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The behaviour of the edible winkle, littorina littorea l. in rock pools on shores differing in their degree of pollution

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THE BEHAVIOUR OF THE EDIBLE WINKLE, __Littorina littorea L.__,

IN ROCK POOLS ON SHORES DIFFERING IN THEIR DEGREE OF

POLLUTION.

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the course requirements for the Degree of

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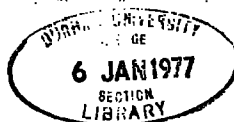
i once heard the survivors

of a colony of ants

that had been partially

obliterated by a cow s foot

seriously debating

the intention of the gods

towards their civilization

                    archy

ACKNOWLEDGEMENTS

Abstract

The variability in distribution and behaviour of the Edible winkle, Littorina littorea L. in rock pools has been examined on an unpolluted shore. The influence of physio-chemical fluctuations in the pool environment is discussed.

Two stretches of polluted coast were then investigated to discover any differences in distribution and behaviour which might be attributable to pollution.

A number of experiments were conducted on the shore to observe the response of winkles in pools to the introduction of various noxious chemicals.

CONTENTS

1.0 Introduction

The precarious environment of the littoral zone is inhabited by a biota variously adapted to physical extremes. The length of subaereal exposure increases along a transect from extreme low water to the level of the highest spring tide. For shore-dwelling animals, most of whom are essentially marine in evolutionary origin, physical conditions become increasingly difficult to tolerate up the transect.

The vertical zone inhabited by a littoral species is often constrained by environmental factors, be they extremes of temperature or perhaps salinity, which tend to vary with the duration of subaereal exposure and hence position on the shore.

That the littoral is mainly colonized by marine groups, many of which still retain pelagic larval phases, is suggested by the fall in species richness as the high water mark is approached from the sea:(Colman 1933). This is rather more true of rocky coastlines than sandy where stranded weed houses a diverse fauna. The fall in numbers of species is perhaps paralleled by a general lessening in species interaction. The vertical range of a species is for this reason more likely to be curtailed on the seaward side by the biological constraints of predation and competition rather than by purely physical ones. This idea is supported by the work of Connell(1961) on competition in barnacles. It also seems to hold for the winkle Littorina littorea L.. This animal would seem to be restricted by physical extremes at the top of the shore but by competition with limpets for space and food, and predation by various crabs towards the Mid-Tide Level.

The presence and abundance of a species at a given locality depends upon the influence of three types of factor; Physical, (for instance see Lewis 1964, Ballantine 1961), Biological, (Connell 1961, Paine 1966) and Geographic. This last refers to the proximity of a population capable of colonizing the area of shore in question.

One might term this a 'distal' factor controlling the distribution of a shore-dwelling species. Other distal factors may include the physical and biological environment experienced by the larval forms.

. It is upon the complex system of the shore that Man's pollution of the seas is most evident. Not only is marine pollution most offensive at the seaside where it intrudes on many aspects of human recreation, it is also very dangerous. The shore is of relatively small extent when compared with the area of sea and land. Partly for this reason it is most vulnerable to wholesale destruction as a viable habitat. Systems that depend on the shore, and here one can include some types of human industry, are thus rapidly affected by littoral pollution. Human consumers at the top of the 'food chain' are directly linked through inshore fisheries to changes in the quality of coastal waters.

Destruction of the shore ecosystem may take place in overt physical forms such as land reclamation or by the more insidious enhancement of the environment with organic compounds and inorganic ions to a point when the water becomes toxic.

A definition of pollution found useful in the course of the present study follows. It is any change in the environment brought about by Man which can be generally assessed as being for the worse. This worsening may be expressed in terms of a reduction in species richness, in diversity of life and habitat, aesthetic qualities and often economic potential, and an increase in mortality, extinction and individual debility. It should be recognized that the various components of pollution, (e.g. industrial and domestic effluent), may not only act synergistically but antagonistically. Thus the effect of a toxin may be counteracted by the increased growth of animals living in an artificially enriched environment:(Genakos 1975).

The dangers of marine pollution have been described in the large numbers of papers dealing with heavy metal poisoning by fish foods, (e.g. Ui and Kitamara 1971), the high concentrations of faecal bacteria in shellfish, (Metcalf, Vaughn and Stiles 1972), destruction of fisheries, (Dewling,

Walker and Brezenski 1972), the slaughter of sea-birds in oil spills and the effect of oil pollution on littoral communities,(Goldacre, Carthy and Arthur 1968).

It is obvious that in the expanse of the sea it is often difficult to link cause and effect. Indeed the effect is frequently most readily noticeable on the sea-shore in the form of corpses of pelagic animals. It is thus well removed in space and time from the cause which may be a tanker spillage well out to sea.

The littoral biota is easily observable and frequently in close proximity to river discharges from populated areas, perhaps the most important source of marine pollution. The outcome of pollution can here be observed in situ, a process which is much more complicated for pelagic ecosystems.

It is highly probable that pollutants affect the fauna and flora of the shore in many ways. If such effects of pollution could be recognized and quantified then this would provide a useful tool for monitoring the impact of industrial Man on the environment. A precise description of the effect is a most necessary requisite for the eventual recognition of the cause. Unfortunately ecologists have had great difficulty in defining the changes caused by pollution super-imposed on the complex of physical, chemical and biological factors already infuencing the shore ecosystem.

Perhaps the most common method of assessing pollution is to record the presence or absence of certain 'indicator species'. Such criteria may indeed mean that the area is polluted but this is only one of a variety of hypothesis which might explain the geography of a species:(see paragraph 4 above). The labelling of an animal as an 'indicator' tends to cause other explanations to be neglected. One is generally left with a number of untestable alternatives from which a prosecuting ecologist is likely to select pollution using Occam's Razor in a rather prejudiced manner.

More recently ecologists have concentrated on characteristics of the community such as 'diversity' in attempts to find parameters sensitive to pollution:(Bellamy, John and Whittick 1968, Sheppard 1976). Although fairly

successful for the sub-littoral community of the Kelp holdfast, the measurement of community parameters on the shore, although it can well be imagined that they respond to pollution stresses, stretches sampling methods and often the taxonomic ability of the ecologist to a degree when the error in the estimate of the parameter is so great that it cannot be convincingly correlated with environmental variables. This is especially so amid the topographical variety of the rocky shore.

An alternative experimental approach has been adopted by some workers, notably at the Orielton Field Station. The effects of certain possible pollutants are determined by field application;(Baker 1971).

Considerable energy has been expended on the determination of LC 50's, (Ottway 1971), a technique commonly used for deciding the 'safety' of various substances released into freshwater bodies.

Such quasi-analytical approaches fight a losing battle against the ever increasing list of pollutants and tell little of the effects on the system as a whole where sub-lethal doses may have far-reaching consequences: (Wildish 1974).

Thus a simple and effective tool for measuring the impact of littoral pollution remains undeveloped. This is exceedingly galling for the qualitative effects of pollution are frequently only too apparent.

In the present study only one of the many habitats on the shore has been considered - shallow rock pools between Mid-Tide Level and Mean High Water of Spring Tides. Littorina littorea L., a very common animal around the British Isles, was observed in this habitat in an attempt to discover consistent behavioural reactions to water pollution resulting in recognizable patterns of distribution.

The Edible Winkle, L.littorea, is happy both above and below water although feeding and movement ceases on a dry surface. Below the water level in rock pools feeding may continue throughout the intertidal period. Alternatively the animals may emerge from the water, withdraw into their shells and await

the return of the tide. Newell in his book 'Biology of Intertidal Animals' remarks that

'<u>L.littorea</u> does not crawl and browse during the whole of the intertidal period, although there is no apparent external factor which prevents it from doing so.'

It was hoped to discover if the time and duration of feeding varies in response to any measureable physio-chemical changes in the rock pool or to other factors external to the pool. The position in which the animal chooses to rest, the 'refuge', be it above or below water, under stones and so forth, may also give indications of the quality of the water in the pool and the condition of the substrate.

During the course of this project a number of experimental manipulations of the rock pool environment were performed in an attempt to test two conflicting hypotheses:

1) that <u>L.littorea</u> in a polluted environment are under physiological stress to a degree that they are unable to tolerate the 'natural' extremes of, for instance, salinity in the pools or high concentrations of toxins.

2) That winkles in a polluted environment are able to tolerate such unpleasantness better than those living in a 'clean' area because of acclimatization of the individual and adaption by the population.

The structure of the study may be summarized as follows:-
The physio-chemical variation of rock pools in the zone between Mid-Tide Level and Mean High Water Spring was investigated at Boulmer in Northumberland, a site regarded as relatively unpolluted:(see page 9). A baseline study of the behaviour of <u>L.littorea</u> was then conducted in these pools. Various experiments were performed to determine tolerances and avoidance behaviour. Rock pools at Marsden Bay,(Durham), and Hartlepools' Point,(Cleveland), were investigated for comparison. These two sites are situated close to the mouths of the Tyne and Tees respectively and are considerably polluted.

It was hoped at the staart of the project that quantitative observations on the behaviour of a single common and easily recognizable animal in an accessible habitat might provide a simple means of measuring pollution: in effect to calibrate the winkles' expression of distaste for the polluted environment.

2.0 General Site Description

2.1 Boulmer, Northumberland: O.S. Sheet 81, NU 266 145 *

The coast at Boulmer is low and backed by stabilized dunes. Below a patchy sand and shingle beach is a very large area of rock, several square kilometres of which are exposed at low tide.

The rock is sandstone of the Carboniferous Millstone Grit Series. In places it becomes very coarse and studded with quartz pebbles. The southward-dipping axes of gentle folds parallel the shore. Cross-bedding is well developed and contributes to the uneven relief of the rock surface. Water accumulates in the many concavities to form large numbers of pools at low tide. The sandstone is friable and fairly easy to erode. Thus the terrain is smoothly rounded rather than rugged.

There is a great variety of habitats within the intertidal area. The scarp and dip faces of the rock ledges provide a choice of aspect and drainage, large boulders are common, weed is plentiful and pools range from the small and ephemeral found on the upper shore to large expanses of water about MTL.**

The diversity of the flora and fauna reflects both the variety of habitats and the extent of the intertidal area which ensures the maintenance of considerable populations of many species. One of the more spectacular denizens is the brittle star <u>Ophiothrix fragilis</u> which is very common in the mid-tidal pools where it may reach 0.16 m in diameter.

Boulmer does not suffer to a great extent from the physical presence of Man. Although throughout the year considerable numbers of people

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* Sheet numbers refer to the Ordnance Survey 1:50,000, second series

** Henceforth the following abbreviations will be used:-

MHWS: Mean High Water at Spring Tides   MLWN: Mean Low Water at Neap Tides

MHWN: Mean High Water at Neap Tides   MLWS: Mean Low Water at Spring Tides

MTL: Mid-Tide Level

arrive with buckets to 'pick winkies', their overall effect on the
environment and the winkle population appears to be slight.

2.2 Marsden Bay, Durham: O.S. Sheet 88, NZ 398 663

The beach at the north end of Marsden Bay is sandy above the high
tide mark but becomes increasingly rocky down-shore. The loose rocks
present are of variable size, ranging from small pebbles through cobbles
to boulders. The nodular Magnesian Limestone rocks which form the low
cliffs that surround the Bay protrude at the northern corner into a low
headland. The hollows in the weathered limestone outcrops readily retain
water to form pools.

As at Boulmer the range of habitats is large; the vertical and horiz-
ontal surfaces of the bedrock, the numerous pools, loose rock as well as
the variety of finer clastic sediments. However, the areal extent of
the intertidal zone is much less and the gradient of the shore considerably
greater.

The younger visitors who flock to Marsden in the summer often prove
to be keen investigators of the littoral fauna. It seems likely that most
of the larger stones on the shore are up-ended at least once a season,
and considerable numbers of animals removed.

2.3 Hartlepools' Point, Cleveland: O.S. Sheet 93, NZ 533 338

The study area selected at Hartlepool was on the windward side of
the point just beneath the wall of the promenade.

Here the Magnesian Limestone is predominantly oolitic. The bedding is
of slight and variable dip, a structure which has given rise to a
series of flat-topped ledges. At low tide about 100 m of rock are
exposed below the promenade. The Neap Tides rise to within 0.5 m of the
base of the sea wall covering all but a small fraction of the natural
outcrop.

The rock surface is generally smooth and swept clean of boulders and other coarse clastics.

The range of habitats is restricted to the vertical and horizontal surfaces of the ledges and the numerous small pools found on the weathered bedding planes. Weed cover, largely Fucus serratus, does not extend much above MTL.

The somewhat limited fauna in this area is probably fairly undisturbed by the actual preence of Man: the occasional people with buckets are there to pick sea coal rather than shellfish.

2.4 Comparing the three sites

The Tyne and Tees estuaries are major influences on the overall environment at Marsden and Hartlepools' Point in terms of salinity, sediment input and pollution. In neither of these sites, however, is there any faunal element peculiar to the estuarine environment and it is on this criterion that they are classified as 'normal marine' together with Boulmer which is far from the mouth of any major river.

A number of authors have examined the evidence for pollution both of the littoral and sub-littoral on the north-eastern coast: (Bellamy, Bellamy, John and Whittick 1967, John 1968, Jones 1970, Starkie 1970, Genakos 1975 and Sheppard 1976). Table(1) summarizes the types of pollution which appear to be most influential at the three sites.

There is a striking contrast between the coasts of Northumberland and Durham. The latter suffers a high sediment load of coal-washings, 'fly-ash' and other river borne particulate matter, high concentrations of domestic sewerage and industrial effluent of great variety. The presence of a southward residual movement in the offshore currents ensures that most of the material entering the sea from the Tyne, Wear and Tees is swept towards the south and away from the Northumberland coast.

Transparency is a useful measure of water quality in the marine environment. Although in some parts a highly turbid sea occurs naturally through erosion of a soft coastline this can hardly be said to be true of the east coast

until one moves south into Yorkshire. Thus the murk of the Durham coastal waters may be largely attributable to pollution. On this basis the sea off Hartlepool would appear to be more polluted than that off Boulmer or Marsden. At most times of the year it is virtually black and, indeed, a frequent sight less than two kilometres offshore is the modified tanker 'Cleveland County' discharging sludge into the sea.

The transparency of the water at Marsden, although not exceeding 5.0 m, is much greater. Boulmer is by far the 'cleanest-looking' of the sites.

It would appear that turbidity is the major factor in the impoverishment of seaweeds on the Durham coast: (Bellamy 1968). For instance at Boulmer the Brown Seaweeds,(Phaeophyceae), are represented by Laminaria digitata, L.hyperborea and Saccorhiza polyschides around the upper limit of the sub-littoral. Ascophyllum nodosum, Fucus vesiculosus and F.serratus dominate the middle shore while F.spiralis and more especially Pelvetia canaliculata extend upwards to MHWN.

P.canaliculata is the only common Brown Seaweed found on the upper shore at Marsden which gives the impression of being rather bare of plants. F.serratus and F.vesiculosus are plentiful below MTL. The waving fronds of a dense kelp forest, predominantly the two species of Laminaria, can be seen at low water.

The lower shore at Hartlepools' Point is mainly covered with F.serratus. A distinct line just above MTL marks the upward limit of dense weed growth. A somewhat subdued forest of kelp exists in the sub-littoral.

In terms of exposure all three sites face towards the north-east quarter. However, Boulmer is protected by an extensive area of offshore shoals. The Littorinids have been used as indicators of exposure: (Evans 1947). Littorina neritoides occurs over a larger vertical range on a more exposed shore. On the sea wall at Hartlepool this animal is found up to 3 m above MHWS, a maximum of 2 m at Marsden but less than 0.5 m at Boulmer where it is uncommon. Lewis 1964 suggests that Littorinids are not found below MHWN

on very exposed shores. This seems to almost be the case at Hartlepool but not at Marsden.

When a cross-section of the fauna and flora are compared using the methods of Ballantine 1961 Boulmer is best described as 'sheltered', Hartlepool's' Point as 'semi-exposed' and Marsden as 'fairly sheltered'. The sites were classified using in particular Fucoids, Barnacles and Nucella lapillus in an attempt to assesss exposure independent of the vertical range of Littorinids.

It should be remembered that the degree of exposure in the micro-environment of the refuges suitable for winkles may not parallel that experienced by other organisms such as Fucoids unable to avail themselves of this type of protection. The availability of refuges at Marsden may be an important reason for the relatively larger numbers of L.littorea found here than at Hartlepools' Point.

Fig.(1) illustrates the zonation of some of the commoner plants and animals.

SITE	BOULMER*	MARSDEN*	HARTLEPOOLS' POINT
SUSPENDED SOLIDS mgl^{-1}	18	58	70
FAECAL BACTERIA l^{-1}	9,000	100,000	160,000
'PHOSPHATE' μgl^{-1}	1.74	2.78	71.9
'NITRATE' μgl^{-1}	10.5	19.0	140
VISIBILITY m	6 - 15	0 - 5	0 - 5
NATURAL SOLIDS IN SUSPENSION	LITTLE	MODERATE	MODERATE
Pb MEAN CONC.IN μgl^{-1} FOR Mytilus edulis	125 $\pm$ 20.6	343 $\pm$ 99	289 $\pm$ 39
QUALITATIVE POLLUTION	SLIGHT	MODERATE	V. HEAVY

Table (1): Some comparative figures for pollution at the three sites,

(compiled from Bellamy,Bellamy,John and Whittick(67), John(68),

Jones(70) and Starkie(70)).

* Measurements actually made at Beadnell Bay,(6 Km north of Boulmer),
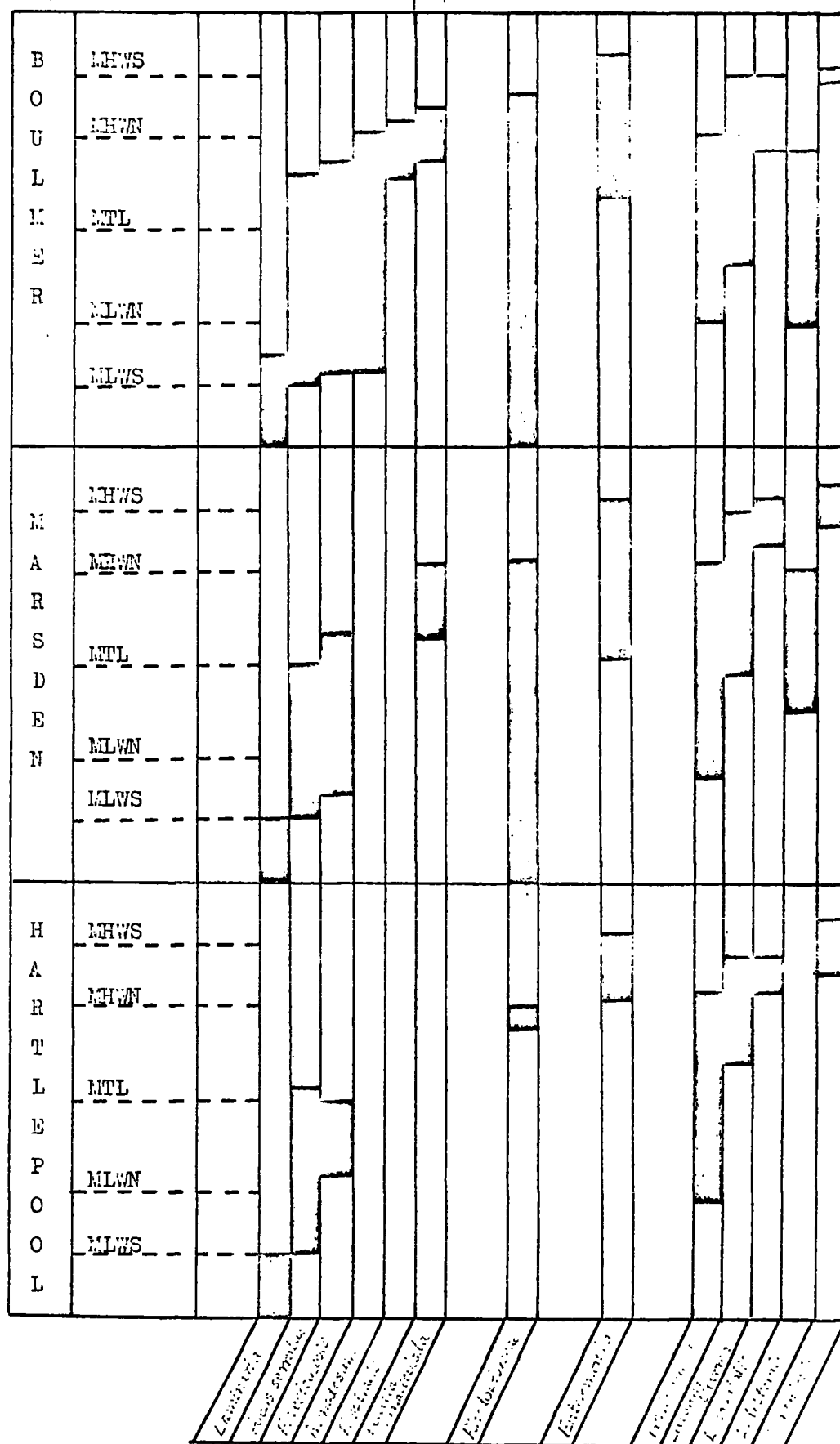
and Souter Point,(at the south end of Marsden Bay).

B
O
U
L
M
E
R

MHWS

MHWN

MTL

MLWN

MLWS

M
A
R
S
D
E
N

MHWS

MHWN

MTL

MLWN

MLWS

H
A
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O
L

MHWS

MHWN

MTL

MLWN

MLWS

Fig.(1): Vertical range of certain key taxa at the three sites

3.0 The Rock Pool Environment

The easily recognizable and definable habitat of the intertidal rock pool
has long attracted the attention of biologists. Reviews of the classific-
atory stage in their study can be found in Newell's 'Biology of Intertidal
Animals' and in Clark 1968. Perhaps the most commonly used classification
is that of Levander 1900 who recognized four different types of pool
in a 'brackish water zone' between the sea and freshwater; Sub-saline,
Splash, Intertidal or Seawater and Algal. The first three reflect the
position of the pool on the shore. Intertidal pools are inundated by the sea
at some stage of the tidal cycle: Splash pools, as the name suggests, are
only reached by splashes at high water while Sub-saline pools occupy an
intermediate position between Splash pools and freshwater. Essentially the
three types lie along a gradient in salinity. Algal pools are formed when
water is dammed behind rafts of seaweed thrrown up onto the shore.

It is the range of variation in physio-chemical parameters, the speed
with which such extremes develop and the frequency of occurrence that are
perhaps most significant for the biota of rock pools. These characteristics
of a pool should allocate it in a rigorous classification. The many
intermediate types of pool which defy cursory labelling make Levander's
system somewhat unsatisfactory. Despite this Clark 1968 found it a useful
basis for her work and further defined each type of pool with curves showing
the frequency of occurrence of various salinities.

The present study was confined to Intertidal or Seawater pools in the
upper part of the eulittoral zone. Such pools are subject to inundation at
least once during a lunar cycle, or, at the other extreme, connected to
the sea for varying periods at every high tide. The occurrence and duration
of connection with the open sea is the prime factor influencing the
environment of the rock pool: (Ganning 1971, Pyefinch 1943, Stephenson,
Zoond and Eyre 1934). Each pool is unique in this respect.

Salinity, pH, oxygen saturation and temperature are variables that have

been measured and monitored in rock pools by a number of researchers including those mentioned in the preceeding paragraph.

Salinity is generally greater but less variable in Intertidal than in Splash or Sub-saline pools, although evapouration may result in super-saturation with salts or rainfall in considerable dilution:(Clark 1968).

The water temperature in pools depends on air temperature and movement, the temperature of the bedrock, the thermal properties of the rock with regard to conduction and radiation, the transparency of the water in the pool and, perhaps most importantly, upon the volume and surface area of the water body itself. The great diurnal fluctuations in water temperature were first remarked on by Klugh 1924 who came to believe that temperature is the overriding factor controlling the biota of rock pools. In north temperate regions, for instance, intertidal rock pools may be the only habitat in which marine organisms are subject to freezing.

From concurrent records of oxygen saturation and pH it has become evident that the two are strongly connected: (see especially Pyefinch 1943 and Ganning 1971). The departure from a normal seawater pH of about 8.2, (Emery 1969), depends upon an imbalance between the rate of algal photo-synthesis and total respiration. During photosynthesis oxygen is evolved while carbon dioxide is removed from the water and the pH rises. During the night photosynthesis ceases and the amount of carbon dioxide in the water increases as respiration continues. The pH lowers as the level of dissolved carbon dioxide rises.

