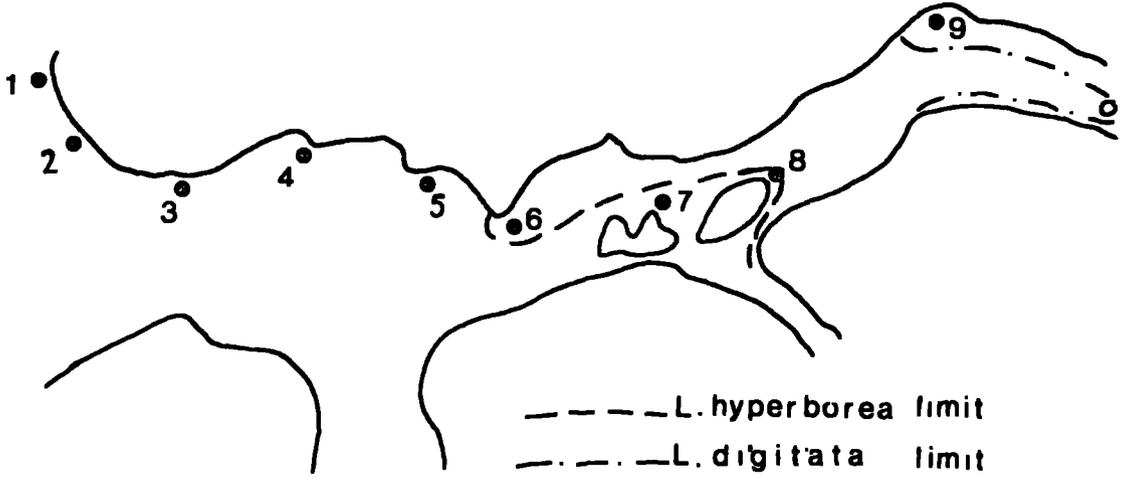


FIGURE 14 KELP DISTRIBUTION (HORIZONTAL) IN LOCH SUNART.

salinity is an important factor in the extinction of this species in the loch.

The Holdfast Fauna

A summary of the species data is presented in Table 8. The three dominant classes are Lamellibranchia, Polychaeta and Ophiuroidea. About half of the species were evenly distributed, with the remainder occurring infrequently at single sites giving the appearance of a small species shift along the transect. To help appreciate whether or not this shift was significant Sorrensen's similarity coefficient was calculated for each pair of sites.

Table 9

Site Number	2	3	4	5	7
1	59	57	63	66	63
2		58	64	64	54
3			58	47	52
4				64	48
5					62

The coefficients ranged from 47 to 66% but there is no difference between coefficients obtained from adjacent or widely separated sites. There is probably no significant qualitative change in species along the salinity gradient. The apparent shift of species in Table 8 is simply the result of the order in which the species are listed. The situation (discussed more fully in a later chapter) is caused because at any site a small proportion of the species occur commonly and widely while the remainder occur rarely. Thus the ordering of species to bring together those occurring at each site could automatically give rise to this kind of pattern.

It is known that fauna associated with mesohaline waters is often poorer than that of oceanic water (Remaine and Schlieper 1971). Therefore the numbers of species and animals per litre of holdfast space were compared for each site (Table 10). (Three litre samples were not used since only between 1.2 and 2 litres were actually collected from each site. Everywhere else three litre standard samples are used).

Table 10

Site	Species litre	Numbers litre	Diversity	95% limits
1	29	285	7.8	1.6
2	25	217	7.0	1.7
3	22	161	7.5	1.9
4	27	280	8.0	1.8
5	26	201	7.0	1.7
7	29	228	9.0	2.1

No gradient exists with any of the numerical characteristics. This is perhaps expected since the laminaria does not really grow in the low salinity water. Thus the infaunas are always in approximately the same salinity and are not subjected to a marked gradient.

There is no evidence to support the proposal that salinity affects the holdfast infauna of Loch Sunart.

Discussion

The environment in the loch with its reduced and probably fluctuating salinity is undoubtedly harsher for marine organisms than that of the Sound of Mull, in ionic terms at least. That an influx of freshwater

eventually has a drastic effect on L. hyperborea is demonstrated by the horizontal and vertical distribution of the alga. In contrast reduced salinity over the range tolerated by Laminaria hyperborea has no discernible effect on the holdfast infaunas. Presumably ecesis and/or growth of the salinity sensitive alga is precluded before faunistic changes can become large enough to be measured.

This is significant from the point of view of using the holdfast unit for environmental monitoring. In his North Sea work Jones (1973) recognised a faunistic group defined as "estuarine-polluted". He distinguished this from his polluted group, implying that estuarine conditions had some effect on his holdfast infaunas, a finding which contradicts those discussed above. However the existence of Jones' estuarine-polluted grouping was based on the observation that eight species were exclusive to it. Six of them have since been found in this study in clean and non-estuarine sites which places his grouping in doubt, and throws further doubt on the validity of using indicator species for these purposes.

In view also of the fact that the lowest salinity that can be tolerated by L. hypertorea is considerably higher than that normally associated with estuarine conditions, it is suggested that his estuarine-polluted grouping is without foundation, and that fresh water can be disregarded as an influencing variable.

II GEOLOGICAL EFFECTS

The possibility that the geological nature of a site effects the holdfast ecosystem was investigated. Geological and other substrate characteristics are of paramount importance in terrestrial ecology, in that they determine the supply of both water and nutrient to the plant.

In contrast, the large majority of benthic marine plants take their nutrient from the water rather than from the substrate, and any effects on the biota attributable to different rock types may be expected to be small. However, because of the different chemical compositions of rocks, and because of their different erosion rates and hardnesses, the possibility was examined that the holdfast infauna might be influenced by the rock to which it was fixed.

Suitable locations for the study of geological effects were found in the Shetland Islands (figure 15). These islands have within a small geographical compass a wide range of rock types which outcrop into the sea. Six of these were visited (see figure 15).

The main chemical and geological characteristics of the six sites are listed, in order of rock hardness, in table 11. The order was arrived at by combining a number of geological and petrological characteristics. (Genakos Y. Personal Communication). The hardness or sheering strength of a rock is only a small indication of its weathering rate and speed of erosion.



Serpentine



Gneiss



Granite



Schist



Limestone



Sandstone

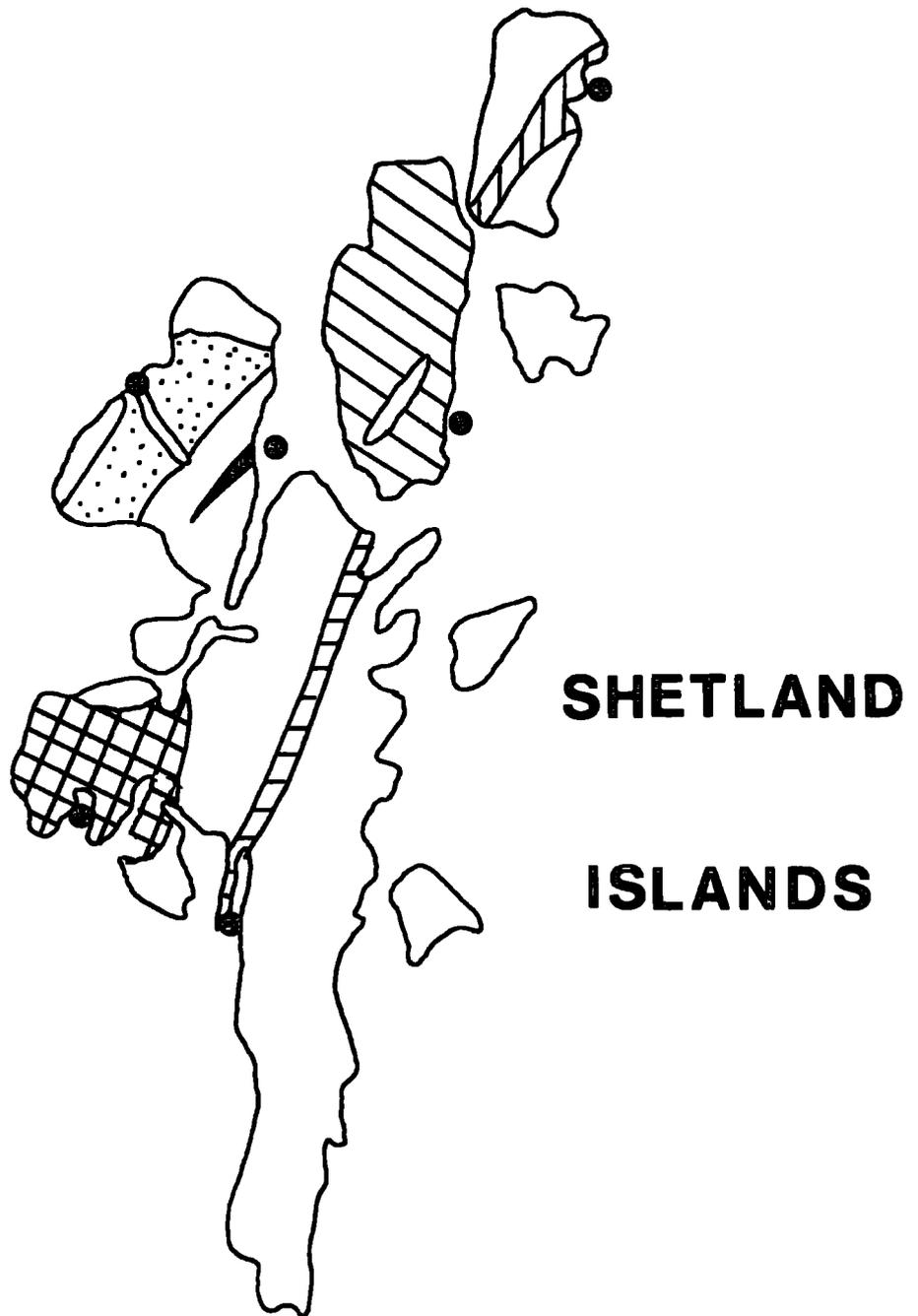


FIGURE 15

Table 11

<u>Granite</u>	Intrusive igneous rock. Weathered. Composed of feldspar, quartz and mica. Main elements of granite are firstly silica and silicates with aluminium second.
<u>Gneiss</u>	Mica - plagioclase gneiss. A metamorphosed rock with injection of magma along the parallel cleavage planes. Composed mostly of feldspar, with smaller amounts of quartz, mica, sericite, and hornblende. Main components again are silica and aluminium, but has higher amounts of Ca, Mg, and Fe than has granite.
<u>Serpentine</u>	Intrusive igneous rock showing some mineral and textural reconstruction. Composed mainly of green magnesium silicate. Noted also for a high content of some toxic elements, e.g. Ni.
<u>Schist</u>	Calc schist, veined and penetrated by granitic material and at this site layered in structure. Composed of quartz, biotite hornblende, chlorite and talc. Al, Mg and Fe are therefore the main components after silica.
<u>Limestone</u>	Crystalline limestone and calc-silicate rock, sedimentary and regionally metamorphosed. CaCO_3 is the main component.
<u>Sandstone</u>	Old Red Sandstone. Composed of quartz and other particles bound with calcium carbonate and iron oxides.

(references:- Ordnance survey (geological survey) maps of Scotland. Maps 1 and 2, and Field R.M. 1952 (Geology).

Feldspar - silicates of Al + smaller amounts of K, Fe and Ca.

Quartz - SiO_2 .

Mica - Silica + Al, K, Fe, Mg.

Sericite - K + mica.

Hornblende - silicates of Fe, Mg and Ca.

Biotite - Fe, Mg + mica.

Chlorite - hydrous silicates of Al, Fe and Mg.

Also marine weathering differs from land weathering in terms of chemical attack and the severity and type of abrasion, so that this subjective ranked order may be inexact. A footnote to table 11 gives the major cationic components of each dominant mineral, although in addition to these all rocks except the more pure crystal types contain a wide range of trace elements. Of special interest here however is serpentine which contains an unusually high load of supposedly toxic metals. This enabled attention to be focused on the possible effects of heavy metals in the absence of man-made pollution.

Site descriptions

The locations of the sites varied considerably with respect to exposure and steepness of slope, and the following site characteristics are relevant (see figure 15).

- Granite Ronas voe HU274838. West facing on steep (45°) slope in mouth of voe. Exposed only in north westerly weather. No strong currents.
- Gneiss Burravoe HU534815. East facing 30° slope. Exposed in easterly weather and has definite but weak tidal currents.
- Serpentine Harold's wick HP665114. East facing and very steep slope. Very exposed in easterly weather but has no strong currents.
- Schist Ollaberry HU377798. 30° slope. Rarely subjected to rough weather due to short fetches on most sides. Currents stronger than at other sites but not exceeding 4 knots.

Limestone Whiteness voe HU384425. Gentle slope; may be rough in strong southerly wind, otherwise very protected. Tidal movements only. Substrate of boulders on sand. Shallow.

Sandstone Gruting voe HU251462. Gentle slope in voe and protected at any angle of weather. Tidal movements only and substrate of boulders. Shallow.

Heavy Metals

It is believed that none of the sites has ever been subjected to industrial or domestic pollution. Only "natural" heavy metals are thus present and these only in the serpentine to any extent.

Analysis of the rocks for trace elements was not undertaken because the total amount of heavy metals is not an indication of their availability to biota. As availability is more relevant the concentration of metal present in two forms of biota was estimated instead.

(1) Stipe tissue of L. hyperborea was analysed for the selected trace elements. The results are shown in Table 12:

Rock type	Table 12				
	Pb	Cu	Metal content in ppm \pm standard errors.		
			Ni	Zn	Cd
Granite	15.3 \pm 1.8	2.9 \pm 1.8	12.2 \pm 3.8	43 \pm 3.3	1.4 \pm .02
Gniess	10.2 \pm 1.1	1.6 \pm .16	Trace	30 \pm 1.4	0.6 \pm .2
Serpentine	12.9 \pm 1.4	3.2 \pm 1.1	2.8 \pm .7	60 \pm 6.	2.8 \pm .4
Schist	2.3 \pm .4	3.6 \pm .7	5.8 \pm 1.1	58 \pm 8.0	3.0 \pm .4
Limestone	3.5 \pm .6	2.8 \pm .2	5.9 \pm 1.3	5.9 \pm 5.	0.23 \pm .12
Sandstone	6.4 \pm 1.0	2.1 \pm .3	8.7 \pm 1.3	72 \pm 4.3	2.3 \pm .63

No particularly low or high values are noted. With lead there appear to be two groups of readings: from approximately 10 to 15 p.p.m. in the hardest rocks and 2 to 5 p.p.m. in the softer three rocks. No high values were recorded for the stipe tissue on the trace element rich serpentine.

Gniess showed the lowest values for both nickel and zinc.

(2) The second species chosen for this study was Patella vulgata. Five large individuals were taken from M.L.W. at every site except from sandstone where none were found. The mode of feeding of this species is worth noting as it consists of scraping algae off rock, a method which probably causes considerable entrainment of rock particles into the animal's digestive system. Table 13 presents the data:

Table 13

Rock Type	Metal content in p.p.m. \pm s.e.				
	Pb	Cu	Ni	Zn	Cd
Granite	3.2 \pm 1.8	8.1 \pm 2.3	7.8 \pm 3.8	145 \pm 19	
Gniess	7.9 \pm 3.7	7.1 \pm 2.0	13.7 \pm 2.4	117 \pm 14	Not done
Serpentine	3.9 \pm 2.2	4.7 \pm 0.5	29.4 \pm 5.0	76 \pm 8	
Schist	6.1 \pm 1.5	8.9 \pm 2.8	5.3 \pm 1.8	132 \pm 27	
Limestone	5.7 \pm 1.9	4.7 \pm 0.6	5.9 \pm 1.8	111 \pm 8	

The levels of nickel in the limpets living on the serpentine were significantly higher than those from all other rock types. Between serpentine and gniess the level of significance corresponded to $p = .05$ and between serpentine and all other rock types the significance was

higher ($p = .01$). With zinc two differences were noted; the zinc concentration in the serpentine limpets was significantly lower ($p = .05$) than those from granite and limestone. The mean value of 76 p.p.m. was lower also than those of the other rock types, though not significantly so on account of the greater range of concentrations of the latter.

These results suggest that serpentine is different in terms of nickel and zinc from the other rock types studied, at least as reflected in the last species.

Holdfast fauna

Table 14 below presents a summary of the numerical values of the fauna found at each site:

Table 14

Rock type.	Species/3 litres	Numbers/3 litres	Diversity
Granite	42	676	9.5
Gneiss	34	412	8.0
Serpentine	38	437	8.5
Schist	36	397	9.0
Limestone	31	382	8.5
Sandstone	34	249	10.0

Granite was high in both species numbers and numbers of organisms, while sandstone was low in total numbers. The other four sites were similar to each other, and all six had similar diversity values. Due mainly to the raised numbers on granite and the low numbers on sandstone

there is perhaps an impression of a decrease in faunal abundance from the hardest to the least hard rocks.

A summary of the species found and their distribution is shown in Table 15. The pattern seen is similar to that along the Loch Sunart progression of sites (table 8), in that there is a substantial group of species which are evenly distributed and others which are infrequent and which occur at a few sites only. As with Loch Sunart, the impression of a species shift is probably misleading and is due to the scattered distribution of uncommon species to which as much weight is given visually as is to the common species.

The following table of similarity coefficients confirms that no qualitative gradients along a hard-soft axis is proved:

Table 16

	Gneiss	Serpentine	Schist	Limestone	Sandstone
Granite	56	55	52	46	50
Gneiss		52	48	47	49
Serpentine			43	47	57
Schist				48	48
Limestone					58

Values range from 43 to 58% with no difference between coefficients for closely and widely separated sites.

As there has however been shown to be a possible decline in total numbers along the hard-soft axis, a study of the more common species is

TABLE 15

SPECIES	Granite	Gneiss	Serpentine	Schist	Limestone	Sandstone
<i>Amphipholis squamata</i>	2	3	2	1	1	1
<i>Pomatoceros triqueter</i>	1	2	1	2	2	2
<i>Porcellana longicornis</i>	1	1	+	+	2	+
<i>Hiatella arctica</i>	1	+	+	1	+	+
<i>Nereis pelagica</i>	+	+	1	+	+	1
<i>Ophiothrix fragilis</i>		+	1	+	+	+
<i>Asterias rubens</i>	+	+	1	+	+	+
<i>Spirorbis borealis</i>	+	+	+	+	+	+
<i>Tonicella rubra</i>	+	+	-	-	+	
Nereidae	+		+	-	-	+
<i>Mytilus edulis</i>	+	+	+		+	+
<i>Harmothoe</i> sp.	-	+	+	+		+
<i>Acanthochitona discrepans</i>	+		+	-		-
<i>Psammechinus miliaris</i>	-	-	+	-		
<i>Balanus balanoides</i>	+		-	-		+
Amphipoda	-	+		-		-
<i>Modiolus modiolus</i>	+		+		-	+
<i>Heteranomia squamula</i>	+	+	+			-
<i>Ophiocomina nigra</i>		-	-		-	-
<i>Lepidochitona cinereus</i>	-			-		
<i>Lineus longissimus</i>	+	+		-		
<i>Halichondria panicea</i>	-					-
<i>Gibbula cineraria</i>	-	-				+
<i>Antedon bifida</i>	+				+	
<i>Ampithoe rubricata</i>	+	-			-	
<i>Acmaea tessulata</i>	+	+	+			
<i>Henricia sanguinolenta</i>	-	-	+			
<i>Actinia equina</i>	+	-	+			
<i>Modiolus barbatus</i>	+	+	+			
<i>Patina pellucida</i>	+		-			
<i>Sargartia troglodytes</i>	-		+			
<i>Carcinus maenas</i>	-					
<i>Xantho</i> sp.	-					
<i>Nymphon</i> sp.	-					
<i>Eunemertes</i> sp.	-					
<i>Venerupis pullastra</i>	-					
<i>Echinus esculentes</i>	+	+				
Nemertine	-					
<i>Eunice</i> sp.		+				
<i>Ophiopholis aculeata</i>		+				
<i>Filograna implexa</i>		+				
<i>Chlamys distorta</i>		+				
<i>Tellina tenuis</i>		-				
<i>Acanthochitona</i> sp.		-				
<i>Acmaea virginea</i>		-				
<i>Venerupis</i> sp.		-				
<i>Ascidia</i> sp.		+	+			
<i>Galathea dispersa</i>		+	+			
<i>Pinnotheres pisum</i>			-			
<i>Galathea intermedia</i>			-			
<i>Aplidium proliferum</i>			+			
<i>Anomia ephippium</i>			-			
<i>Nereis diversicolor</i>			-			
Gammarid 1.				+	-	
<i>Ensis arcuatus</i>				-		
<i>Amphipholis</i> sp.				-		
<i>Chlamys</i> sp.				-		
<i>Cancer pagurus</i>				-		
<i>Littorina</i> sp.				-		
Ophiuroidea				-		
Anomiid				-		
Porifera				-		-
Gammarid 2.				+		
<i>Lacuna</i> sp.					-	-
<i>Serpulida</i> sp.					+	
<i>Harmothoe impar</i>					-	
<i>Lepidonotus</i> sp.					-	
Nematoda						+
<i>Lineus ruber</i>						+
Cirratulidae						-
Polychaeta (Eunicidae?)						-

necessary to show which of these are responsible. All species which contribute more than 10% of the total numbers in any site are tabulated below, with their percentage abundance.

Table 17

Species	Granite	Gniess	Serpentine	Schist	Limestone	Sandstone
<u>A. squamata</u>	34	39	35	13	9	6
<u>P. longicernis</u>	11	6	5	3	5	2
<u>P. triqueter</u>	11	24	10	29	22	23
<u>H. arctica</u>	5	2	4	18	2	4
<u>D. fragalis</u>	0	2	7	0	2	1
<u>A. rubens</u>	3	3	5	2	5	2

The polychaete Pomatoceros triqueter was slightly more abundant in holdfasts from the softer rocks, while the brittle star Amphipholis squamata is substantially more abundant on the harder rocks. The latter distribution may have some significance. However the brittle star is well known to be migratory and patchy in its distribution. Probably no one species is responsible for the raised numbers in the granite samples.

Discussion

No conclusive evidence is found that the type of rock affects the nature of the holdfast infaunas. Population differences are judged to fall within the range of sampling variation, and it is of particular interest that serpentine, which contained elevated concentrations of nickel, did not appear to give rise to abnormal populations.

III DEPTH, EXPOSURE AND SEDIMENTATION EFFECTS

These three variables were studied together. Their action and effects are difficult to separate since all are closely connected. For example depth is inversely related to exposure, and in turn exposure affects sedimentation. Turbulence and strong wave action prevents sedimentation, while increased depth leads to "quieter" water with less turbulence and more sedimentation. The effects of exposure on marine fauna are however not limited to those of sedimentation; there are the physical effects of exposure as well, namely the sweeping away of non attached forms, the prevention of settling, and the washing away of gametes before fertilization. For all these reasons exposure has often been an important consideration in descriptions of marine life (Lilly et al 1953).

To investigate the effects of depth on holdfast infaunas three depth transects were studied. In addition holdfasts from two exposure gradients were also studied. The depth transects were from the Shetlands, the Hebrides where the deepest ranges were found in this investigation, and from the North coast of France at Port Levi, near Cherbourg. The slopes of the sea bed in these regions were 45° , 20° and less than 5° respectively. All three regions were considered to be unpolluted. The exposure gradients were those already used in other connections, namely the sites along Loch Sunart and from the Shetlands.