Pools with large quantities of algae exhibit a much larger diurnal fluctuation in oxygen concentration and pH than those in which the biomass is mainly animal. Typically the highest values of both parameters are reached during mid-afternoon. In contrast the lowest occur in the early hours of the morning before there is enough light to begin photosynthesis.

Ganning 1971 concluded that there was generally no shortage of oxygen

in the pools which he studied. However, he did record a diel movement
of the Gastropod _Limnaea peregra_ out of the pools in the early hours
and back during late morning which he suggested might be inresponse to
fluctuations in oxygen partial pressure and pH.

In the marine environment where the inorganically induced pH is relatively
constant it is possible to measure either oxygen concentration or pH and
estimate the unknown parameter graphically; see Appendix (1). It may be
more convenient to measure pH and estimate oxygen saturation because of
the problems of supersaturation causing oxygen bubbles to form on the
surface of plants and be trapped beneath the surface film.

In a large pool organisms will experience an environment considerably
buffered from extremes of temperature and salinity. Thus even at the same
level on the shore the smaller pools will show more extreme fluctuations
than the larger. A simple zonation of pools on purely physio-chemical
criteria is therefore impracticable.

The effects of pollution on conditions in rock pools are described in
the most general terms in Carthy and Arthur 1968. Also relevant is the paper
by Cairns, Heath and Parker 1975 on the effects of temperature upon the
toxicity of chemicals to aquatic organisms. Kontogiannis and Barnett 1973
examined the effect of oil pollution on the survival of certain copepods
in rock pools. They concluded that the death of the copepod was partly
due to the toxic effects of the oil but also to oxygen starvation, the oil
acting as a barrier to oxygen diffusion across the surface of the pool.

In general it seems that rock pool pollution causes an already extreme
environment to become even more extreme, often to the point when conditions
become intolerable for the original inhabitants.

3.1 Rock pools at Boulmer

Most of the pools investigated are situated in a zone between MHWN
and MHWS and were selected to represent the great variation in depth
and volume. The largest pool, (12), had an estimated volume of 250 1,
a depth of 0.5 m and an area of 1.2 m^2. In contrast the smallest, (11),
was initially 0.025 m deep with a volume of 2.9 1 and a surface area
of 0.09 m^2. The dimensions of all the pools which were studied in detail
are given in Appendix (2).

Of the pools examined in this zone only 12 and 15 had a reasonable
diversity of macro-organisms; occasional Fucus spiralis, Catenella repens
and Enteromorpha (intestinalis) among the larger algae, the animals
represented by Patella vulgata, Balanus balanoides, L.littorea, L.saxatalis,
a few anenomes and gobies. Pools 1, 3, 6-11 were impoverished by comparison.
Only the two species of Littorinid were reasonably common. A fringe of
Enteromorpha was present around the margins of some of the pools.

By mid-June it had become apparent that the shallower pools all dried up
in the period between Spring tides, weather permitting. Of those mentioned
above only 12 and 15 remained filled throughout their period of severence
from the sea.

The rate at which the volume of a pool diminishes through surface
evapouration increases exponentially as the ratio of surface area to
volume increases. Thus if the depth of the pool is initially within a
certain critical range, (assuming a similar pool morphology), then the
likelihood of drying up is very great. Outside this range the decrease in
water depth due to evapouration is slow and pools are likely to remain
until the next tides. At Boulmer this range was 0.10 - 0.15 m during June
but increased to 0.25 m in the course of the very hot July.

By the end of July most of the plants and animals that had distinguished
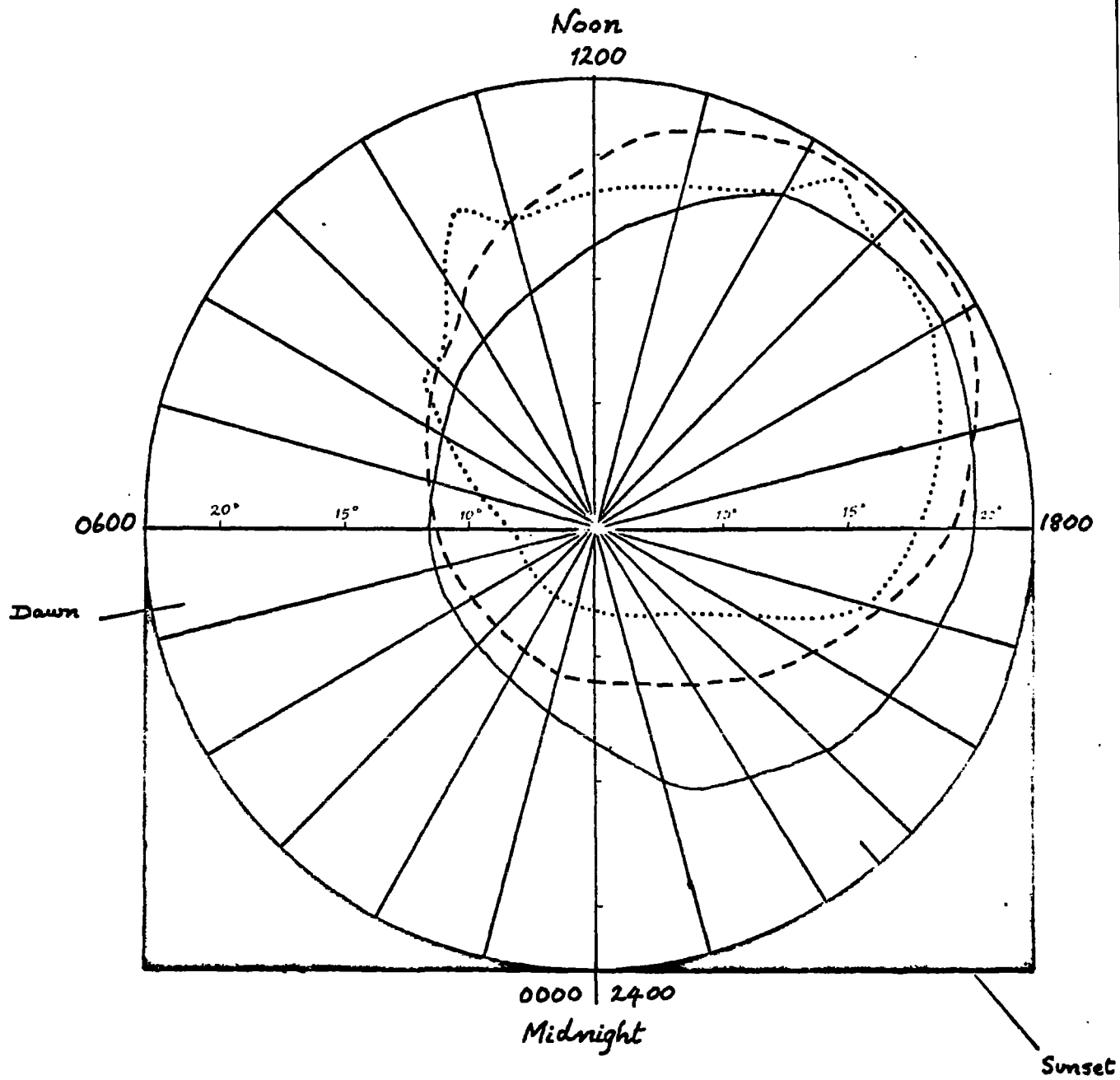the deeper pools had disappeared leaving only the Littorinids.

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Fig.(2): Temperatures at Boulmer over twenty-four hours: (8-9/5/76)

〰〰 Water temperature in pool 12 °C

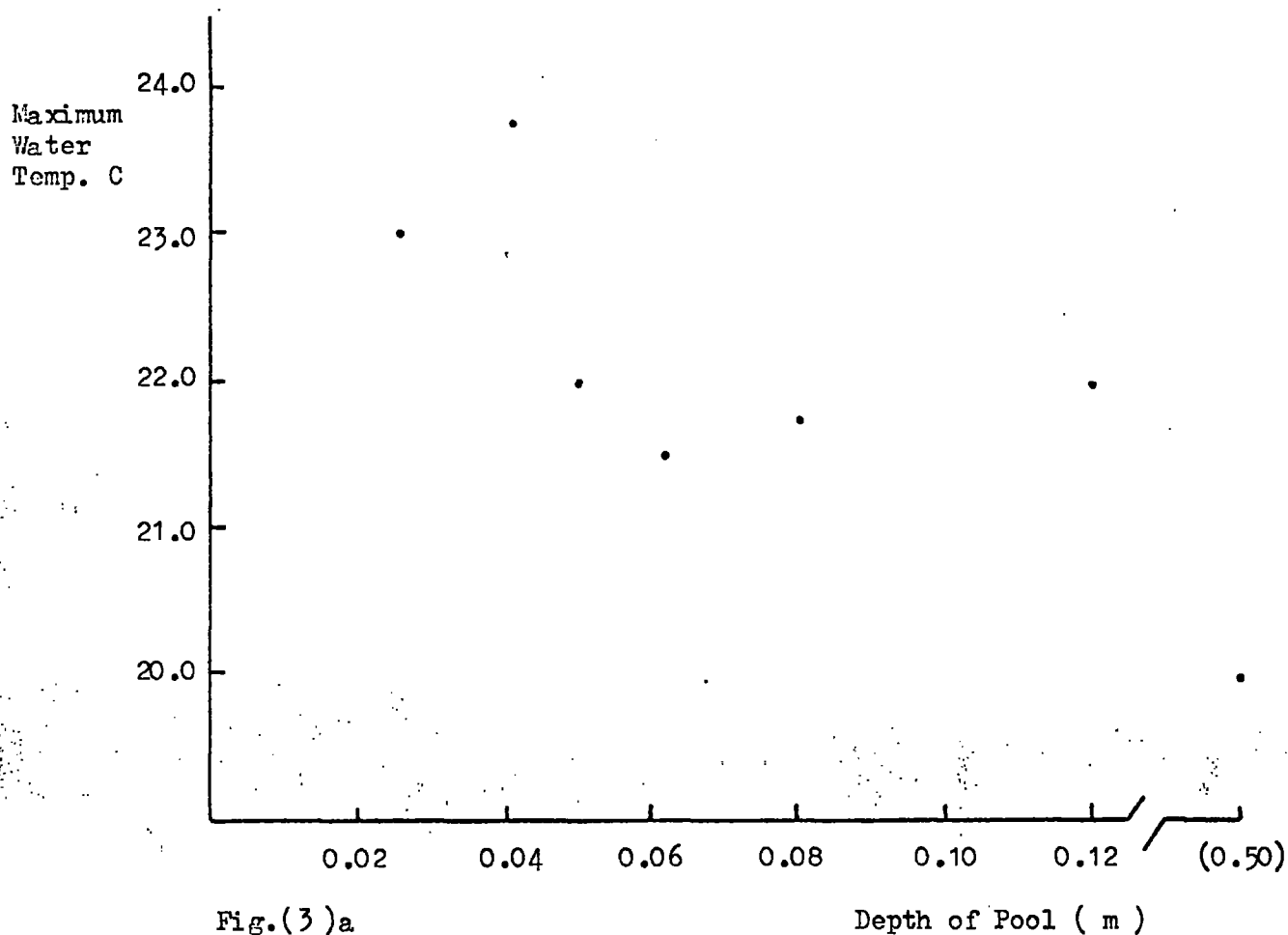- - - - Water temperature in pool 2   °C
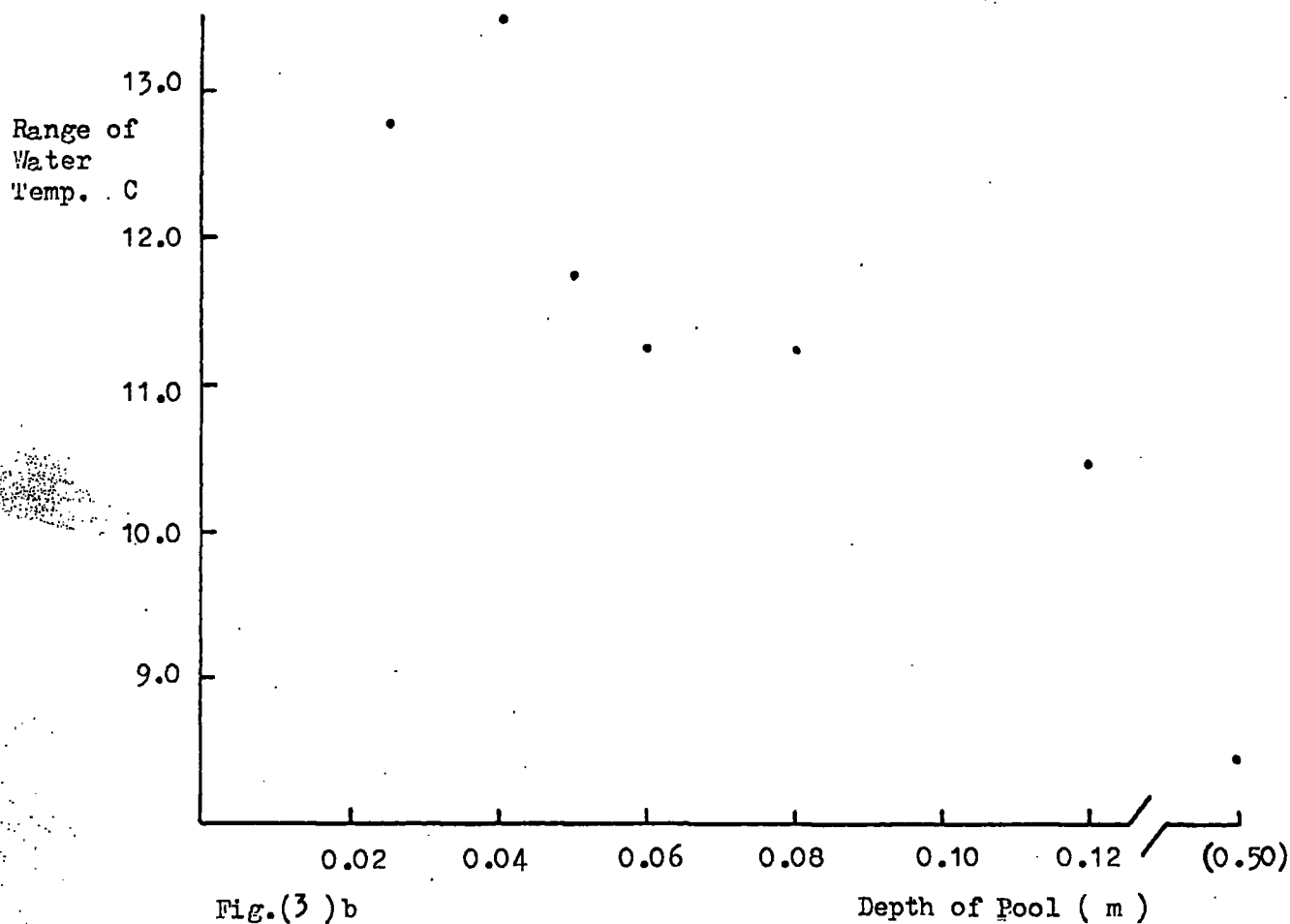
······· Air temperature °C

Fig.(3)a

Fig.(3)b

Fig.(3): Pool depth plotted against maximum recorded temperature,(a),

and range of variation, (b), in pools at Boulmer for a
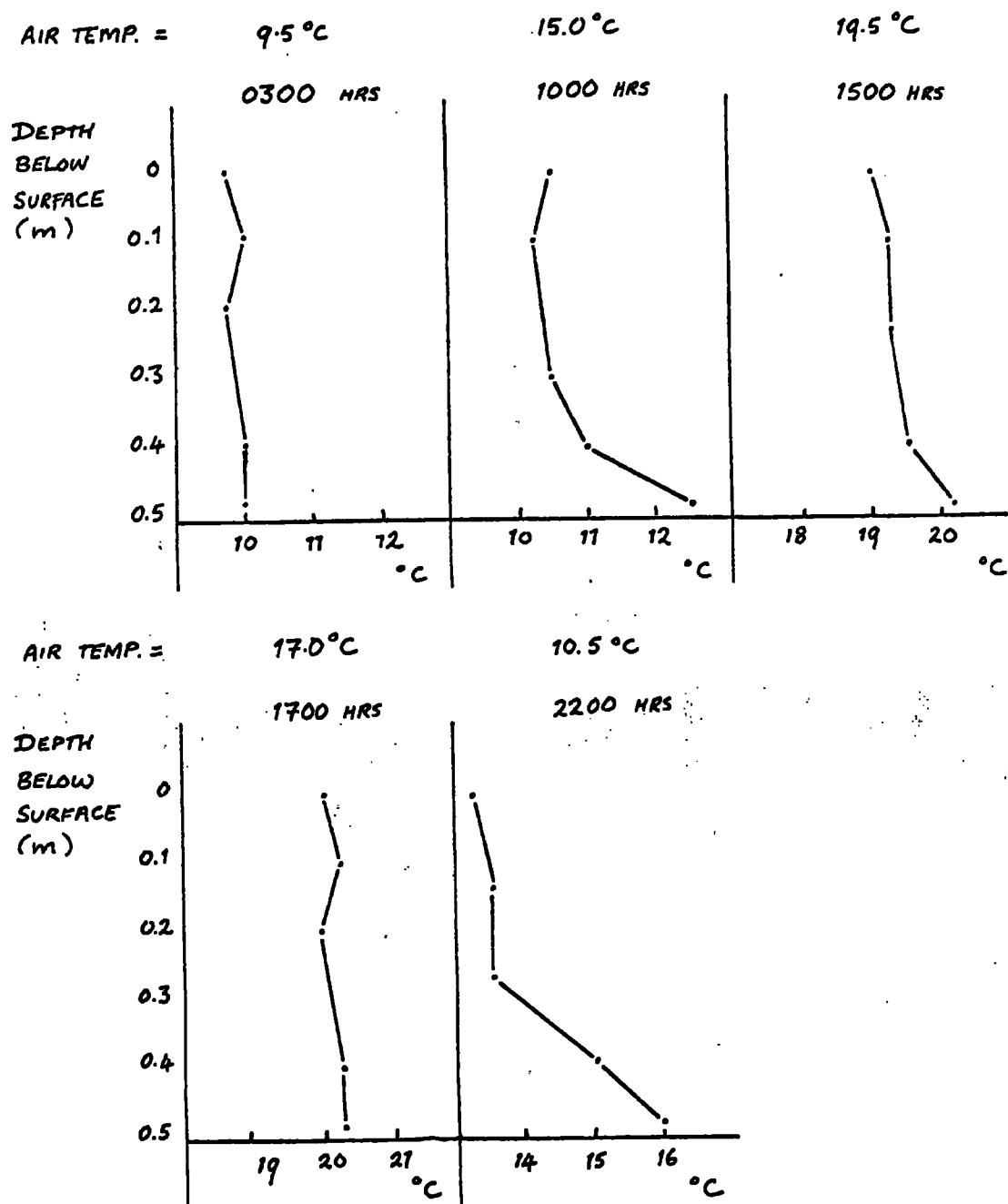
twenty-four hour period; 8-9/5/76

Fig.(4): Temperature Profiles in Pool # 12 at Boulmer:

[Date: 8 and 9, 5, '76]

3.11 Temperature variation

All temperatures were measured using a standard mercury thermometer calibrated from 0 to 60° C.

The changes in water temperature in pools 2 and 12 over a period of twenty-four hours are illustrated in Fig.(2). Not only is the variation in temperature greater in the shallower pool 2 but the maximum value is reached earlier in the day. Pool 12 is slower to warm up in the morning but retains the heat of the day much further into the night. The highest temperatures are reached when the sun is shining: at other times the shallow pools follow quite closely the variation in air temperature.

Fig.(3a) graphs the relationship between depth of pool and maximum temperature attained during one twenty-four hour period. As might be expected they are inversely proportional. A similar result is obtained for depth of pool plotted against range of variation: (Fig.(3b)).

Water temperature was measured 0.02 m above the floor of the pool and the air temperature at the same distance above the surface. It was thought that a measure of water temperature in this position would perhaps be one most relevant to winkles. The necessity for taking the water temperature in a standard position is demonstrated in Fig.(4) where the temperature profiles at different times of day are illustrated for pool 12. Until mid-afternoon the bottom warms faster than the surface waters. (This is only the case when the pool is being insolated.) The temperature near the surface reaches and slightly surpasses that of the bottom in the late afternoon. At night the surface waters cool rapidly while the bottom remains relatively warm until the early hours of the morning.

The maximum temperature recorded in pool 12 was 33°C in late June. At this time the water did not cool below 16°C at night.
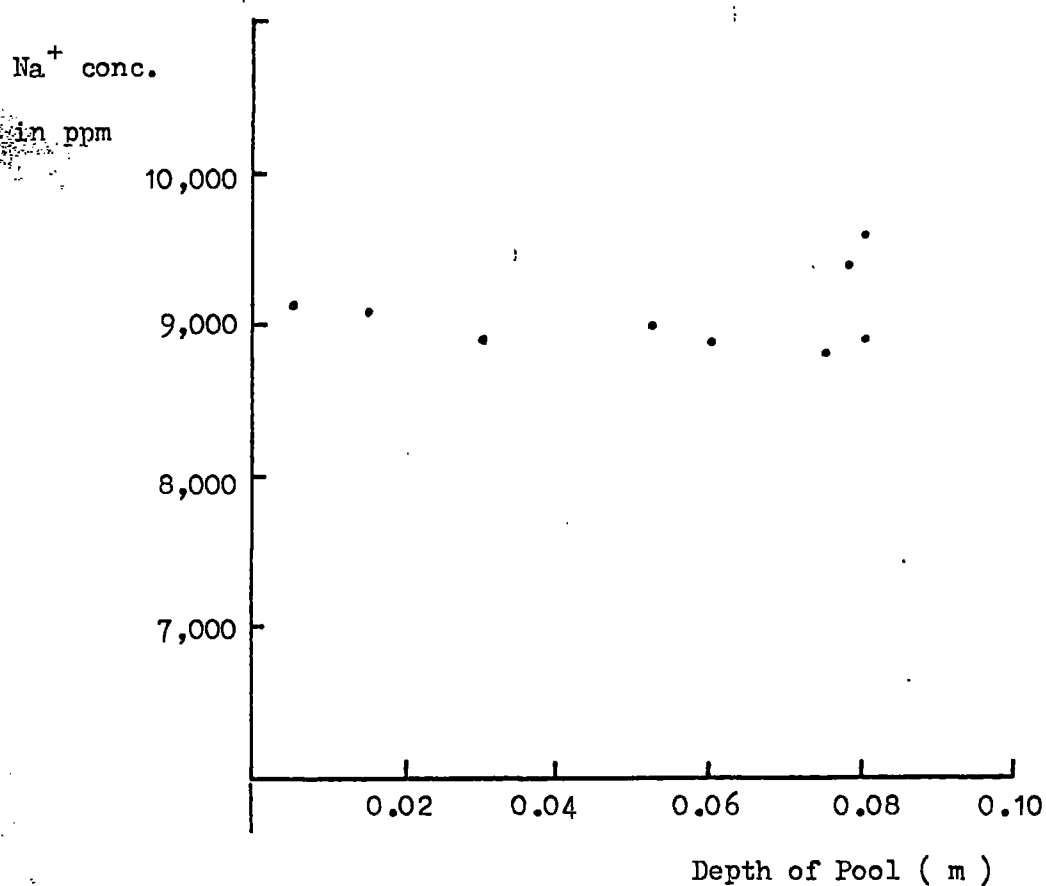
Na$^+$ conc.

in ppm

Depth of Pool (m)

Fig.(5): Na$^+$concentration plotted against depth of water

remaining in pool 10: Boulmer 9/5/76

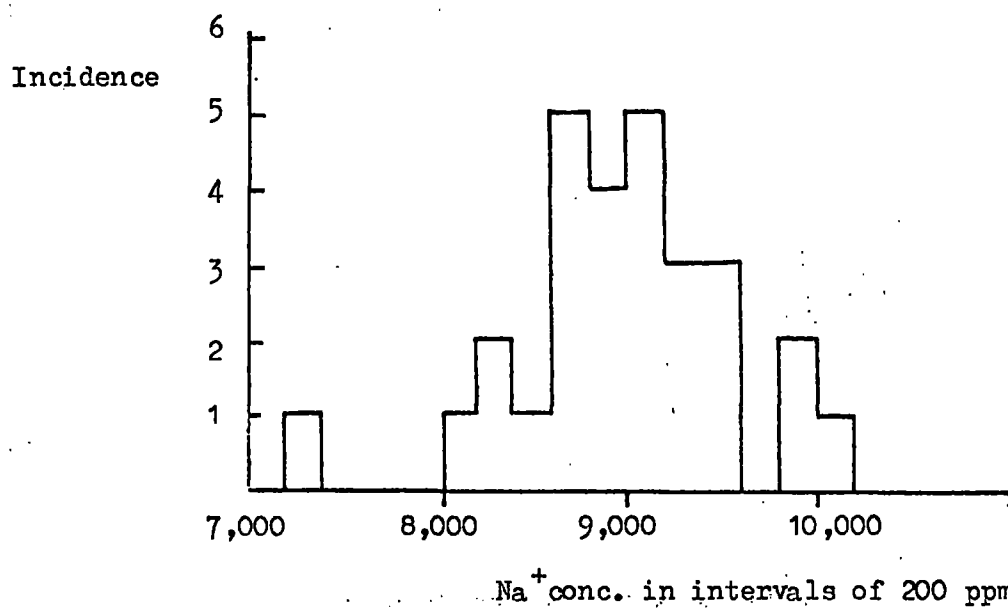Incidence

Na$^+$conc. in intervals of 200 ppm

Fig.(6): Incidence of various Na$^+$concentrations in pools

on the upper shore at Boulmer during the period

8-10/5/76.

3.12 'Salinity'

This was estimated indirectly by determining the concentration of Sodium ions in the samples by flame photometry. Water was withdrawn from the pools using a 10 ml pipette, placed in a small plastic sample tube and transported back to the laboratory. 1 ml of the sample was then dispersed in 250 ml of distilled water and a small beaker of the resulting solution placed beneath the suction tube of the photometer. This machine had previously been calibrated with a 100 ppm Na^+ solution. The correct Na^+ concentration in the original sample could then be calculated by multiplying the reading on the galvanometer by any scale correction for errors in the zero and span, and then by 250.

Repeated determinations on a single sample revealed an error of $\pm$ 100 ppm for this method of analysis.

An average figure for Na^+ concentrations in the ocean of 9,580 ppm is given in Sverdrup, Johnson and Fleming 1942. It is therefore possible to estimate the chloride concentration in the samples by multiplying by the ratio

$$\frac{\text{Average } Cl^- \text{conc. in seawater(ppm)}}{\text{Average } Na^+ \text{conc. in seawater(ppm)}} = \frac{17,200}{9,580} = 1.795$$

As has been noted above a number of pools dried up during the course of observations. It seemed likely that the ionic concentrations might reach high values during this process. In Fig.(5) Na^+ conc. is plotted against the depth of water remaining in pool 10. No increase in 'salinity' is noticeable.

In fact the drying out of the pool actually occurred in the late evening when evapouration rates are low. Probably the water level in the pools at Boulmer depends not only upon rainfall and evapouration but also on the height of the water table in the permeable sandstone that contains them. If the disappearance of water from pool 10 is simply because of
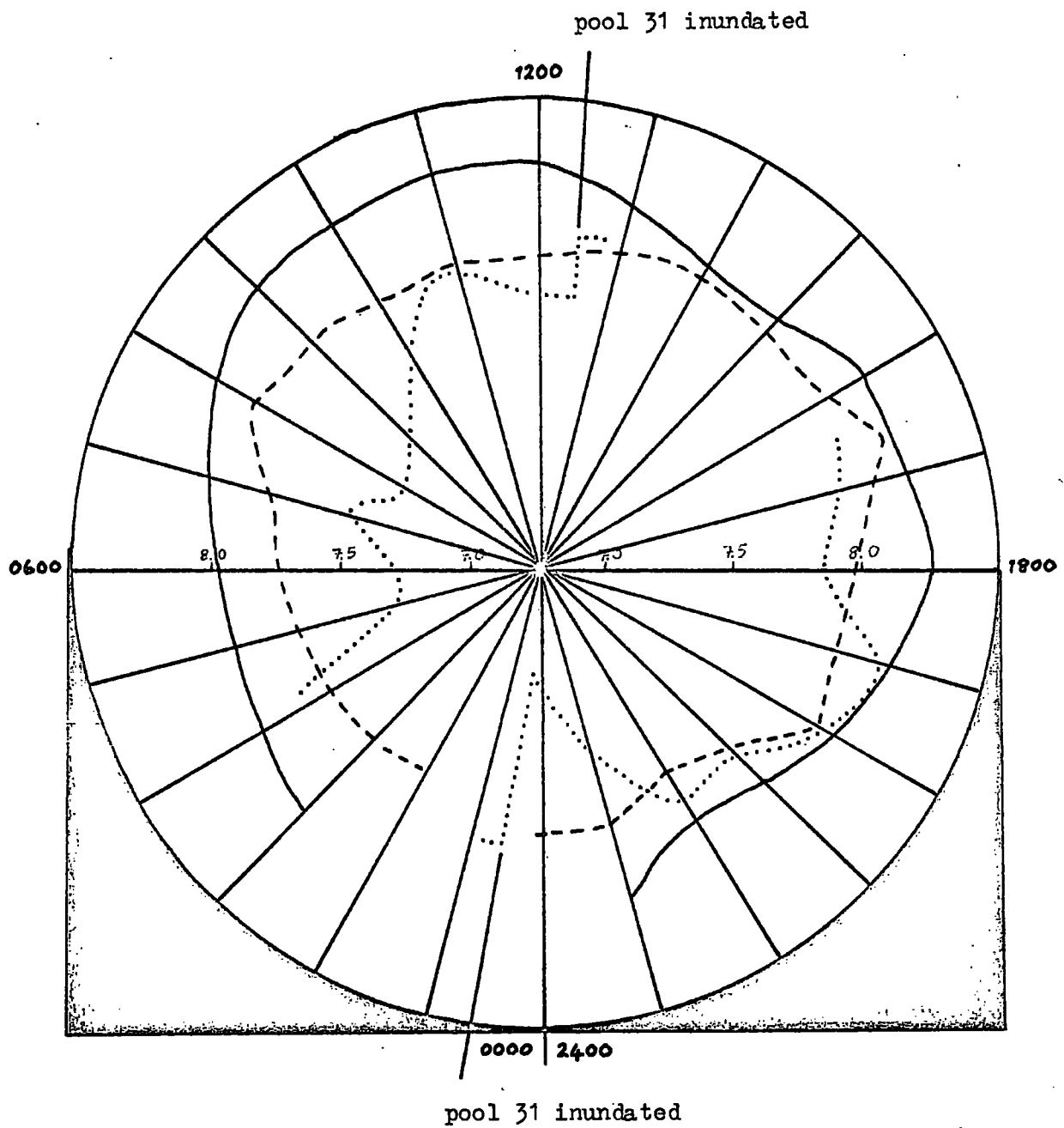
Fig.(7): pH monitored over twenty-four hours at -

Boulmer, pool 15, 23/5/76

Hartlepools' Point, pool 31, 25/6/76

"   "   " 29,   "

movement down through the interstices of the rock then no increase in ionic concentration could be expected.

The movement of water through the rock at Boulmer must considerably modify the extremes of salinity which might otherwise develop in the pools. Indeed the water level in pool 15 was observed to move up and down slightly, presumably in response to tidal rhythms, despite being apparently unconnected with the sea. This movement is out of phase with the tides and probably depends on the movement of small amplitude waves inland along the water table by a capilliary mechanism.

The highest Na^+ conc. recorded in any of the pools at Boulmer was 10,450 ppm and the lowest 8,000 ppm. Most of the pools fell in the range 8,500 to 9,600 ppm which is somewhat lower than the concentration measured in the open sea during May;(9,800 ppm). Fig.(6) records the frequency of occurrence of various concentrations in the pools during the month of May.

3.13 pH

Monitoring the pH in pool 15 over a twenty-four hour period revealed no marked difference from that of the sea:(see Fig.(7)).

A portable pH meter was used. It was calibrated with standard solutions made up to pH4.2 and pH9.6 and checked with narrow range pH paper. These instruments are notoriously temperamental, however, and the error involved in taking a pH reading may be as great as $\pm$ 0.15 units.

The meter recorded a range of readings between 7.9 and 8.3 for the open sea measured on various days and the pH in the pool did not stray outside these limits. The lack of fluctuation in pH may be expected because of the low algal biomass inpools at this level on the shore:(Pyefinch 1943). Apparently respiration does not increase the concentration of carbon dioxide at night to a point where the pH is measureably affected.

3.20 Rock pools at Marsden Bay

A number of pools were selected for study about and above the level of
MHWN. Pool 21A, just below MHWS, was bare of macro-algae throughout the
period of observation and the only large faunal elements seen were the
winkles L.littorea and L.saxatalis. L.neritoides, though present on the
rocks just above this level, was absent from the pool itself.

Pools 18, 20, 21 and 22 are at the level of MHWN and are therefore
refreshed by the flood tide on almost every day of the year. L.littorea,
Balanus balanoides, an occasional Patella vulgata and numbers of tiny
worms with endolithic tubes were present together with Ulva lactuca,
Enteromorpha and some Rhodophyceae.

Further down the shore the pools become increasingly weedy. Fucus serratus
and Ascophyllum nodosum are common. Enteromorpha growth is frequently
excessive. The exposed rock in the mid-tidal area is generally barren of
weed, perhaps kept in this condition by the numerous limpets.

3.21 Temperature

It seems reasonable to assume that pools of depth and volume comparable
to those at Boulmer will show similar temperature characteristics. A
rigorous comparison would require the production of Temperature/Frequency
of Occurrence curves for the pools at both sites.

3.22 'Salinity'

The Na^+conc. in the waters off Marsden was measured as 7,890 ppm on
the 2nd. of June. The concentrations in the pools around MHWN varied from
7,320 to 7,630 ppm on this date, a dilution which may be explained by rain
early on the morning of the 2nd..

Samples were taken from pool 21A on a number of occasions during June.
The Na^+conc. ranged from a minimum of 6,890 ppm on the 8th. to 9,900 ppm

at the end of the month, after the start of the heat wave which presumably accelerated the evapouration of water from the pools. It would seem that the extent of variation in ionic concentration in the highest pools at Marsden is greater than that at Boulmer. A likely explanation for this difference is the contrast in the permeabilities of the rock substrates. The limestone matrix is altogether much 'tighter'.
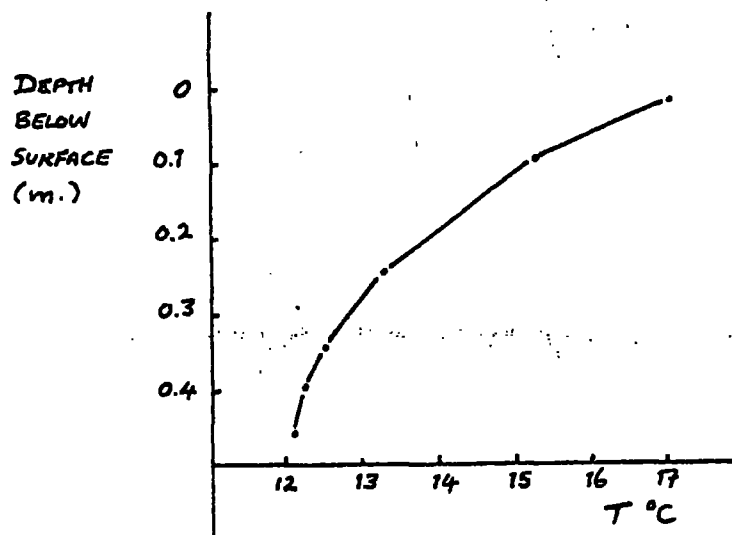
3.23 pH

This was not measured at Marsden.

Fig.(8): TEMPERATURE PROFILE IN POOL #25 AT HARTLEPOOLS POINT

[DATE: 16.6.76 , TIME: 1315 , AIR TEMP.: 17°C]
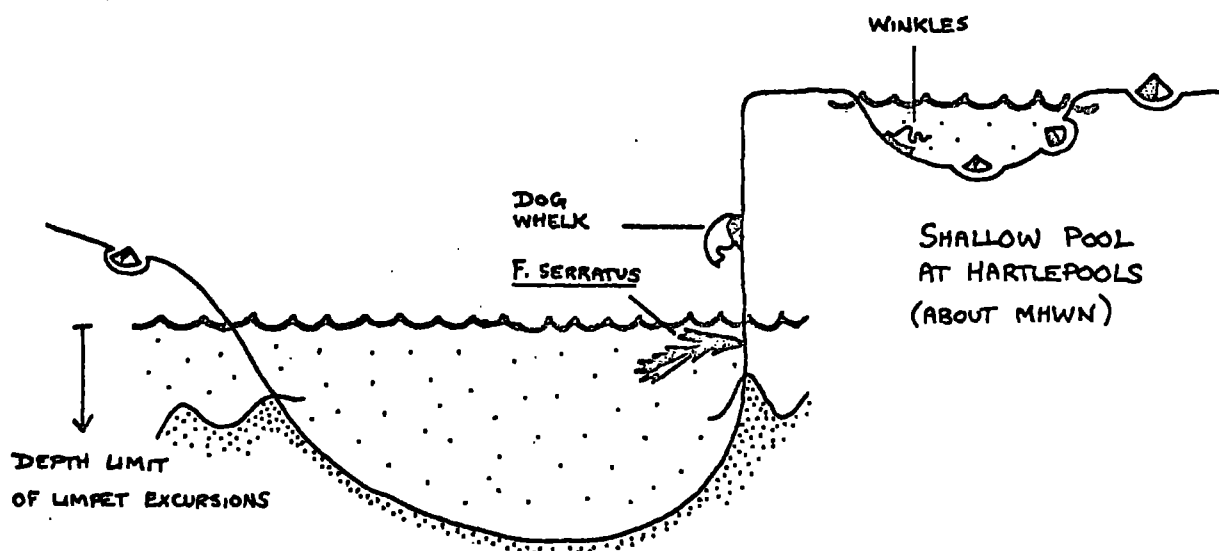
Fig.(9): DEEP POOL AT HARTLEPOOLS POINT
(BETWEEN MHWN AND MTL)

⊙ : DEPOSITS OF GREY SILT FIXED BY ALGAL MATS

△ : LIMPETS

3.30 Rock pools at Hartlepools' Point

From MTL to mWHN the pools at Hartlepool tend to be quite large reaching depths of 0.5 m. The bottom is frequently invisible because of the extremely murky water. Fucoids, almost entirely Fucus serratus, do not grow in these pools except as a fringe around the margins:(see Fig.(9)). It is common to see the sides of the pool relatively clear of sediment to a depth of, 0.1 - 0.2 m. Below this depth the rock surface is covered with a slimey grey deposit which inplaces reaches a thickness 0.015 m. This film is composed of silt which supports a heavy growth of filamentous diatoms, at least during the early summer. Beneath the microscope this diatomaceous growth resolves into long strings of oblong tests bound in gelatinous sheathes.

Only two animals were observed to live in this material; a species of Harpacticoid and an Ostracode. Patella vulgata is extremely common on the exposed rock surface where, at low tide, they are to be found resting in self-wrought hollows in the limestone.

Few limpets or winkles were seen resting or feeding below the surface of these rock pools during the intertidal period. However, it is most probably the downward excursions of limpets at high tide that keep the upper parts of the pools free from silt and algal growth. It may be that below a certain depth the sediment load deposited from the column of still water trapped in the pool at low tide becomes too great for the limpets to continually remove. P.vulgata seems unable or disinclined to crawl and browse over the surface of sediment bound by these slimey algal mats. .

Shallow pools at about the level of MHWN are to be found on the ledges just below the promenade. Those less than 0.15 m deep are clean of bottom sediment and the transparency of the water is such as not to obscure the pool floor to any discernible degree. Limpets, L.littorea and L.saxatalis are common resting and feeding both above and below the surface. Some Rhodophyceae and Enteromorpha are present but there are no Brown Seaweeds
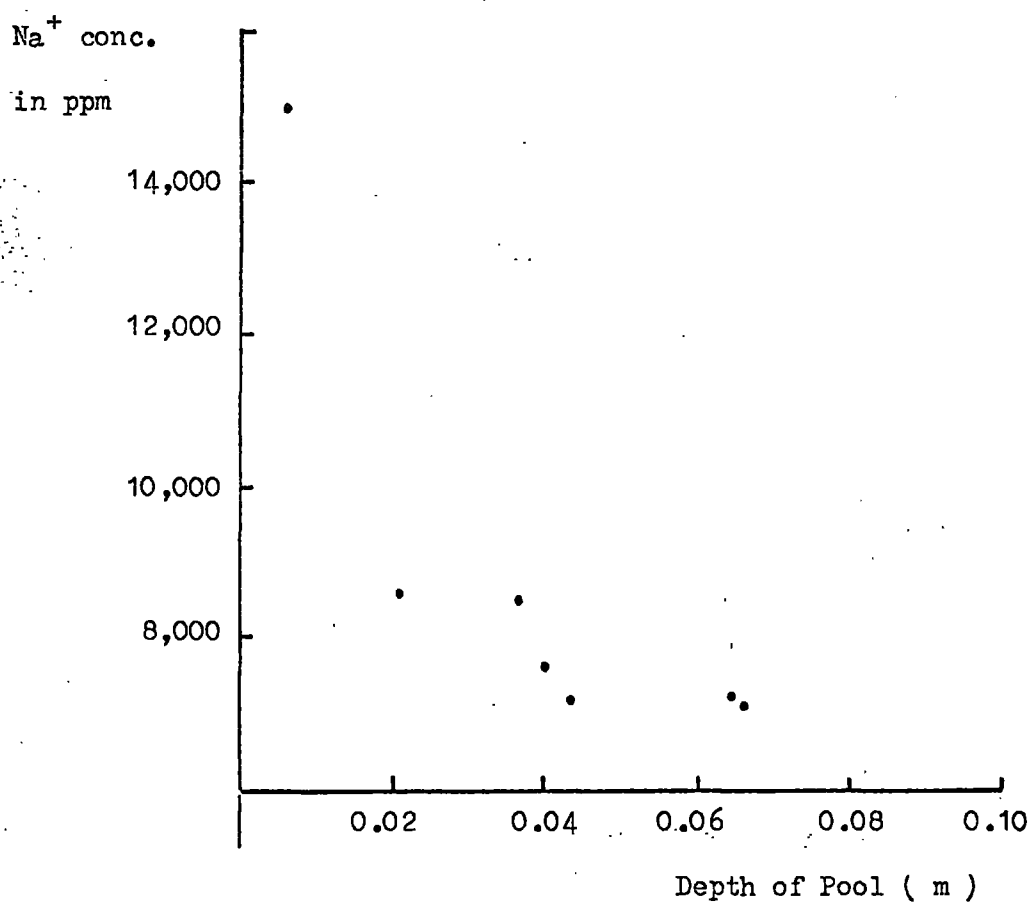
Fig.(10) : Na⁺concentration plotted against depth of water

remaining in pool 22: Hartlepools' Point 25/6/76

at this level. In some pools anenomes are common.

As noted at Boulmer the macro-algae and the anenomes were only found in pools which were not observed to dry up during the periods of exposure.

Pools 29 and 30 were the highest examined at Hartlepool. They are situated between MHWN and MHWS and in such a position as to be severed from the sea for up to four days during Neap tides. A sparse fringe of _Enteromorpha_ was present in pool 29 when observations began in May but became bleached and eventually disappeared by late June. The only animals noted in these pools were specimens of _L.littorea_.Sediment accumulation did not appear to be great at this level on the shore.

3.31 Temperature

A temperature profile for the deep pool 31 is given in Fig.(8). Unlike Boulmer the water does not heat from the bottom: the turbid water prevents radiation penetrating more than a fraction of a metre. The temperature in the pool rapidly decreases with depth.

The temperature in the shallower pools behaves similarly to that of pool 2 at Boulmer in closely following the fluctuations in air temperature.

3.32 'Salinity'

The Na^+conc. in pool 31 did not differ from that of the sea; (7,300 ppm on the 25th. of June). During the afternoon of this day the water in pool 22 was sampled as it dried out. The ionic concentration can be seen to increase as the water depth decreases, reaching a measured extreme of 15,000 ppm Na^+:(see Fig.(10)). There was no suggestion of percolation through the rock as at Boulmer and an encrustation of salt was left after the complete evapouration of the pool.

The variation in 'salinity' of pool 29 during June was from 7,150 to 7,350 ppm, a rather small range when compared with that in pool 21A at Marsden. This may reflect its somewhat lower position on the shore.

3.33 pH

An average figure for the pH of the open water off Hartlepool is
7.8 $\pm$ 0.2. The twenty-four hour monitoring of pH in pool 31 reveals that
in daylight hours it does not rise much above 8.0 but may drop as low as
7.0 at night:(see Fig.(7)). This is doubtless due to the respiration of
the bacteria and algae in the silt deposits at night and the turbidity
of the water inhibiting daytime photosynthesis. One may therefore deduce
that animals in this pool experience quite low oxygen concentrations towards
early morning. It may be that such conditions discourage limpets from
resting below the surface.

In contrast the pools higher on the shore,(e.g. pool 29), do not display
fluctuations of this kind. Perhaps the animals grazing on the algae
keep the vegetable biomass down to a level where its metabolism does not
significantly, or measureably, affect the pH.

4.00 Littorina littorea as an object for investigation

The Littorinidae are common intertidal organisms throughout the world. They are, as their name suggests, one of the few groups of animals limited to the littoral zone, at least in the adult stage. Some species, for instance Littorina littorea, retain a planktonic larval phase. Others, such as L.saxatalis, are viviparous. It is perhaps strange that the smallest British winkle L.neritoides is found highest on the shore yet still has a planktonic larva. A general description of the British Littorinids may be found in 'The Sea Shore' by C.M.Yonge.

L.littorea is a common animal on the north-east coast reaching a maximum length of 30 mm at Boulmer. Probably for the reason of large size it is popularly known as the 'Edible Winkle' and is subject to harvesting on some sections of coast.

Usually found between MTL and MHWS on a variety of shore types from muddy to rocky, L.littorea is most likely to be confused with the 'Rough Periwinkle, L.saxatalis, a species of similar habits and general appearance. The former is most easily recognized by the following characteristics:-

(i) The colour, which is a uniform grey-green.

(ii) The striking set of dark rays on the inner lip of the aperture.

(iii)The less rounded aperture. The growing edge of the shell joins the final whorl at an acute angle.

(iv) The marked surface sculpturing.

With some practice it becomes possible to rapidly distinguish the two species.

Spawning in the Edible Winkle occurs in early Spring. A few weeks later the young winkles return from a short life in the plankton to settle on the shore. They grow rapidly to become sexually mature after about eighteen months. It is frequently possible to recognize several generations in a shore population but it seems unlikely that individual winkles live for more than about five years.

Winkles have attracted the attention of many zoologists over the last
fifty years. Most of the studies performed upon the group have either
been essentially physiological, being concerned with the animal's tolerance
of extreme environments;(Crapp 1971, R.G.Evans 1948, Fraenkel 1961,
G.E.Newell 1964, R.C.Newell 1969, R.C.Newell and Pye 1971,1973, R.C.Newell,
Pye and Ahsanullah 1971, Sandison 1966 and Todd 1963), or behavioural;
(Bock and Johnson 1967, F.Evans 1961,1966, Hayes 1929, Jansson 1960,
G.E.Newell 1958a,b, E.E.Williams, I.C.Williams and Ellis 1975).

Of the physiologically orientated experiments the most relevant to the
current study are:-

(i) The work of Fraenkel who determined the lethal high temperature for
three marine invertebrates including L.littorea. During the course of his
experimnets he identified four responses to high water temperatures in the
winkles listed below in order of increasing severity.

(a) Snails crawl out of the water.

(b) They become fixed to the wall of the vessel under water but usually
show little activity.

(c) The animal begins to stretch out of its shell.

(d) The operculum is firmly closed.

Behaviour of types (a) and (b) was observed to be frequent under natural
conditions during the present study.

(ii) R.C.Newell and Pye studied the effect of temperature and body weight
on oxygen consumption by L.littorea. It seems that larger winkles have
a lower oxygen consumption per mg than smaller. Increasing the temperature
considerably reduces the consumption of smaller individuals but has a
progressively slighter effect as the size increases.

(iii)R.C.Newell, Pye and Ahsanullah examined the differences in feeding
rate,as expressed by radular movement, of winkles kept in a laboratory
tank in which the conditions and rhythms of the shore were carefully

simulated. They found that smaller animals radulated faster than larger. Increases in water temperature up to 25°C raised the number of radular movements in an approximately linear fashion but where was some degree of acclimation above this temperature expressed by a gradual reduction in feeding rate. However, it turned out that the most important factor determining radular activity was the position of the animal on the shore. Winkles from high up on the shore exhibited high rates of radulation which reflect the need to make up for lost feeding time during the prolonged periods of subaereal exposure.