(a) Depth Gradients

The following table presents the numerical data for the three depth gradients.

Table 18

Depth Metres Below	Shetlands HU495697		Hebrides NG045815		Pt. Levi 49045'N. 1 ⁰ 29'E	
	Species/ 3 litres	Number/ 3 litres	Species/ 3 litres	Numbers/ 3 litres	Species/ 3 litres	Numbers/ 3 litres
M.L.W.						
3			36.7	206		
6	27.6	333			32.0	270
9			38.6	324	25.5	275
12	32.2	322			31.0	335
15			32.9	585	37.5	324
18	28.0	384				
21			27.5	336		

The consistency of the values in these three widely separated regions and at all the different depths within them is striking. One exception is the numbers of animals in the 15 metre Hebrides collection where the elevated numbers are attributable to Pomatoceros triqueter.

No trends with depth are revealed. The 18 metre collection from the Shetlands, was comprised mostly of young plants of age 4 and so this result is included for completeness only, although it compares closely with the other sites.

From the above values it is evident that holdfast infaunas are not markedly affected by depth.

The species concerned are listed in table 19. Examination of their nature reveals that the species found at the different depths are not unique to that depth and most have been found over a wide depth range.

HEBRIDES SPECIES LIST					SHETLANDS SPECIES LIST					PORT LEVI SPECIES LIST				
	3m	9m	15m	21m		6m	12m	18m		6m	9m	12m	15m	
<i>Heteranomia squamula</i>	1	+	+	+	<i>Pomatoceros triqueter</i>	2	2	2	<i>Patina pellucida</i>	+		+	+	
<i>Pomatoceros triqueter</i>	+	1	1		<i>Eulalia viridis</i>	-	+		<i>Balanus balanoides</i>	2				
<i>Ascidia</i>	-	-	-		<i>Amphipholis squamata</i>	2	2	2	<i>Hydroides norvegica</i>	+	1	-		
<i>Ophiothrix fragilis</i>	+		-		<i>Ascidia</i> sp.	+	+		<i>Porcellana longicornis</i>	1	1	1	1	
Caprellidae	-				<i>Asterias rubens</i>	+	+	+	<i>Cucumaria saxicola</i>	-	-		+	
<i>Hiatella arctica</i>	1	1	1	1	<i>Ophiothrix fragilis</i>	+	+	+	<i>Chthamalus stellatus</i>	+	+	+	1	
Nereidae	+				<i>Nereis pelagica</i>	1	+	1	<i>Nereis pelagica</i>	1	1	1	+	
<i>Lagisca extenuata</i>	+	+			<i>Hiatella arctica</i>	1	1	1	Kowertini	-				
<i>Nereis pelagica</i>	1	1	1		<i>Acanthochitona crinitus</i>	+	+	+	Sabellidae	1	1	+		
<i>Acanthochitona crinitus</i>	-	+	+		<i>Mytilus edulis</i>	+	-		<i>Calliostoma zixyphinum</i>	-	-			
<i>Jorunna tomentosa</i>	+				<i>Porcellana longicornis</i>	+	+	+	<i>Pilumnus hirtellus</i>	+	+	1	-	
<i>Modiolus modiolus</i>	+	+	+		<i>Leander</i> sp.	-	-		<i>Diodora apertus</i>	-				
<i>Filograna implexa</i>	+				<i>Filograna implexa</i>	+			Amphipoda	-				
<i>Lacuna vincta</i>	-				<i>Galathea dispersa</i>	-			<i>Gibbula cinerarea</i>	+		-	-	
<i>Balanus balanoides</i>	1	1	1	1	<i>Henricia sanguinolenta</i>	-			<i>Tricolia pullus</i>	+				
<i>Harmothoe impar</i>	1	+	+	+	<i>Hydroides norvegica</i>	+	+		<i>Lysidice ninetta</i>	-	+	+	+	
<i>Jassa falcata</i>	-				<i>Tonicella rubra</i>	-	-		<i>Pomatoceros triqueter</i>	+				
<i>Myxilla</i> sp.	1				<i>Gammarus</i> sp.	+	-		<i>Myxilla</i> sp.	+	1	+		
<i>Eulalia sanguinea</i>	+				<i>Harmothoe impar</i>	+	+	+	<i>Sphaeroma rugicauda</i>	+				
<i>Tealia felina</i>	1	+			<i>Lineus ruber</i>	-	-		<i>Spirorbis borealis</i>	+		+		
Serpulida	-				<i>Acmaea tessulata</i>	-			<i>Harmothoe impar</i>	-		-		
Syllidae	1				<i>Heteranomia squamula</i>	-	-	1	Sipunculida	-				
<i>Patina pellucida</i>	+		-		<i>Idotea</i> sp.	+			<i>Cucumaria lactea</i>	+			+	
<i>Porcellana longicornis</i>	-	+	1		<i>Littorina neritoides</i>	+			<i>Filigrana implexa</i>	+	1	+		
<i>Nassarius incrassatus</i>	+	+			<i>Actinia equina</i>	-	-		<i>Acanthochitona</i> sp.	-		-		
<i>Musculus marmoratus</i>	-	+	+		<i>Modiolus barbatus</i>	-	-		<i>Lacuna vincta</i>	-		+		
<i>Actinia equina</i>	-	-	+		<i>Lineus longissimus</i>	-			<i>Branchioma vesiculosum</i>	+	1	-		
<i>Orchomenella nana</i>	+	1	+		<i>Gibbula cineraria</i>	-			Porifera	-				
<i>Lepidonotus squamatus</i>	-				<i>Serpula vermicularis</i>	+			<i>Hiatella arctica</i>	-				
<i>Modiolus barbatus</i>	+	+	+		<i>Tellina</i> sp.	+			<i>Balanus perforatus</i>	2		2		
<i>Ascidia</i> sp.	-				<i>Echinus esculentus</i>	+			Porifera(2)	-	-	-		
<i>Amphipholis squamata</i>	+	1	1	2	<i>Balanus balanoides</i>	+	+		Decapoda	-				
<i>Elminus modestus</i>	-				<i>Psamechinus miliaris</i>	+	+		<i>Sabella pavonina</i>	+	1	-		
<i>Hydroides norvegica</i>	+				<i>Ophiocoma nigra</i>	-			<i>Chlamys varia</i>	-		-		
<i>Nymphon</i> sp.	-				<i>Modiolus modiolus</i>	-			<i>Nudibranchia</i>	-				
<i>Pycnogonum</i> sp.	-				<i>Patina pellucida</i>				<i>Fusus</i> sp.	-				
<i>Antedon bifida</i>		+	+		Nereidae	-			Terebellidae			1		
<i>Ophiopholis aculeata</i>	-				<i>Spirorbis borealis</i>	+			<i>Ampithoe rubricata</i>	-				
<i>Talitrus saltator</i>	-				<i>Limacea clavigera</i>	-			<i>Musculus discors</i>	+		-		
<i>Kellia suborbicularis</i>	+	+	+						<i>Axinella</i> sp.	+				
<i>Gammarus</i> sp.	-								<i>Rissca variabilis</i>	+		+		
<i>Tonicella rubra</i>	-	+	+						<i>Asterina gibbosa</i>	+		-		
<i>Chlamys didortia</i>	-								<i>Platynereis dumerilii</i>			3		
<i>Pilumnus hirtellus</i>	+								<i>Orchomenella nana</i>	+				
<i>Chlamys varia</i>	+	-							<i>Ocenebra erinacea</i>	-				
<i>Calliostoma zixyphinum</i>	-								<i>Trivia arctica</i>	-				
<i>Hyas araneus</i>	-	+							<i>Bispera voluticornis</i>				+	
<i>Asterias rubens</i>	+	+	1						<i>Ophiothrix fragilis</i>	-				
<i>Cucumaria saxicola</i>	+								<i>Syllis</i> sp.	-				
<i>Nassarius reticulatus</i>			-	+					<i>Lepidonotus squamatus</i>	-				
<i>Phylodoce maculata</i>			-						<i>Eulalia</i> sp.	-				
<i>Nereis virens</i>			-						Serpulida	-				
<i>Psamechinus miliaris</i>			+						<i>Distonus variolosus</i>				+	
<i>Gibbula magus</i>			+						<i>Baseodiscus delineatus</i>	-				
<i>Potamopyrgus jenkinsi</i>			-						<i>Munida</i> sp.	-				
<i>Trivia arctica</i>			-						<i>Phylodoce maculata</i>	-				
<i>Cancer pagurus</i>			-						<i>Pinnotheres pisum</i>	-				
<i>Acmaea tessulata</i>			-	-					<i>Sagartia elegans</i>				+	
Cirratulidae				+										
<i>Eunemertes nessii</i>			-											
<i>Arca lactea</i>				-										

There are no species in the deeper ranges which do not occur elsewhere much shallower (see Appendix E), with the occasional exception such as Arca lactea whose only occurrence anywhere was at 21 metres off the Hebrides.

(b) Exposure Gradients

Inseparably mixed with depth is the factor of exposure. In view of this it would seem likely that the above depth gradients are effectively exposure gradients as well. Similarly the sites along Loch Sunart and around the Shetlands can also be ordered in terms of exposure.

In Loch Sunart (see figure 11) the exposure gradient runs from site 1 (most exposed) to site 8. In the Shetlands the sites can also be ordered accordingly to relative exposure though with less certainty. The order is Serpentine, Gneiss, Schist, Limestone, Granite and Sandstone (see figure 15).

It is remembered that no marked faunistic gradients were seen along Loch Sunart. Similarly no marked differences were found between the Shetland sites.

(c) Sedimentation

Both exposure and depth are intrinsically mixed with sedimentation. Where water is calmest, sedimentation is often highest since the scouring effect of even moderate water movement can keep rock surfaces clear of sedimentation (Postma 1967). With a build up of sediment the habitat is altered, and with this alteration should come a change in the holdfast fauna. Where sedimentation is highest there may be a greater density of

detritus feeders, and where currents are strongest there is often a greater number of suspension feeders (Lilly et al 1953; Scarrett 1960). A trend in either of these two trophic categories in the holdfast faunas therefore could be interpreted as evidence that exposure or sedimentation is having some effect.

The following table presents the numbers of animals and numbers of species in these two trophic categories as studied along the Loch Sunart and the Shetland exposure gradients.

Table 20

Loch Sunart

<u>Numbers</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>7</u>
Detritus	0	0	0	0	1	1
Suspension	236	182	140	224	177	198

No. Species

Detritus	0	0	0	0	1	1
Suspension	13	13	9	13	14	15

Shetlands

<u>Numbers</u>	<u>Serpentine</u>	<u>Gneiss</u>	<u>Schist</u>	<u>Limestone</u>	<u>Granite</u>	<u>Sandstone</u>
Detritus	0	0	0	0	0	+
Suspension	36	68	86	99	89	53

No. Species

Detritus	0	0	0	0	0	1
Suspension	9	10	9	11	10	11

Little evidence of sediment gradients is obtained from these results although the presence of Nereis diversicolor in Loch Sunart at sites 5 and 7, and nematodes (larger than 2mm) in the Shetland Sandstone site

may be taken to indicate some sediment increase in the more sheltered sites.

Discussion

None of the gradients considered above appear to significantly affect the holdfast faunas. A reason for these in a sense negative results must be looked for in the nature of the holdfasts.

Located on the sea floor the holdfast has above it a dense forest of plants up to 3 metres tall, which offers a resistance to water movement in the same way that a terrestrial forest resists wind. The effect is readily noticed by divers, and is also reflected in the progressively reduced "streaming" shown by the stipe epiphytes as the sea floor is approached. This suggests that the environment around the holdfasts is less prone to the effects of currents than is bare rock.

The presence of the holdfast tissue still further increases this protection. It has been shown (Chapter 3) that about 38% of the total holdfast is occupied by plant tissue. Probably species living in holdfasts enjoy considerably stabilised conditions with respect to exposure and are not subjected to extremes, a point recognised by Scarrett (1960), Jones (1970) and Moore (1971). The uniformity of holdfast habitat with respect to exposure is therefore comparatively high, even between regions.

The relationship between water velocity and sediment build up is reciprocal but not linear (Postma 1967) and only in very calm conditions will a build up of sediment be large. Laminaria hyperborea does not grow to normal or average size in very sheltered conditions, nor can it grow well in conditions of high sediment, but grows optimally in conditions of

moderate to strong water movement (John 1967). Thus extreme sediment conditions are unlikely to affect the holdfast.

The kelp itself only occurs within limits of exposure and sedimentation which are considerably inside the total spectrum of sea conditions.

Extremes of sedimentation at the base of a kelp forest are usually less than those on bare rock deeper than it (Bellamy et al 1968). This was shown to be the case in Shetland. Here, twelve "sweeps" were made to collect or note all species that occurred outside holdfasts in a two metre wide swathe from 30 metres to the surface. No attempt was made to count the numbers of each species on each sweep; only their presence was recorded. The data from each sweep was then divided into sections of 3 metres depths and tabulated (table 21). The slope of the rock face was 45° and the kelp did not grow below 15 metres.

The key of table 21 is modified from the usual, in that although for example the number 5 still means 80% or more it here means that the species occurred in 80% or more of the twelve swathes. This introduces an element of qualitiveness into the results.

It was noticed that sedimentation on the floor of the kelp bed was minimal throughout its depth range while that on the bare rock from 18 to 30 metres appeared to be greater. The sediment was due to a bed of hydroids and other filamentous organisms largely absent within the kelp bed, which trapped the silt forming a bed of soft material 0.5 cms. thick. Table 21 shows a more or less distinct difference of fauna above and below 15 metres. Group A are species which occurred universally,

group B are those mostly above 15 metres and group C are those predominantly below 15 metres. Such a division may be fortuitous in that none of the species in group C are specifically soft-bottom or detritus feeding forms, but nevertheless the division exists and two blocks as distinct and divisive as this cannot be formed using any other depth as a pivot.

It has been stated that the kelp forest offers a resistance to water movement, and so when particle bearing water is slowed down by the kelp, particles would be expected to fall out of suspension. This undoubtedly happens and some sediment is always present in and around holdfasts. Despite this the uniformity found in a kelp bed and experienced by holdfasts from different regions is much greater with respect to exposure and sedimentation than it is to most other variables.

FOUR ENVIRONMENTAL VARIABLES POSSIBLY
AFFECTING HOLDFAST FAUNAS

1. Heavy Metals

Introduction

The terms heavy metals and toxic metals have often been used interchangeably to denote a wide range of elements. Passow (1961) defined heavy metals as those having a specific gravity of five or more, which is satisfactory providing it is accepted that less dense metals can be toxic, e.g. Aluminium, arsenic; and that not all the heavier metals are toxic in moderate concentration. Either term can be used provided it is clear which elements are being referred to and there is a knowledge of their toxicity.

Bryan (1971) suggested that mercury, silver and copper are exceptionally toxic, with cadmium, zinc, lead, chromium, cobalt and nickel following in that order. The exact order though must depend in part on the test organism and on the salt or compound of the metal under consideration. It was decided to limit the study to the following heavy metals, cadmium, copper, lead, nickel, and zinc, the effects of which have been studied in some detail on certain organisms.

The effects of heavy metals both in isolation and with others have been investigated, as have their effects when acting in conjunction with other parameters such as water hardness, reduced oxygen concentration and

temperature, pH and salinity extremes.

Of a wide range of marine animals Wurtz (1962) believed molluscs were the least resistant to high levels of heavy metals and were the first to be eradicated. Skidmore (1964) found that the toxic effects of zinc and copper were strongly synergistic, as were zinc and nickel. He believed the effects of zinc and copper were closer to being additive. Lead-zinc mixtures, lead-mercury and copper-mercury mixtures have all been found to have synergistic actions (Grey and Ventilla 1971; 1973). These authors also found that any combination of copper, zinc and mercury would synergistically inhibit growth of copepods, although in concentrations of less than parts per billion some combinations had the opposite effect and growth was stimulated.

It is generally conceded (Wilson 1972) that the most important variable in the toxicity of copper (to fish) is the mitigating effect of increased water hardness. The same applied to zinc whose toxicity is reduced by calcium, especially the carbonate salt (Skidmore 1964). In this connection pH is important. A raised pH alleviates the toxicity of several elements by causing them to precipitate (Wurtz 1962) while a lowered pH raises their toxicity by allowing them to dissolve and thus increasing their availability.

Polluted environments often suffer from low oxygen levels which appears always to increase the toxicity of heavy metals (Herbert and Vandyke 1964; Skidmore loc cit). Likewise lowered salinity and both lowered and raised temperature may increase toxicity (Vernberg and O'Hara 1972; Wurtz loc cit). It must be said that not all authors agree on which pairs of metals and other environmental parameters are synergistic or simply

additive. Brown (1971) for example believed that any mixture of copper, zinc, and nickel are more nearly additive (in their harmful effects on rainbow trout) than synergistic, but the majority of authors concur with the above outline.

These authors substantiate the belief that the elements chosen for analysis in this study are toxic to marine life generally and very often in a more than additive fashion. Many of the elements are bound intracellularly and once concentrated they may remain so even when the organism is transferred to clean water (Lockhart et al 1972). The literature shows that the effects of heavy metals on marine organisms range through all the expected sub-lethal manifestations of poisoning such as growth inhibition (Grey and Ventilla 1971 ; Sheppard and Bellamy 1974), genetic damage (Beardmore 1975; Skerfving et al 1970), cancer (Barada 1975), and teratogenicity (Epstein 1970), to death.

These gross effects are merely the manifestations of biochemical disorders, but the reasons why, at the biochemical level, these gross effects occur are less clear, despite considerable work on sub-cellular and enzymic interactions (Schutte 1964; Danielson 1970). Lead has probably been subjected to more attention than any other heavy metal. It has long been known that lead impairs the integrity of cell membranes allowing major essential cations such as K^+ to leak out (Davson and Danielle 1938). It is also known to inhibit calcium metabolism such as that at neural junctions (Silbergeld et al 1974) which emphasises why such small quantities can be very toxic. Waldron and Stoffen (1974) review the metabolism of this element, which although considerable, lags behind the more easily obtained knowledge of its effects at the whole animal level.

This applies to other elements as well. Cadmium disrupts general enzyme systems such as the key oxidative phosphorylation pathway (Jacobs et al 1956). It also accumulates in and damages the digestive and renal systems (Mullin and Riley 1956). Copper binds with proteins on the animals' gills rendering them non-functional (Wilson 1972). Zinc also accumulates in gills and by coagulating their proteins induces the gill epithelium to slough off (Burton et al 1972). With zinc however evidence is accumulating on some beneficial effects of raised zinc concentrations, such as in haemoglobin metabolism and healing (Wright and Dormandy 1972; Underwood 1971; and Dash et al 1974).

Because of these very varied effects it is understandable that metals often act synergistically. Similarly metals acting in a less than optimum environment (oxygen lack, temperature extremes etc.) will have a more severe effect. Situations of less than optimum environment for certain organisms commonly occur in polluted areas.

Probably the only reason why these elements are toxic at all is because tissues concentrate them. There is no evidence to suggest that tissue concentrations as low as those found in sea water could harm the organism. From the evidence of the damage caused to organisms subjected to metals in laboratory experiments, the damage that would be caused by levels in the parts per billion range would probably be "unnoticed" by the organism. Indeed several elements such as zinc and copper are essential in minute amounts and are only toxic when raised. Each tissue concentrates different metals by differing amounts (Pontreath 1973), and it is only the ability of tissues to concentrate them, their inability to prevent their

uncontrolled entry into the body, or their inability to excrete them once absorbed, that leads to biological damage.

Interestingly, many of the factors such as decreased oxygen, changes of pH or salinity that synergise with the metals' toxic effects, also increase the rate of accumulation of the metal (Bryan 1971 ; Coleman et al 1971 ; O'Hara 1973). The situation for the animal in such conditions is thus part of a vicious circle; small changes in, for example, oxygen level, coupled with small levels of toxic elements leads to an ever increasing accumulation of the elements and enhanced damage by them.

Experiments demonstrating the responses of whole animals to heavy metals in the laboratory are numerous though not very representative of natural conditions. The levels used are often higher by several orders of magnitude than those found in even the most polluted marine situation. The effects of these elements in lower, more natural concentrations is less clear.

Analysis for heavy metals

A suitable tissue was sought for estimating the relative heavy metal concentrations at each site sampled. Laminaria hyperborea tissue was the only material collected in quantity at every site, but prior to placing any reliance on it experiments were carried out to determine 1) that the tissue could absorb or adsorb dissolved heavy metals; 2) that the amount taken up was related to the concentration in the water; and 3) whether the time that the plant was in the water affected the tissue concentration.

A total of 80 sections of stipe tissue were placed in normal sea water or in sea-water enriched with nickel, lead, cadmium, zinc, copper and manganese in concentrations of 0.125, 0.25 or 0.5 parts per million. After overnight agitation the tissues were analysed for their concentrations of these metals.

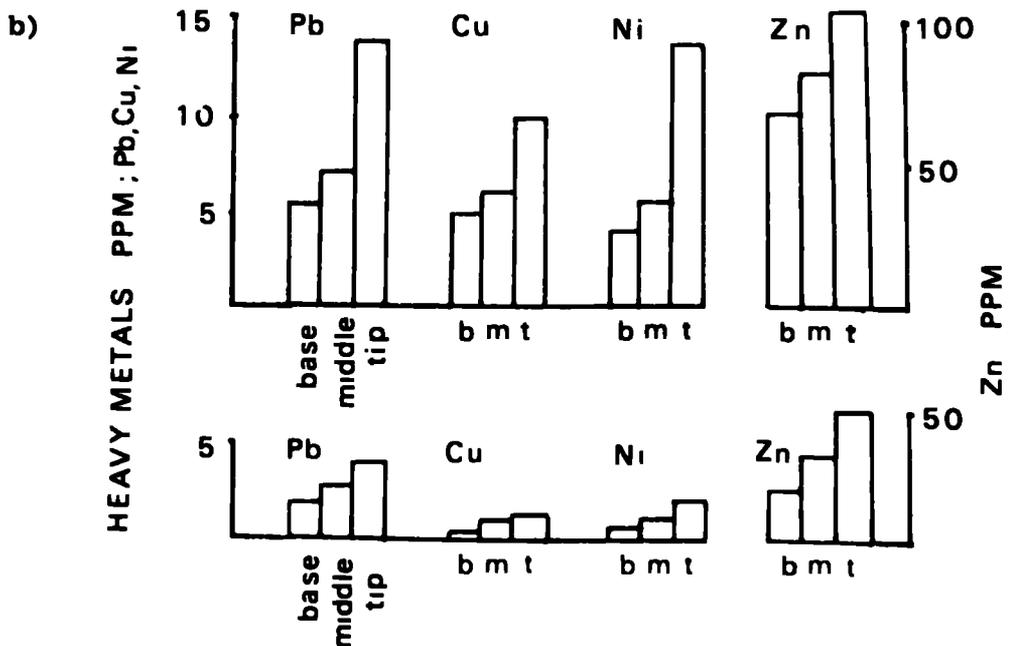
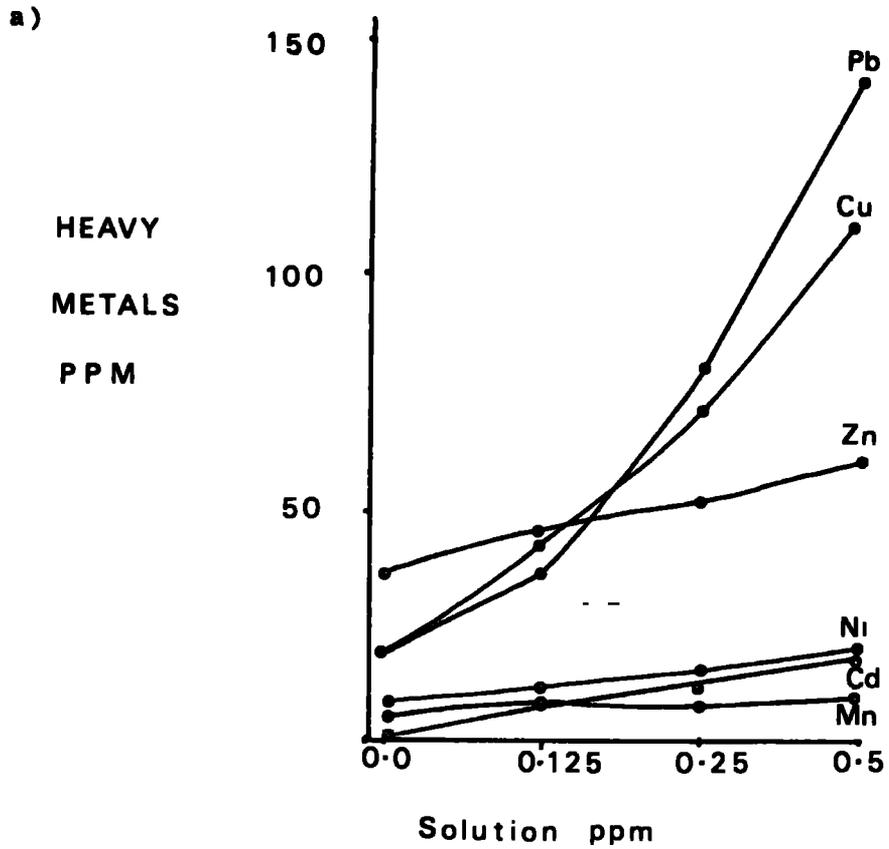
The results are shown graphically in figure 16a. In all cases except that of manganese there was an uptake of the metal. Cadmium and lead showed the largest (about eightfold) concentration between the normal and the 0.5 ppm enriched seawater. Copper, zinc and nickel also showed progressive tissue increases with concentrations related to the seawater concentration. Following this experiment no further investigations of manganese were undertaken since its usefulness in monitoring seemed doubtful. Possibly the plant tissue was able to regulate the uptake of this element. With the other elements some form of ab- or adsorption, into the plant material took place. This has been reported for other phaeophytes (Bryan 1969; I.M.E.R. 1975) and is probably attributable to colloids (Black and Mitchell 1952).