It should be noted that pool-dwelling animals are not constrained to feed only at high water and should not need to increase their rate of radulation. (iv) In his work on oxygen consumption Sandison demonstrated that time of day had a barely significant influence on respiration in L.littorea. (v) Todd determined a survival time of less than twelve days for L.littorea living under conditions of reduced salinity;(11,200 ppm Cl⁻).

Behavioural studies on winkles have concentrated on describing their movement on the shore in terms of a limited number of 'taxes'. The chief goal of these investigations seems to ahve been to discover a simple behavioural mechanism by which winkles maintain their littoral zonation.

Initial observations suggested a simple sun-compass reaction which would enable the winkles to orientate themselves and so produce their typically 'U'-shaped feeding trails. However, accumulated evidence now suggests that reversals in behaviour can occur; animals may commence feeding as photopositive but later become photonegative. They may exhibit positive and negative geotaxes as well. Newell summarizes his researches up to 1972 in the following manner:

'..... so that many gradations between the use of a purely light-compass reaction with reversal of response, and a geotaxis with reversal of response, may be expected to occur in specimens collected from shores where a great variety of slopes are colonized.' (Biology of Intertidal Animals, p 140.)

It also seems that <u>L.punctata</u> navigates by recognizing the distant image of the shoreline:(F.Evans 1961).

Perhaps the complex of clues to which winkles respond in a given situation is not particularly amenable to this kind of analysis.

4.10 The advantages of choosing rock pools in which to study the behaviour of <u>L.littorea</u>

(i)   The rock pool between MHWN and MHWS which may be separated from the sea for periods of several days, provides an arena for observing the behaviour of the animals undisturbed by tides.

(ii)   The influence of tides is largely removed. There is unlikely to be any increase in feeding rate to compensate for periods of enforced non-feeding.

(iii) The environment of the pool can be easily manipulated for experiments.

(iv)   It is easy to keep track of individual winkles.

(v)   The pool provides a simple choice for the animals; to stay below the surface and feed, or to haul out above water to rest.

(vi)   The winkles are in their natural environment. Most of the work on the physiology and even the behaviour of <u>L.littorea</u> has been performed in the laboratory. The present author attempted to persuade a group of animals to behave 'normally' in a laboratory tank filled with water collected at the same site,(Boulmer), as the winkles. The tank was brightly illuminated, the lights being controlled by a timer set so as to provide the same number of daylight hours inside as there were outside. Changes in water level were not simulated since the specimens were collected from upper pools above the current high tide mark. The water was circulated through a U.V. sterilizer to prevent excessive algal and bacterial growth.

Despite these arrangements an AAI, (see page 39), of more than 5.0 was calculated from observations on fifty animals over a twelve hour period. This high figure suggests that the animals were behaving in a completely
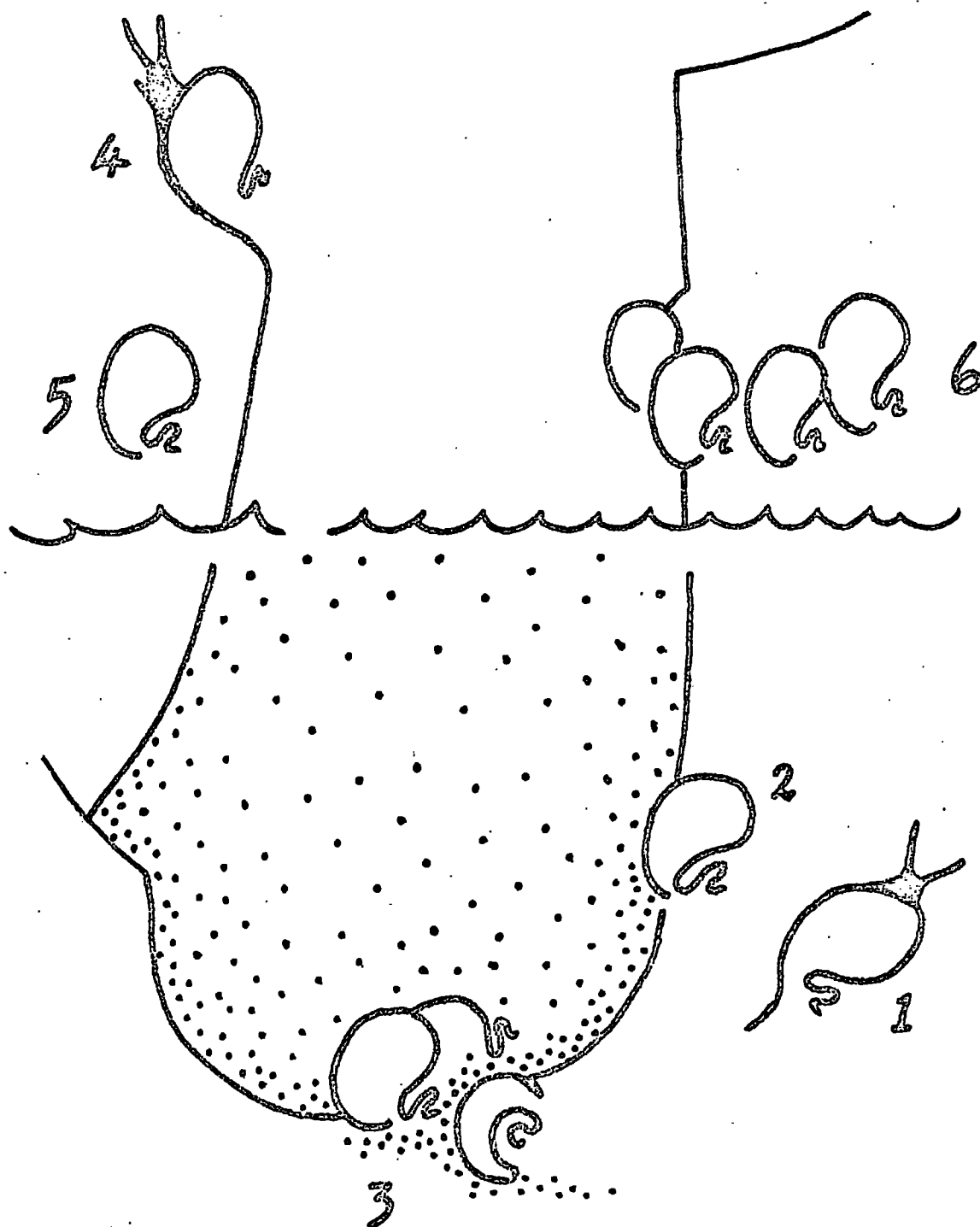
Fig.(11). Schematic rockpool showing the six types of Winkle
position and activity recognised in this study.

Score.

1	Animal below water surface	, moving with tentacles extended.
2	"	"	"	"	, stationary with tentacles retracted.
3	"	"	"	"	, clumped with tentacles retracted.
4	"	above	"	"	, moving with tentacles extended.
5	"	"	"	"	, isolated with tentacles retracted.
6	"	"	"	"	, clumped with tentacles retracted.

abnormal fashion. In most cases winkles introduced to the tank rapidly climbed the sides and remained unmoving just above the water's edge. The tracks of occasional short excursions below the surface could be clearly seen in the sand on the floor of the tank. In most cases winkles seen underwater had just fallen from the sides of the tank and were attempting to regain their former positions.

The great difference in behaviour between captive and wild suggests that the molluscs are alert to changes in their surroundings and that their capture, transport and subsequent release into the tank was sufficient to cause bewilderment and 'abnormal' behaviour. An established laboratory population would have provided a useful control for some of the experiments performed in this study. For instance, the animals could have been subjected to differently polluted water collected from the three sites and their reactions recorded. However, the preliminary results from the tank suggested that experiments of this kind would have been suspect. The laboratory approach was therefore discarded and observations restricted to the field.

4.20 Method used for recording winkle behaviour

An arbitrary decision was made to exclude from consideration any winkles more than 0.2 m above the surface of the pool or in such a position as to be separated from the pool by a convexity.

Six categories of behaviour were recognized for individuals living in or about the rock pools. These are listed below and summarized in Fig.(11).

Score: (1) Animals moving and feeding beneath the water surface; the most active category.

(2) Isolated individuals below the surface but stationary with tentacles retracted.

(3) Animals in clumps below the surface, stationary with tentacles retracted. Clumps are composed of three or more winkles separated by not more than the width of a shell:(in practice about 0.01 m).

(4) Moving and feeding above the surface of the water. This only

occurs when the surface of the rock is moist.

(5) Animals stationary, typically 0.01-0.05 m above the water surface

with tentacles and body retracted into the shell. The operculum

is usually in position and the entire weight of the shell is

supported by dried mucus around the rim of the aperture.

(6) Clumped individuals in the same immobile condition described

under (5). These 'clumps' are often linear arrangements of

winkles at a similar height above the water.

It is quite common to see winkles fall off the surface of the rock and
roll back into the pool. This tends to happen if a group of quiescent
winkles is approached noisily or if not enough attention is given to the
position of the observer's shadow. In some cases this dislodgement may be
done in order to recommence feeding below the surface. Usually a winkle that
rolls to the bottom of a pool will right itself and travel up the pool
side to regain its original post. However, during the course of some of
the experiments conducted in this study conditions in the water deterred
the winkle from opening its shell underwater and it remained at the bottom
of the pool. In this unfortunate state they are distinguishable from
categories (2) and (3) by the orientation of the shell. A 'happy' winkle
will always attempt to turn its shell so that the aperture and foot faces
the substrate. Such dislodged animals were scored as (6).

The six categories are ranked partly in order of decreasing activity
and also so as to easily distinguish between winkles above and below the
water surface. A single observation on a winkle consisted of scoring its
behaviour on the scale (1) to (6). The sum of the scores may be divided by
the number of winkles observed to give an 'Average Activity Index' or 'AAI'.
Obviously such an index can refer either to observations on a single animal
over a period of time or to an 'instantaneous' description of the behaviour
of all the winkles in the pool.

4.30 Statistical analysis of results

It should be noted that nothing can be assumed about the distribution of winkle observations between the six categories. The AAI is not the mean of a normal distribution; it is simply one way of summarizing the results.

The method of observation outlined above produces a classification of activities. As such the results should be considered 'distribution free' and are not, in their initial form, amanable to analysis with parametric statistics.

Comparisons made between sets of results are best supported with the X^2 test. One disadvantage of the X^2 is that it is not necessarily valid if expected values are low. If it proved advisable the results were manipulated to ensure expected values greater than five. This was done by first adding the number of scores under category (6) to those in (5) and recalculating the expected values. If these were still too small then the number under (5) to (4) and so on. For specific purposes it was possible to reduce the results to a 2X2 contingency table.

The X^2 reveals the degree of homogeneity between columns of figures. The probabiltiy quoted in standard tables is that of obtaining a X^2 as large, or larger than that given, if the null hypothesis is true and the columns are homogeneous. If the probabiltiy was less than 0.01 then for the purposes of this study the null hypothesis was rejected and a real difference in observed behaviour established.

One useful result of proving sets of score frequencies to be insignificantly different was that they could then be summated and used for further comparisons.

Plotting the AAI enabled rapid visual identification of areas of homogeneity which could then be tested with X^2.

4.40 Method used for the experimental manipulation of the pool environment

Small pools of not more than a few litres volume were selected for experimentation. The exact volume was determined by siphoning the contents into a large graduated cylinder.

Ideally the winkles already in the pool were used but if these were insufficient in number specimens in nearby pools were collected and quickly placed in the experimental pool.(The winkles did not seem to be much affected by such rapid displacement.) Usually about twenty-five animals were observed per experiment.

The salinity of the pools was gradually reduced by adding small increments of tap water. A standard minimum of thirty minutes was allowed after each environmental change. Since on one occasion several winkles were observed maintaining a speed of 0.1 m min^{-1} it seemed that thirty minutes was adequate time for the animals to respond. After this time had elapsed the pool was approached and the behaviour of the winkles scored. The salinity was then further reduced.

Using a similar method various chemicals were also introduced to pools and the effects of ever larger concentrations obsereved. The smallest volume used was 0.01 ml and was added to the water with a syringe followed by a brief stir with a glass rod.

Experiments of this kind can take several hours so care was taken to observe a group of control animals in a nearby pool undisturbed except by occasional agitation with the rod.

4.50 Additives

The reactions of winkles to varying concentrations of the following 'pollutants' were recorded:-

(i) Durham tap water

(ii) Acetic Acid; 99.5% + CH_3COOH

(iii) Urine

(iv) B.P. Lubricating Oil

(v) Benzene

(vi) 'Citron Vert' detergent

	BOULMER		MARSDEN	HARTLEPOOL	
Percentage of Total Population	84 %	16 %	100 %	83 %	17 %
Mean Length (mm)	14.8	5.7	12.5	8.5	1.0
Standard Deviation	2.30	2.45	2.30	1.75	-
Standard Error	0.23	0.26	0.9	0.22	-

Table (2): Description of the sub-populations of L.littorea

found at the three sites during June, 1976

5.00 Notes on the demography of L.littorea at the three sites

Winkles from the study pools were collected and measured across their maximum linear dimension; the axis which runs from apex to aperture. The cumulative percentages of winkles in the various size classes were then plotted on probability paper.

It is possible to identify discrete normally-distributed sub-populations from these curves:(see Southwood 1968). A normal distribution approximates to a straight line when plotted on this kind of paper. If two age classes are present in the population then two straight line segments are likely to appear separated by a kink.

In this study the sub-populations or age classes were identified and the graphic mean and standard deviation determined for each. Table(2) summarizes these population parameters for the three sites.

Winkles smaller than 0.002 m were ignored during the observational work because they are easy to lose and more difficult to identify to species.

The larger age classes at the sites may be compared using Student's 't'. The majority age class at Boulmer is significantly larger than that at marsden,('t'= 2.16, p<0.03, d.f.=∞), and at Hartlepools' Point, ('t'= 9.4, p<0.001, d.f.=∞). Similarly the mean at Hartlepool is significantly less than at Marsden;('t'= 3.8, p<0.001, d.f.=∞).

It seems reasonable, though now impossible to prove, that these three sub-populations are of approximately the same age. They are likely to have settled on the shore in early 1974. The smaller age class at Boulmer is probably last years settlement which for some reason seems to have missed Marsden and Hartlepool. This year's recruitment, though present, were still less than 0.002 m in June.

ACTIVITY SCORE	Group A		Group B	
	No.	%	No.	%
1	33	55	30	50
2	13	22	13	22
3	4	7	3	5
4	1	2	4	7
5	7	12	6	12
6	2	3	4	7

Table(3):   Activity of Group A,(mean length = 5.7 mm), and

Group B,(meah length 14.8 mm), in pool 15;. 24/5/76.

ACTIVITY SCORE	8/5		9/5		10/5		11/5	
	No.	%	No.	%	No.	%	No.	%
1	126	14	30	15	25	17	31	15
2	373	41	91	45	61	42	99	48
3	335	37	80	40	58	40	78	37
4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0

Table(4): Afternoon activity in pool 12 from 8/5 to 11/5/76

6.00 Some aspects of variation in the behaviour of pool winkles

at a single site;(Boulmer).

6.10 Variation due to size differences between individuals

Sixty winkles of various sizes were collected from the upper pools at
Boulmer. Each was dried with tissue paper, painted with a number, measured
and, after about forty minutes, released into pool 4. The paint used was
a quick drying enamel but nevertheless tended to flake off the shells,
especially when one winkle crawled, radulating, over the back of another.
The behaviour of the released winkles was scored at intervals from 1945 hrs
on 22/5/76 to 0820 hrs on 24/5/76.

For each individual the AAI for the period was calculated and plotted
against length of shell. No pattern could be discerned in the resulting
scatter of points. A correlation coefficient calculated for a regression
line fitted by the method of least squares through the points was 0.13.
This is so low that it would seem that behaviour is not influenced by size
of animal, at least over the size range 14.0' - 23.0 mm.

Another experiment was performed in which the behaviour of two groups
was observed. Group A consisted of twenty animals belonging to the minority
age class at Boulmer with a mean shell length of 5.7 mm. In contrast
Group B comprised twenty from the older class with a mean of 14.8 mm.
The summed behaviour scores for Group A in pool 4 and Group B in pool 15
over the period 1400 - 1630 hrs on 24/5/76 are shown in Table(3).

As can be seen the behaviour of the two groups is remarkably similar;
there seems to be no consistent size dependent difference:($X^2 = 0.82$,
$p > 0.8$, d.f.= 3). It is likely, however, that below a certain size, perhaps
2 - 3 mm, differences begin to emerge.

This negative result, though somewhat unexpected, is not necessarily in
conflict with Newell's conclusion that rates of activity decrease with

age and increased size. The type of observation made in the present work is sensitive to duration of activity rather than rate.

6.20 Variation through twenty-four hours

Results from observations made on winkles in pool 12 on 8 - 9/5/76 are given in Fig.(12), and for pool 2 in Fig.(14).

The animals appear to be most active just after dawn. The numbers feeding are significantly greater between 0500 and 0600 hrs than during the succeeding hour;($X^2 = 39$, $p < 0.001$, d.f.= 2), or indeed at any other time of day. From 0700 hrs onwards the winkles become less active until they reach a plateau of activity which lasts from 0900 to 1600 hrs.(The results for this interval are homogeneous: $X^2 = 4.59$, $p \approx 0.4$, d.f.= 5.)

In the early evening there is a slight increase in numbers feeding but this gradually declines through the night until the early hours when the animals are most inactive.

Thus a very distinctive change in behaviour coincides with dawn; the AAI drops from around 3.0 to 1.25 in one hour.

Another way of monitoring the activity over a twenty-four hour period is illustrated in Fig.(13). The distance of feeding winkles from their refuge was measured. The refuge in this case was a large stone and individuals could be associated with the stone by following their tracks on the pool floor.

The results show that the animals tend to be found closer to the refuge during the afternoon but move further out as evening approaches where they remain fairly evenly distributed until morning. The furthest excursions take place towards midnight but such journeys are performed by rather few winkles, which keeps the average activity in the population fairly low.

47

Fig: 13 . POOL # 12 ; 9,5,'76 . DISTANCE (m.) OF FEEDING WINKLES FROM REFUGE

HORIZONTAL BARS = PERCENTAGE OF FEEDING WINKLES , SCALE 1 CM. = 10%

AAI

6.0

5.0

4.0

3.0

2.0

1.0

0000　　　0 600　　　1200　　　1800　　　2400 hrs.

dawn　　　　　　　　　　　sunset

%
Activity

100

50

0
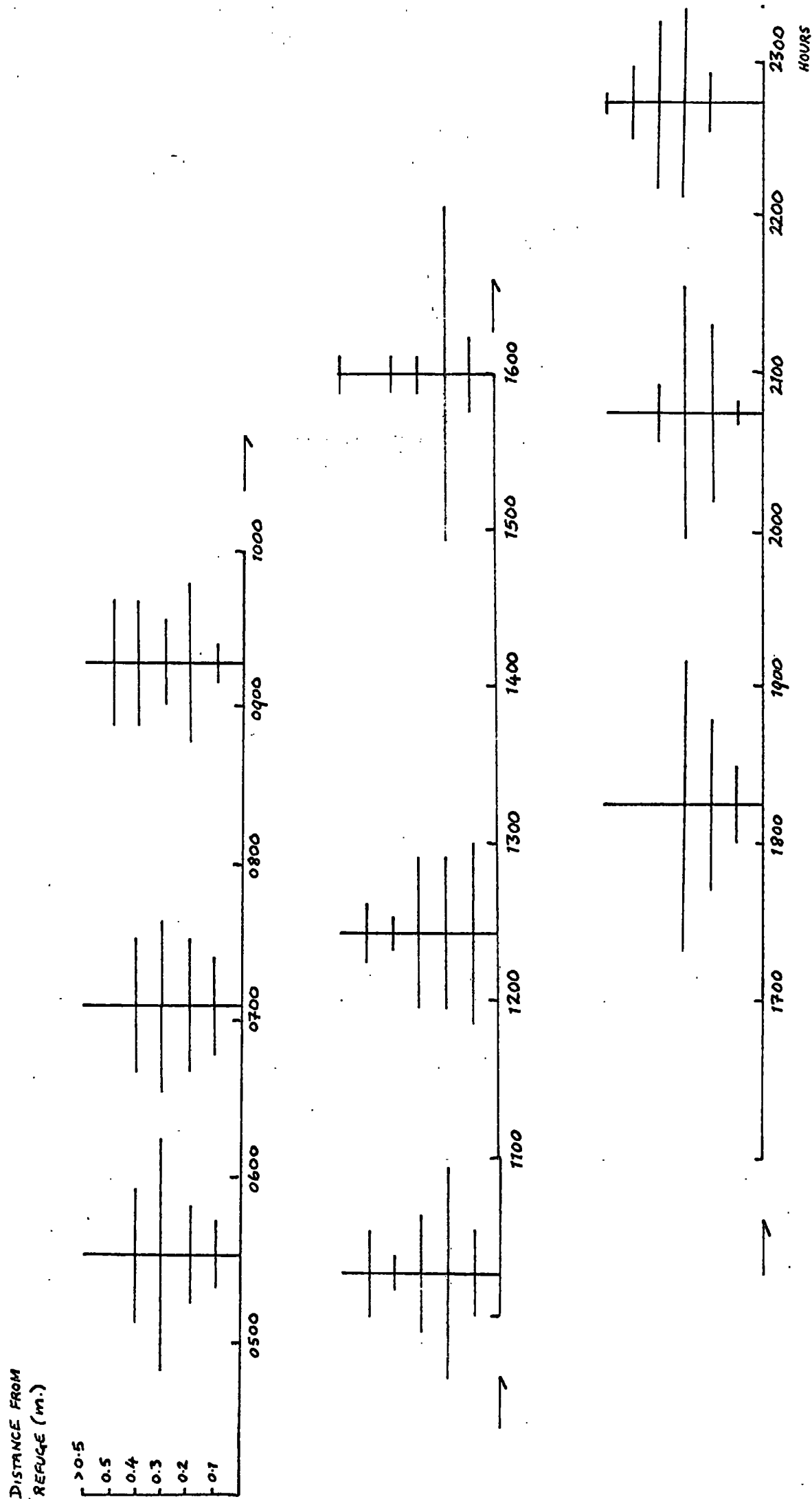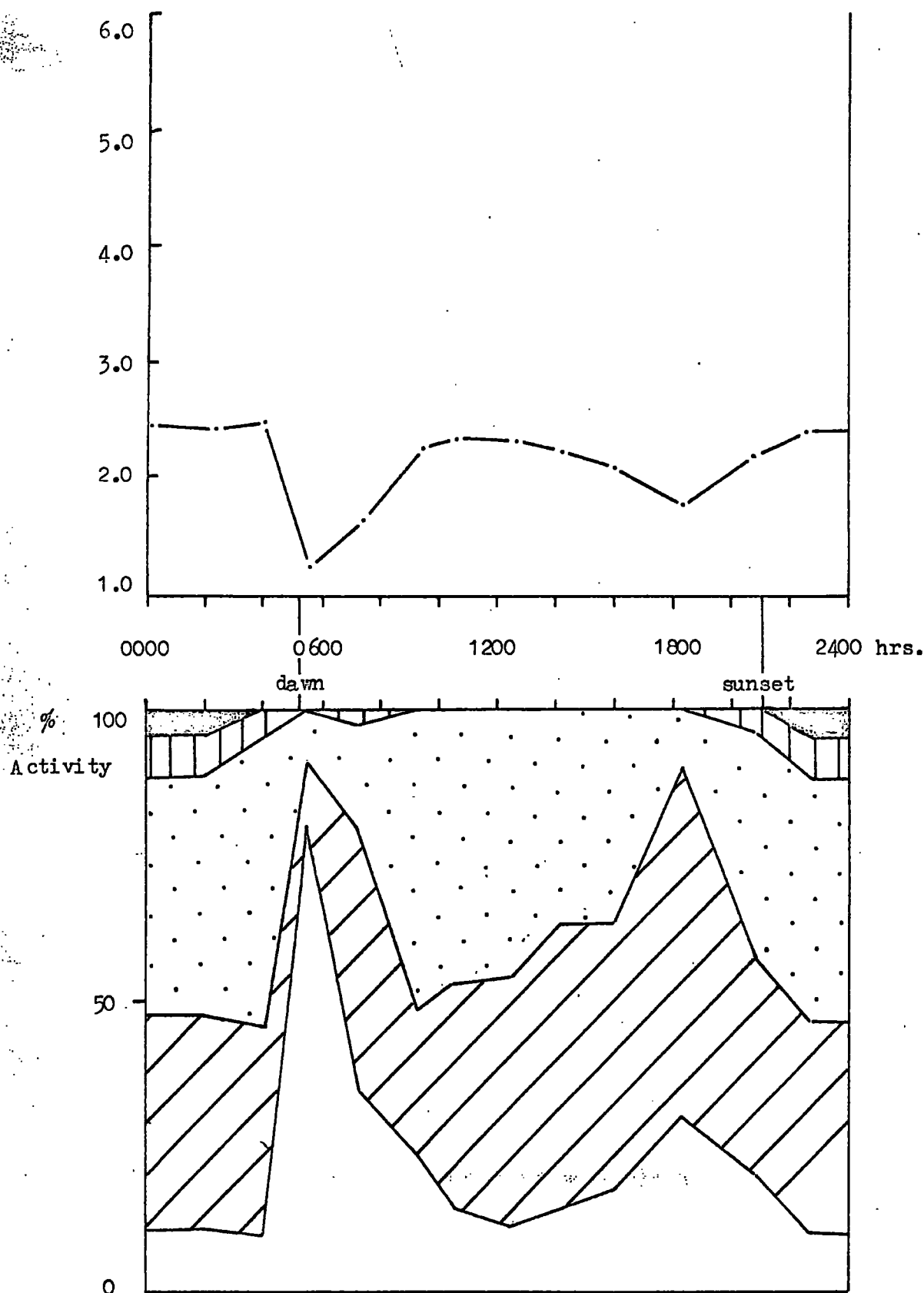
Fig.(12) : Average Activity Index, (AAI), and Percentage Activity
recorded over a twenty-four hour period at Boulmer,
pool 12 , 8/5/76