With the lower concentrations found in the sea the time of exposure to the heavy metals might be another parameter determining their level in the tissue. To test this, two series of analysis were carried out on different aged sections of the kelp frond. Base, centre and tip sections of fronds collected from the unpolluted site at St Abbs (grid reference NT 908692) and from the polluted site at Marsden were analysed for a range of heavy metals. The sampling was carried out in October (1973) so the ages of the sections were approximately one month, four or five months and eight months old respectively. The results are shown

FIGURE 16 a, b

a) HEAVY METAL UPTAKE CHARACTERISTICS OF L. HYPERBOREA.

b) IN VIVO ABSORPTION BY DIFFERENT SECTIONS OF FROND.



in figure 16b. In all cases the concentrations were in the order base<centre<tip. The overall levels were higher at the polluted site but the pattern at both sites was the same.

The findings from these experiments show that 1) L. hyperborea stipe tissue does take up all the heavy metals investigated except manganese; 2) the uptake is proportional to the media concentration and 3) with in vivo uptake seawater where concentrations are low the time factor is important. Laminaria stipe tissue would therefore seem to be suitable for the determination of the relative amounts of heavy metals at the sites sampled. Because of the importance of the time factor the standard section chosen for analysis was the base of the stipes of five year old plants.

Total Heavy Metal Index

The results of the analysis for heavy metals at each site are contained in Appendix C. An index entitled Total Heavy Metals (THM) was then built up from the readings obtained from each site (Table 22). Each element was taken in turn and the sites were ranked from 1 to 35 (least to most) of that element. The five lists of rankings were then averaged to make a final average ranking of sites. The position of any one site in the list is therefore its place, relative to all the other sites, according to the average amounts of the five "toxic" elements considered. The ranking approach was taken so that each element would contribute the same weighting to the final order of sites. Since the readings of Cd ranged from 0.35 - 3.4 ppm whilst those of Zn were 11.0 to 85.0 ppm the use of actual concentrations instead of rankings would have given different and disproportionate weightings to the different elements.

Table 22

Site rankings for heavy metal concentrations

<u>Site</u>	<u>Sector</u>	<u>Pb</u>	<u>Cu</u>	<u>Ni</u>	<u>Cd</u>	<u>Zn</u>	<u>Ranked Mean</u>
Cellardyke	I	1	8	19	8	11	1
Peterhead	I	16	26	2	3	7	2
Aberdeen	I	30	11	9	1	5	3
Caithness	I	13	16	5	17	6	4
Seaton	IV	2	1	10	26	16	5
Fraserburgh	I	6	3	15	32	10	6
St. Abbs	I	28	6	1	2	29	6
Montrose	I	4	20	5	26	11	6
Falmouth	II	3	9	24	17	16	9
Portencross	III	23	15	22	10	1	10
Port Erin	III	14	17	7	10	24	11
St. Agnes	IV	29	28	4	5	8	12
Kingsbarns	I	5	14	19	21	15	12
Ballycastle	III	12	4	29	30	3	14
Plymouth	III	31	18	3	6	22	15
Durdle Door	IV	32	5	16	15	20	16
Robin Hoods Bay	II	19	7	28	16	18	16
Penzance	IV	34	27	10	4	14	18
Dunbar	I	11	13	14	20	31	18
Loch Sunart	III	9	10	25	22	19	20
Kimmeridge	IV	22	2	22	33	13	21
Lossiemouth	I	17	18	11	28	26	22
Port Ysagden	III	24	23	11	17	25	22
Souter	II	35	24	11	7	23	22
Bangor	III	10	34	27	14	21	25
Corsewall	III	26	21	30	23	9	26
Jersey	IV	18	12	25	29	26	27
Scarborough	II	8	29	35	10	28	27
Oxwich	III	20	32	8	25	30	29
Whitby	II	15	25	34	10	31	29
Sennen	IV	25	31	31	31	4	31
Marsden	II	33	29	17	9	35	32
Redcar	II	7	33	21	34	33	33
Newbiggin	II	27	35	32	35	2	34
Flamborough	II	21	22	33	24	33	35

- N.B. 1. No heavy metal data was obtained from the Hebrides.
 2. Peterhead (reference NJ133457) was sampled for heavy metals only and these results are included here.

In fact the THM order is very close to the orders of the individual elements; every element correlated significantly (at least to $p = .05$) with the values of THM. The index thus reflects closely the values of each element, and smooths out some of the vagaries that occasionally occurred with some sites, (e.g. see values for Newbiggin).

It can be shown that each element contributes about equally to building the THM index. The equation predicting THM from the five elements is:

$$\text{THM} = 5.25 \text{ Cd} + 0.11 \text{ Ni} + 0.46 \text{ Pb} + 0.18 \text{ Zn} + 1.75 \text{ Cu} - 9.81$$

The normalised version is:

$$\text{THM} = 0.42 \text{ Cd} + 0.35 \text{ Ni} + 0.35 \text{ Pb} + 0.39 \text{ Zn} + 0.34 \text{ Cu}$$

The latter shows very similar values for each element. Cd at 0.42 contributes the most to THM and Cu at 0.34 the least, but the differences are small. The index is therefore probably a good indicator of the heavy metal loads found at each site.

Trends and regional differences in Total Heavy Metals

Taking each sector in turn (see Table 22) the highest levels of THM occurred in sector II where the mean value was 28.5, $sd = 6.6$. The lowest were found in sector I whose mean was 8.0 $sd = 7.1$. This difference is significant ($p = .05$). Sectors III and IV were midway with mean values of 19.6 ± 7.2 and 17.1 ± 8.0 respectively. It is interesting to note that the highest and lowest means refer to adjacent regions both in the North Sea. It would seem unlikely therefore that there is a distinct North Sea basin or zone with respect to heavy metals. The average level in the North Sea is no more than that in the Atlantic or South coast sectors. The differential within the North Sea however is steep.

Figure 17 shows the general trends of THM around the whole study area. The arrows progress from lowest value to highest and are only drawn where a correlation of THM with latitude or longitude was significant. The statistical method used is described in Appendix A. The correlation and its significance showing the degree of the relationship is written above the arrows, and the regression, showing the steepness of the slope is written below the arrows.

Taking all the sites together first, THM correlates significantly with longitude, the levels increasing eastwards (central arrow). The steepness of the gradient is in the order of one THM unit per degree longitude. There was no overall North-South trend.

Taking each sector in turn the only correlation found within a single sector was the slight one in section III, where there was a tendency for THM to increase southwards. Neither the correlation nor the steepness of the slope were large.

Taking the North Sea as a whole strong relationships were seen with both latitude and longitude. It should be noted that latitude and longitude values are closely correlated in the North Sea sites ($r = .859$ $p = .001$). Because of this the heavy metal increase eastwards may only be a consequence of its increase southwards, or vice versa. The value depicted in Figure 17 is that with latitude and it shows a steep slope for THM which increases southward at nearly 7 units per degree latitude. (The slope was 7.8 units per degree longitude).

TOTAL HEAVY METAL GRADIENTS.

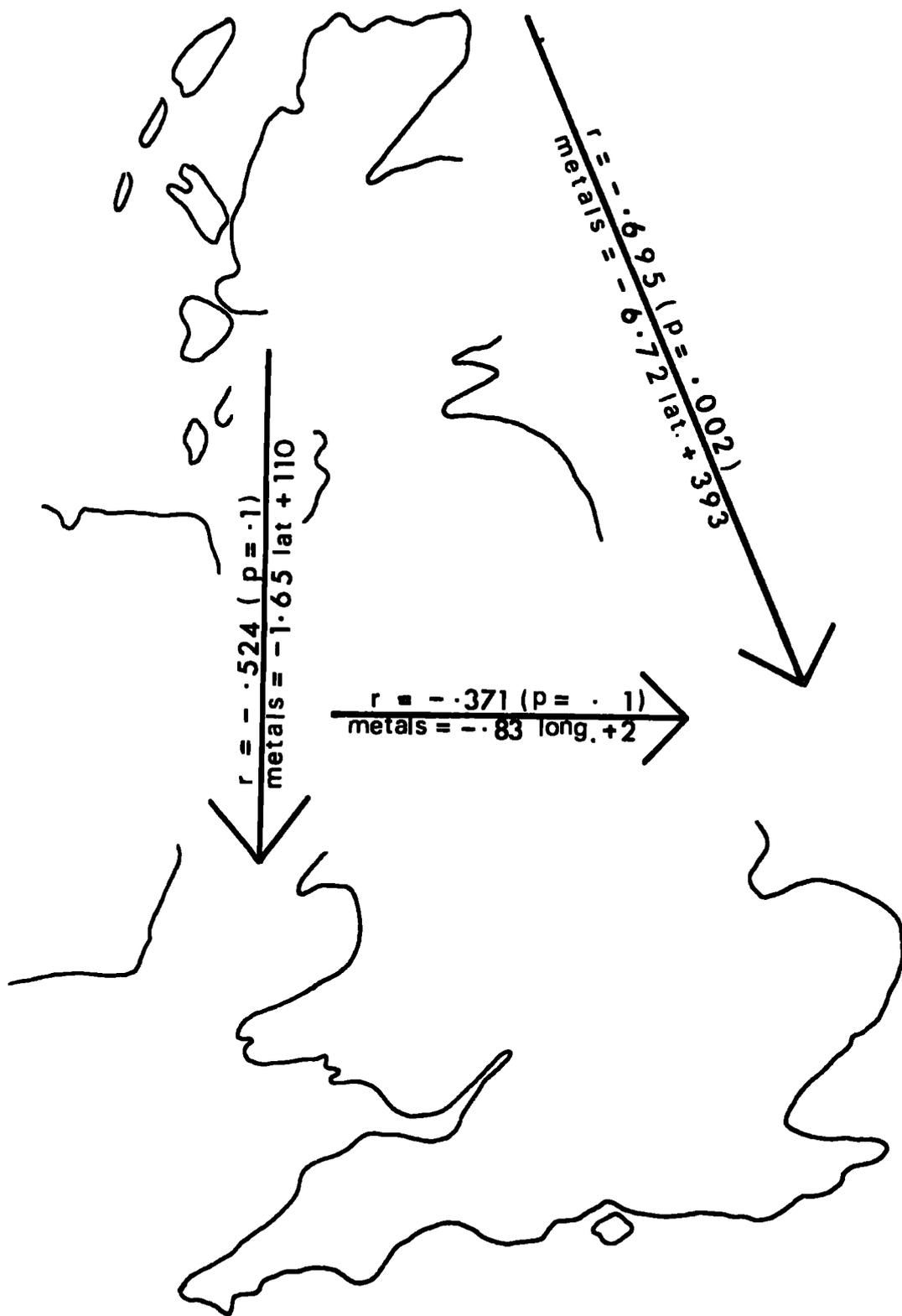


FIGURE 17

The broad conclusions of the pattern of THM are:

- (1) That the English coast sector of the North Sea is the most "polluted" of all the sectors in terms of the heavy metals studied.
- (2) The least levels were found in the Scottish North Sea region such that a steep gradient is formed down the British North Sea coastline.
- (3) A slight trend is seen in sector III.
- (4) Over Britain as a whole there is an increase eastwards.

The possibility that Total Heavy Metals affects the holdfast infaunas is investigated later in this study.

2. Water Clarity

The clarity of a body of water is one of its most distinctive and in biological terms important characteristics. The transmission of light through water has been studied in detail by Jerlov (1951) and the more specific biological effects of light on Laminaria has been investigated by Kain (1966).

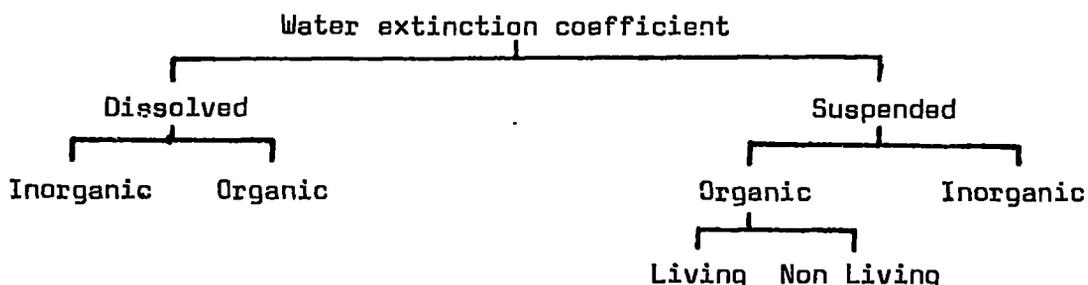
It has been shown earlier in this thesis that light itself is of little apparent importance to the fauna; at three sites there was no significant change in holdfast composition with increasing depth or with decreasing light. The factors which are of importance to the fauna are suspended and dissolved compounds in the water, which may be measured in several ways, one of which is the reduction in light penetration.

Light transmission is geometric and is described fairly well by the equation

$$\frac{dI}{dt} = -kI$$

where I = intensity of the incident light, t = depth and k = the water extinction coefficient. The value k is thus the main factor which determines light penetration and water clarity. Very clear water has a k value of 0.03 and absorbs 50% of the incident light in the first metre and 90% in the first 20 metres. Open ocean water remote from land or reef masses may have a k value of .1, and coastal water a value of .3 upwards (Krebs 1972).

The main factors affecting k are summarised below.



In different bodies of water the components may assume different degrees of importance, but all the components are interdependent.

Methods of measuring the components

(a) Overall Clarity

Spot checks on water clarity can be made using a number of modifications of the Secchi disk method. Longer term measurements using in situ apparatus suffer from the problems of sediment and biota on the sensors.

(b) Dissolved Materials

Technically it is possible to analyse sea water for almost all dissolved substances and analysis for many is now routine (Strickland and Parsons 1968). The problems inherent in this are many however and are summarised as follows.

1. The very low concentrations of many of the compounds leads to high analytical standard error.
2. Certain of the compounds, such as nitrogen, phosphorous and silica compounds have such rapid turnover rates and are buffered so strongly by sediments (Bulter and Tibbits 1972) that the results obtained have limited value. Compounded with this is the problem of formation and secretion of organic materials by marine life.

3. In recent years the fact that double carbon bonds absorb ultra-violet wavelengths has been used for estimating dissolved carbon. At the beginning of this study the method was used along the North East England coast. Early in the work however, several large and at present uncorrectible interferences were revealed making the method unusable. In view of its continued use by many authors the study is recorded in detail in appendix E, although it was discarded as a means of analysis here.

(c) Suspended Materials (Organic and inorganic)

Single readings of suspended matter can be simply obtained using a variety of filtration techniques. Moore (1972) has attempted to gain a more continuous or integrated pattern by using in situ sediment traps, but encountered difficulties due to disturbance by storm conditions.

In the study of pollution by sewage the assessment of suspended coliform bacteria has been extensively and successfully used (Watson and Watson 1968 ; Henriksson 1969). The main problems here relate to the short life of faecal organisms when exposed to sea water.

Overall Problems

In addition to the above specific difficulties, any method for assessing overall water clarity or a component of it is subject to the following limitations:

(1) Owing to the enormous heterogeneity of input, currents and mixing, collections should be taken at each site at regular short intervals if a meaningful extrapolation is to be allowed.

(2) Even if a mean value is obtained it may have limited value unless the extremes of the variation have also been noted since the latter may be of far greater significance. For example the mean dissolved oxygen is of little importance if the lowest value is zero, and readings of mean dissolved phosphate may be of less importance than pulses high enough to stimulate algal blooms. Likewise Laminaria may survive periods of no light interspersed with periods of good water clarity, but not a sustained clarity below their compensation point. -

There is certainly a need therefore for some integrated assessment of water clarity when attempting to study the ecology of marine ecosystems.

Kelp "phytometer"

One satisfactory way of obtaining an integrated year-round index of "pollution" by suspended material can be achieved using the "phytometer" method of Bellamy et al (1967, 1970, 1973) who showed that the depth range of the kelp varied with the amount of suspended matter in the water. It was shown that a reduction in the depth range of L. hyperborea could be attributed to reduced light penetration. This reduction in depth range is brought about by all forms of suspended material both from natural sources and from industrial and domestic pollution.

Although the depth range or site performance correlated closely with suspended material Bellamy et al (loc cit) found that the individual performance of the plants was little affected except at the extreme lower edge of its depth range. Where light appears to be "barely sufficient" the growth of each plant was not reduced. A complete set of data on the

performance of the kelp over its depth range at one site is presented in Appendix 9. This illustrates the effect of a marked reduction of individual performance at the extreme lower limit of the depth range.

These observations find support from the work of Drew (1969, 1971) on the photosynthetic efficiency of algae. He showed that efficiency of carbohydrate synthesis increased with depth until it approached the maximum theoretically possible after which growth ended abruptly.

The depth to which kelp grows at each site is therefore used as an integrated index of water clarity. The following table gives the values found in this study (depths in metres).

Table 23

Sector		Sector II		Sector III		Sector IV	
Caithness	23	Newbiggin	2.5	Hebrides	25	St. Agnes	14.7
Lossiemouth	11	Marsden	2	L. Sunart	25	Sennen	21.2
Fraserburgh	23	Souter	3	Portencross	7.6	Penzance	15
Aberdeen	10	Redcar	4	Sallycastle	15	Falmouth	17
Montrose	10	Whitby	9.5	Corsewall	7.6	Plymouth	12
Kingsbarns	7	R. Hoods Bay	6.5	Bangor	15	Seaton	6
Cellardyke	7	Scarborough	6.8	P. Erin	16	Durdle Door	-
Dunbar	10	Flamborough	9.5	P. Yeagden	12	Jersey	18
St. Abbs	16.4			Oxwich	9.5	Kimmeridge	12.1
Mean	13.4		5.5		14.5		15.1

Of all the sites studied only at Durdle Door in Dorset did the substrate give way to sand before light became limiting to the growth of kelp. Similar mean values were found for all sectors except Sector II which showed a much restricted mean depth range.

The trends are shown in figure 18. Over Britain as a whole (central arrow), there is increasing clarity from East to West. Interestingly along the only sector orientated East-West, i.e. along the South coast, no similar gradient was revealed. This will be discussed later.

In the North Sea the clarity increases northwards overall, but the results from sectors I and II show a pivot around the coast of Durham where very poor water clarity conditions appear to exist. Water clarity increases both northwards and southwards from this point.

In sector III there is a significant but less steep gradient, such that the waters of the Scottish West coast, appear on average to be clearer than those of the Irish Sea.

The causes for a reduction in water clarity are discussed later when it is shown that industrial and domestic pollution in the N.E. England sites must be at least a major cause of the loss of clarity there, and evidence is presented which largely discounts natural turbidity as being a prime cause in this region.

"Clarity" is regarded as a second variable which possibly affects the holdfast fauna. Measured by the depth range of the kelp it encompasses all parameters which have an affect on light transmission through the water.

WATER CLARITY GRADIENTS.

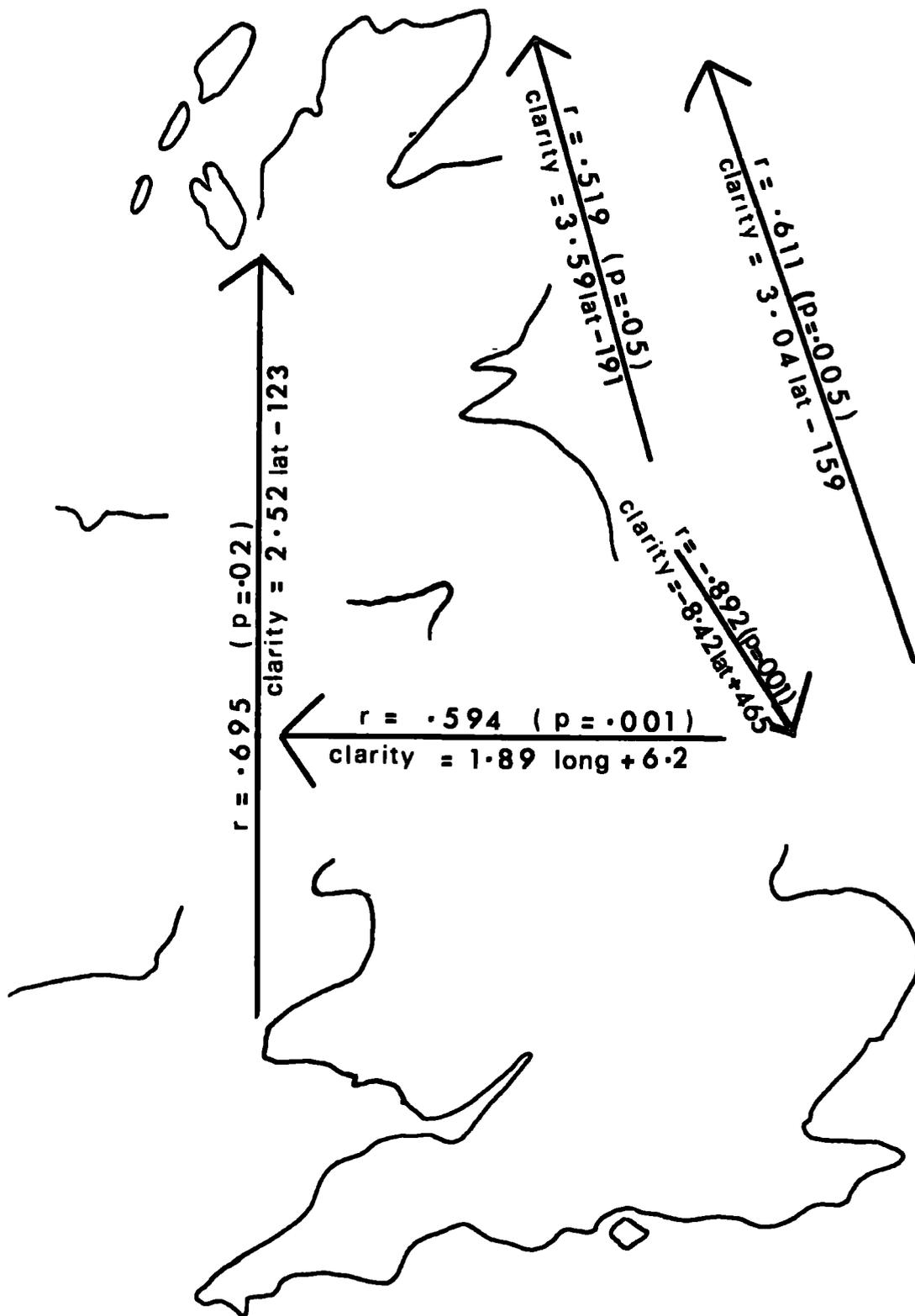


FIGURE 18

3. 4. Latitude and Longitude

In addition to the two variables Total Heavy Metals and Clarity the effects of geographical location were examined on the assumption that this also has a bearing on holdfast fauna. Since all species have a geographical range of some sort it seemed probable that significant patterns would emerge over the 1000 x 500 kilometer range of this survey. Latitude and longitude were therefore included as variables, making a total of four to be considered.

The four variables

It is possible that these four variables in fact measure more or less than the four actual dimensions. For example, possibly geographical location might be only one real dimension although it requires two apparent variables to locate it. In contrast relative heavy metal load and water clarity need only one measurement each for their location.

Conversely one variable might measure more than one theoretical dimension, or one variable might be more or less completely accounted for by, or contained within another. As an illustration, Total Heavy Metals might simply be a component of Clarity.

Therefore the degree of complication and duplication shown by the four variables was determined, and the justification was assessed of regarding them as being entire in themselves or whether they were measuring more or less than the four theoretical dimensions claimed for them.

This was most suitably done with principle component analysis, a branch of factor analysis. This is a straightforward way of transforming the four variables into another hypothetical set of variables, called factors.

The factors are constructed from the variables so that each variable contributes a varying amount towards the factors. Factor 1 is the best summary of linear relationships exhibited in the data and accounts for more of the variance in the data as a whole than do any other combinations of variables or parts of variables. Factor 2 accounts for the largest part of the remaining variance, and so on until the number of factors equals the number of variables when all the variance is used up. In the method chosen, although not necessarily, each factor is orthogonal (uncorrelated) to the others.

Two implications of this are as follows. 1) If a variable loads substantially on to more than one factor it means that the variable measures more than one theoretical dimension (Nie et al 1970; Comrey 1973). 2) If two variables load on to the same factors in the same way than those variables are measuring the same thing. In this way the structure of the data can be seen and the validity of the variables can be assessed.

The four variables, THM, Clarity, Latitude and Longitude, were subjected to this form of principle component analysis. The following structure emerged:

	<u>Table 24</u>			
	Factor 1	Factor 2	Factor 3	Factor 4
Latitude	.9858	-.1407	-.0904	.0139
THM	-.1443	.9978	-.0670	-.0137
Longitude	-.1020	-.0697	.9488	.2906
Clarity	.0181	-.1508	.2959	.9431

It is clear that one variable loads very substantially onto one factor each and onto other factors by only a minimal amount. Also one factor represents only one variable. The correspondance between each variable and its factor is high. The square of the values, x 100, is the percentage of the variables variance accounted for by that factor. Thus it can be seen that each factor is very similar indeed to one variable.

It can be concluded that the variables are uncomplicated and measure only one theoretical dimension each. Also there is no duplication of variables, so that, in the earlier example, THM is not merely a component of Clarity. The variables are all approximately orthogonal to each other as well.

For the purpose of this study it is perfectly adequate to leave the variables as they are. Had the loadings been radically different the factors would have to have been substituted for the variables.

THE FAUNA

The Faunistic Patterns

The numbers of species, the total numbers of animals and the diversity of a three litre sample at each site are listed in table 25 together with the averaged value for each sector. The English North Sea region, sector II, has the highest number of individuals but the fewest species, which together produces the lowest diversity. The Scottish North Sea region, sector I, shows the highest diversity, but is little different from the West and South coast sectors. In the latter region one site at Seaton was exceptional and had a very large spatfall of Mytilus on every holdfast collected. This site is the only one that falls out of the overall South coast pattern and was situated close to a sewage outfall.

The gradients of these values, correlated with latitude and longitude are shown in figure 19. The correlation coefficient, r , of either number of species (Sp) number of animals (N) or diversity (α) with latitude or longitude is written above the arrows, and the "steepness" of the gradient is indicated below the arrows in the form of its regression equation. As in the two previous figures only significant relationships are depicted.

With all the sites combined (central arrow) there is a gradient of increasing species richness and diversity in a westward direction. No general North-South gradient appeared from the data to hand.

Table 25

	<u>Sites</u>			<u>Sectors</u>		
	N	Nsp		N	Nsp	α
Caithness	458	42.2	11.5			
Lossiemouth	503	27.7	6.2			
Fraserburgh	342	44.1	13.5			
Aberdeen	300	31.6	8.5	676	34.7	8.0
Montrose	1866	23.3	3.6			
Kingsbarns	253	31.8	9.5			
Cellardyke	436	30.	7.1			
Dunbar	776	39.1	8.7			
St. Abbs	1151	43	8.5			
Newbiggin	3150	24	3.5			
Marsden	778	24.9	4.8			
Souter	1475	25.3	4.0			
Redcar	6630	21.9	2.9	.1692	27.5	4.5
Whitby	421	36.4	9.0			
Scarborough	248	31.6	9.5			
Robin Hoods Bay	282	22.	5.5			
Silwick	556	33.5	7.5			
Hebrides	558	35.5	8.6			
Loch Sunart	767	43.3	10.8			
Portencross	613	49.7	13.0			
Ballycastle	102	23	9.3	562	30.0	6.9
Corsewall	874	20.9	3.9			
Bangor	338	32.	8.7			
Port Erin	225	22.7	8.2			
Port Ysadgan	343	21.3	5.6			
Oxwich	1234	21.3	3.8			
St. Agnes	563	47.4	12.2			
Sennen	539	47.7	12.5			
Penzance	340	43.9	13.5	1164	34.9	6.8
Falmouth	808	41.4	9.3			
Plymouth	700	44.	10.5			
Seaton		24.7	3.5			
Durdle Door	112	20.1	7.5			
Kimmeridge	124	27.	10.0			
Jersey	131	18	5.2			

FAUNISTIC GRADIENTS.

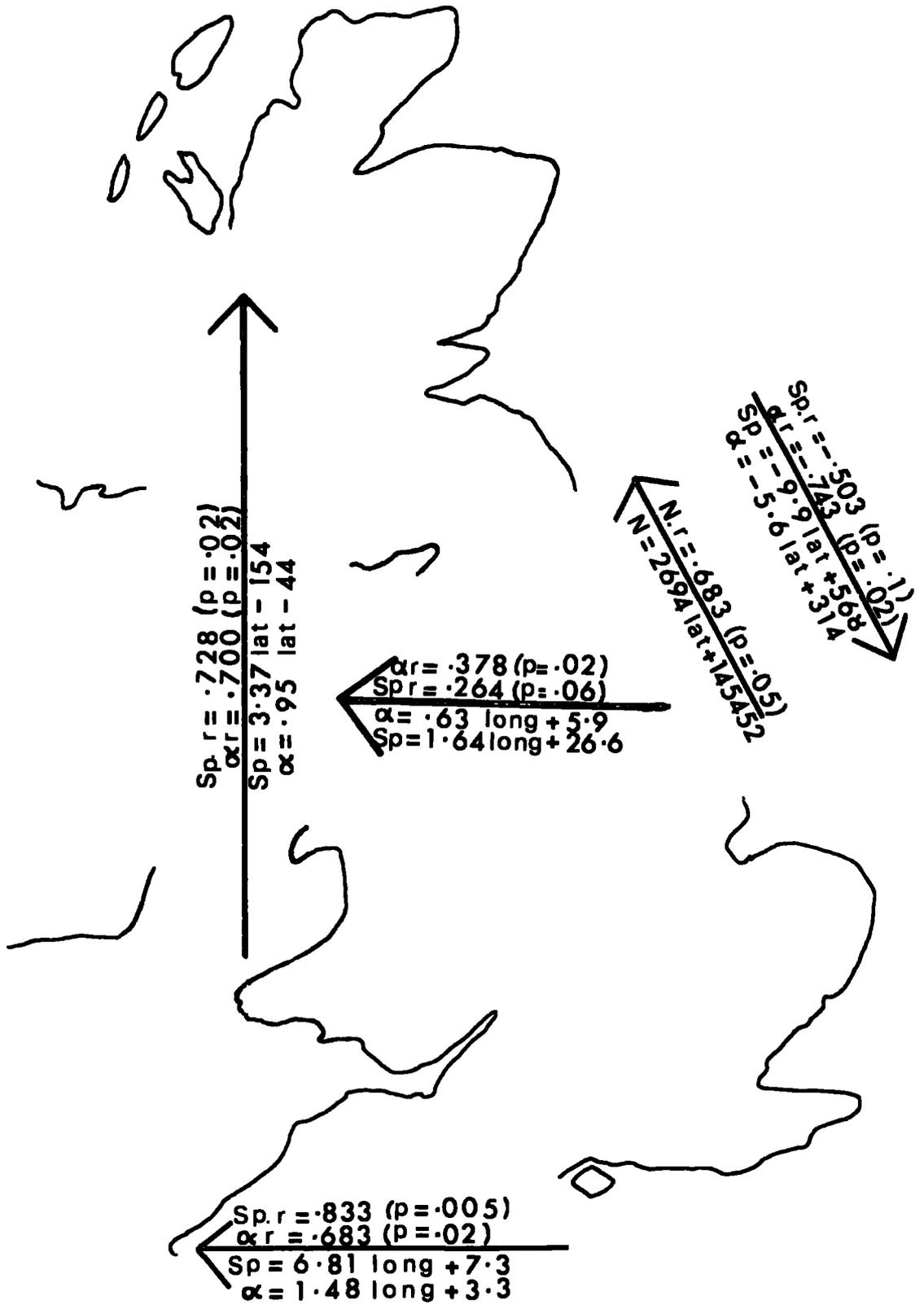


FIGURE 19

Sector I showed no faunistic gradient with latitude or longitude. In sector II total numbers increased steeply northwards from the Yorkshire to the Durham coast. Simultaneously, species richness declined, and with it, diversity. The southernmost sites in this sector such as Whitby and Scarborough are similar in numerical composition to some of the least polluted sites elsewhere in Britain, so that the gradients of species and numbers along this coast appears to be caused by the inclusion of the more northerly sites of sector II, namely those between Redcar and Newbiggin. This is in agreement with the results of Bellamy et al (1967) and Jones (1970).

Elsewhere other trends are apparent. Along the West coast, sector III, a North-South gradient of species richness and diversity appeared. It would have been desirable to divide this sector into two parts, an Irish Sea/Bristol Channel region and a West Scotland region. However, too few samples prevent this. There is the possibility however that an Irish Sea/Bristol Channel "basin" exists which is low in species compared to the Scottish West coast.

Sector IV showed three clear trends. The number of species, numbers of animals and diversity all increased westwards. This finding compares well with the work of Crisp and Southward (1958) on rocky intertidal animals in the English Channel, which were found to decrease in both richness and abundance as the eastern Channel basin was approached. Exactly the same situation obtained with the holdfast faunas along the South coast. However due to the absence of L. hyperborea East of the Isle of Wight, only the Western half of the South coast is involved in

this study compared to the whole South coast region in the study of Crisp and Southward.

All the gradients seen in figure 19 may have several causes. The trends may be due in some cases to zongeographical trends, other natural factors, or may reflect gradients of industrial and domestic pollution. The reasons for the trends in each sector can be elucidated at least in part by examining the statistical relationships of the fauna to the four environmental variables.

Relationships of fauna with Total Heavy Metals and Clarity

The following table presents all the significant correlations that existed between total numbers, number of species and diversity with either THM and Clarity.

Table 26

Sector	Variable pair	r	p
I	Sp Clarity	.599	.05
II	N Clarity	-.623	.05
	Sp Clarity	.635	.05
	Clarity	.743	.02
III	Sp THM	-.659	.05
	THM	-.786	.01
IV	None		
North Sea	Sp Clarity	.753	.001
I + II	THM	-.398	.05
	Clarity	.663	.002
All sites	Sp THM	-.270	.05
	Sp Clarity	.459	.005
	THM	-.294	.05
	Clarity	.606	.001

In every instance where there is a correlation between a faunistic attribute and THM or Clarity, a "deterioration" of the environment (increase in THM or decrease of Clarity) correlates with a fall in species richness and a fall in diversity. In sector II a fall in Clarity also correlates with a rise in the total number of organisms. No exception to this occurred.

These relationships are perhaps the "logical" effects of a deterioration of the marine environment, whether by pollution or by natural turbidity. However there were as many coefficients that were not significant as those that were. For example on the South coast neither of the environmental variables correlated significantly with any of the three faunistic attributes. In certain of the sectors however, the above correlations speak strongly of a meaningful relationship between the environmental variable and the holdfast fauna. In sector II Clarity appeared to have some importance, while in sector III THM showed significant correlations. The relative importances of these two variables, and their importance relative to the geographical variables latitude and longitude, were elucidated further with the help of multiple regression analysis.

The Relative Importances of the Four Variables

The four variables were regressed onto 1) number of species, 2) total numbers of animals and 3) diversity (Tables 27, 28 and 29). The independent variables in each equation are written in order of their importance. The one which accounted for the largest part of the variance of the dependent variable is written first, the one which accounted for the second largest part is written second and so on. Only those variables accounting for 2% or more of the variance are included. Only the final step of each

Table 27

Species numbers

1) All sites -

Species = .76 Clarity -.12 THM + 24.6
 %variance accounted for by : Clarity = 30%
 +THM = 32%
 All 4 = 32.3%

2) North Sea sites

Species = 1.0 Clarity + 21.5
 variance : Clarity = 72. %
 All 4 = 75.9%

3) Sector I

Sp = 1.09 Clarity - 2.12 lat - 2.17 long + 146
 variance : Clarity = 63%
 + Lat. = 70%
 + Long. = 72.5%

4) Sector II

Sp = 1.34 Clarity - 0.25 THM + 12.7
 variance : Clarity = 65.5%
 +THM = 74.5%
 All 4 = 75.5%

5) Sector III

Sp = 2.92 Lat - .27 THM - 125
 variance = Lat. = 35.0%
 +THM = 38%
 All 4 = 50%

6) Sector IV

Sp = 6.81 long + 7.29 (.001)
 variance : Long = 86%
 All 4 = 91%

Table 28

N

1) All sites

$$N = -97.1 \text{ Clarity} + 2079$$

%variance accounted for by : Clarity = 13%
 All 4 = 13.4%

2) North Sea sites

$$N = -42.0 \text{ Clarity} + 39.47 \text{ THM} + 911$$

variance : Clarity = 12%
 + THM = 18%
 All 4 = 19.4%

3) Sector I NS

4) Sector II NS

5) Sector III
 $N = \text{NS}$

6) Sector IV NS

Table 29

Diversity

1) All sites

$$\alpha = .27 \text{ Clarity} - .05 \text{ THM} + 5.4$$

% variance accounted for by :

Clarity	=	37%
+ THM	=	39%
All 4	=	40%

2) North Sea sites

$$\alpha = .375 \text{ Clarity} - 0.29 \text{ Long} + 4.1$$

variance :

Clarity	=	58.7%
+ Long	=	59.5%
All 4	=	60%

3) Sector I

$$\alpha = .305 \text{ Clarity} + 4.5$$

variance :

Clarity	=	44%
All 4	=	48%

4) Sector II

$$\alpha = .395 \text{ Clarity} - 2.31 \text{ lat} + 130$$

variance :

Clarity	=	66%
+ Lat	=	68.7%
All 4	=	68.7%

5) Sector III

$$\alpha = -.26 \text{ THM} + .52 \text{ Lat} - 15.3$$

variance :

THM	=	56.1%
+Lat	=	64.5%
All 4	=	68%

6) Sector IV

$$\alpha = 1.492 \text{ long} + 3.3$$

variance :

Long	=	54%
All 4	=	74%

equation is written in the tables, although several steps had to be computed to arrive at this part, using firstly all the variables together and then selectively omitting each. Written after each equation is the percentage of the dependant variable's variance which is accounted for as each independant variable is added to the equation.

Thus an impression can be gained of 1) which variables affect the holdfast fauna appreciably, 2) the relative "importance" of each variable to the fauna compared to the other variables and 3) the different degrees of importance of each variable in the different sectors.

Examining species number, (Table 27) first, it can be seen that water clarity has the overwhelming effect, both in the North Sea as a whole and in sectors I and II separately. After clarity, latitude has some significance along the Scottish coast and heavy metals are implicated along the English section. However with about two thirds of the variance of species numbers being accounted for by clarity, this variable can be assumed to be of paramount importance in the North Sea.

Along the West coast latitude is implicated as being the most important of these four variables. Heavy metals are implicated slightly. All four variables together account for about half of the species number variance.

Along the South coast the most important of the four variables considered is clearly longitude which accounts for the very high figure of 90% of the variance. None of the other three variables contribute significantly, and the remaining 10% of the variance could easily be due



to sampling error alone.

A very similar pattern emerges when diversity is the dependant variable, (Table 28) the only real difference being that in sector III total heavy metals assumes more importance, moving from second to first place. In all cases where Clarity is effective its effect on species numbers and diversity is to increase them. When THM is effective it tends to decrease species numbers, and diversity. In the table for total numbers however (Table 29) this situation is seen to be reversed a fall in clarity and a rise in THM lead to greater total numbers of animals.

It needs to be emphasised that variables not measured may certainly be very important. For example, in sectors III and IV where latitude and longitude are implicated respectively, the important factors may be latitude or longitude per se but are very likely to be unmeasured parameters which correlate very highly with them. Salinity, temperature and current are possible examples. Crisp and Southward (1958) described salinity and sediment gradients along the South coast (although these were only marked East of the sites which form the basis of this study), and similar physical gradients exist down the West coast (Lewis 1964).

Thus latitude and longitude are both general and comprehensive variables in the same way that Clarity and THM are comprehensive variables. Clarity encompasses both pollution by sewage and natural turbidity (cf. the controversy between Jones and Moore) ; THM encompasses industrial pollution and a variety of weathering and natural environmental parameters. Likewise latitude and longitude represent a range of unmeasured physical attributes. The broad nature of these four

variables have been an advantage in that they have enabled the factors which influence the holdfast fauna to be greatly narrowed down, and the study has shown that in the different sectors different variables assume most importance. Further analysis of the faunal communities clarifies some of these variables, and throws light on the changes of the ecology of holdfasts under different conditions.

TROPHIC ANALYSIS

The regressions indicate the gross effects each variable has on the holdfast fauna. It was felt that more information about the nature and the effects of the variables may be obtained by examining the nature of the species that appear or disappear along the various gradients.

To this end, all species were categorised into one of the following trophic groups; carnivore, herbivore, omnivore, detritus feeder and suspension feeder. It is realised that the last two categories describe how the animal feeds rather than what it feeds on. It is because of this that they are valuable categories descriptively. The animals in the suspension feeder category for example are almost all planktonic omnivores which will utilize suspended detritus and non-living organic material when present. Detritus feeders are also largely omnivorous but both categories are considered as being distinct here because of their unique positions in the food web. The bibliography used in determining the trophic category of each species is listed within the references. The lists compiled by Jones (1970) proved especially valuable.

The numbers of each species and the total numbers of animals in each category were calculated for each site, using three litres of holdfast space as the sample. This provided the "density" of each category at each site. The density variable is not a transformed one, as for example percentage presence of each category would be, and can be used directly. By showing directly the number of each feeding type at each site, per unit sample size, it distinguishes between two sites which may have

the same percentage of one category but different numbers of them.

1) North Sea : Sectors I and II.

Table 30 shows an array of all the more common species (that is those which occurred at three or more of the sites) in the North Sea. The sites are ordered along the gradient of "Clarity" which was indicated above to be the most important of the variables studied in this region. The species have been subjectively ordered into three groups, A, those which occur right across the gradient, B, those which are present mainly in the clearer sites and C, those which are present in largest numbers in the less clear waters.

Group B is very heterogenous, containing representatives from many phyla and from all the trophic categories especially herbivores, carnivores and omnivores. In contrast, all the species of group C except one are suspension feeders.

To test the significance of these observations correlations were calculated of water clarity with both the total numbers of animals and numbers of species in each trophic category. The correlations are presented in the following table.