SCORE:　1　□□□　　3　□·· ·□　　5　□□□□

　,2　▨▨　　4　□— —□　　6　▨▨
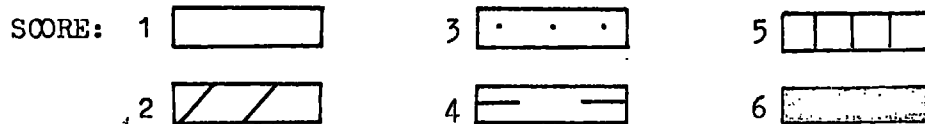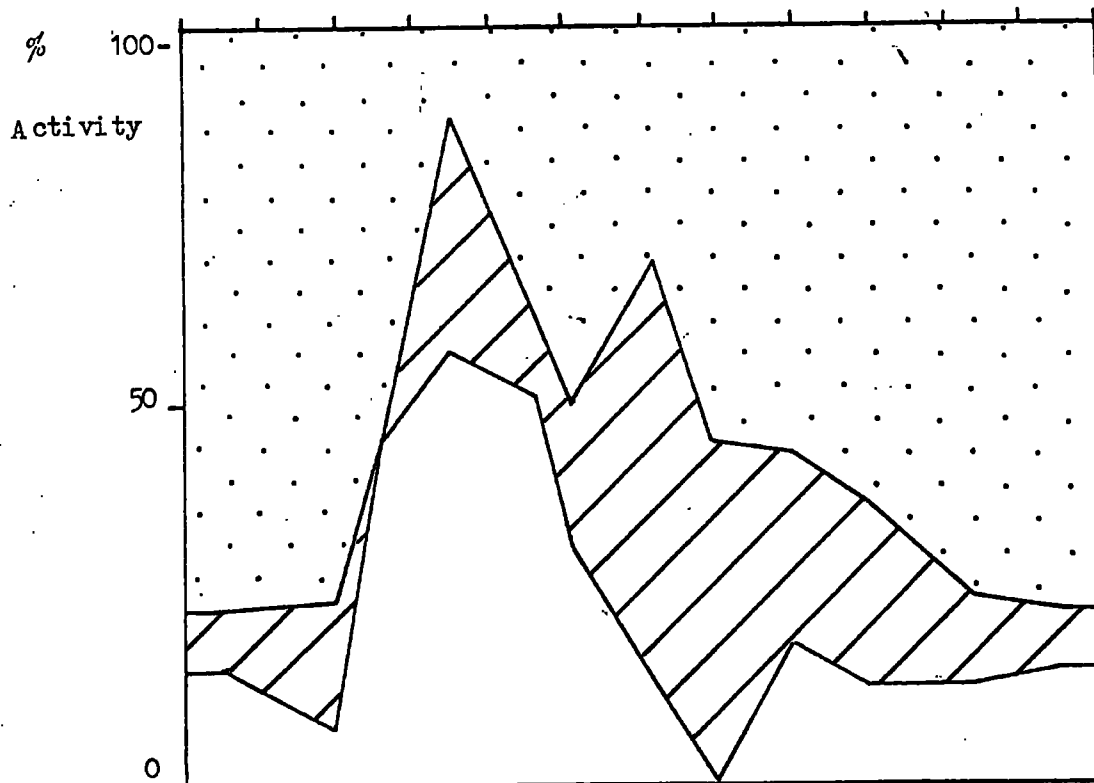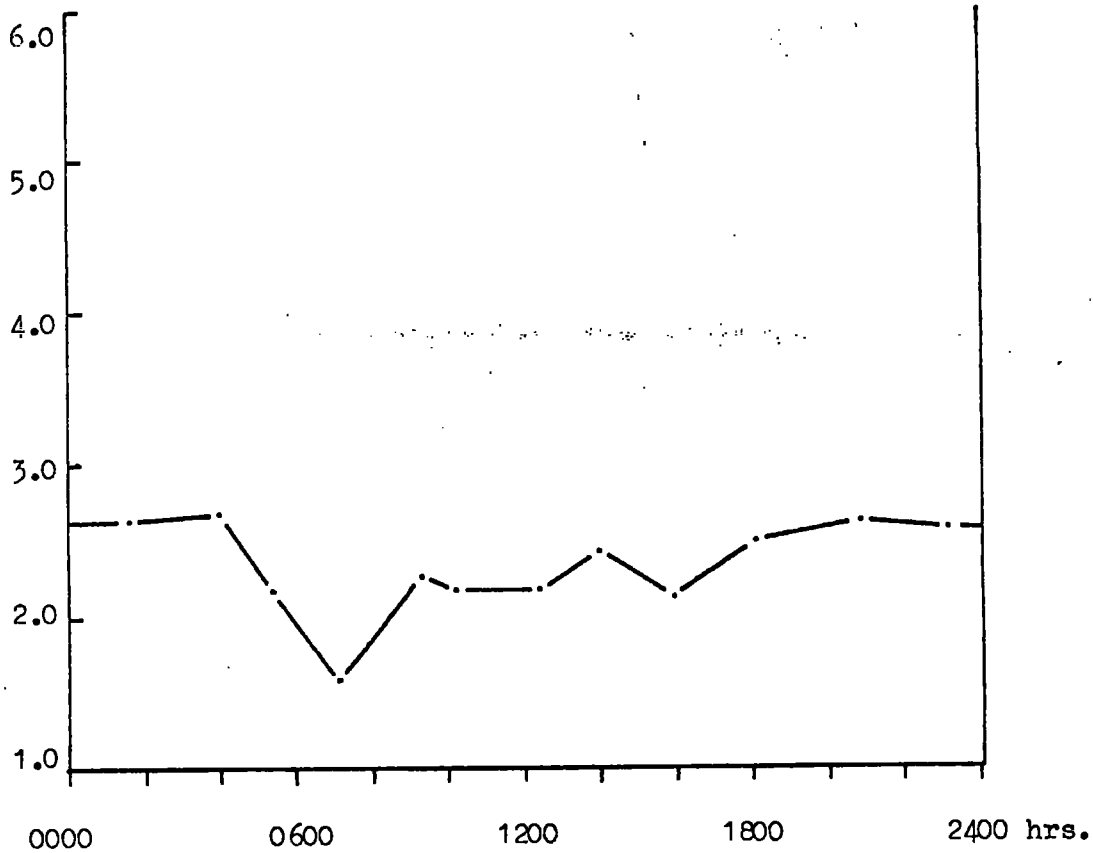
Fig.(14): Average Activity Index, (AAI), and Percentage Activity recorded over a twenty-four hour period at Boulmer, pool 2, 8/5/76

SCORE: (As for page 48 .)
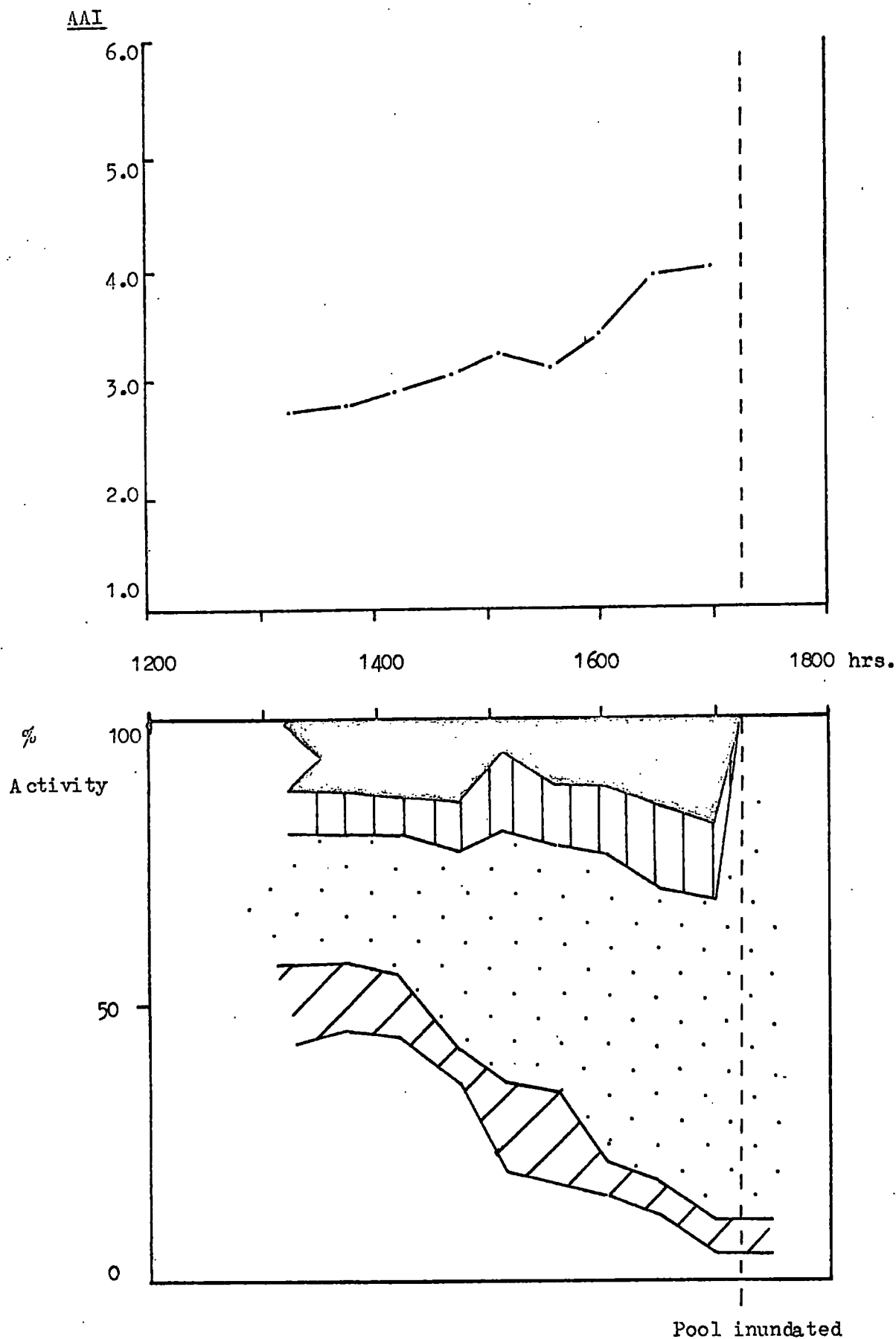
Fig.(15): Average Activity Index, (AAI), and Percentage Activity
recorded over a six hour period at Hartlepool,
pool 23, 16/6/76

SCORE: (As for page 48.)
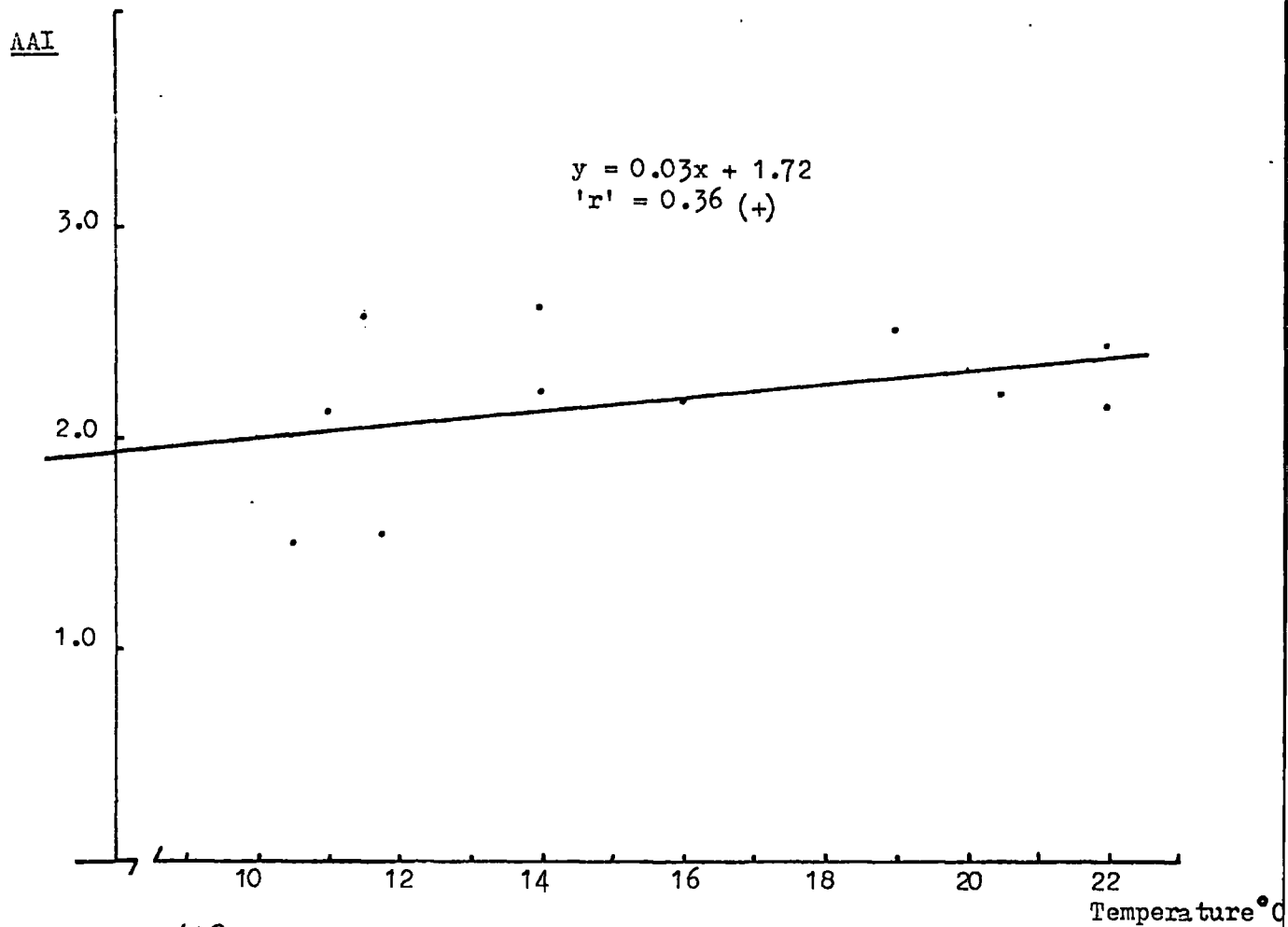
Fig.(16): Average Activity Index v. Water Temperature in
Pool 2 at Boulmer, 8,5,'76.
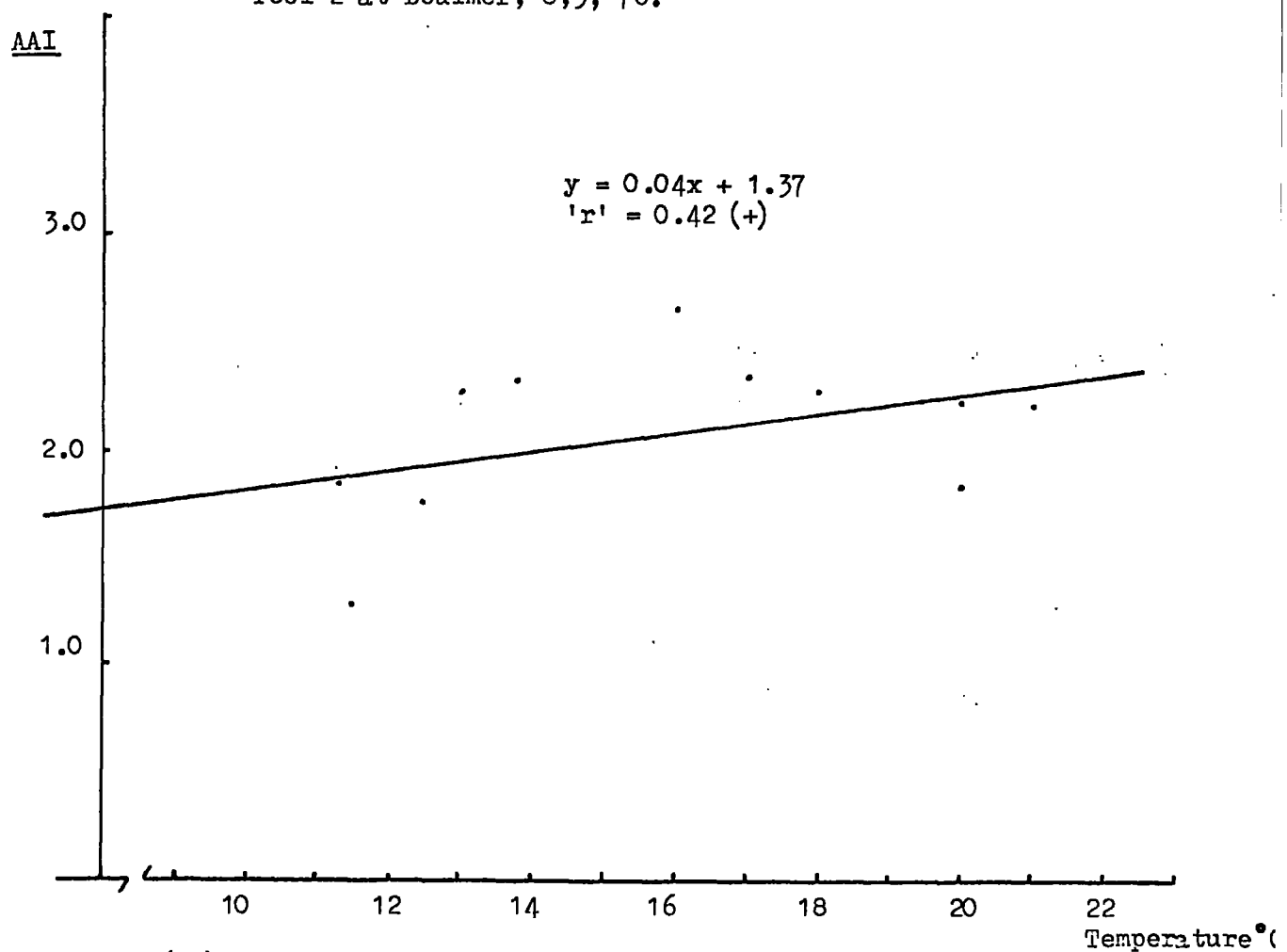
Fig.(17): Average Activity Index v. Water Temperature in
Pool 12 at Boulmer, 8,5,'76

6.21 Variation due to temperature changes

The activity in the pools does not seem closely correlated with temperature. The water temperature during the most active period had not increased from that recorded in the hours before dawn. The plateau in activity was reached by 0900 hrs at which time the temperature in the pool had barely risen to 13°C. The continued rise in temperature until 1600 hrs is not reflected in any further changes in activity.

Regressions of water temperature against AAI for animals in pools 2 and 12 are given in Figs.(16) and (17). 'r' is positive but low. One might therefore claim that there is a slight reduction in activity with increasing temperature.

Observations made during June suggest that at temperatures higher than about 25°C winkle behaviour in the pools begins to be modified. When the water in pool12 reached 33°C no winkles were observed feeding; all were clumped in refuges below water except for a small number hanging around the pool margins.

6.22 The influence of changes in oxygen tension in the pool

Inhibition of winkle activity by oxygen depletion in Boulmer pools seems unlikely. Nevertheless the most inactive period is during the early morning when low oxygen tensions could be expected to develop. However, the small fluctuations in pH do not suggest progress towards such unfavourable conditions.

6.23 Tidal rhythms

The tide did not appear to influence the behaviour of winkles in pools 2 and 12 on the 8 - 9/5/76. The high water mark on this date was some thirty metres from the study pools so perhaps this is hardly surprising.

ACTIVITY	Pool 4		Pool 12	
SCORE	No.	%	No.	%
1	5	12	25	17
2	5	12	60	42
3	11	25	60	42
4	0	0	0	0
5	2	5	0	0
6	20	46	0	0

Table(5): Afternoon activity in pool4,(below High Water),

compared with that in pool 12, (above High Water),

on 25/5/76.

ACTIVITY	2		12		6		8		10		11	
SCORE	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1	13	21	126	14	76	21	8	17	11	11	5	7
2	25	39	373	41	224	60	3	6	30	31	19	28
3	26	40	335	37	58	16	9	19	11	11	4	6
4	0	0	0	0	2	1	0	0	0	0	0	0
5	0	0	0	0	6	3	5	11	8	8	5	7
6	0	0	0	0	0	0	21	45	36	37	34	51

Table(6): Activity in pools at Boulmer across the shore

6.30 Variation over the days that the pool is severed from the sea

Pool 12 was cut off from the sea on 5/5/76 and not inundated again until 11/5/76.

The distribution and activity of winkles in the pool was recorded at 1300 hrs every day from 8/5 to 11/5. The results are given in Table(4). The χ^2 confirms the apparent homogeneity of the data:(χ^2 = 1.32, p$\approx$0.97, d.f. = 6). One is able to conclude that there is no progressive change in winkle behaviour over this period.

Obviously this does not apply to shallow pools such as 6 which disappear. In these cases the winkles retreat to refuges as they become gradually exposed during the drying up process. They make little attempt to remain below the dropping water surface. When pool 6 became completely dry all the winkles were found clumped in the refuge; a crack running along the edge of the pool.

6.40 Variation between pools; (i) Down the shore

At any time other than during high Spring tides pools are to be found both above and below the level of high water. Those below are isolated from the sea for not longer than twelve hours while those above may not have been refreshed by inundation for several days. It is likely that winkle behaviour differs considerably in the two types of pool.

Pool 3 was compared with pool 12 during the afternoon of 25/5/76. The former became submerged by early evening.

In pool 3 large numbers of winkles were clumped around the pool above the water surface:(see Table(5)). Only a small percentage were feeding.

It seems that winkles subject to a tidal regime tend to synchronize their feeding by the arrival of the tide. Crawling to a position just above the water surface enables them to become immediately aware of the imminent flood as the level in the pool rises. Winkles in the upshore pools have no such method of synchronization.

The approach of the tide has a definite effect on those winkles feeding

in the lower pools. Consider the observations made on winkles in pool 23 on 16/6/76:(see Fig.(13)).

From 1400 - 1535 hrs there is no significant variation in the proportion of winkles feeding:(X^2 = 15.4, p<0.01, d.f. = 3). The splashes from breaking waves did not reach the pool until 1645 hrs by which time the AAI had risen to 4.0 from 2.8. No animal was seen feeding when the ledge finally became submerged at 1715 hrs.

Winkles must either have a well-developed sense of tidal periodicity or they can somehow sense the approaching flood. Perhaps they are warned by reverberations in the rock generated by breakers.

6.50 Variation between pools; (ii) Across the shore

Pools at the same level on the beach vary in their morphology and topography. It is important to know by what degree the behaviour of winkles is influenced by such differences.

Pools 2 and 12 at Boulmer represent extremes of morphology. The former is shallow with gently sloping sides. The winkles retreat to a refuge in the form of a large stone in the centre of the pool. In contrast 12 is deep with near vertical sides.