Table 31

	Species	Total numbers
suspension feeders	.385 (p= .1)	-.402 (p = .05)
herbivores	.523 (p=.02)	.533 (p = .02)
carnivores	N.S.(+value)	N.S.(+value)
omnivores	.540 (p=.02)	.672 (p =.002)
detritus feeders	N.S.(+value)	.382 (p = .1)

TABLE 30
NORTH SEA SPECIES DISTRIBUTION

Clearlest water → Least clear

		Caithness	Fraserburgh	St. Abbs	Lossiemouth	Whitby	Montrose	Aberdeen	Dunbar	Flamborough	Kingsbarns	Cellardyke	Scarborough	Robin Hoods Bay	Redcar	Souter	Newbiggin	Marsden
NERE	PELA	+	+	1		1		+	+	1	+	+	1	1	+	+	+	1
AMPH	SQUA	+	1	1	1	+	1	+	+	+	+	-	+	+	+	+	+	+
HETE	SQUA	+	1	+	1	1	4	1	2	1		1	+	2	+	+	2	1
ASTE	RUBE		1	+	+	+	+	1	+	+	+	+	+	-	+	+	-	+
FCMA	TRIQ	1	1	1	3	+	+		1	1	2	+	+	+	+		+	+
FATI	FELL	+		-	-			+	-			+				+	+	+
HIAT	ARCT	2	1	+	+	1	+	1	1	1	1	-	1	2	+		1	+
BALA	BALA	2	+	+	+	+	+	2	+	+		4	1		-	1		+
OPHI	FRAG	+	-	+	1	+	+	+	+	+	+	+	+	+			+	+
LEPI	SQUA	+	+	+		+		+	+	+		+				-		+
MODI	BARB	1		+	+	+	+	+				+				+	1	-
VERR	STRO	+		1			+	+		+	-	-	-			+		+
EULA	VIRI		-	+		+			-			-	+		+		-	-
NEMA			1			1	+	+	+			-			+			
HARM	INPA	+	-	+		+		+	-			+				+	+	+
HENR	SANG	+	+	+		+		+			-	-			+	+	+	+
ACTI	ECUI	+	+	+			-	+	-			+				+		+
AMFH	RUBR			+		+		+	+	+		1				+		-
PINN	PISU	-	+			+		-	+	+		+		-				
TONI	RUBR	-		+			-	-	+			+				+		-
CIRR	CIRR		-	+					-			+	+					-
ACAN	COMM			-		+			-			-	-	-				
OPHI	NIGR			+		+		1				-	-					
PYCN	LITT	-				-	-											+
GAMM	SPEC			+		-						+						
EUNE	NEES	+	-								+				+			
LINE	LONG	-	-					-										+
TEAL	FELI						-	+							+			
LITT	LITT	+		-												+		
NEME		-						-										+
PORC	LONG	+	+	1	+		+	+	1		+	+	+				-	-
CANC	PAGU	+	-	+	-		-	+			-						-	-
MONI	PATE	+	-			+	1		+	1		+						+
FILO	IMPL	+	+	+	+				+		+	+						
NERE	VIRE		-	-		+	+	-		-	-							
OPHI	ACUL	+	+	1		+	1			-								
ACAN	CRIN	-	+		-				-								-	-
STRO	DROB		+	+		-											-	-
LINE	RUBE	-		+				+										-
NASS	INCR	+		-				-	-									
PERI	CULT	-	-			-		-										
PSAM	MILI		+	+	+				+									
TELL	TENU	+	-			-							-					
SERP	VERM	+	-							-								
ACHA	TESS	-			+				-									
GIBB	CINE	-		-					-									
SAGA	ELEG	+				+								-				
NYPP	SPE2	-				-							-					
MODI	MODI	+	+	+	+	1	+	+	+	1	+	2	1	5	2	2	1	
SABE	SPIN					1	+		2	2	2	-	+	1	2	+	4	
NYTI	ECUL	+	-	+		1	+	+	+	+	1	-	+	1	1	+	+	
NERE	DIVE										-	-			+		+	-

A

B

C

It is thus obvious that a decline in water clarity correlates with an increase in the total numbers of suspension feeding organisms, but with a decrease of the numbers found in all other trophic categories and with a decrease in the number of species of all trophic categories. Inspection of the earlier table 30 clarifies the situation, showing that the increase in suspension feeders is accounted for in large part by the increase in the numbers of Modiolus modiolus and Sabellaria spinulosa alone. It is of interest to speculate on the possibility that the massive increase in the numbers of these two suspension feeders might be responsible for the decrease found in the numbers of all other organisms simply by physically excluding them. These two species are amongst those described by Jones (1970) as being adventive in organically enriched water.

2) South Coast

Table 32 summarises the South coast data. Longitude, which was indicated to be the most important of the considered variables in this sector, was correlated with both total numbers of organisms and numbers of species in each trophic category.

Table 32

	Species	Total numbers
suspension feeders	.595 (p = .1)	.548 (p = .1)
herbivores	N.S.	.671 (p = .05)
carnivores	.952 (p = .001)	.810 (p = .01)
omnivores	.929 (p = .001)	.610 (p = .01)
detritus feeders	N.S.	N.S.

In all cases where the correlations were significant all attributes increased from East to West, including the total numbers of suspension feeders. Thus it would seem that along a gradient caused by factors other than pollution; by natural turbidity, sedimentation and salinity, (Crisp and Southward 1958) there is no increase in the numbers of suspension feeders. Of interest here is Seaton, which showed a very large number of Mytilus and which was situated close to a sewage outfall.

3) West Coast

As both THM and latitude appeared to be important in sector III correlations of trophic structure were calculated against both of these variables. The results are presented in Tables 33 and 34.

Table 33 (with THM)

	Species	Total numbers
suspension feeders	N.S.	.750 (p = .01)
herbivores	-.683 (p = .02)	N.S.
carnivores	-.567 (p = .05)	N.S.
detritus feeders	-.677 (p = .05)	N.S.
omnivores	-.500 (p = .1)	N.S.

Table 34 (with latitude)

	Species	Total numbers
suspension feeders	N.S.	N.S.
herbivores	N.S.	.592 (.1)
detritus feeders	N.S.	N.S.
omnivores	N.S.	N.S.

Taking the correlations with THM (table 33) first; increasing THM correlates with a decreasing species richness of all categories except suspension feeders. The total numbers pattern is exactly the

reverse; suspension feeders numbers was the only group to show an increase with increasing THM.

In contrast there are no highly significant correlations with latitude (Table 34).

Again it would seem that THM, a parameter linked to pollution, correlates with a decreasing richness of all trophic categories except the suspension feeders.

Discussion

Although the situation is complex a number of definite lines worthy of further consideration emerge from this study.

It would appear safe to conclude that both a decrease in water clarity and an increase in THM correlate with a decrease in trophic diversity coupled with an increase in the number of suspension feeders. It is therefore of interest that along the South coast gradient, where the marked differences between the fauna and flora of the eastern and western basins of the Channel have been attributed to natural causes, no such reciprocal relationship was recorded.

It would seem not unreasonable to conclude that in the absence of enrichment of the marine environment by organic material (N.B. there are no large industrial complexes discharging into the section of the Channel studied, and many of the coastal towns adequately treat their sewage); with decreasing species richness and trophic diversity there is no concomitant increase of suspension feeders. It must be accepted

that this could be due to zoogeographical reasons alone, although the presence of an anomalous site at Seaton mediates against that argument.

It is of interest to speculate that in the eastern half of the South coast sector the holdfast space is underutilised (see Table 25 which showed that these sites were low in both total numbers and species numbers). Only where there is organic matter present, as at Seaton, does the space become filled by the adventive suspension feeders.

It would therefore appear to be very difficult to argue that the holdfast faunistic gradients shown along the East coast sectors have nothing to do with organic pollution.

DISTRIBUTION OF SELECTED GROUPS

The distribution of certain groups of organisms proved to be of interest and of relevance here. Firstly the distribution of the mollusca, the largest phylum present is briefly discussed. Following this, some aspects of the geographical distribution of the species as a whole are examined.

1) The Molluscs

Of the 252 macroscopic species found, 75 or about 30% were molluscs. Of these, three were ophistobranchs, six were chitons, and the remainder were divided about equally between the prosobranchs and the bivalves.

The species found are shown in table 35, where the order of sites follows the water clarity gradient. It can be seen that there is 1) a reduction in the numbers of prosobranchs in the less clear water, and 2) that the distribution of bivalves is more evenly spaced although there are high densities of some of them in the less clear sites.

To help determine the cause of the decline of prosobranch species numbers the same multiple regression approach used for all species earlier was adopted. The results (table 36a) show clearly that water clarity is the most important variable in this survey in determining prosobranch species richness. Heavy metals are implicated significantly, but the geographical parameters were not significant.

Table 36(b) shows the analysis repeated for the bivalves. None of the four variables showed the same amount of importance in determining

Table 36a

Prosobranch species numbers = $.217 \text{ Clarity} - .069 \text{ THM} - 2.0$ ($p=.001$)

Clarity accounts for 35.5% of variance

Clarity + THM accounts for 43.5% of variance

Clarity + THM + Lat + Long accounts for 47.0% of variance

Table 36b

Bivalve species numbers = $.204 \text{ Clarity} + 3.35$ ($p=.01$)

Clarity accounts for 20.9% of variance

Clarity + THM + Lat + Long accounts for 21.5% of variance

bivalve species richness as they had in the prosobranch case, and only Clarity was significant.

Of the four variables considered, water clarity, or lack of it due to suspended particles, is the overriding determinant of molluscan species richness. Neither latitude nor longitude appeared to be important in determining species richness. The English North Sea coast has the least clear water and is also the most Easterly sector, but it appears to be the former variable that correlates with species richness, not the latter. The Scottish North Sea is considerably richer.

Bivalve species numbers are less affected than those of prosobranchs. A more marked effect shown by some bivalves in water of low clarity is that their total numbers increase.

The dietary behaviour of the molluscs is relevant here. Bivalves are almost all suspension feeders, and their greater numbers in the least clear waters reflects the greater food supply to these organisms. Prosobranchs are usually herbivores, carnivores, or both, and possibly their decline in areas of low water clarity shows a loss of their food base.

2) Geographical distribution of selected species

Of the 252 species collected from the 35 main sites only a few showed any marked pattern of distribution. Table 37 presents those species which had such a distribution. They include those which occurred in only one or some of the sectors, and others which occurred more

generally but which had a heavy weighting towards one region. The species are selected from the total list, compiled in Appendix D.

Group A contains eight species which occurred either mostly in the North Sea but with occurrences on the West coast, or which occurred mostly on the West coast but with occurrences in the North Sea. This group is the least distinct of the five but contains perhaps the more northerly species.

Group B contains those species which were absent from the West coast, occurring in this study in the North Sea and South coasts only. Group C are those which were found only in the North Sea. It contains three species of which two, the echinoderms Strongylocentrotus and Henricia are known to be confined to the North Sea. Group D are those which were absent from the North Sea but which occurred elsewhere.

Two sponges have, however, been included in this grouping which did have occurrences in the North Sea. Group E contains the southernmost species. These occurred largely in sector IV but in some instances were found further North as well. This group included the polychaete Lysidice ninetta and the pheasant shell Tricolia pullus, both Atlantic species of lower latitude.

All these groups might exist for geographical reasons only. The North Sea basin is most marked in this respect having several species exclusive to it or from it. However this basin contains some of both the most and least polluted water, but this factor has little effect on several of the species of groups A, B or C which are found in both the clearer and more polluted sites equally. The North Sea / rest of Britain division is probably the largest single geographical division

that occurs around Britain and would seem to be more defined than a North / South division.

The southern group E is also fairly definite. The South coast of Britain is the northernmost extreme for Lysidice and Tricolia, both of which were commonly found in holdfasts on the Normandy and Brittany coasts of France (unpublished data). Perhaps the strangest group is B, the species found everywhere except on the West coast. All three species have a reported distribution which includes other regions so although this division seems clear it is perhaps a chance result.

Species whose frequency was less than three sites were ignored in this table.

3) Similarity Matrices

The question of species distribution can be elaborated on with the help of similarity coefficients.

Sorenson coefficients (see Appendix A) were computed for every pair of sites, which yielded over 600 values in all. This coefficient, it is emphasised, depends upon species presence only and ignores numbers of each organism.

Table displays of all the coefficients are presented in two ways (figure 20a and b). The key of the values in the tables are such that percentage similarities are simplified to classes of 10 percentage points, e.g. 5 = 50 - 59%. The exceptions are that - = 20 - 29% and + = 30 - 39%. The latter two symbols were chosen because they are less

dense visually making the patterns which exist in this large body of data easier to see.

In the first array (figure 20a) the coefficients are arranged such that the highest values cluster in the centre of the matrix. When this is done, the site pairs in the centre of the matrix are found, without exception, to be those of sites situated in the North Sea.

The similarities between sites in the North Sea are thus higher than those between any other sites, and higher than those between a North Sea site and any other. The fact that the North Sea contains both the cleanest and most polluted, turbid, or heavy metal laden sites seems to be of little importance here. The North Sea sites clearly have a greater common pool of species amongst them, despite a range of environmental conditions, than sites from other regions.

The lack of an effect by clarity, the variable with the largest effect on species numbers both in the North Sea and generally is illustrated in the second array (figure 20b). Here the axes were arranged such that the central sites are those which have the least water clarity, and the sites at both ends are those with the greatest clarity. It can be seen that the central cluster of high values has been spread out. Geography is clearly the most important factor in determining the similarity of species between sites. Species presence or absence would seem not to be determined or affected much by environmental conditions, a point which is of interest and which will be returned to later in the discussion.

DISCUSSION

Two of the most important attributes which determine the characteristics of a site are 1) Numbers of species in a given sample size together with measurements of their abundance and distribution and 2) the trophic state of the community, (Reish 1972). Both of these attributes are given full attention in this study of holdfast infauna. Several faunistic and trophic gradients have been identified, as have some of the environmental parameters influencing them.

In contrast few of the sections of this thesis are concerned with species presence / absence data alone and none with the associative techniques as used for example by Moore (1973b, 1974). The reasons for this will become apparent.

Jones' approach to the problem of interpreting holdfast data was to establish groups of species which seemed to form associations and relate these to environmental conditions such as "polluted" "estuarine-polluted" or "clean". He also discussed trophic differences to support this and surveyed the species which were present in, or which disappeared from different groups of sites. Moore's approach was to regard each holdfast as a single sample, of which approximately 5 were collected from each site, and subject the species data to multivariate analysis. Jones formulated groups of species which appeared to be formed by gradients of pollution, while Moore attributed the divisions observed by him to natural turbidity firstly and to pollution to a lesser extent. The results contained in the present work for the coast with which the above authors were concerned, namely the North Sea, show that faunistic differences are

closely related to and probably largely affected by the variable termed Clarity. The question should be asked therefore what the causes are for a decrease in water clarity along the North Sea coast: pollution or natural turbidity?

Jones (1970, 1973) and Bellamy (1970) have maintained that large inputs of sewage and industrial effluents on the Durham and North Yorkshire coast are the main causes of the reduced water clarity and quote, amongst other things, the very high coliform counts along this stretch to substantiate their belief that sewage is a very important factor in the sub-littoral environment of this region. Moore (1972, 1973a) on the other hand favours the belief that the loss of water clarity is due to exposure, river outflows (even if not laden with sewage) and to the erodible rock along the Durham and North Yorkshire coast. The following reasons would suggest that the latter causes are unlikely.

- 1) The Durham coast where the effects in this study are most evident is comprised mainly of magnesium limestone. This rock is much less erodible than the North Yorkshire boulder clay whose holdfast faunas were very like those of clear water.
- 2) There is erodible rock outcropping at other sites in Britain such as Dorset which is fairly exposed but which despite its soft rock supports rich kelp growth to depths considerably greater than those found at any of the English North Sea sites, and which therefore has clearer water.
- 3) River outflows into the North Sea not laden with sewage have no discernable effects on coastal clarity or holdfast fauna outside a very small radius from their estuaries. For example the Tweed which is larger than the Tees, Tyne and Wear and which flows through similar terrain

before reaching the sea. The sites at Dunbar and St. Abbs are closer to the Tweed estuary than several sector II sites are to the other three rivers and yet do not show the same sort of holdfast community structure or restricted depth range of the kelp. Only polluted rivers flow into the grossly affected region.

4) There is however no significant difference in weather conditions between the English and Scottish sectors of the North Sea. Tidal currents in the two sectors are almost identical (Eisma 1973) and extreme sea conditions and highest waves are more common in the Scottish sector (Stride 1973). Also the distribution of mud and sandy mud beds offshore in the North Sea are concentrated more off the Scottish than English coast (McCave 1973). Thus a marked increase in natural turbidity off the English coast compared to the Scottish North Sea coast would seem to be unlikely.

5) In figures 18 and 19 it was shown that both water clarity and faunistic characteristics of the holdfast pivoted around the more northerly sites of the English North Sea sector. Clarity increased both North and South of this point, as did species richness and diversity. This distribution certainly eliminates weather effects.

It is probable that the loss of water clarity seen in sector II is attributable in large part to pollution. Moore (1972) found that the environmental parameters of sea state, tidal range and river flow accounted for only 28% of the variance of suspended solids. This is not a high value and leaves room for other factors to be important. It is suggested that sewage is one significant one. Certainly sewage discharges into this region are high (Watson and Watson 1968), and it remains that a large rise in the number of suspension feeding organisms is found here

which presumably require large quantities of suspended organic matter as a food source. In the North Sea it is suggested that "Clarity" can be interchanged with "Sewage Pollution" with little loss of accuracy. Elsewhere around Britain the causes of loss of clarity are less clear, but elsewhere it is not a very important variable, determining the make-up of the infauna.

Moore does not in fact exclude sewage pollution as being a contributing factor. In his paper (1973b) he asserts a minimum of four times that pollution is one significant factor which influences his faunistic groupings. Despite this he claims that this is ".....further evidence for either the lack of a uniform widescale pollution effect or at least its low effectiveness if any such distribution exists". He believed that pollution was only associated with his animal groupings by implication, because his clear water grouping was unpolluted (!) and because he did not find any indicators with which to divide turbid sites into turbid / polluted and turbid / unpolluted groups. This would be natural if the turbidity was caused even in part by pollution.

It is of interest to note that otherwise the conclusions of Moore and Jones are not radically different.

Methods of Data Analysis

Both of the above authors placed emphasis on species presence / absence information. Moore particularly approached his data in this way and built elaborate statistical treatments on it. The appropriateness of this form of approach in holdfast work is therefore examined.

The Holdfast Fauna Community

The sea contains far fewer species than does the land although it occupies a far larger proportion of the Earth's surface. There are for example 13,500 species of marine plant (Halstead 1972) whereas there are over 200,000 recorded terrestrial Angiosperms and Pteridophytes alone (Preston 1962). The animal kingdom is more diverse at the species level than the plant kingdom and 500,000 species of animals are found in the sea. On land however, there are many times this number of invertebrates, and twice this number of insects alone. The most common explanation of this is that terrestrial environments are more varied, and variable, and the great range of species have evolved in relation to this diversity. There are apparent contradictions to this however, such as Sander's (1968) findings that deep water samples have shown species richnesses equalling those of shallow tropical waters although the former environment is assumed to be more stable than the latter.

Preston (1962, 1962b) discusses species / area relationships in two types of terrestrial situation, island and continents. He took islands to be "isolates" while areas of mainland he designated "samples". An island generally has fewer species on it than does an area of mainland the same size, but the rate of species increase with area is greater on islands.

The two rates of species increase are as follows. In the equation $\text{Species} = C \cdot \text{Area}^z$, where C is a constant measuring the number of species in a unit area and z is a constant relating species increase with area increase, for a wide range of island situation $z = 0.3$ while for mainland situations z falls between 0.15 and 0.24 (Krebs 1972). Krebs (loc cit)

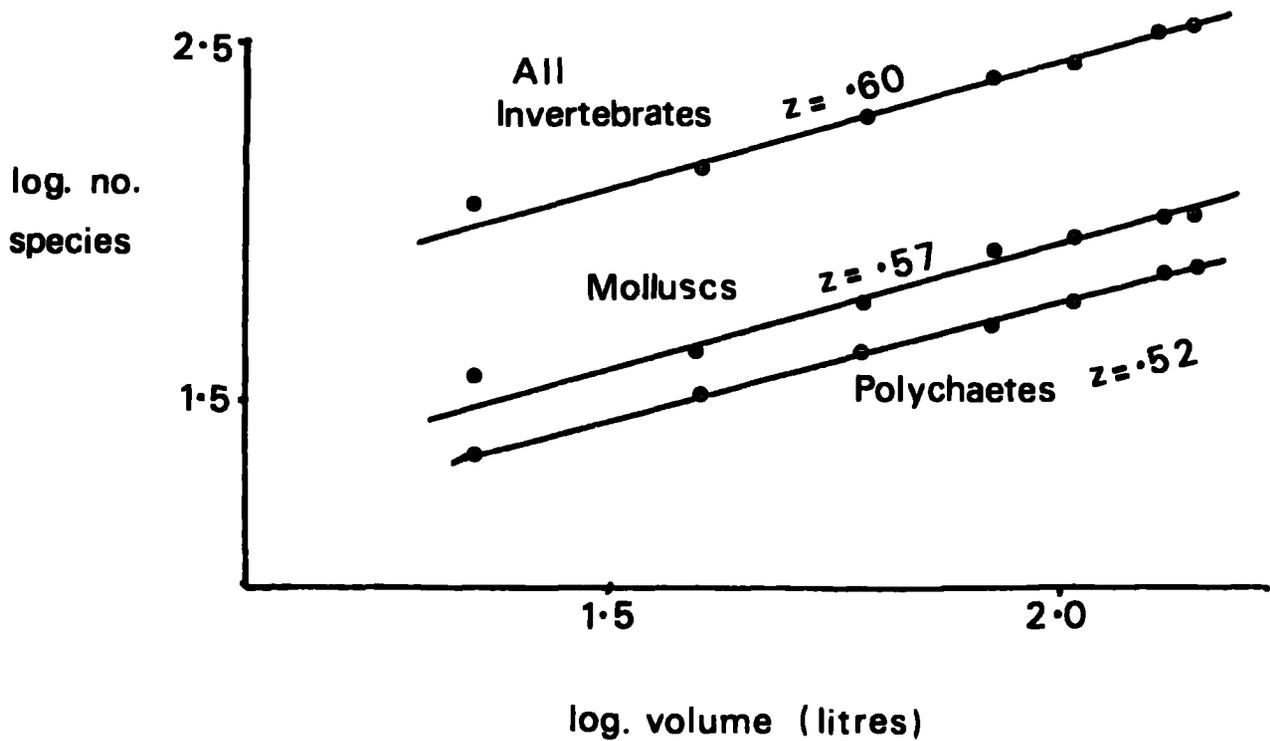
and Preston (1962, 1962b) illustrated this with a wide range of examples.

The slope (z value) was therefore calculated for the marine fauna collected in the course of this study using both the two largest groups collected and the fauna as a whole (figure 21). The values of z were higher than any found in terrestrial situations. That for Molluscs is 0.57, for Polychaetes 0.52 and for total invertebrates it was 0.60. The rate of species increase in holdfasts is thus double that in terrestrial examples, a finding which may disagree with Krebs suggestion that the z values of 0.15 - 0.3 may reflect an unknown ecological law.

The question arises of whether the sample size of this marine situation is at all comparable to those of the cited terrestrial situations. The sizes of the latter are the areas of islands and continents, which are obviously larger in terms of space by many orders of magnitude. However in terms of species richness they are not necessarily larger. There are more mollusc species in 137 litres of holdfast space than there are amphibians and reptiles in the West Indies (MacArthur and Wilson 1967), ants in the West Indies (Fischer 1960), snakes in the U.S.A. or mammals in Canada (Simpson 1969). There are about as many molluscs in this number of holdfasts as there are fish in Europe or in the North American Great Lakes (Lowe - McConnell 1969) and about as many Polychaetes as there are Canalid copepods in the upper 50 metres of the whole Pacific Ocean! (Fischer 1960). In terms of species richness therefore the holdfast's sample size is fairly comparable.

FIGURE 21

GRAPHS OF LOG. INCREASE OF SPECIES WITH
LOG. VOLUME, FOR MOLLUSCS, POLYCHAETES,
AND TOTAL INVERTEBRATES, ACCORDING TO
EQUATION: $S=cA^z$



Smallest sample is Sector I, then adding
Sectors II, III, IV, Shetlands, France and
Bantry Bay.

The explanation for the richness of the holdfast fauna must in part be because in some of the terrestrial examples considered the species concerned are large. However other groups cited such as ants and copepods are not and an explanation must lie in the nature of the holdfast.

Rough estimations show that there is approximately one litre of holdfast space per square metre of rock, involving from 5 - 10 holdfasts, which occupy only about 5% of the rock surface. This small percentage however, contains the bulk of the species in that square metre. The holdfasts act as a sink or a pool for the region's fauna.

Perhaps the obvious attraction of the holdfast is the shelter it affords. Shelter is however not the same as protection since the holdfast attracts predator and prey alike. Many species are attracted to shelter though this does not apply to all species, especially suspension feeders (Foster 1958; Lilly et al 1953).

A second reason for the attraction of holdfast is that they contain a large surface area for their size, and the surface of the haptonema branches is very suitable for species attachment (see chapter three).

A third reason may be due to a situation in which the presence of a few animals will attract others, or more of the same species until saturation is reached. The presence of prey may for example attract predators, and there are numerous short food chains amongst the holdfast infauna (Scarratt 1960; Jones 1970).

Whatever the reasons are, the rate of species increase with sample size is rapid and more so than for the cited terrestrial and pelagic examples. The indication is that this rate of species increase is as rapid at any one site as it is for the pooled wide range of sites used in Figure 21, since the calculated slope for all species at Loch Sunart, the most extensively sampled single site, is also about 0.5.

Quite clearly therefore the number of holdfasts which it is possible to collect at any one site will contain nowhere near the majority of animal species which actually occur at that site in holdfasts. A collection of 20 holdfasts should contain those species which are common or abundant, (five or ten holdfasts will with much less certainty), but will not include many of those species whose distribution is sparse.

This reveals a limitation with the method, or more accurately a limitation on ways of interpreting the results. Firstly it is clear that analytical methods which rely on species presence / absence data can have no meaning if absent species have a good chance of becoming present with an increase of sample size, or with a second sample of the same size. Secondly when different areas are being compared the same sample size should be used in all cases. This limitation however should be observed in all ecological studies and is not unique to holdfast work. The identity of individual species making up the community is, in the context of pollution monitoring, of less importance than the nature of the community as a whole. If the nature of the community is studied the holdfast remains a perfectly acceptable and useful sample unit. Species numbers per unit volume,

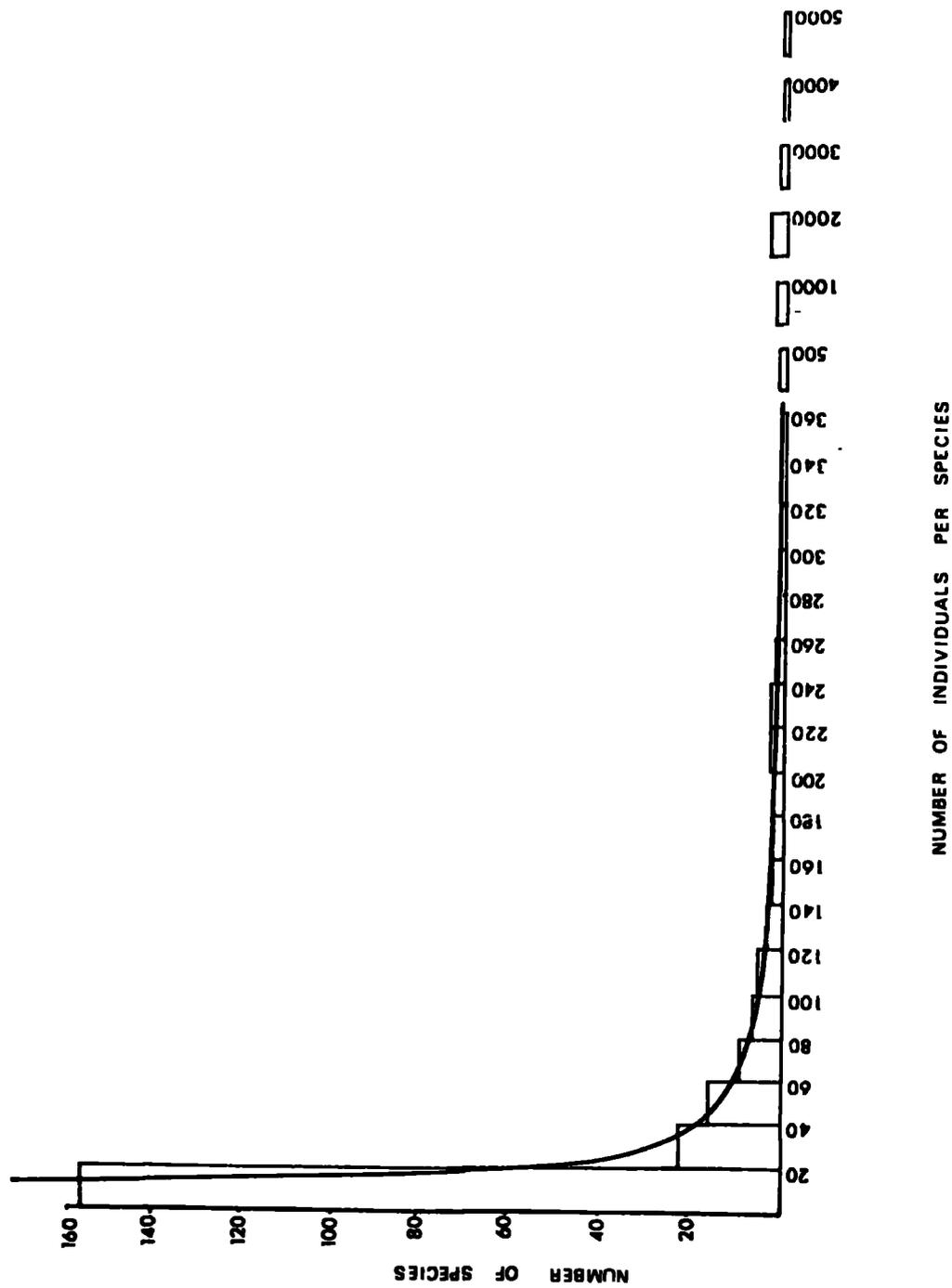
the density of the common species, and particularly the trophic structure of the community should be the prime factors to be investigated. Although it should not be said that any species is "unimportant", perhaps the fact of whether a herbivore is of this species or that is of less importance than the fact of it being a herbivore, especially if, had the holdfast been collected an hour later it might have moved away to be replaced by another species.

The intrinsic structure of many animal population is often logarithmic (Fisher, Corbett and Williams 1943) with most species occurring singly or with a few occurrences and a few species occurring abundantly. This is also the situation in holdfast populations (figure 22) where the frequency distribution is a near perfect log curve; (The apparent mode to the right of this curve is caused by the shortening of the horizontal axis). In fact, out of the 252 species found in the survey 65 occurred only once. Only eight occurred more than 1,000 times and these, with the exception of Nereis pelagica, were all suspension feeders, most of which were those which appear to be "adventives" in polluted water (Jones 1970).

The fact that a large number of uncommon species will not be collected is perhaps not as important in the pollution monitoring context as the fact that the abundant species are. The proportion of the latter to the total fauna will not change whatever the sample size is. In conclusion it may be stated that if the nature of the whole community, and particularly its trophic state is studied, the holdfast community remains an effective monitoring unit.

FIGURE 22

FREQUENCY / DISTRIBUTION CURVE OF
TOTAL HOLDFAST SPECIES.



INTELLIGENT NATURAL HISTORY

Elton (1966) said; "I believe that even in this elaborately technical age reconnaissance at the level of intelligent natural history is a necessary precursor of all successful ecological research in the field, because it defines the natural context of habitat interspersion and the communities occurring there, as well as suggesting what is practically possible to study and measure with a given amount of labour and time".

Today more and more elaborate and complex methods are being tried in the pursuit of solutions to ecological problems. The use of ever more complex mathematics has been progressing at what must be almost an exponential rate. The rate cannot slow down either for at least a decade, for new statistics are continually being devised and there is a time lag of several years between their inception and widespread use, so that, like the DDT story, even if no more were produced they will still increase until 1990.

One field of mathematical ecology undergoing this popularity is that concerned with models. Another is "straight" multivariate statistics. However more than one caution has been sounded about over-enthusiastic use of many of these new statistics. Krebs (1972) has said that he fears that the computational techniques now available far outstrip the available ecological data and understanding, and that ecological insights cannot be gained from combining complex mathematics with primitive information. Models, which are an aid to understanding the real thing should not be mistaken for being the real thing.

The reason for such disproportionate steps forward in modelling and statistics is mostly due to the increasing availability of computers. Although there is no doubt of the usefulness of this it does mean that many statistics are performed simply because they can be performed and with little effort. The difficulty when using these statistics comes not from computing them but in justifying their use afterwards; a point which is evident from many published papers including some on topics with which this thesis is concerned. The ease with which computers can produce "results" has given rise to the adage that one can "make as many mistakes in a few microseconds as you would in 800 years with a pencil and paper" (Bevan 1973). Put more succinctly : Garbage in - garbage out. Statistics designed for one job may just not be valid if used for another.

For example, a commonly used treatment now is that revolving around divisive techniques, or dendograms. Sites are split into two groups on the basis of the presence or absence of that species which leads to more heterogeneity in the whole data set than any other species. The outcome is that the two groups of sites resulting from the division are each considerably more homogenous than was the whole. This process continues, to defined limits, until several groups are left, each containing a relatively homogenous group of species. This treatment of results has been widely used by phytosociologists (Shimwell 1968), but has been used and advocated for holdfast work as well (Mocre 1973b). The method however ignores the numerical composition of sites. Whether the holdfast is jammed with thousands of mussels or whether its fauna is very diverse is not considered. In the context of this work it has been shown that this latter detail is of the greatest importance, and is possibly more important than the identity of the non-dominant species.

This method should be used with extreme caution in any study, but especially when dealing with mobile species. It relies on species presence/absence, but a very common reason for a species not being present is simply that it just had not got there, or that it was not in that collection because it had wandered away, or because the sample was too small. It is unreasonable to always suppose that an animal's absence from a sample is because there is something in the environment that has prevented it permanently from being there. Jones (1970) defined a rare species (in a holdfast) as one that was present only once in a collection. Thus rare species need larger samples to find them. Thus to divide sites into groups on the basis of presence / absence data will give different answers with different sizes of sample, and even with duplicate samples the same size. Increasing the holdfast sample size will tend to make uncommon species common, and absent species present. Presence or absence loses its meaning in the context. To illustrate this it was mentioned that Jones had a division of polluted/estuarine organisms, based on his observation that eight species occurred in the Firth of Forth that were absent elsewhere. It was shown that larger samples revealed six of them in clean and non-estuarine conditions, which clearly invalidates this group. It is quite easy, with the data presented in preceding chapters, to set up another group of species as being found only in estuarine polluted conditions instead of Jones' group, except that larger samples still would perhaps invalidate this group and substitute another group in its place, and so on. The same can be said of Moore's results. His dendograms were drawn with splits based on species which showed the required behaviour for that sample size only. With increasing size of sample and increasing recruitment of species the dynamics of the total sampled fauna change continuously. Heteranomia could be the basis of a

division if the samples were small enough and it was the commonest species present. This method, and others like it, should only be used if there is reason to believe that the absent species are absent because they should be absent for definite reasons, and should not appear at all in that site. It seems clear that the methods used in interpreting faunal results must be subjected to scrutiny first. This author is unqualified to judge on the suitability of this method in the study of vegetation patterns, but the method was devised with the study of large tracts of vegetation in mind where many samples are taken and most of the plants species under study within them will be recorded. Most of the species occurring at any one site are not recorded with a small collection of holdfasts. Recourse to Elton's "intelligent natural history" would have shown the unsuitability of this method for manipulating the data from holdfast work. Scrutiny of the chosen method is all the more important when it is realised that a complex association analysis for example, giving attractive results, could be obtained with data obtained in this study with the use of 6 punched cards and twenty minutes labour, which makes its use very tempting indeed.

Most large computer installations have many programs publicly available. In this thesis frequent use was made of the computer. Most regressions and correlations were done using a public program, as was the extraction of factors in the single example of principle component analysis. Elsewhere use was made of it as a typewriter, to print out tables of species at different sites with the orders of species and sites being dictated. The same program was used to print out the similarity coefficient matrices. These uses are not inconsistent with this authors' emphasis on "natural history" being of paramount importance in primary survey work, and the belief that ecological data and understanding needs time to catch up with computational techniques (Krebs loc cit). Although

it would be of interest to construct a model of the holdfast system, with all the variables that have been shown to have an effect on the ecosystem being included, simple multiple regressions are just as effective in problems of this order of complexity (Stein 1968), and are a lot simpler to use. Against this however, it has been stated (Paulik 1968) that models are less likely to mislead in cause - effect situations. Doubtless all approaches will continue to flourish.

This study is currently being extended and expanded. Eight further sites have since been sampled along the Channel and Atlantic coasts of France where Laminaria hyperborea grows. The sampling rationale here was identical to that adopted for this preliminary but central survey, and it is hoped that this system of sampling and monitoring will be extended along a large section of the European coastline. In the more southerly regions L. ochroleuca replaces L. hyperborea as the dominant macrophyte, but in the light of the findings on the comparison of the two it would seem that this species can be used with equal success.

As has been discussed elsewhere (Bellamy 1972 ; Sheppard 1975) the large scale use of amateur divers has been shown to be both entirely reliable and successful as the means by which extensive surveys can be completed, and this resource will continue to make extensions of this survey possible.

SUMMARY

- 1) To determine whether the holdfast's texture had any effects on the infauna, the fauna from two similar species of kelp are compared. Some sedentary species were found to be affected, but no noticeable effect was found for the majority of the species.
- 2) Sample size should be measured in terms of volume of holdfast space, not as number of holdfasts. The absolute minimum sample size is one litre, although three litres is a "safer" minimum sample especially in species rich areas.
- 3) Fresh water inflows were not shown to have any significant effect on holdfast faunas. The kelp dies before the salinity fall becomes marked enough to induce changes.
- 4) Geological substrate has no discernable effects on the fauna. The heavy metal rich serpentine rock had no noticeable effect.
- 5) Depth, exposure and sedimentation had no marked effects on the holdfast fauna. The nature of the holdfast and the environment at the foot of the kelp forest account for this.
- 6) Heavy Metal gradients were defined around the U.K. The levels were measured using a ranked index which gave equal weight to five heavy metals.
- 7) Water clarity gradients were defined around the U.K. It was measured using a kelp "phytometer" method.

- 8) The validity of using the heavy metal index, the water clarity index, and the variables latitude and longitude were assessed. Each is acceptably unique and independent.
- 9) The faunistic gradients around the U.K. were determined. Species poor regions were defined along the Durham coast and the eastern end of the South coast.
- 10) The influence of the four variables in (8) on the fauna were assessed. In the North Sea, Clarity was shown to be significant. Heavy Metals were important along the West coast and a "geographical" gradient was revealed along the south coast.
- 11) The trophic structures of the holdfast faunas of each site were studied in the light of the faunistic gradients shown to exist. Briefly, in sectors I, II and III where pollution can be marked, numbers of suspension feeders has a reciprocal relationship with numbers and diversity of other types. Where pollution is high or water clarity low, suspension feeders are most numerous and species are fewest. Along the South coast (where there is no heavy metal or clarity gradient) there is a decline in all trophic categories attributable here to "longitude", but which is probably due to other unmeasured variables such as temperature, salinity, sediment.
- 12) Mollusc distribution, being the largest phylum present, was studied. The findings support those found above.
- 13) Sorenson similarity coefficients which depend on presence / absence information, showed that similarity between sites is a function of their geographical location and distance between

sites. (The North Sea is particularly homogenous.) Pollution has no effect on the similarity coefficient.

- 14) Species showing geographical distributions are indicated.
- 15) The reasons for the "distortions" of the fauna on the Durham coast are shown to be probably attributable to pollution rather than to natural turbidity.
- 16) The nature of the holdfast as a sample unit is discussed. Species increase with space in this habitat is very rapid, although the population's distribution maintains a good log-normal fit. Even with very large sample sizes the presence or absence of many species seems to be subject to almost complete randomness.
- 17) The validity of using presence / absence data is discussed. It is shown to be quite inappropriate in holdfast work. Numerical attributes of the fauna, i.e. Number of animals, number of species, diversity, in a fixed sample size, and its trophic structure, are meaningful. By using these the holdfast proves to be a good environmental monitoring unit.

Appendix A

The Collections

The holdfasts were collected with the aid of diving equipment from a depth midway between the surface and lower limit of the kelp. At this point large plants could always be found. The depth varied with the sites and ranged from 14 metres in West Scotland to 2.5 metres on the Durham coast.

The holdfasts were removed by sliding a knife between the haptera and the rock and levering upwards. Only those having a regular conical shape were selected in the interests of uniformity in samples. Any that were not removed intact were discarded. Immediately after removal each was placed in a polythene bag whose neck was sealed with bands to prevent the loss of species.

Preliminary Laboratory Work.

Each holdfast was aged according to Kain (1963). Each hapteron was then cut off and every animal of 2mm or more in any dimension was removed for identification. The taxonomic keys used are listed in the references, but expert help was sought for several groups, notably the molluscs and polychaetes. Even so a small proportion of the animals could only be identified to genus, and some, notably some polychaetes, only to family.

Determination of holdfast volume.

Volumes were first determined by using the Archimedes principle of

water displacement. The holdfast was enclosed in a flimsy polythene bag and immersed in water in such a way that it hugged the holdfasts' contours. From this volume was deducted the volume displaced by the hapteron tissue after the holdfast had been dissected. Later the volumes were determined by reading them off the line in figure 9 after ageing them.

Data treatment

Once identified and counted the numbers of species and the total numbers of animals were determined in a fixed volume, for each site. Sample size was standardised at 3 litres of holdfast space. Usually the holdfasts collected from each site totalled between 2 and 4 litres. To determine the numbers of animals in three litres, their cumulative numbers as each holdfast was added, was regressed onto their cumulative volume. (Only those of 4 years old or more were used.) The regression line was computed by the method of least squares, and the numbers in three litres was calculated from the regression equation.

The number of different species was determined in a similar way. Unlike total numbers, which increased linearly with volume, species numbers increased in non-linear fashion (see figures 2a, 4 and 5). The curves were always very close to logarithmic curves, at least up to the three or four litre samples used in this study. Therefore species increase was regressed onto log. volume and the number in three litres was calculated from the regression equation. It is stressed that there was always approximately three litres of holdfast space on which to perform the regressions. The values for three litres were not in other words, obtained from extrapolating from a much smaller volume.

The significance of every regression was checked by analysis of variance. If the F value was significant it inferred that the scatter of points about the regressed line was small. Always the lines of best fit proved to be very close fits; the significance of F being always at least .05 and usually much less.

Where regressed lines were compared (eg Chapter 3) the standard deviation of the regression coefficient was also computed. It is realised that when two species/log. volume lines were compared the statistics were carried out on transformed (logged) data, so that what was actually compared was the increase with log. volume, not the increase with volume. Therefore although conclusions concerning the increase with volume may be logically inferred they have not in fact been proved.

Emphasis is placed on diversity only where it is used to help determine minimal sample size. Here (chapter 4) three indices were used. Elsewhere the index used is always Fishers' alpha. This was chosen because its mathematical construction is particularly relevant. It was found by Williams (Fisher, Corbett and Williams 1943) that "with high number of N the relationship between the number of species and the log number of individuals becomes practically a straight line." This exact situation is found for holdfast communities and the use of alpha is therefore appropriate.

Heavy Metal Analysis

Heavy metal analysis formed an important part of the work. Those selected for analysis included the base of the laminaria stipe, Patella

vulgata occasionally, and where found Asterias rubens and Echinus esculentus.

Analysis in all cases was by atomic absorption spectrophotometry, on a Perkin Elmer 403 instrument. Elements assayed were copper, lead, cadmium; zinc; nickel and manganese.

Strong interferences exist however for most of these elements. These are caused by the high concentrations of calcium, sodium, magnesium and potassium in the solutions which artificially raise the heavy metal readings. These therefore were also estimated, so that the necessary corrections could be applied to the heavy metal results. These interferences (Waughman and Brett personal communication) are linear in the ranges found here, and the increased readings caused by each of these four major cations are additive to each other. The following equations describe the interferences from these four elements on each of the heavy metals:

$$\begin{aligned} \text{Cu interference} &= 1.5 \times 10^{-5} \text{Ca} + .38 \times 10^{-5} \text{K} + .49 \times 10^{-5} \text{Na} + .74 \times 10^{-5} \text{Mg} \\ \text{Pb interference} &= 14.9 \times 10^{-5} \text{Ca} + 2.1 \times 10^{-5} \text{K} + 2.1 \times 10^{-5} \text{Na} + 10.5 \times 10^{-5} \text{Mg} \\ \text{Ni interference} &= 14.2 \times 10^{-5} \text{Ca} + 1.7 \times 10^{-5} \text{K} + 3.8 \times 10^{-5} \text{Na} + 1.5 \times 10^{-5} \text{Mg} \\ \text{Zn Interference} &= 1.9 \times 10^{-5} \text{Ca} + 0.33 \times 10^{-5} \text{K} + 0.2 \times 10^{-5} \text{Na} + 7.5 \times 10^{-5} \text{Mg} \\ \text{Cd interference} &= 2.4 \times 10^{-5} \text{Ca} + 0.28 \times 10^{-5} \text{K} + 0.9 \times 10^{-5} \text{Na} + 0.33 \times 10^{-5} \text{Mg} \\ \text{Mn interference} &= 1.72 \times 10^{-5} \text{Ca} + 0.25 \times 10^{-5} \text{K} + 0.23 \times 10^{-5} \text{Na} + 4.9 \times 10^{-5} \text{Mg} \end{aligned}$$

These amounts are deducted from the reading obtained for the heavy metal to give the "true" value of the heavy metal.

The tissues were prepared for analysis by a wet digestion procedure. Between one and two grams dry weight of material was left overnight in 20 mls. nitric acid and 5 mls. perchloric acid (both "Analar" grade). Then the mixture was boiled almost to dryness until it became clear. After this the solution was made up to about 50 mls. filtered, and adjusted accurately to 100 mls. The solution was then ready for analysis.

Statistical analysis

Many of the variables obtained in the course of this work were not normally distributed, for example the latitude and longitude of the sites. Therefore when correlations were used in the data treatment a ranked correlation coefficient was employed. The one chosen was the frequently used one by Spearman. It was always computed using the "SPSS Statistical Package" of Nie et al (1970), as were all regressions and the Factor analysis.

In the qualitative assessment of sites a coefficient of species similarity was employed (Sorrensen's'). This coefficient, which ignores the numbers of animals and depends on species presence alone has the formula:

$$\frac{2 \times \text{no. species common to both sites}}{\text{no. species in A} + \text{no. species in B}}$$

This is multiplied by 100 to express it as a percentage. Since the calculation of similarity between every pair of sites involved over 600 calculations a fortran program was written for this.

Interpretation was also helped by the use of a program developed for phytosociological use (Wheeler 1974). This program prints out tables of

species richness with sites ordered horizontally and species listed vertically in any dictated orders. Thus visual impressions can be gained of the species distribution. The complete table, from which other tables were drawn, is in Appendix D, where the sites are ordered according to sector and the species are listed from most to least frequent. The abundance of each species is represented on a seven point scale. - indicates that one animal of that species occurred at that site; + indicates more than one was found but that they comprised less than 5% of the animals at that site; 1 means 5 - 20% and 2 - 5 means 20 - 100% in intervals of 20%.

APPENDIX B

Kelp Performance.

A value for year round, integrated water clarity was derived from the depth to which the L. hyperborea grew. Bellamy et al (1967; 1970) have shown that as depth increases kelp performance alters very little until the extreme lower edge of their depth range is reached, when individual performance falls rapidly to extinction. Figures 23a, c and Figures 24a, c, illustrate this. Generally there is no significant difference between the performance curves for kelp collected from 6 - 15 metres below M.L.W. At 18 metres however the performance is significantly lower and no kelp existed at 19 metres. Though typical of all sites these results were obtained from Port Levi, France. Here L. ochroleuca was only slightly less abundant than the L. hyperborea, and a direct comparison of the two species was made possible. Interestingly the same response to depth is seen with L. ochroleuca (Figures 23b, d and 24b, d) and is, if anything, more marked. Below the Laminaria bed at this site rock apparently suitable for kelp growth persisted to at least 30 metres, indicating that light, or water clarity, become limiting.

These comparisons are also of interest in the context of chapter 3 in which the holdfast faunas of the two species are compared.