In both these pools emergence from the water is rare and times spent feeding and resting below the surface are similar:(X^2 = 1.48, p≈0.6, d.f.= 3) , see Table(6).

If one looks at pools with more extreme topographies a somewhat different story emerges. Those with overhangs and crevices near the water surface are seldom without a quota of winkles utilizing such refuges:(see Table(6)).

The figures for pools 6,8,10 and 11 are perhaps slightly misleading since these pools were in the process of drying up and winkles tend to be stranded in their refuges. Nonetheless a considerable variation in the proportion of animals above the water surface and the degree of clumping must be assigned to differences in relief.

ACTIVITY	May		June		July	
SCORE	No.	%	No.	%	No.	%
1	126	14	15	20	22	18
2	373	41	32	43	48	39
3	335	37	27	36	52	42
4	0	0	1	1	0	0
5	0	0	0	0	0	0
6	0	0	0	0	0	0

Table(7): Activity in pool 12 over three months

Results such as this lead one to suspect that the most useful category of behaviour with which to compare pools is percentage feeding. It is arguable that categories (3) to (6) are too dependant on the peculiarities of the terrain. However, it is possible to choose pools of similar size and shape, free of large cracks and other rugosities.

6.60 Variation over the months of the study

Table(7) shows afternoon records for winkle behaviour in pool 12 in May, June and early July. There are no significant differences: $(X^2 = 2.69, p > 0.7, d.f. = 5)$.

By late July and August the numbers of winkles to be found at all sites had considerably lessened. This was most dramatic at Boulmer on the extensive upper shore. The very high temperatures reached in July must have caused high mortality. The activities of winkle pickers may also have contributed.

Having examined the nature of variation in winkle behaviour at a single site it is possible to formulate a strategy for comparing sites which minimises such 'in-site' variation. This greatly improves the chances of identifying 'between-site' variation.

Pools at different sites should be above current high water. They should not have been inundated for at least forty-eight hours. Water depths should exceed 0.1 m and pools with deep cracks and overhangs be avoided. It is safest to examine the winkles between the hours of 0900 and 1600 when the behaviour is fairly uniform. It is possible that aberrations in behaviour could result from excessively high water temperatures;(greater than 25 C.

7.00 Winkle behaviour at different sites

7.10 General remarks

Of the three sites examined by far the greatest numbers of winkles live
on the rocks at Boulmer. They extend in quantity from MTL to just below
the height of normal Spring tides. At low water many are exposed on the
rock surfaces. They are found in pools both deep and shallow, in cracks,
under weed and beneath stones. They are absent only from under larger rocks
where the substrate has become blackened with sulphides and anaerobic.

In the extensive pools about MTL there are fewer winkles away from the
refuges provided by stones and rocks. It is probable that their numbers
on the open floor of the pool are limited by the numerous crabs, in particular
Eupagurus bernhadus, the common hermit, and the shore crab, Carcinas maenas.

Many winkles are found in the ephemeral pools on the upper shore
which regularly dry out during their period of severence from the sea.

At Marsden L.littorea are only common up to the level of MHWN. In a zone
of pools just below MHWN the winkles reach an abundance comparable with
that found at Boulmer. The most striking difference in their distribution
is that few are to be found exposed on the rock surface; they are either
beneath the water or taking refuge under stones. Because the densities in
Marsden and Boulmer pools are roughly equal the numbers of inactive, emergent
winkles found at the latter site is probably not a density dependant
phenomenon.

There are very few animals to be seen in small ephemeral pools around
MHWS at Marsden. They are restricted to the deeper and more permanent
pools.

There are not only fewer winkles at Hartlepools' Point than there are
at the other two sites but their vertical range on the shore is much more
limited. They are common in shallow pools just below MHWN; elsewhere they
are scarce. In the deep pools on the middle shore they remain below the

ACTIVITY SCORE	BOULMER		MARSDEN		HARTLEPOOL	
	No.	%	No.	%	No.	%
1	126	15	14	13	9	9
2	373	45	59	56	5	5
3	335	40	30	28	88	86
4	0	0	1	1	0	0
5	0	0	1	1	0	0
6	0	0	0	0	0	0

(a) Pools above high water; (2, 12, 21A, 29, 30).

ACTIVITY SCORE	BOULMER		MARSDEN		HARTLEPOOL	
	No.	%	No.	%	No.	%
1	30	23	38	40	61	40
2	15	12	48	51	36	24
3	18	14	8	8	52	34
4	0	0	1	1	0	0
5	6	5	0	0	0	0
6	60	47	0	0	2	1

(b) Pools below high water; (4, 17, 25 - 28)

Table(8): Winkle activity in pools at the different sites

water surface but do not venture into the silty depths, preferring to remain scattered about the pool margins.

As at Marsden very few animals are found exposed on the rock surface. Ephemeral pools do not contain many individuals.

7.20 Comparing the behaviour in the pools

The best comparative figures for winkle behaviour at the three sites are shown in the top half of Table(8). Taken together these ratios are obviously different and this is confirmed by a X^2 for all the data: (X^2 = 91.3, p < 0.001, d.f. = 4). However, it is the Hartlepool results that are most peculiar.

At Boulmer and Marsden the ratio of the three categories, (1):(2):(3), is similar: (X^2 = 0.22, p ≉ 0.6, d.f. = 1). Winkles feed for about 14% of the time. The percentage feeding at Hartlepool is rather lower, 9%, but the main difference lies in the high percentage found clumped below the water surface.

At none of the sites do winkles habitually haul up above the water in pools high on the shore. They prefer to remain below the surface where their activity is best expressed as percentage feeding. On this criterion there are no significant differences between sites.

The high degree of clumping at Hartlepool cannot be explained in terms of a more complex pool topography. Instead it suggests that a larger percentage of winkles elected to remain totally inactive below the surface: in effect the pool population divided into two groups, one inactive and the feeding and resting for periods comparable to those observed at Marsden and Boulmer.

If one examines pools below the high water mark, (see the bottom of Table(8), it is clear that there is one striking feature that distinguishes the distribution of winkles at Boulmer. Approximately 50% of the pool's

inhabitants are above the water surface. The Marsden and Hartlepool winkles are seldom found in such a position and remain underwater where 40% can usually be observed feeding. Perhaps feeding is restricted at high water unlike Boulmer where it often seems to be initiated by the flood tide.

Most probably this difference is related to the degree of exposure experienced by the winkles at high water. In the calm conditions of Boulmer feeding animals are unlikely to tbe dislodged as they move over the rock surface. The turbulent sea at Marsden and Hartlepool may cause such excursions to be rather more dangerous.

8.00 The reactions of winkles to various pollutants introduced to the pool

8.10 The method used for performing these experiments is described on page 41.

The reponse of the experimental population to increasing concentrations of pollutant is illustrated in the following figures where the Average Activity Index, AAI, is plotted against concentration in ppm.
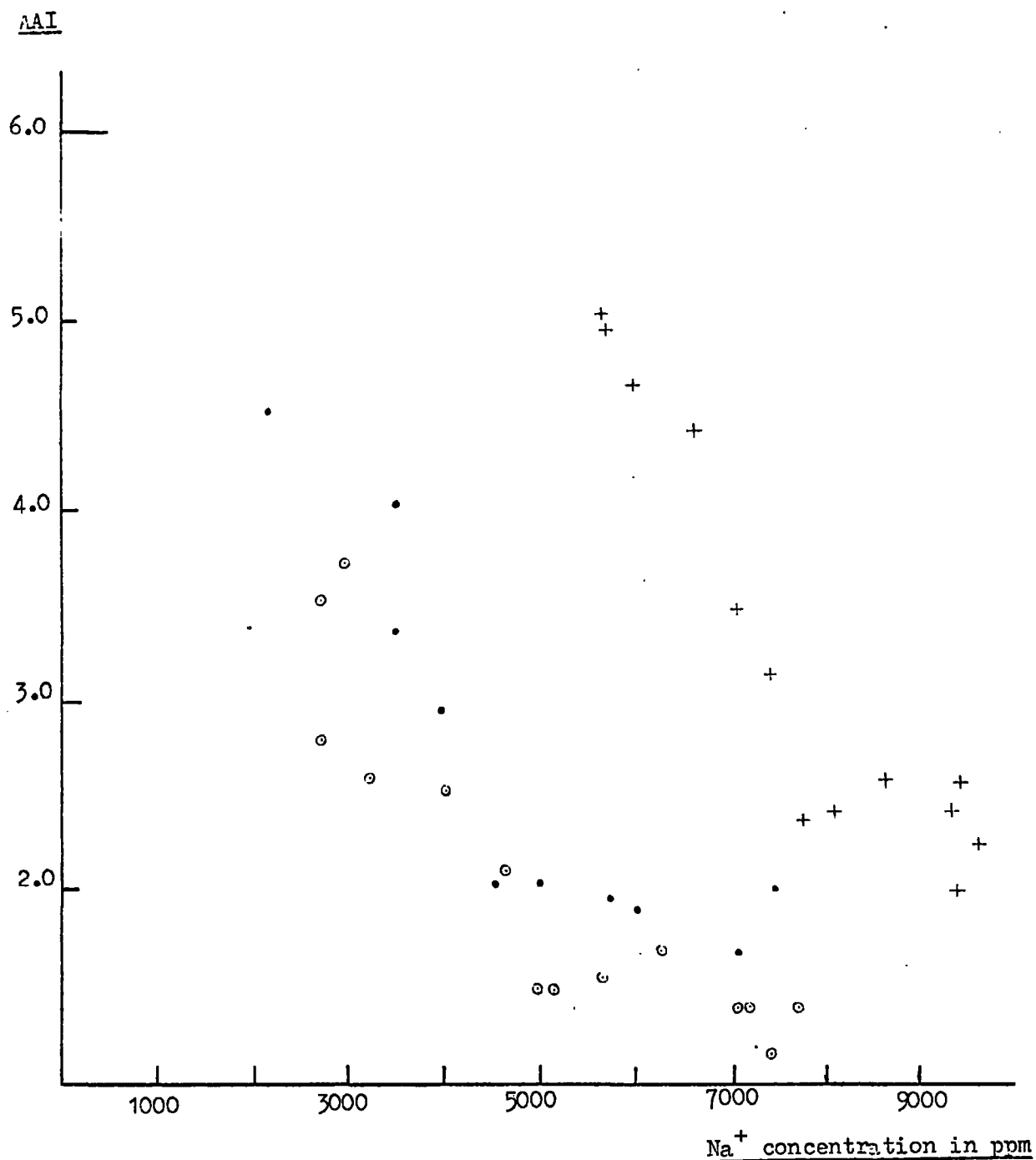
Fig.(18): Changes in Average Activity Index, (AAI), with differing

Na$^+$ concentrations in the pool water

+ Boulmer, pool 16, 22/5/75

○ Marsden, pool 18, 2 and 8/6/76

• Hartlepools' Point, pool 25, 16/6/76
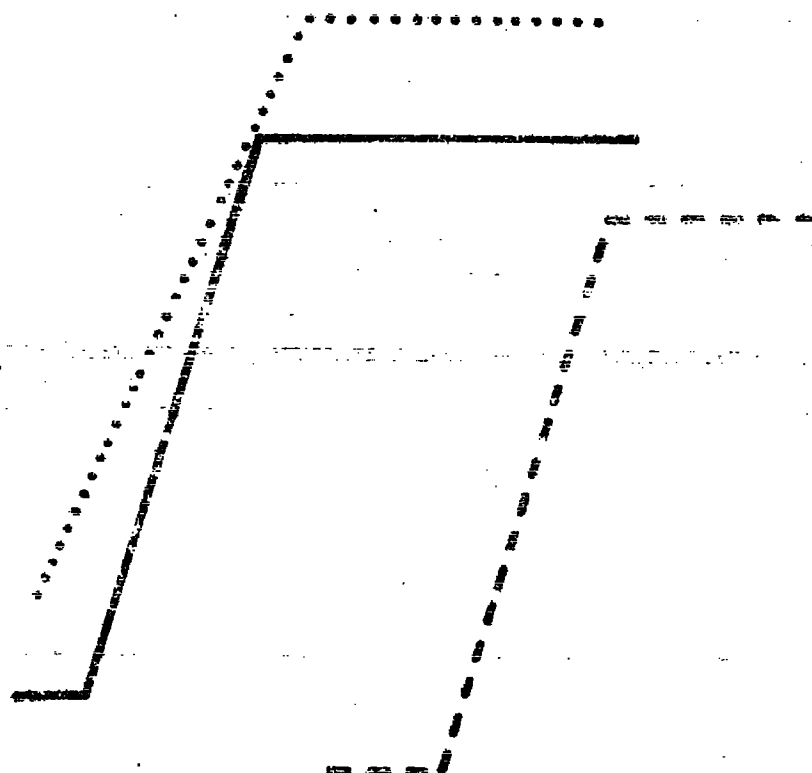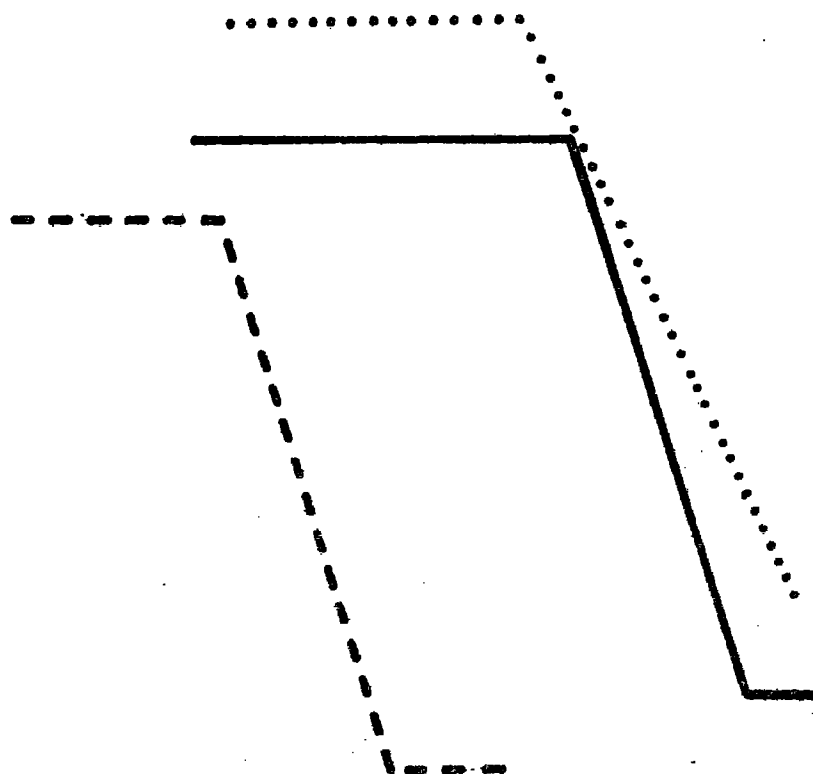
8.20 The effect of reducing the salinity in the pools

The reponse curves illustrated in Fig.(18) are typically 'Z'-shaped: reducing the ionic concentration from 'normal' values initially had little effect but below a certain concentration the winkles began to vacate the pool. This occurred over a range of concentratiOns probably related to differences in individual tolerance of dilution. A few winkles did not emerge but remained inactive below water. These animals kept the AAI under five. Further dilutions did not increase this figure.

It is interesting to note that, although the thresholds of response at Marsden and Hartlepool were similar, the winkles at Boulmer reacted more rapidly and began to leave the pool when the Na^+ concentration had been reduced to 7,800 ppm.

Since the commonly experienced salinities at Marsden and Hartlepool are both somewhat lower than at Boulmer this difference in response may indicate that the winkles are acclimatized to waters of lower salinity. At all three sites the threshold of response is approximately 2,500 ppm Na^+ below the initial value at the start of the experiments.

Natural dilutions tolerated by L.littorea vary from 4,600 ppm Na^+ in the Baltic to 6,400 ppm Na^+ on the Norwegian shore of the North Sea: (data compiled by Brattegard 1966).
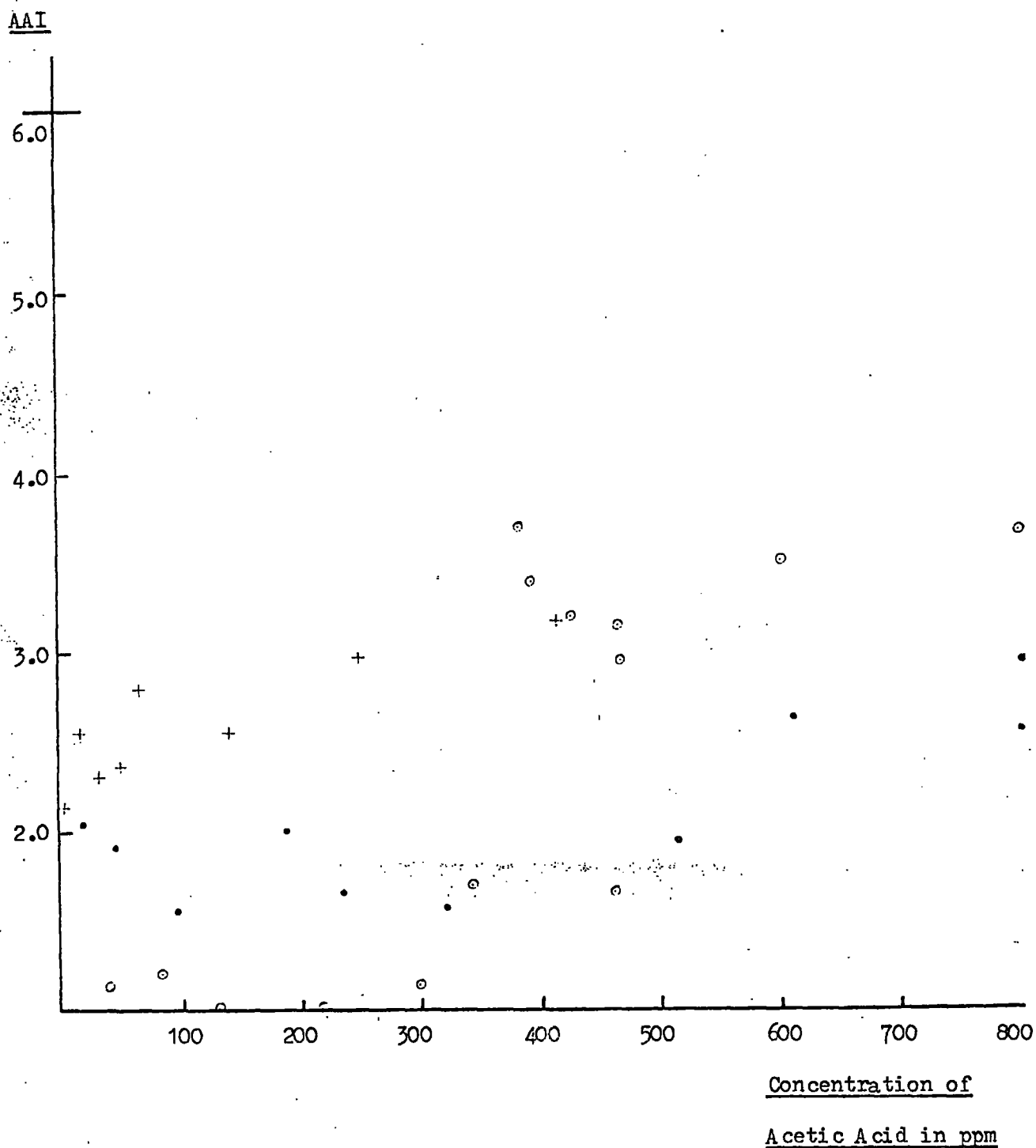
Fig.(19) : <u>Changes in Average Activity Index, (AAI), with differing</u>

<u>concentrations of Acetic Acid in the pool water</u>

+ Boulmer, pool 16C, 10/8/76

⊙ Marsden, pools 20 and 21, 23/6/76

• Hartlepools' Point, pool 25, 25/6/76
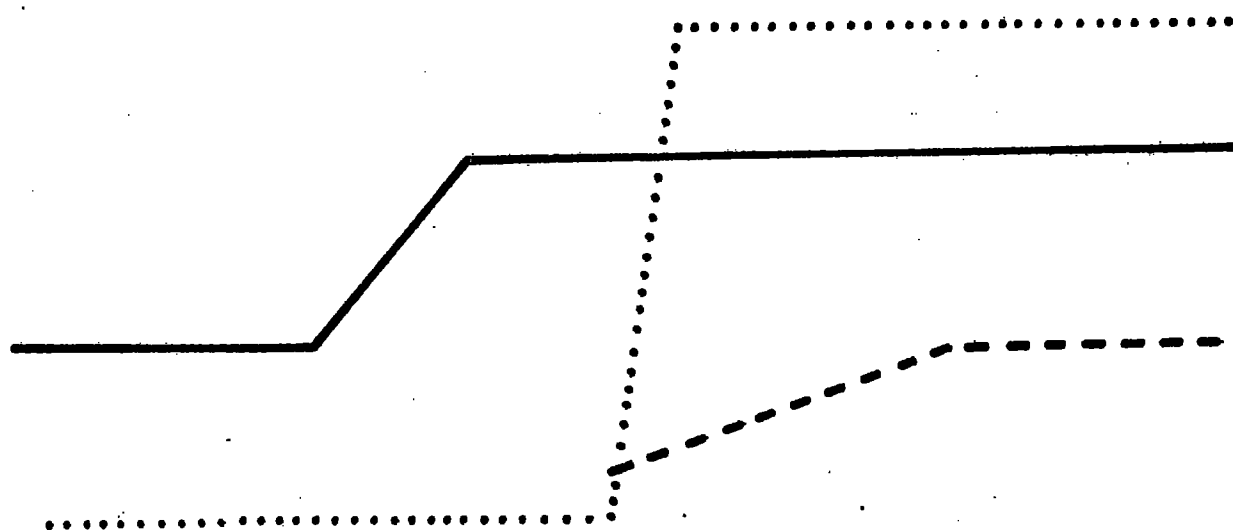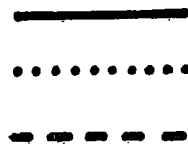
8.30 The response to increasing concentrations of Acetic Acid

At Marsden winkles clearly responded to concentrations in excess of
350 ppm by emerging from the pool and becoming inactive.

The curves for Boulmer and Hartlepool do not reveal such a definite
reaction. However, it is clear that avoidance behaviour began at the latter
site as the Acetic Acid concentration approached 500 ppm. At Boulmer,
although a threshold is not apparent, the winkles may well have been respond-
ing to concentrations as low as 200 ppm.

It is difficult to explain why the various populations of winkles
should respond differently to a chemical which must be rarely encountered
in the natural environment. One hypothesis might involve the mean size
of the animals: the slightly smaller winkles at Hartlepool may be unable
to respond as rapidly as larger individuals at other sites.

Alternatively it is a temptation to attribute such differences to
the degree of pollution. Animals at the most polluted site, Hartlepools'
Point, may be more tolerant of chemical peculiarities in their environment.