Figure 23 a - d

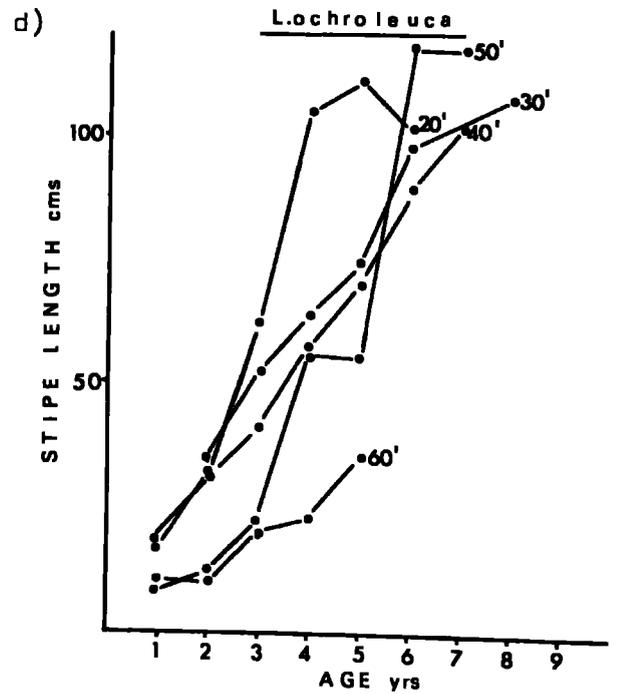
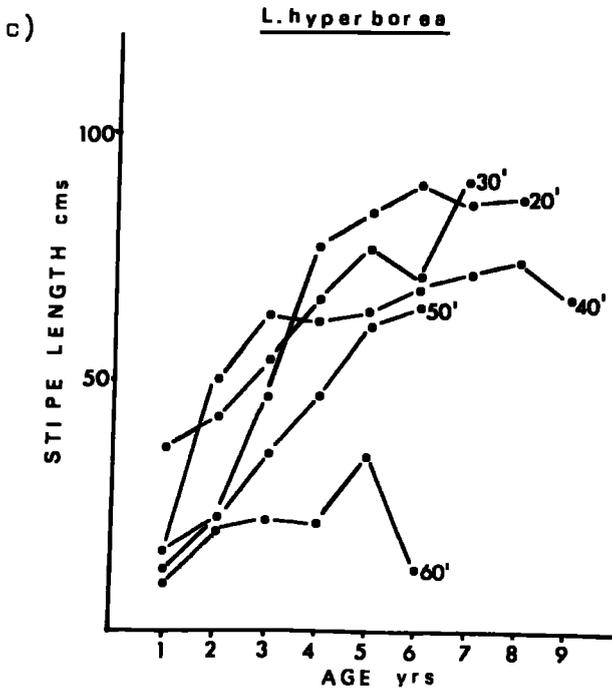
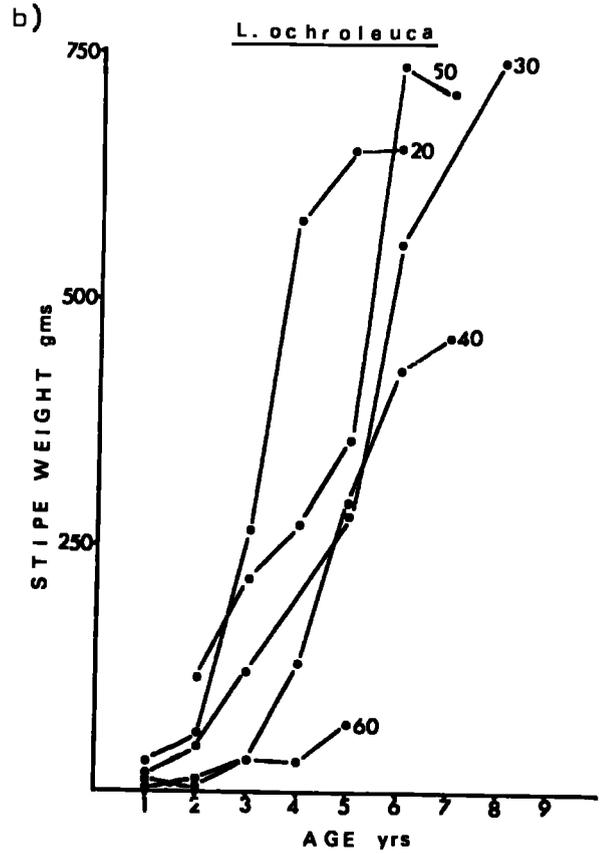
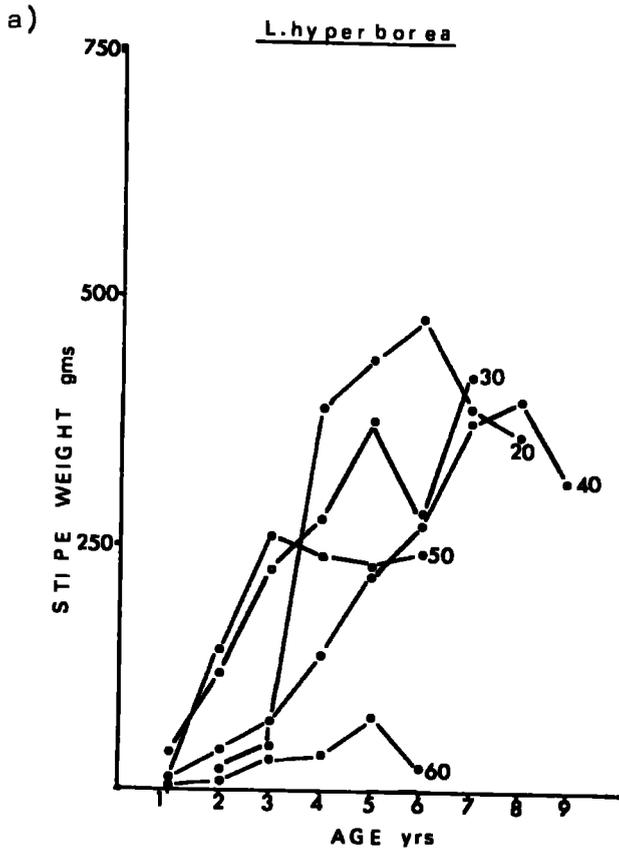
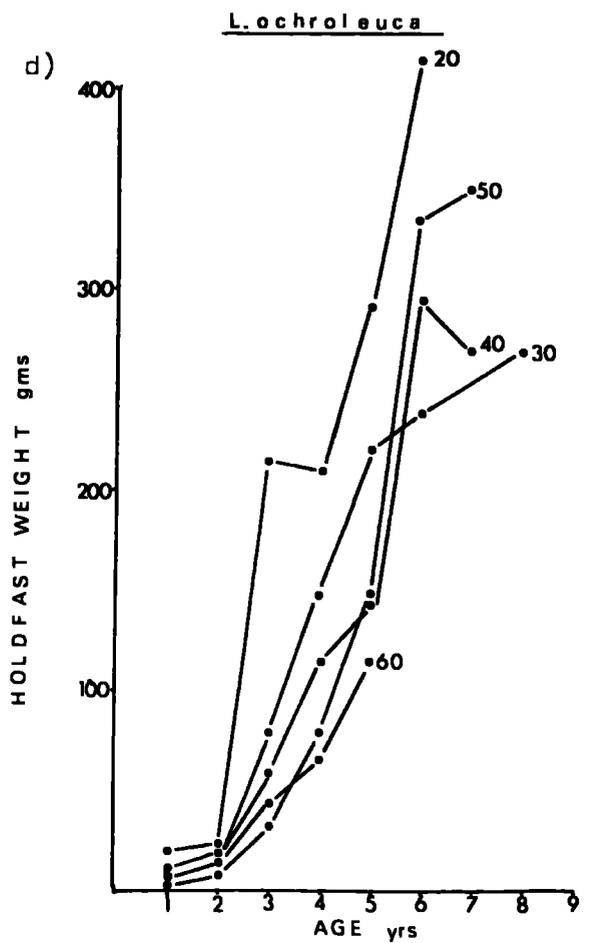
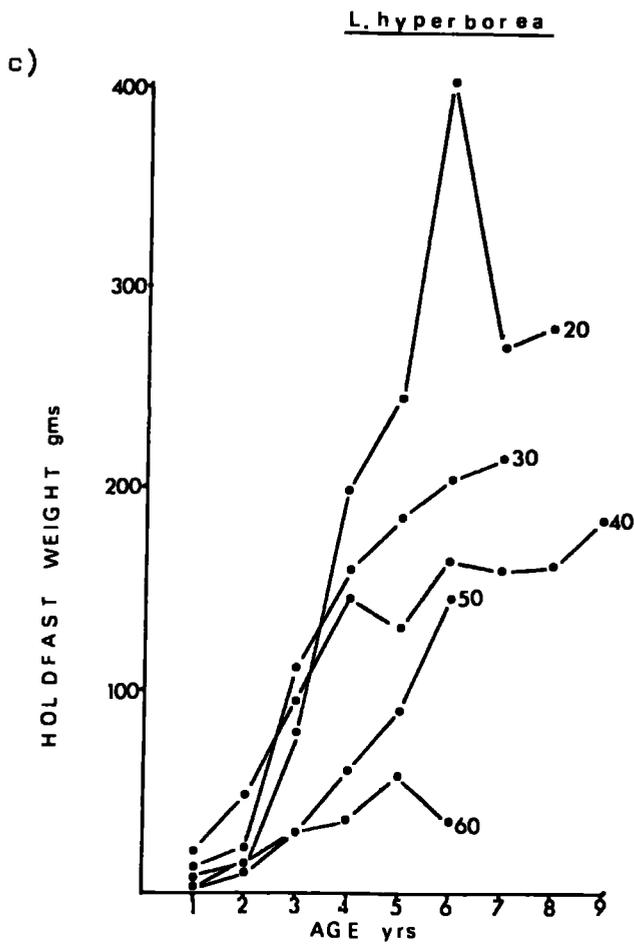
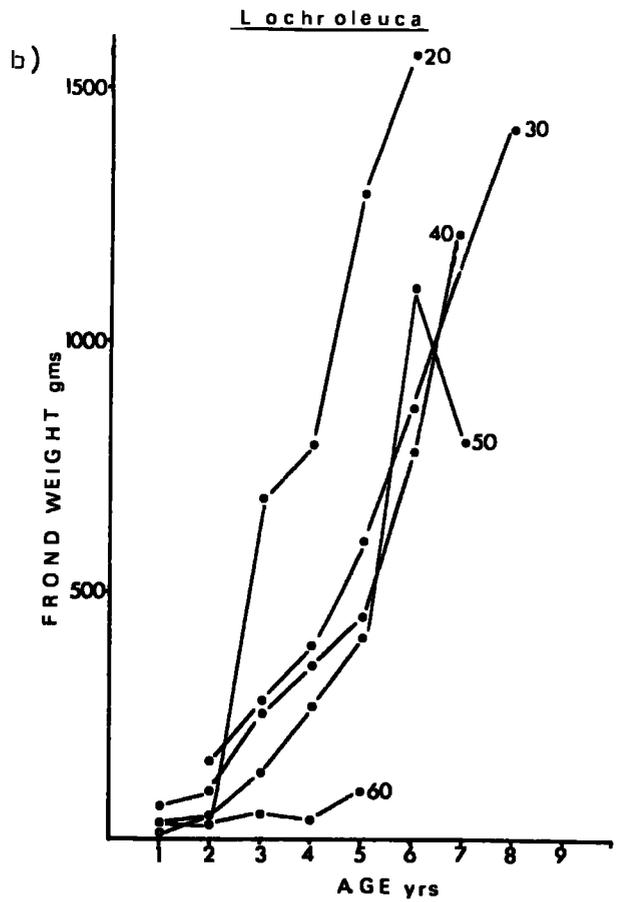
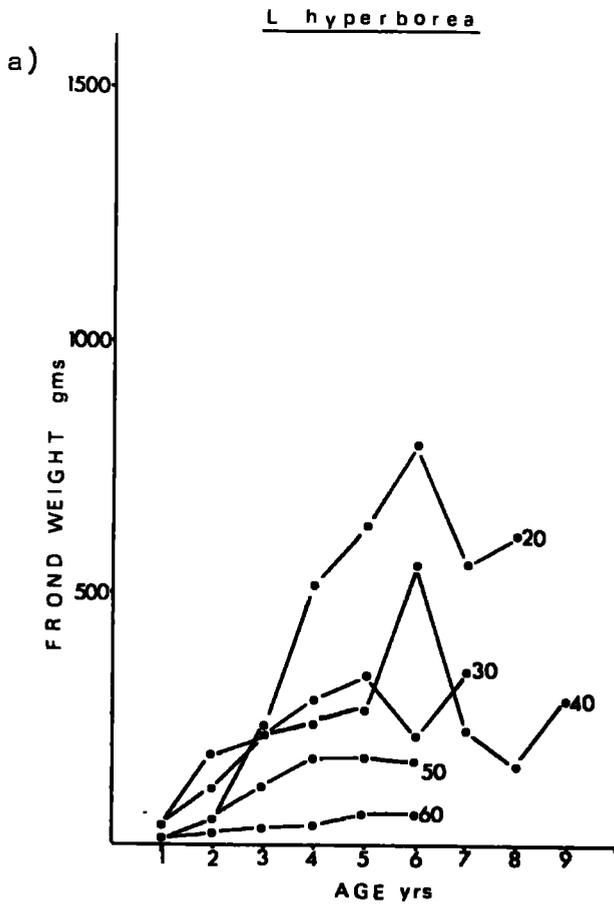


Figure 24 a - d



APPENDIX C

Heavy Metal Concentrations in *L. hyperborea* stipe \pm standard errors

Site					
Caithness	8.3 \pm .93	2.60 \pm .23	5.2 \pm .22	1.01 \pm .20	21.0 \pm 1.2
Lossiemouth	9.5 \pm 1.30	2.67 \pm .20	7.0 \pm 1.10	1.80 \pm .50	26.7 \pm 1.3
Peterhead	9.5 \pm .90	3.22 \pm .18	4.0 \pm .80	.39 \pm .08	21.7 \pm 1.1
Fraserburgh	7.0 \pm .41	0.75 \pm .17	9.7 \pm .80	2.60 \pm .30	25.2 \pm 6.0
Aberdeen	20.0 \pm 4.6	2.42 \pm .81	6.4 \pm .50	0.35 \pm .08	20.5 \pm 1.7
Montrose	5.4 \pm .82	2.90 \pm .45	4.6 \pm .35	1.54 \pm .11	48.6 \pm 3.4
Callardyke	5.0 \pm .33	1.43 \pm .18	10.6 \pm 1.91	0.80 \pm .23	30.0 \pm 4.7
Kingsbarns	6.0 \pm .41	2.53 \pm .57	10.6 \pm 2.04	1.10 \pm .28	31.5 \pm 6.0
Dunbar	8.1 \pm .97	2.50 \pm .13	7.3 \pm .38	1.06 \pm .10	70.1 \pm 7.6
St. Abbs	15.8 \pm 5.52	1.36 \pm .15	1.0 \pm .92	0.56 \pm .06	55.0 \pm 6.5
Newbiggin	14.0 \pm 1.01	8.80 \pm 1.20	28.0 \pm 5.01	3.41 \pm .90	14.1 \pm 1.2
Marsden	24.4 \pm 2.87	3.50 \pm .70	10.0 \pm 1.21	0.91 \pm .06	85.0 \pm 10.3
Souter	42.6 \pm 3.91	3.00 \pm .29	9.0 \pm 1.18	1.00 \pm .07	35.0 \pm 2.2
Redcar	7.0 \pm 1.92	7.40 \pm .81	11.1 \pm 1.49	2.40 \pm .40	74.0 \pm 5.0
Whitby	9.3 \pm .72	3.15 \pm .57	113. \pm 37.	0.91 \pm .12	61.5 \pm 11.0
Robin Hoods Bay	10.0 \pm .59	1.30 \pm .22	15.0 \pm .08	1.00 \pm .06	33.1 \pm 4.5
Scarborough	7.5 \pm 1.08	3.50 \pm .22	155. \pm 48.0	0.90 \pm .14	57.7 \pm 6.0
Flamborough	10.2 \pm 1.6	3.00 \pm .21	104. \pm 36.0	1.40 \pm .11	81.3 \pm 14.0
Loch Sunart	7.9 \pm .74	2.20 \pm .19	13.0 \pm 1.10	0.20 \pm .08	58.0 \pm 0.5
Portencross	12.9 \pm .41	2.54 \pm .26	12.0 \pm 3.80	0.90 \pm .07	14.0 \pm 2.4
Ballycastle	8.1 \pm .20	0.80 \pm .01	16.0 \pm 3.00	2.00 \pm .15	16.4 \pm 3.1
Corsewall	14.6 \pm 2.70	2.96 \pm .34	16.4 \pm 3.70	1.20 \pm .25	24.2 \pm 5.6
Bangor	7.9 \pm 2.10	8.60 \pm .92	14.0 \pm 1.80	0.37 \pm .08	96.8 \pm 4.7
Port Erin	8.5 \pm .71	2.92 \pm .23	5.8 \pm .81	0.90 \pm .22	46.6 \pm 6.0
Port Ysagden	13.2 \pm 2.50	3.06 \pm .55	8.4 \pm .52	1.00 \pm .16	52.8 \pm 5.3
Oxwich	10.1 \pm .93	5.56 \pm .34	6.0 \pm .21	1.50 \pm .30	58.4 \pm 4.4
St. Agnes	18.0 \pm 3.10	3.28 \pm .60	4.5 \pm .52	0.52 \pm .15	24.0 \pm 1.8
Sennen	14.3 \pm 1.60	5.33 \pm .44	24.0 \pm 10.01	2.10 \pm .21	18.1 \pm 3.4
Penzance	27.8 \pm 7.52	3.25 \pm .14	6.8 \pm .90	0.45 \pm .08	30.8 \pm 6.0
Falmouth	5.3 \pm 1.21	2.01 \pm .23	12.5 \pm 3.80	1.01 \pm .20	32.4 \pm 6.0
Plymouth	20.8 \pm 8.11	2.66 \pm .22	4.2 \pm .50	0.56 \pm .08	42.6 \pm 6.5
Seaton	5.1 \pm .30	0.04 \pm .01	10.1 \pm .35	1.54 \pm .20	32.5 \pm 4.7
Durdle Door	21.5 \pm .20	0.93 \pm .12	10.0 \pm 1.00	0.92 \pm .06	37.8 \pm 3.6
Jersey	9.5 \pm 1.03	2.48 \pm .15	13.9 \pm 1.89	1.70 \pm .10	54.3 \pm 5.6
Kimmeridge	11.1 \pm .11	0.52 \pm .00	12.0 \pm 2.11	3.10 \pm .45	30.4 \pm 4.6

APPENDIX CHeavy Metal Concentrations in *Echinus esculentus* gonads \pm standard errors

Site	Pb	Cu	Ni	Cd	Zn
Fraserburgh	11.0 \pm 2.7	4.3 \pm 1.3	9.3 \pm 1.9	3.3 \pm 1.0	146. \pm 88.
Cellardyke	6.6 \pm 0.9	2.1 \pm 0.2	5.5 \pm 0.6	1.2 \pm 0.2	63. \pm 9.
Kingsbarns	4.0 \pm 0.7	2.2 \pm 0.2	8.3 \pm 1.7	1.4 \pm 0.2	226. \pm 58.
Newbiggin	14.6	7.1	9.0	2.3	55.
Whitby	15.3 \pm 3.9	6.8 \pm 1.6	8.3 \pm 2.9	1.0 \pm 0.3	113. \pm 44.
Scarborough	4.5 \pm 0.6	4.5 \pm 0.6	145. \pm 106.	0.8 \pm 0.4	179. \pm 60.
Robin Hoods Bay	6.2 \pm 1.2	6.2 \pm 1.2	25. \pm 17.4	0.9 \pm 0.5	331. \pm 36.
Portencross	6.3 \pm 1.1	6.3 \pm 1.1	7.4 \pm 0.9	0.8 \pm 0.1	163. \pm 60.
Corsewall	5.0 \pm 1.0	5.0 \pm 1.0	10.5 \pm 1.1	2.1 \pm 0.5	248. \pm 77.
Plymouth	3.5 \pm 0.4	3.5 \pm 0.4	18.0 \pm 3.5	2.3 \pm 0.6	264. \pm 95.

Heavy Metal Concentrations of *Asterias* \pm standard errors

Site	Pb	Cu	Ni	Cd	Zn
Aberdeen	12.8	2.3	48.6	0.7	129.
Cellardyke	29.3 \pm 7.	5.3 \pm .2	62.2 \pm 3.0	0.9 \pm .17	142. \pm 32.
Newbiggin	20.0	8.9	31.0	5.0	19.
Whitby	9.7 \pm 1.1	10.5 \pm .8	109. \pm 13.9	.4 \pm .01	174. \pm 9.4
Scarborough	23.0 \pm 3.5	8.8 \pm .5	100. \pm 20.0	0.0	152. \pm 9.1
Robin Hoods Bay	13.0 \pm 2.1	7.6 \pm 2.3	68.0 \pm 5.4	1.4 \pm .02	161. \pm 4.3
Flamborough	18.1 \pm 3.1	8.4 \pm 1.3	30.9 \pm 2.0	0.5 \pm .08	182. \pm 6.9
Portencross	17.9 \pm .6	10.4 \pm .5	16.1 \pm 1.8	0.6 \pm .03	174. \pm 13.1
Corsewall	10.4 \pm 1.4	18.4 \pm 4.0	73.2 \pm 3.0	1.8 \pm .21	139. \pm 8.7
Falmouth	12.8 \pm 2.3	12.4 \pm .7	11.5 \pm 8.2	1.5 \pm .12	74. \pm 6.2
Plymouth	13.3 \pm 2.2	9.6 \pm .8	54.2 \pm 0.8	2.0 \pm .05	121. \pm 28.
Kimmeridge	14.2 \pm .7	5.3 \pm 1.6	53.4 \pm 3.7	3.2 \pm .10	143. \pm 42.
Seaton	7.0 \pm .8	2.8 \pm .3	36.7 \pm 0.9	1.6 \pm .69	92. \pm 21.

Appendix E.

The use of ultra-violet absorption for measuring the origins, behaviour and fate of dissolved organic compounds in an estuary.

A prolonged attempt was made to use the technique of ultra-violet absorption for measuring the amount of dissolved organic compounds in seawater. The method has been used by a wide range of authors, but while using the method, and in particular while attempting to concentrate the dissolved substances in order to relate absorption to milligrams of carbon, interferences came to light which make the method largely unusable.

Because of the numerous different sources of dissolved carbon compounds a river system was studied from its source to a point on the coast, several miles away from its mouth. The U-V traces for compounds of different origins were compared, and their behavior, with respect to time for example, was studied. Two main categories of sources were shown to exist.

Introduction

On the North East coast of England the river Tyne drains a catchment area of about 1750 square miles, a large part of which is covered with eroding blanket peat which is a rich source of humic materials. On the estuary of the Tyne the Newcastle conurbation discharges large quantities of untreated sewage into the tidal waters. Both the upper catchment area and the city are large sources of organic carbon, which enter the sea together.

An attempt was made to distinguish sewage from the natural "background" carbon, and to estimate the relative contributions of each to the total organic material passing through the estuary.