AAI

6.0

5.0

4.0

3.0

2.0

100   200   300   400   500   600   700

Concentration in ppm of
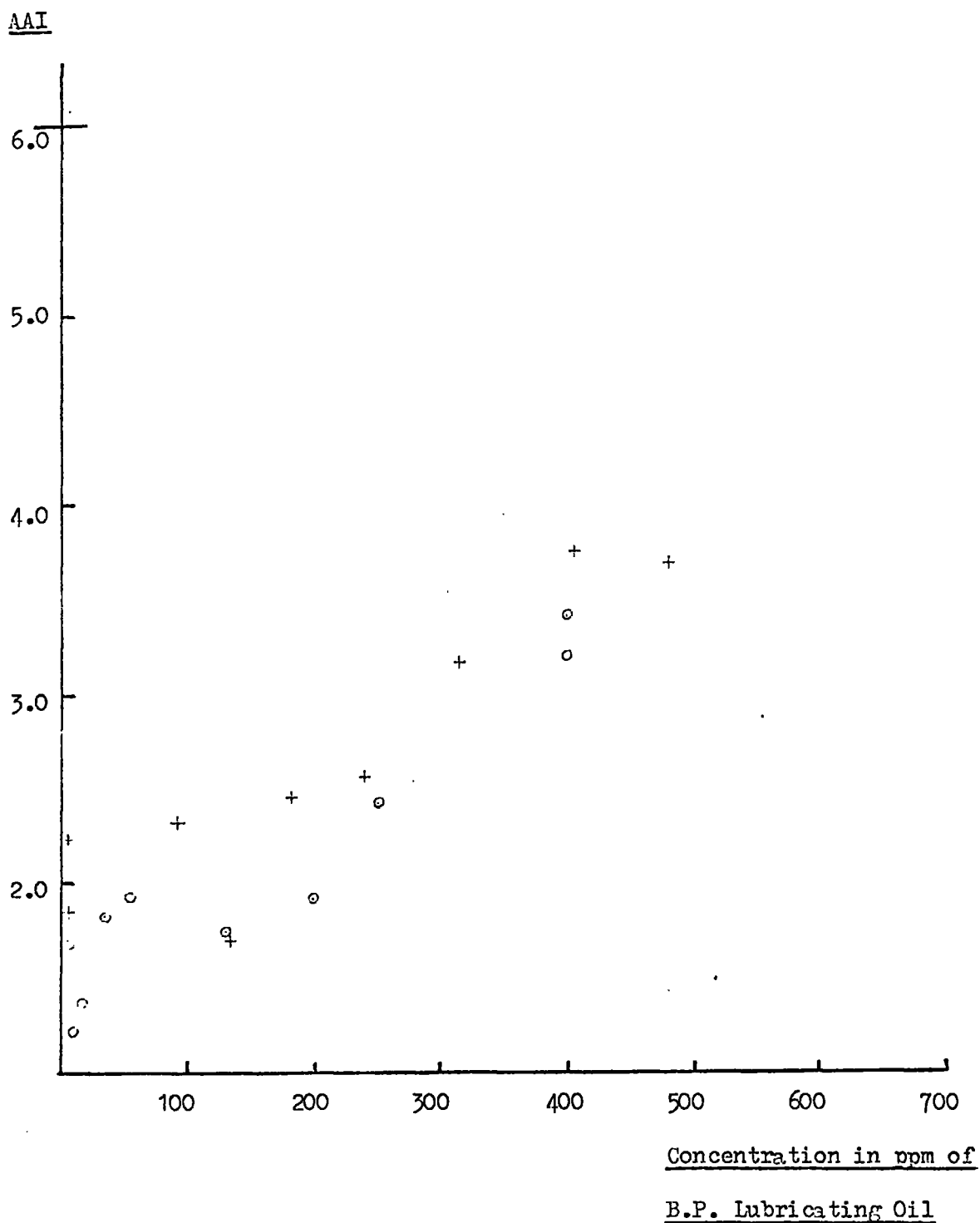
B.P. Lubricating Oil

Fig.(20) : Changes in Average Activity Index, (AAI), with differing

concentrations of B.P. Lubricating Oil

+ Boulmer, pool 16A, 10/8/76

o Marsden, pool 21, 8/6/76
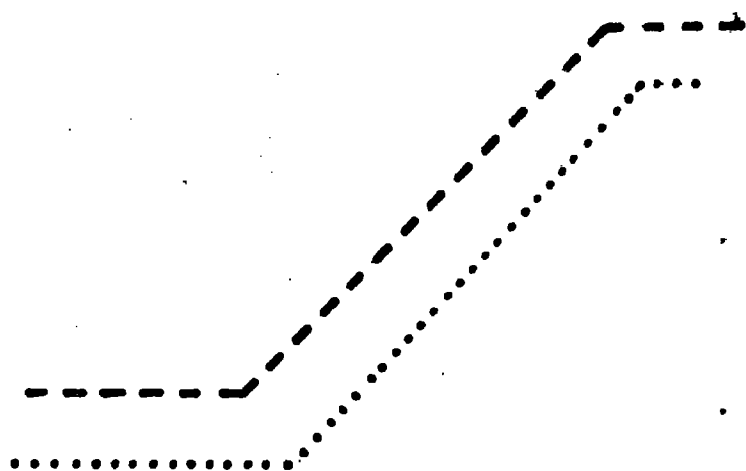
8.40 The response to adding B.P. lubricating oil

Winkles at both Boulmer and Marsden started to respond to additions of oil at concentrations of about 200 ppm. The reaction of most animals was to emerge from the water but some remained clumped and inactive below the surface. It should be remembered that oil is a surfactant and hence concentration in ppm is perhaps an inadequate description of the quantity present.

Surprisingly, animals deep in the water were able to sense some more soluble constituent of the oil and respond accordingly even if this required them to traverse the water/air boundary where the oil concentration is presumably at a maximum.
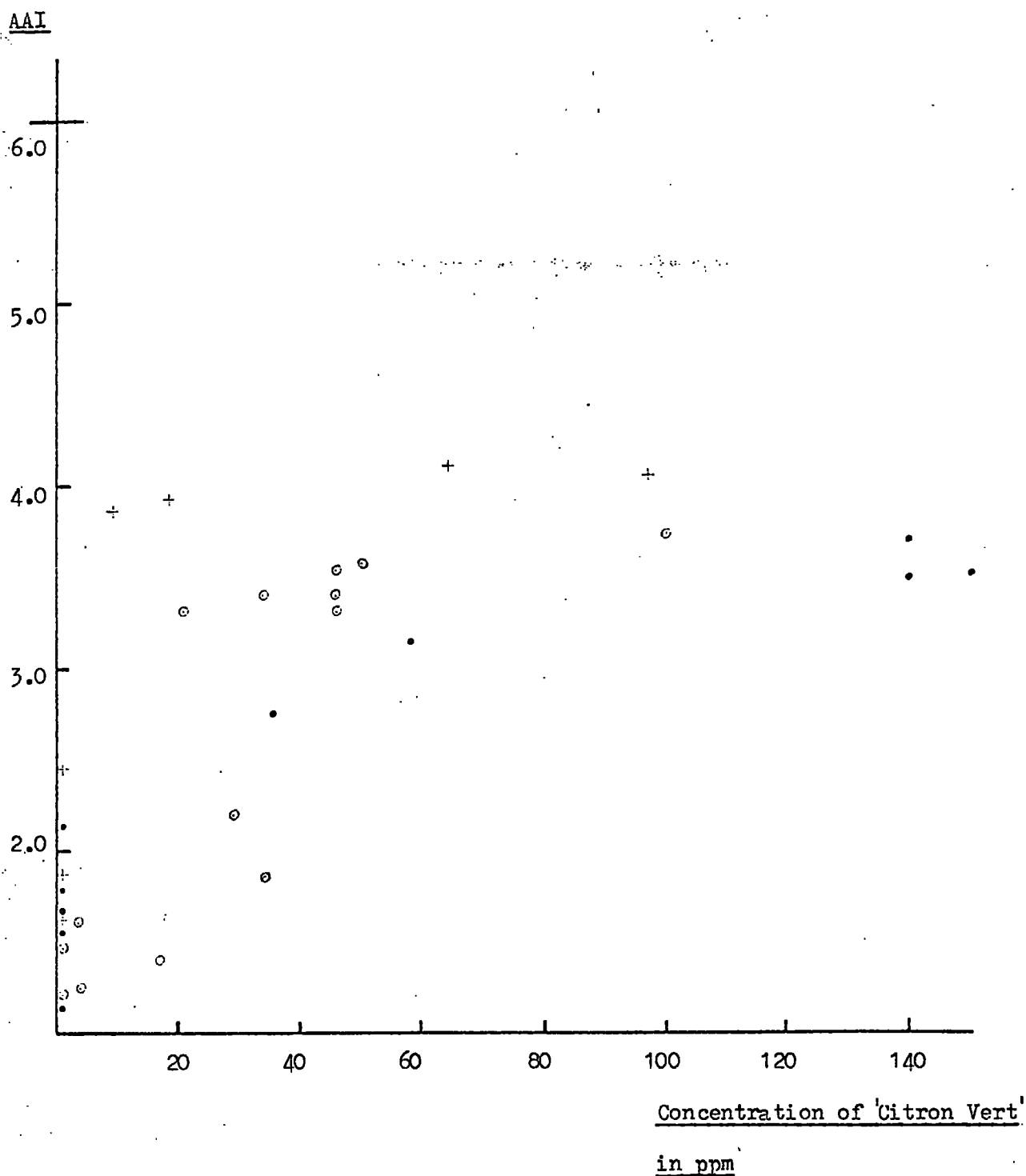
Fig.(21): <u>Changes in Average Activity Index, (AAI), with differing</u>
<u>concentrations of 'Citron Vert'</u>

+ Boulmer, pool 16B, 10/8/76

o Marsden, pools 17 and 20, 8/6/76

• Hartlepools' Point, pool 22, 16/6/76
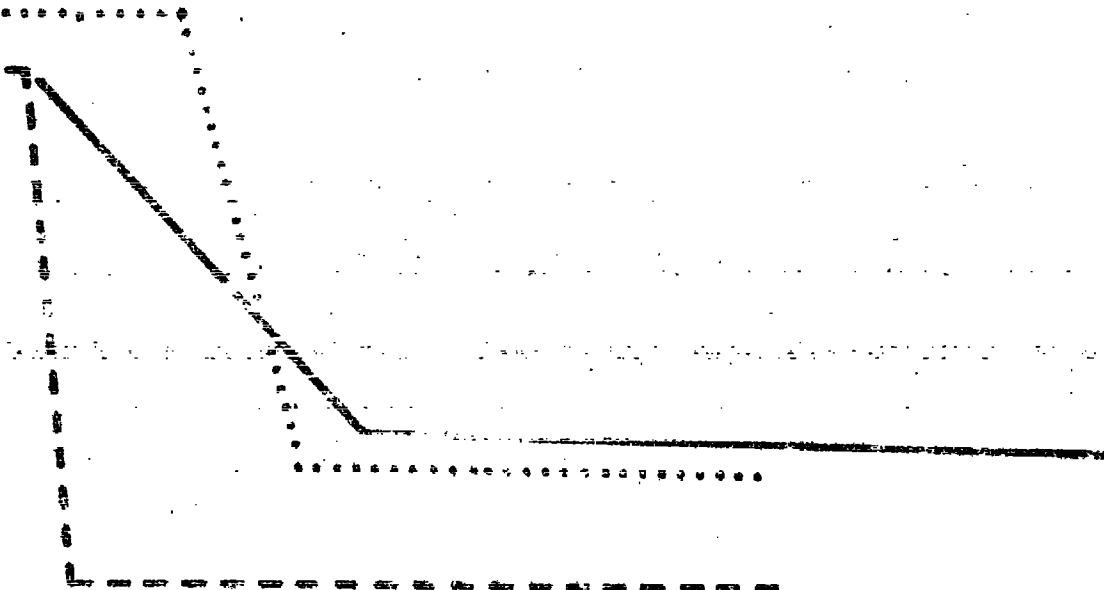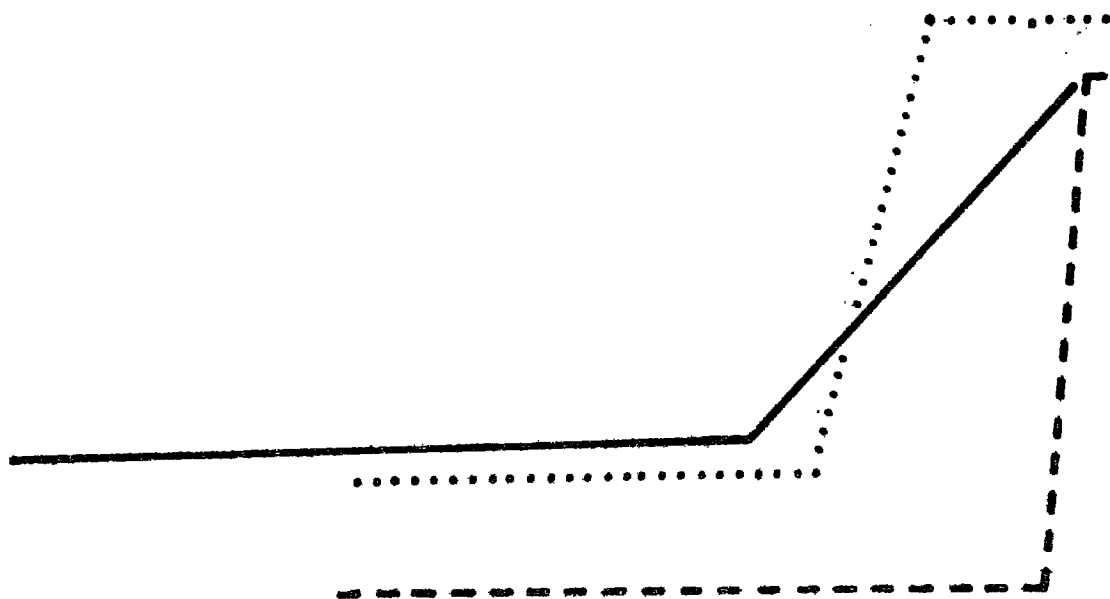
8.50 The reaction to a detergent; 'Citron Vert' washing-up liquid

Winkles proved to be extremely sensitive to 'Citron Vert' and began to evacuate the pools at concentrations not exceeding 25 ppm.

The response in Boulmer pools was somewhat more rapid and vigorous than at the other sites.

The animals were rather more reluctant to pass through the surface film disturbed by detergent than when it was contaminated with oil. Frequently the emerging winkle stopped when its tentacles touched the surface and remained inactive just below the water...
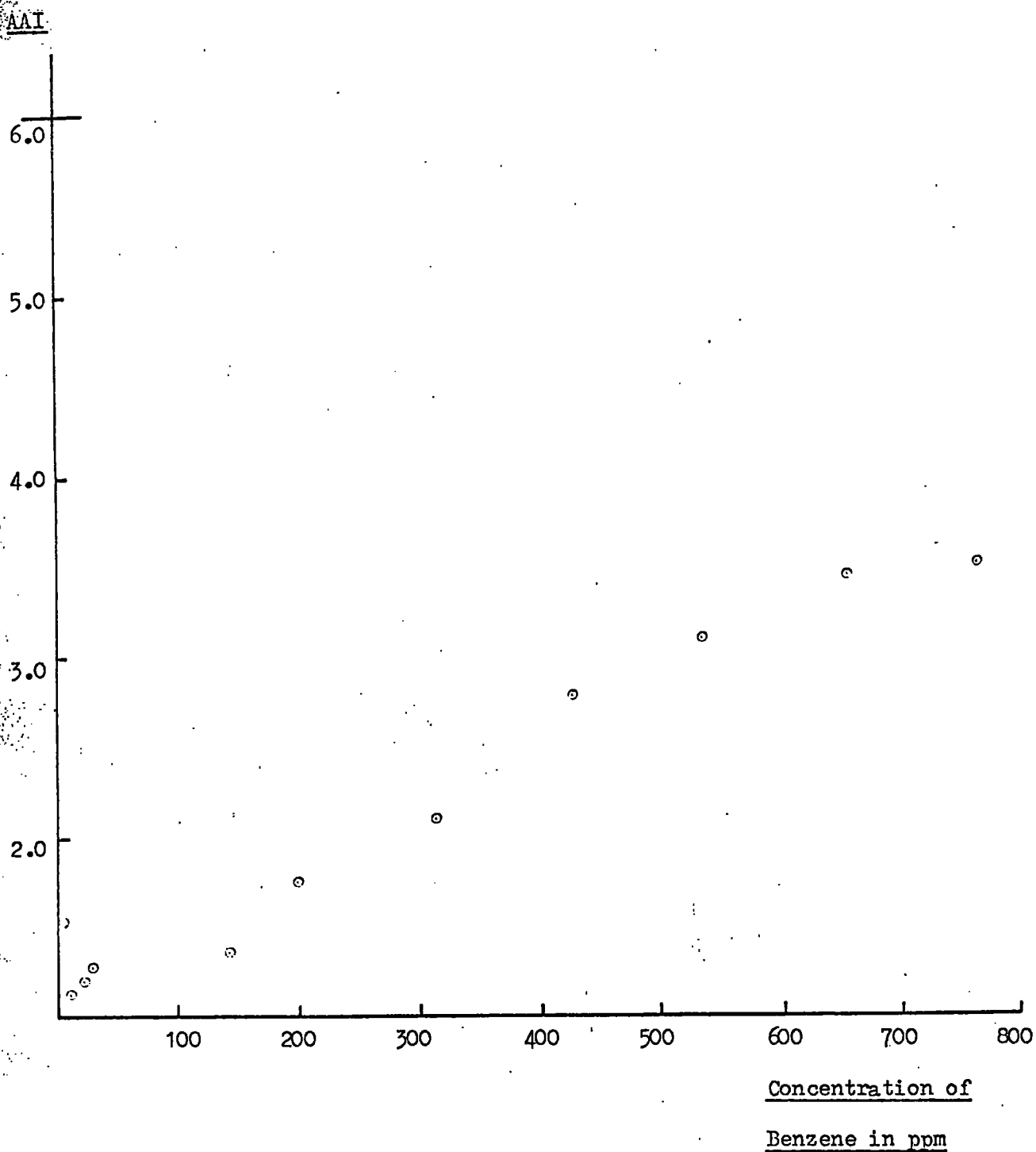
Fig.(22): Changes in Average Activity Index, (AAI), with differing

concentrations of Benzene in the pool water

o   Marsden, pool 18, 23/6/76
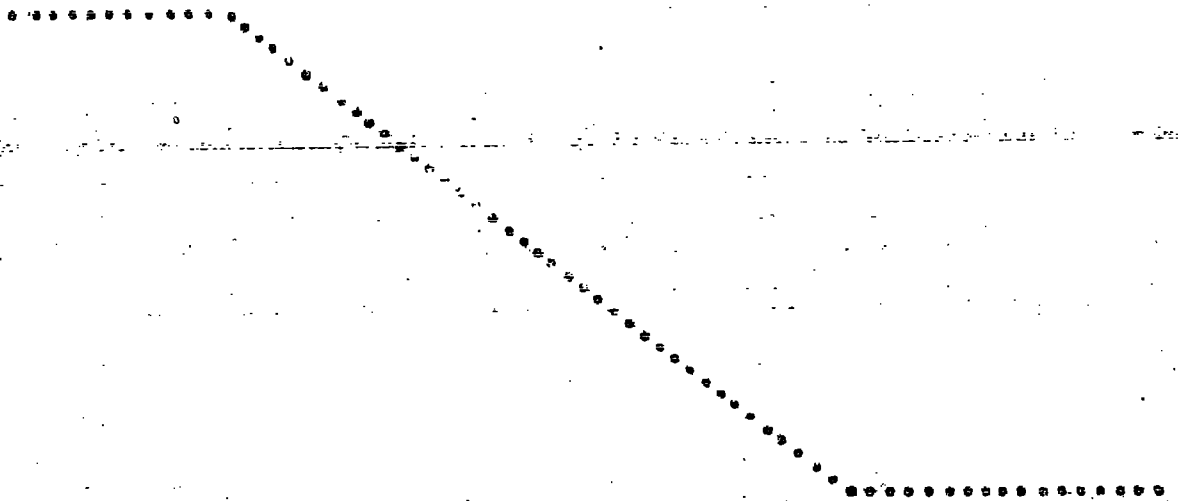
8.60 Winkle response to Benzene

The response, observed at Marsden only, began at concentrations of around 150 ppm and was graduated over an extended range up to 700 ppm. Fewer animals actually left the water and tended to remain inactive below the surface.
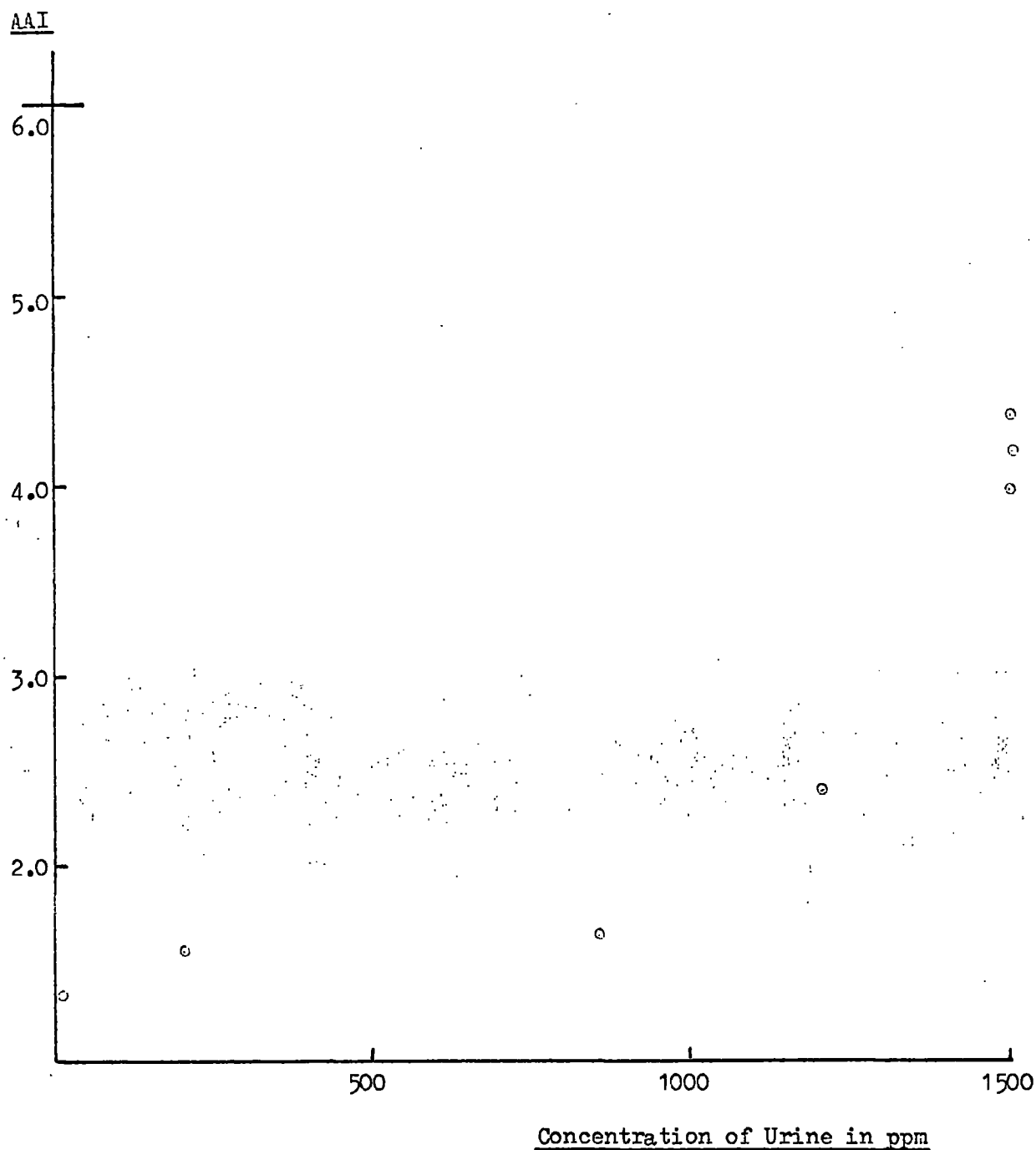
Fig.(23) : Changes in Average Activity Index, (AAI), with differing

concentrations of Urine in the pool water

⊙ Marsden, pool 19, 2/5/76

8.70 Winkle response to Urine

Urine was added to the pool simply because it was an easily available unpleasantry with which to subject the winkles. However, the animals remained unpeturbed until concentrations exceeded 1000 ppm when they began to leave the pool.

9.00 Discussion

The experimental addition of various chemicals to the pools produced two surprising results. Firstly, the reactions of winkles was quite definite in most cases and well expressed by the six point classification of behaviour used in this study. The avoidance reaction generally involved the emergence of the winkles from the water but it was usual for some individuals to remain inactive underwater. Thus AAI scores of five and greater were seldom attained. Secondly, the response curve was often 'S' or 'Z'-shaped, there being a distinct threshold of reaction and also an upper limit beyond which the winkle distribution and activity remained little changed regardless of further additions to the pool.

Although these experiments tell nothing about the chronic influence of pollutants, they do point to the extreme sensitivity of winkles to the introduction of low concentrations to their pool habitat. As a means of determining a comparative effect of various substances when released into the environment this technique of observing the vigour of the behavioural response may be of some interest to those concerned with environmental protection.

The response curves to the same pollutant at different sites suggest that animals from the more polluted sites are somewhat more tolerant of the experimental addition of further noxious substances to their environment. It is important to note that although the initial response has been dulled, in the long term such additions might prove fatal.

Thus the sensitivity of winkles to deliberate pollution may be some measure of environmental quality. A similar result was obtained by Foret-Montardo 1970 who noticed that mussels,(Mytilus galloprovincialis), from polluted waters were less sensitive to detergents than those from unpolluted areas.

The total number, mean size and distribution of L.littorea on the shore would appear from this study to be restricted by littoral pollution

as well as by natural variables such as exposure. It seems likely, for instance, that the range of available habitat is reduced at Hartlepools' Point by excessive sedimentation. The turbidity of the water may also affect the growth of algal foods and this is likely to be an important check on the growth and reproduction of winkles.

There is a suggestion that winkles in the higher pools at Hartlepool are less active than those in similar situations on less polluted shores. However, these results are by no means conclusive and it would seem that there are no great differences in winkle behaviour which can be attributed to variations in pool water quality.

The skeleton of this investigation has been traced and the results have proved indefinite. Further investigation of the behavioural variation would be required to put flesh on the skeleton and conclusively demonstrate that between-site differences exist or not.

It has become reasonably clear, unfortunately, that the behaviour of L.littorea as observed in rock pools is unlikely to provide a useful criterion for defining the extent of littoral pollution at particular sites.

10.00 Summary

(1) Rock pools at Boulmer exhibit large fluctuations in water temperature which depend greatly on the volume and morphology of the pool. pH and salinity do not appear to vary much.

(2) Suspended sediment modifies the temperature extremes which would otherwise develop in polluted rock pools at Hartlepools' Point. Low pH values may be reached in mid-tidal pools during the night. High level pools do not show such fluctuations but do have a more variable salinity than at Boulmer.

(3) Pollution in the form of a heavy nutrient rich sediment load has caused the mid-tidal pools at Hartlepool to deteriorate as a habitat. The animals and plants that live in them have become very limited both in terms of species and numbers. In shallow pools about MHWN the biota is much richer and pollution is not so evident. It is likely that browsers such as limpets and winkles are responsible for the maintenance of their habitat.

(4) Pools around MHWS are similar at all three sites and are characteristically inhabited only by Littorinids. There is some suggestion that Littorina littorea living in Hartlepool pools are less active than those in a similar habitat at Marsden and Boulmer.

(5) Littoral pollution is likely to have had a detrimental effect on the numbers, growth rate and settling success of winkle populations as well as reducing the extent of shore habitats suitable for them.

(6) A baseline study of Boulmer winkles in pools above the then current high water mark showed that the activity of these animals was primarily influenced by the twenty-four hour sun cycle. Other variables seem to have had little effect over the ranges observed.

(7) Comparing the behaviour and activity of L.littorea at the three sites using this knowledge of 'normal behaviour' did not reveal any differences

which could be attributed to pollution. The large numbers of animals exposed on the rock surfaces at Boulmer is more likely to be a phenomenon related to the sheltered nature of the site.

(8) The six-point classification of behaviour used in this study can reveal the avoidance reaction of winkles to various 'pollutants' artificially introduced to their pools. There is usually a distinct threshold concentration above which animals start to emerge from the pool or become inactive below the surface.

(9) Reactions were particularly strong to a detergent which caused rapid evacuation of the pool at very low concentrations. Less violent responses were elicited by oil, benzene, urine, acetic acid and dilution with fresh water.

(10) There is evidence to suggest that winkles from more polluted sites are less sensitive to further exotic additions to the water than those from cleaner areas.

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Percentage Oxygen
Saturation

pH of water in rock pool
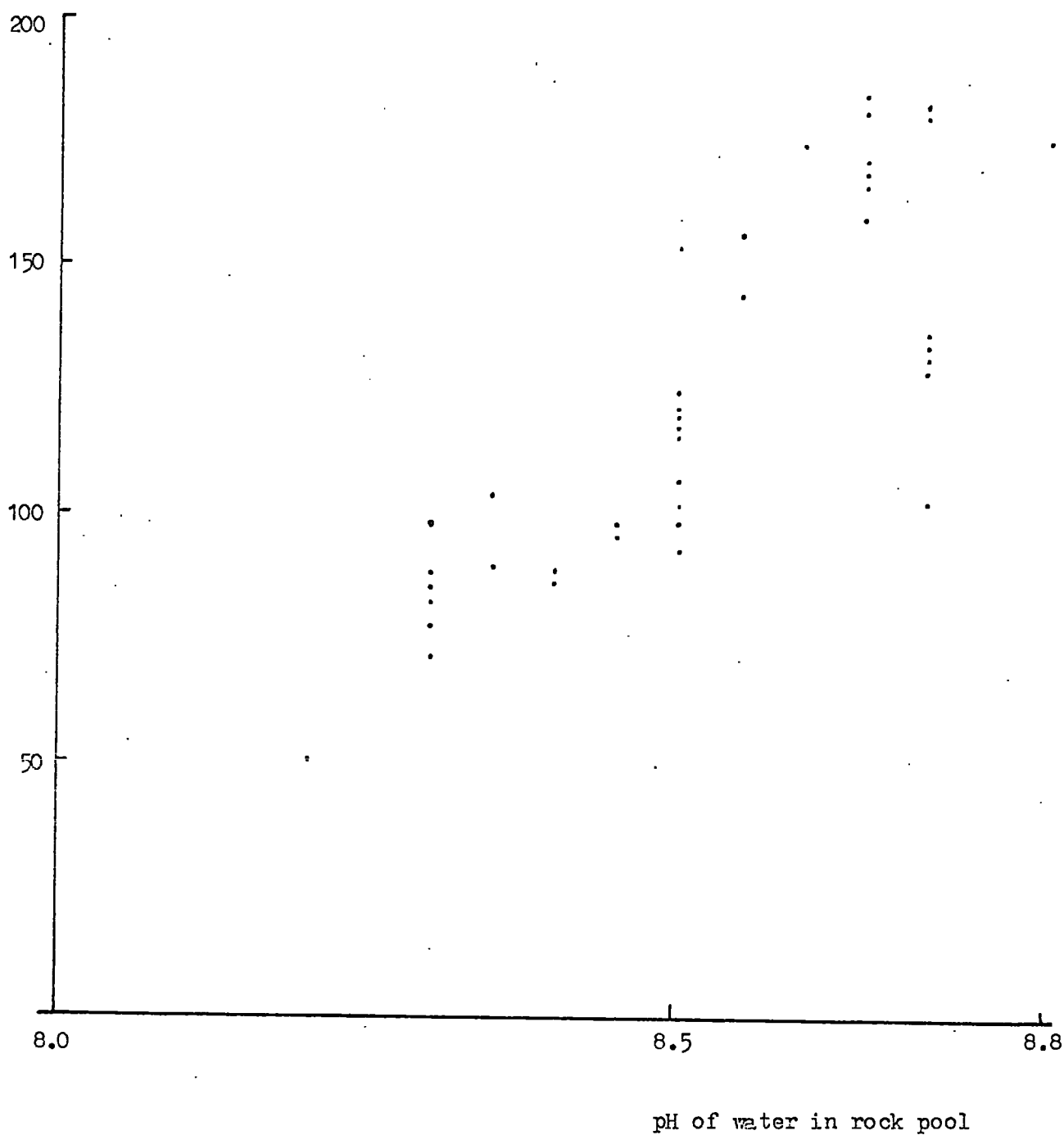
Appendix 1: Relationship between percentage oxygen saturation and pH
in rock pools. Data from Pyefinch (1943).

APPENDIX (2)

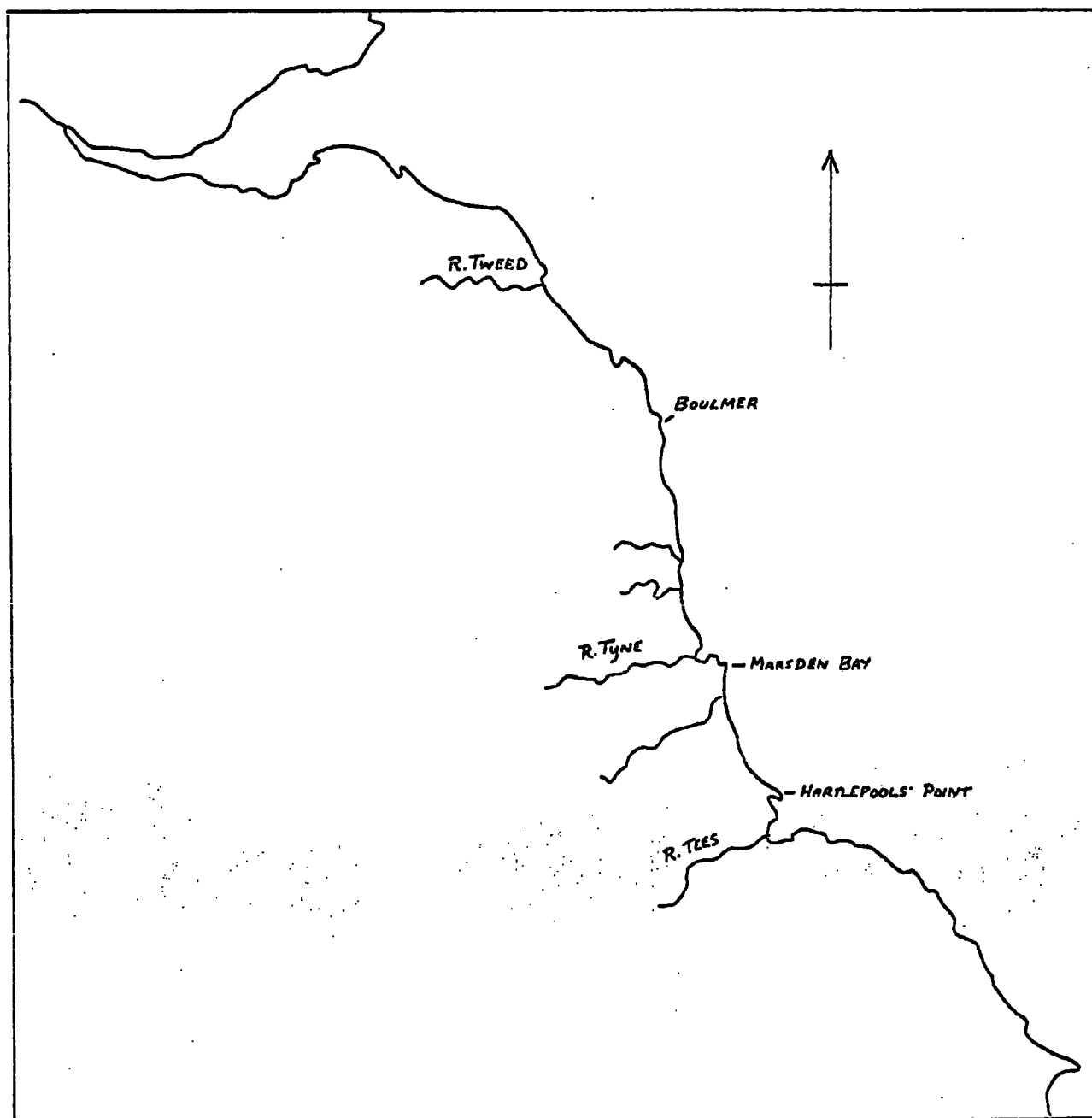| Pool #	Site	Maximum Diameter m.	Minimum Diameter m.	Maximum Depth m.	Volume mL	Ephemeral or Permanent	Position	Remarks.
1	B	1.50	0.40	0.23		P	>MHWN	Some Enteromorpha
2	B	1.60	0.11	0.11		P	>MHWN	Area somewhat variable because of shifting sands
3	B	0.40	0.40	0.13		P	MHWN	Some Pelvetia,
4	B	0.73	0.58	0.18		P	MHWN	Brown, Red + Green Algae, Limpet, Bowl-shaped.
5	B							
6	B	1.00	0.50	0.06		E	MHWN ~MHWS	Dimensions very variable.
7	B	1.00	0.40	0.03		E	"	All shallow pools occupied solely
8	B	1.00	0.05	0.05		E	"	by winkles
9	B	0.90	0.70	0.08		E	"	..
10	B	1.00	0.50	0.08		E	"	',
11	B	0.50	0.30	0.03		E	"	..
12	B	1.00	0.50	0.50		P	>MHWN	Some Enteromorpha, small stones
13	B	3.00	2.00	0.15		P/E	..	Large shallow, silty Enteromorpha
14	B							
15	B	0.70	0.40	0.12		P	"	
16	B	0.28	0.23	0.098		P	^	
16 A	B	0.35 0.45	0.15	0.07	1110	E	~MHWS	Barren except for occasional winkles
16 B	B	0.30	0.25	0.08	1090	E	"	
16 C	B	0.26	0.47	0.12	6110	P/E	"	
17	M	0.40	0.30	0.21		P	MTL– MHWN	Red, Green, Brown Algae. Limpets, winkles.
18	M	0.40	0.35	0.22	8780	P	~MHWN	
19	M	0.20	0.20	0.13	2160	P	"	
20	M	0.21	0.18	0.14	2160	P	"	
21	M	6.35	0.25	0.15	2380	P	"	
21A	M	1.10	0.30	0.32		P	~MHWS	Only Winkles.
22	H	0.30	0.10	0.04	272	P	~MHWN	Winkles, some Limpets.
23	H	0.32	0.20	0.02		P	"	

APPENDIX (3)

Fig.(24): North-east England showing the sites mentioned in the text
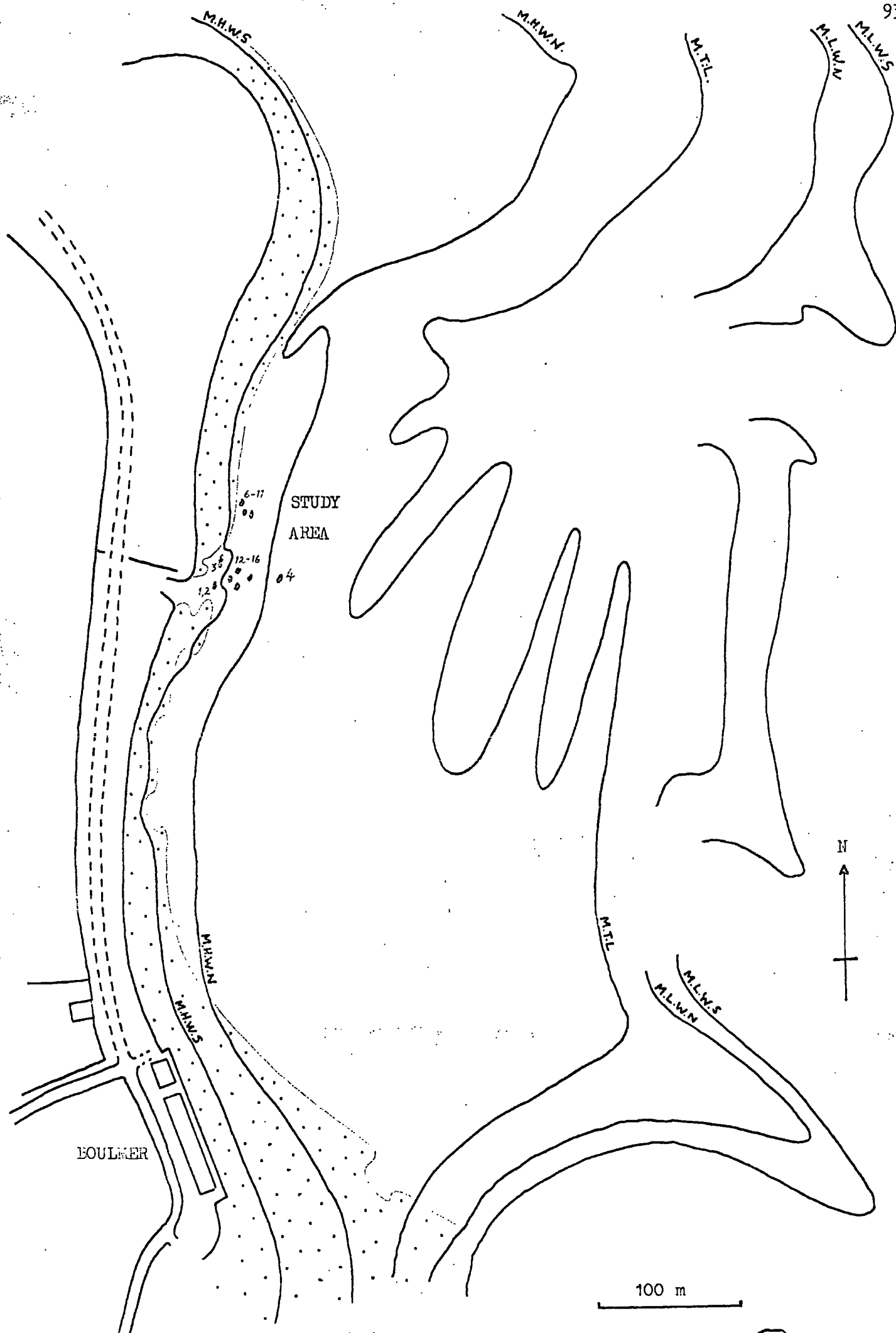
Fig.(25): Sketch Map of Boulmer   Sand: ⬠

STUDY
AREA

BOULMER

N

100 m

M.H.W.S. M.H.W.N. M.T.L. M.L.W.N M.L.W.S

M.H.W.N. M.H.W.S M.T.L M.L.W.S M.L.W.N

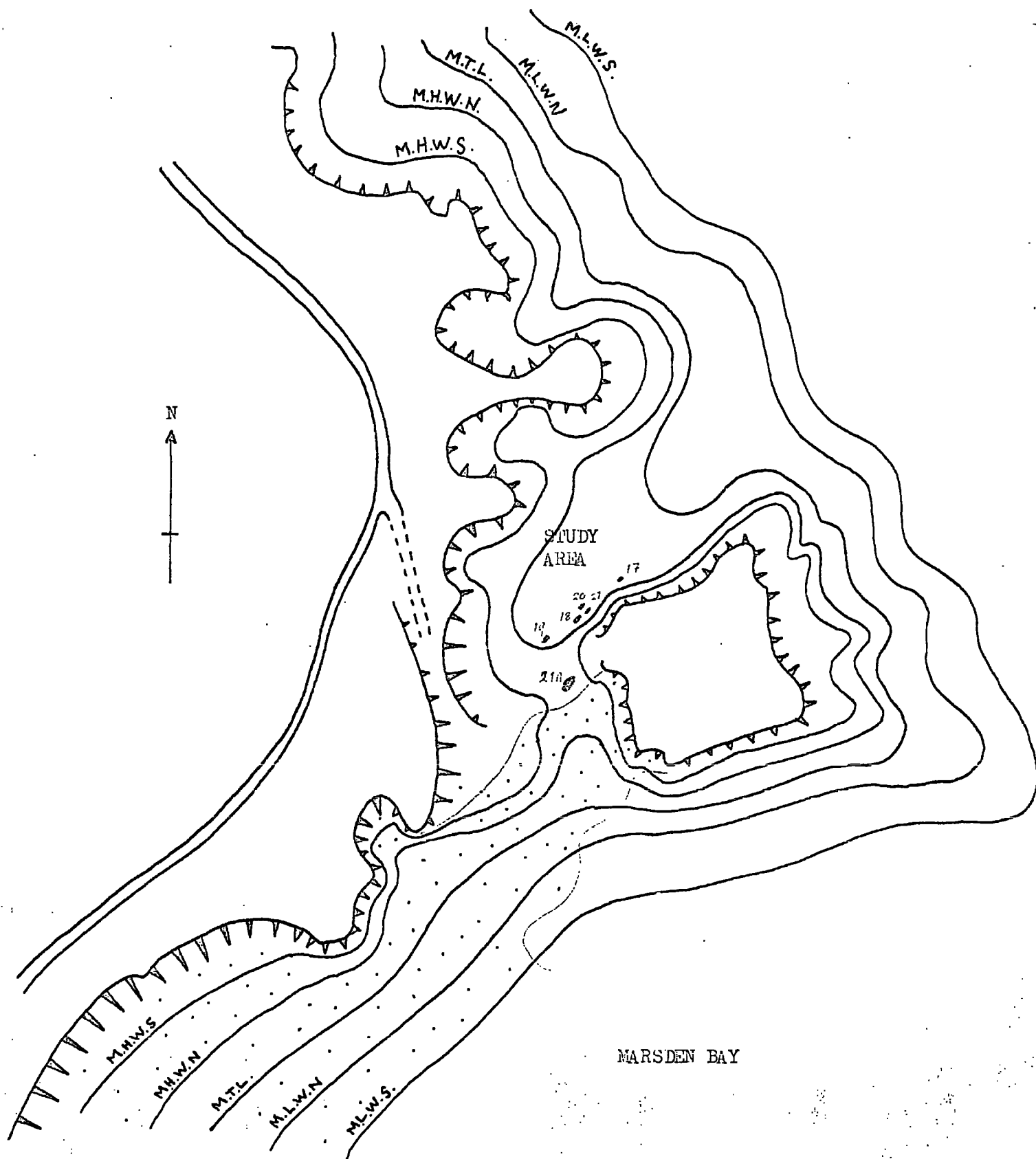Fig.(26): Sketch Map of Hartlepools' Point
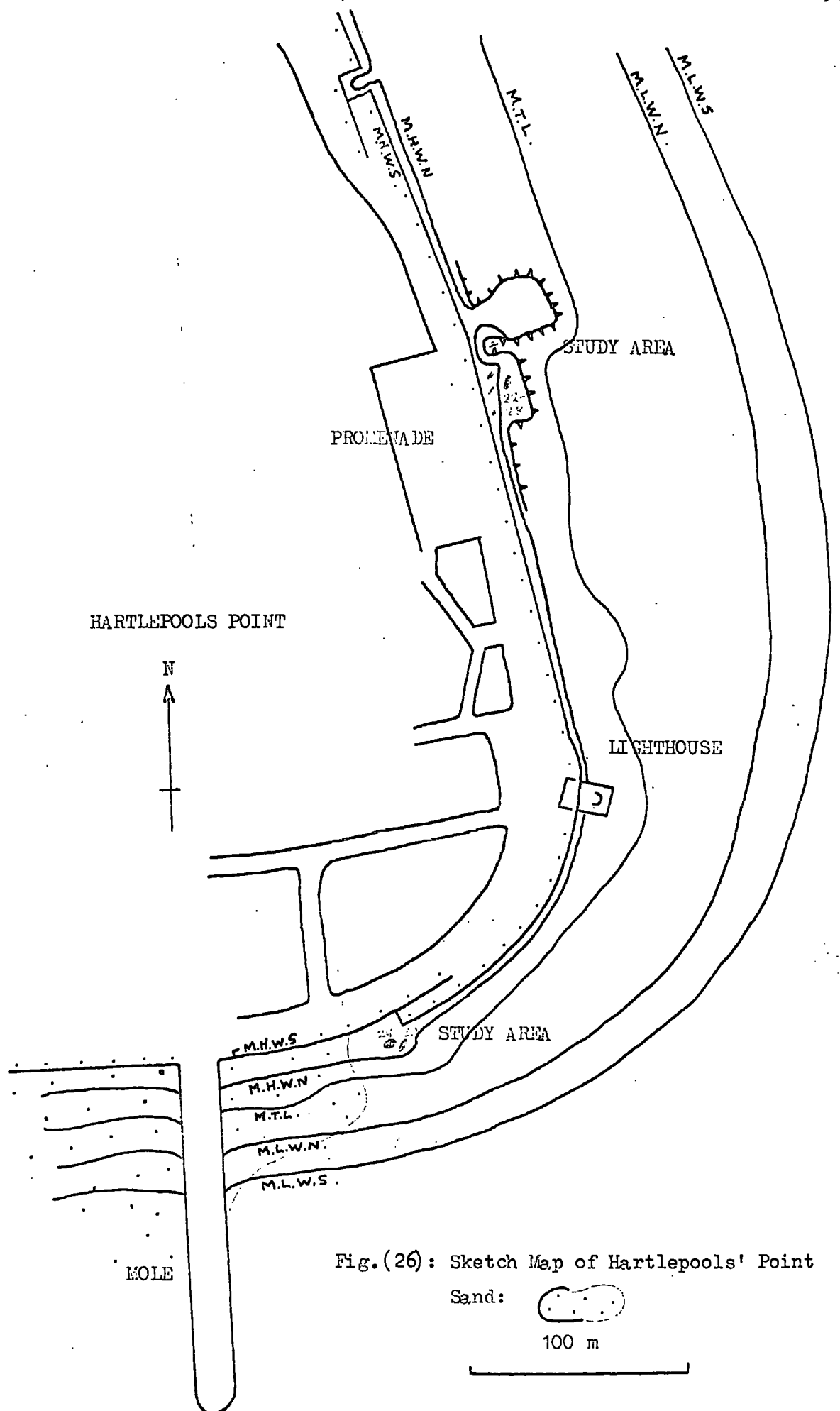
Sand:

100 m

Fig.(27): Sketch Map of Marsden Bay

Cliff Line:

Sand:

100 m