U-V absorption in the range 200-350 nm. is attributable in part to unshared electron pairs, eg. C=C and C=O linkages (Schnitzer and Khan 1972). Humic acids such as those from the peat catchment are phenolic and therefore absorb strongly. As an estimate of dissolved carbon the method of U-V absorption is thought to be superior to Chemical Oxygen Demand (Banoub 1973), and has been used increasingly frequently as a substitute for this and similar tests. The main interfering compound in fresh water is nitrate which absorbs strongly at around 210 nm. In marine and estuarine systems bromide interference has also been reported (Ogura and Hanya 1967), but these only interfere at the lower end of the spectrum and can be ignored at wavelengths above 230 nm.

U-V absorption has seldom been studied in fresh water, although Banoub (1973) used the technique with success in lake water. In estuarine systems Butler and Tibbits (1972) established that in the Tamar estuary dissolved colloids affected the U-V absorption of the water, and that absorption was inversely proportional to salinity. In marine systems a larger amount of work has been done. Ogura and Hanya (1967, 1968) identified the various absorbing components, and found that coastal water had a higher absorption than ocean water, which was attributed to pollution. Foster and Morris (1971) however, in attempting to relate pollution and absorption in sea water concluded that this method was limited in its use.

Due mainly to the supposed extreme homogeneity of the absorbing compounds a wide range of wavelengths have been employed. Sanoub (loc cit) measured at 260 nm; Foster and Morris (1972) used an integrated value of 250-350 nm; while Ogura and Hanya (1967, 1968) used 220 nm and later 230:220 and 250:220 ratios. The strong emission line of the mercury lamp at 254 nm has been used for work on sewage effluent (Dobbs, Wise and Dean 1972). In the sea however, it was found that the absorbing compounds were not homogenous and the choice of wavelength therefore became important. The differences in the wavelength selected may thus have been a cause of the different degrees of success obtained by different workers with this method.

Method

Sampling was carried out in April to June 1974. Absorption readings were measured on a Perkin Elmer recording spectrophotometer with a pair of matched 4 cm cells. Traces between 190 and 350 nm were obtained, but because of the interferences from nitrate and bromide usually only the section above 230 nm was used. With sea water samples in which the concentration of dissolved organic materials was low it was convenient to use an instrument amplification of x 5. For the fresh and estuarine samples the normal x 1 setting was used.

Samples were filtered in the field and placed in ice until reading within six hours. Whatman 42 papers were used throughout which had been previously flushed through with 200 mls. distilled water and left in their filter funnels. Such papers do not contribute absorbing or scattering

materials to the samples, unlike GF/C papers, whether pre-combusted or not, which have been favoured by other workers.

Salinity measurements were made by argentimetry, using the conversions of chlorinity into salinity given by Strickland and Parsons (1968).

Results.

Figure 25 shows absorption traces of water samples taken from four points along the river system. Trace (a) is that of fresh spring water, which is not strictly part of the river at this early point. The negligible absorption above 230 nm shows that almost no organic material was present. Trace (b) is that of a sample of water taken from the moors into which the spring water flows, and from which the river Tyne originates. A large input of organic material occurs at this point (and at the same time the nitrate which is the 205 nm. peak, has been removed by the vegetation). Traces c and d are absorption curves of the young and mature river respectively, and show a progressive decline in concentration of organic material downstream from the source. The whole river system is shown in figure 26a, which illustrates the decline in all tributaries and in the main river as the sea is approached. Figure 26b shows the relative volume of water flow at the same points on the river. The figures are the actual volumes (in $m^3 \times 1000$ per hour) on one day in April 1974. Experiments with stored samples of water from these regions showed that the dissolved compounds were stable for several days with regard to absorption, so it is concluded that the decline in absorption is accounted for by simple dilution of the initial load from the upland catchment. The diluting water, or land runoff had little absorbing water of its own.

On entering its estuary therefore the Tyne contained a substantial and

Figure 25

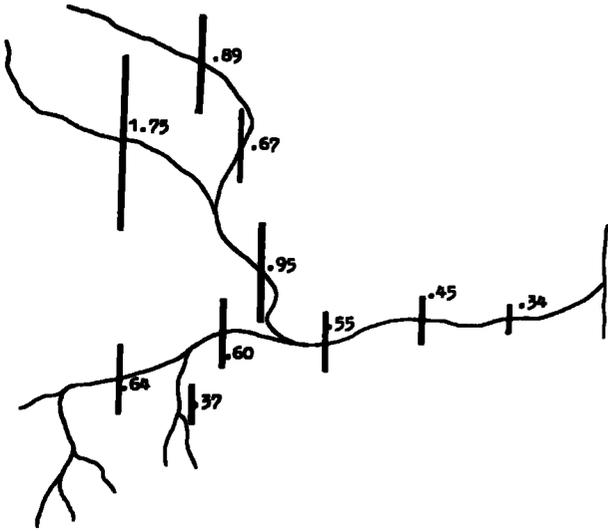
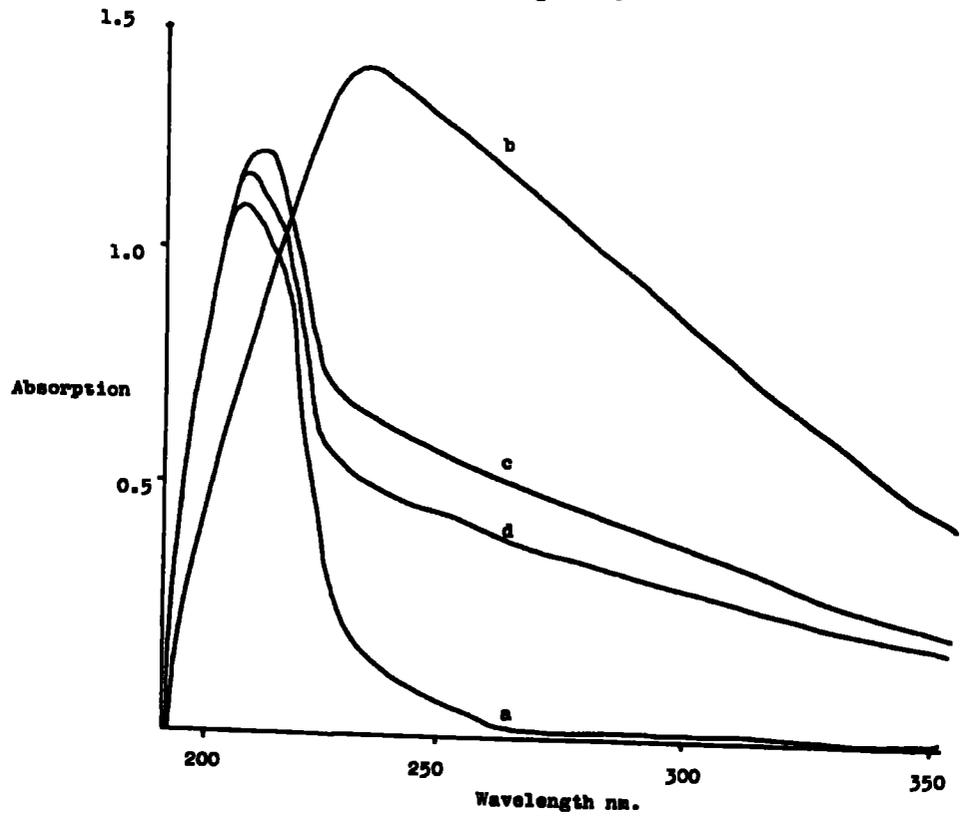


Figure 26a

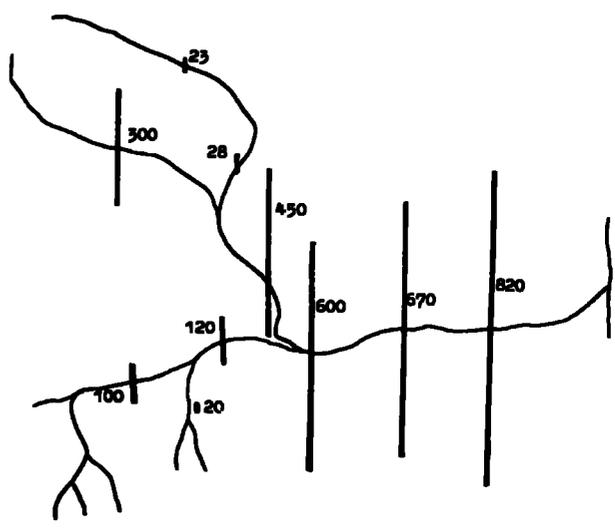


Figure 26 b

measurable amount of stable organic carbon. This can be regarded as the natural background level, onto which is superimposed the organic compounds introduced from the built up areas around the estuary.

A drop in absorption at all wavelengths occurred as soon as the river mixed with sea water. Two factors were investigated as possible causes of this (1) a precipitation of the absorbing compounds by salts and (2) simple dilution. Salinity measurements were used to establish the ratio of fresh water to salt water in the estuine samples.

River water of known absorbance was mixed with sea water in nine ratios between 1:9 and 9:1 and left for 5 days. Reading for absorption after this period showed that the fall in readings were accounted for entirely by dilution. Filtering the samples and re-reading them did not affect the reading, and it was concluded that at all wavelengths between 230 and 350 nm only dilution reduced the readings.

In view of the stability of these humic substances over time and in the presence of sea water it is presumed that they flow out unchanged into the sea almost in their entirety.

In the estuary it is necessary to compensate for dilution caused by tide changes. This is best achieved by eliminating the dilution factor and obtaining a corrected absorption reading which gave the absorption of the river water had it not been diluted by sea water. The following equation was used:

$$\text{Corrected } E = \frac{(E)_{\text{mixture}} \times (S)_{\text{sea}} - (S)_{\text{mixture}} \times (E)_{\text{sea}}}{(S)_{\text{sea}} - (S)_{\text{mixture}}}$$

where E is absorption and S is salinity. (E)_{sea} was taken as .01 and (S)_{sea} was taken as 32 ppt in all cases.

Following the course of the river using the corrected readings a substantial increase in the U-V absorption was detected along an eight mile stretch in the middle of the Newcastle conurbation. In this region 180 outfalls discharge untreated sewage, and this region frequently becomes anoxic in warm weather (James 1973). Random samples taken from near some of the outfalls showed greatly increased readings, and it was estimated that such outfalls were sufficient to raise the absorption by the amount seen.

From this maximum value in Newcastle the corrected values declined as the mouth of the river was approached, despite the fact that there is no decline in industry or population. By the time the mouth of the river was reached the corrected readings were slightly less than they were at the head of the estuary.

To explain this samples were collected from three points along the estuary; from the top, the most polluted part in the middle and from the mouth of the river. After storing for 24 hours at room temperature and at 4° C the corrected values from the central polluted region had converged with and met those of the mouth of the river, and both were progressively less than those from the top of the estuary. This indicates that the sewage is being rapidly "treated" with respect to its U-V absorption properties, leaving only the original resistant humic compounds from the upper catchment area. That treated sewage does not have any significant absorption properties was

corroborated by the fact that downstream from an efficient treatment plant (the Durham City plant on the river Wear) there was no increase in absorption although a 50% increase in total phosphorus was detected.

Therefore it would seem that this method is of little value in the detection of sewage at sea.

Immediately the humic substances were followed out to sea a change in the traces became apparent. Instead of the smoothly descending line typical of the river traces a dip was noticed at around 230 nm, rising to a small peak at 260 nm, after which it continued in a normal uninterrupted fall (see figure 27). This peak and dip have been recorded before (Armstrong and Boalch 1961) although not explained. It was further found that in over 40% of the sea water traces the dip at 240 nm. extended to below the zero reference line. This was at first thought to be an artifact or to an absorbing contaminant in the reference cell of the twin beam instrument. Both these possibilities were eliminated. Neither changing the cells about nor reading against air, both with and without the reference cuvette in position eliminated the effect.

To concentrate the constituents of sea water and to elucidate this effect, river and sea water samples were passed through a column packed with nylon after the method of Sieburth and Jensen (1968). River water lost about 50% of its absorption on passing through the nylon. When sea water was treated however, the column effluent showed a higher absorption than that of the initial sea water, (Figure 27). With both river and sea water, as the nylon became spent the readings of the column effluents approached that of their respective untreated samples, i.e. the fresh water rose and

Figure 27

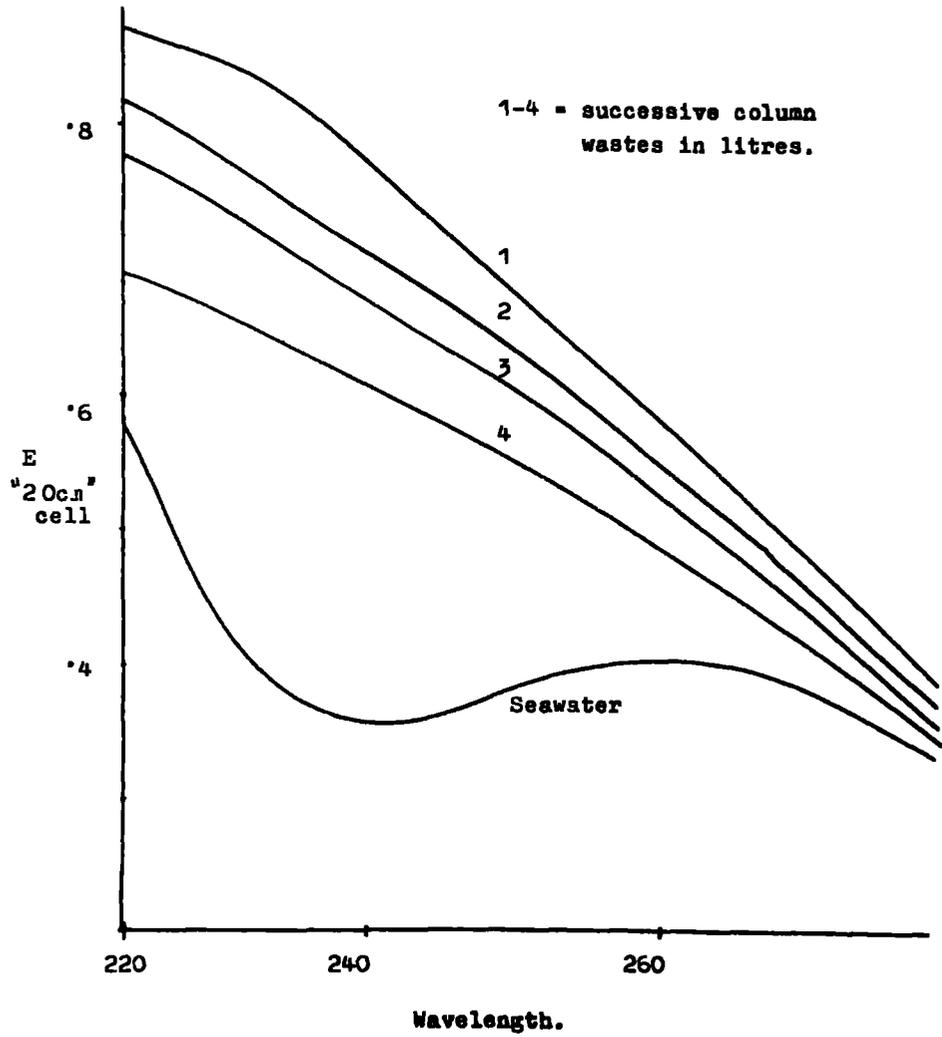
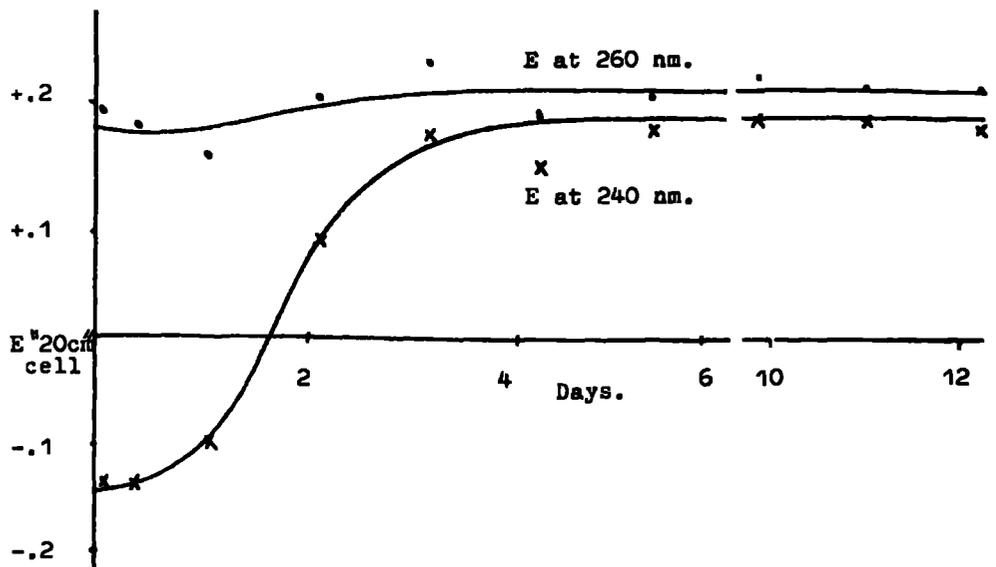


Figure 28



Change of absorption at 240 and 260 nm with Time at 3.5° C.

the sea water fell. It would thus appear that some substance is present in sea water which has the property of reducing its absorption, and which is nylon extractable. The substance can be eluted from the column with 10% NaOH, (and comes off after a fraction containing strongly absorbing material.) After neutralising, the eluate was found to produce a trace typified by a very deep trough at 240 nm and a rise at 260 nm, with the whole trace being well below the distilled water reference line. The fraction thus contained a "negatively absorbing" compound.

It has been observed that river samples showed very little change in absorption with time. In contrast stored samples of sea water showed that while absorption at 260 nm stayed much the same over a two week period, that at 240 nm showed a marked increase during the first four days which largely eliminated the dip at 240 nm. (Figure 28). With storage at two temperatures this increase was found to be dependent on temperature with a Q_{10} of 2.0. Exposure to light had no effect. The same ageing experiments done on the nylon column eluate fractions showed that the absorbance of the second "negatively absorbing" fraction rose with time in a manner identical to the 240 trace of Figure 28. The first, strongly absorbing fraction of the eluate did not change with time.

The findings indicate the presence of two groups of compounds in the sea water, one absorbing light in the normal way over the entire U-V band, and one which has its effect mainly at 240 nm. The latter has a depressing effect which superimposes on the normal curve, though this effect is lost in time. In all probability the substance is the fluorescing and phenol staining substance found by Sieburth and Jensen (1968) when investigating chromatograms of their nylon eluates.

Because of the nature of the construction of spectrophotometers, fluorescence on being irradiated by U-V will be detected by the sensor and recorded as reduced absorption.

In sea water the depression caused by this interference extends across a band of up to 70 nm, although the main effect is at 240nm. It would seem that in sea water therefore this method should not be used for the estimation of total carbon.

In summary it has been shown that (1) This method is of no use in detecting the presence of sewage since the latter quickly loses its absorption properties, and (2) In sea water it cannot be used for the estimation of other carbon compounds either, due to the interferences described.

APPENDIX FDescription of Sites

Aberdeen	NJ955006. Facing East. Steep slope to 40 metres then silt. Moderate exposure. No major rivers. Considerable population and industry, especially shipping, petrochemical.
Ballycastle	55° 12' N. 6° 15' W. Facing North. Steep slope in kelp zone. Moderate exposure. No major rivers. Moderate industry and population.
Bangor	54° 40' N. 5° W. Facing North on East coast. Gentle slope. Slight exposure. In Belfast lough-estuary of river Lurgan. Heavy industry and population especially in Belfast at head of lough.
Caithness	ND385665. Facing East. Very exposed. Steep slope. No rivers. Population sparse and no industry.
Cellardyke	NO579038. Facing South on Fife Peninsular. Gentle slope. Slightly exposed. In Firth of Forth. Moderate population and little industry.
Corsewall	NW979725. North West tip of Wigtown ^{Sea} peninsular. Gentle slope. Moderate exposure. No rivers. Little industry and population.
Dunbar	NT752752. Gentle slope. Possibly severe exposure. Near small river. Little industry and population.
Durdle Doer	SY805802. South facing slope to 15 metres, then sand. Fairly exposed from south. Little industry or population.
Falmouth	SW826315. Facing South East. Gentle slope. Exposure slight. No major rivers nearby. At the collection point population was moderate and industry almost nil.

Flamborough TA255710. East Facing. Slope moderate to 20 metres. Exposed in easterly weather. No nearby rivers. Population: slight and industry minimal.

Fraserburgh NJ955680. North Facing. Steep Slope. Very exposed in Northwesterly weather. No rivers. Population and industry minimal in immediate surroundings.

Hebrides NG045815. South East facing. Moderate slope. Fairly sheltered due to islands. No rivers of importance and almost no population or industry.

Jersey 49° 10' N. 2° 10' W. Strong currents at this site. Moderate slope and fairly exposed. Moderate population but little industry,

Kimmeridge SY907788. South facing. Moderate slope to 15 metres, then gentle until sand. No significant rivers locally and little population or industry.

Kingsbarns NO577150. North East facing by Tay estuary. Gentle slope and fairly protected. River Tay may be important. Population and Industry: sparse around collection site but large 20km further West.

Loch Sunart NM405675. West facing. Steep slope and fairly protected. No detectable fresh water effects. Minimal population and no industry.

Lossiemouth NJ176708. North facing. Steep slope. Moderate exposure. Small rivers Lossie and Spey nearby. Population and industry small.

Marsden NZ397656. East facing. Gentle slope. Moderate exposure. Very near Tyne estuary. Very large population and heavy industry.

Montrose NO713534. East facing. Moderate exposure. Gentle slope. River Esk nearby. Population and industry moderate. Petrochemical industry established.

Newbiggin	NZ316878. East facing. Very gradual slope. Moderate exposure. Near river Tyne estuary. Population and industry very large.
Oxwich	SS512850. South facing. Very gradual slope. Moderate exposure. In Seven estuary. Probably under influence of Swansea, Port Talbot industrial complexes.
Penzance	SW479295. South-facing. Gradual slope. Very protected site. No rivers nearby. Moderate population and industry.
Plymouth	ST478502. Off Plymouth breakwater. South facing. Moderate exposure. Gentle slope. Probably too far out to be affected by river Tamar. Some industry. Population large.
Portencross	NS176488. West facing. Gentle slope. Moderately exposed, No nearby rivers and little population and industry. Nuclear power station nearby.
Port Erin	SC183698. West facing. Moderate slope and exposure. Little industry and population near collection site.
Port Ysagden	SH376220. West facing. Gentle slope and moderate exposure. Little industry or population.
Rædcar	NZ615255. East facing. Very gentle slope. Moderate exposure. Very large population and industry North and South of this site, particularly from Tees estuary.
Robin Hood's Bay	SE960065. East facing. Moderate exposure, gentle slope. Limited population or industry.
St. Abbs	NT908692. East facing. Moderate slope, fairly sheltered site (Petticoe Wick Bay). Minimal population and no nearby industry.
St. Agnes	SW875077. West facing. Very steep slope and fairly exposed site. No rivers or industry, minimal population.

Scarborough TAD49864. East facing. Gentle slope, moderate exposure. Rivers probably too distant or small to be of importance. Large population with some industry.

Seaton SY226880. South facing. Protected site in bay. Under influence of considerable population locally and river Axe, but little industry.

Sennen SW346265. West facing. Very steep slope to 20 metres then more gentle. Very exposed in westerly weather. Minimal population, no industry.

Souter NZ411642. East facing. Very gentle slope. Moderate exposure. Near to Tyne and Wear estuaries. Very large population and industry.

Whitby NZ910113. East facing. Gentle slope. Moderate exposure. Some industry and fairly large population nearby.

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