CUMACEAN   ZOOGEOGRAPHY

The zoogeography of Tasmanian shallow water marine

zoobenthos exemplified by some Cumacea

by

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STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university except where indicated clearly in the text. To the best of my knowledge and belief this thesis contains no copy or paraphrase of material previously published and written by another person, except where due reference is made in the text of this thesis.

Alan J. Dartnall

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## ACKNOWLEDGEMENTS

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# 1.                    PREFACE

This thesis incorporates the results of studies into
the distributions of the Cumacea whose members are one of
the groups of animals living in shallow water sands off
eastern Tasmania.

My approach assumes that patterns of animal distribu-
tion exist.   This may be regarded as an expression of
belief.   However, as MacArthur (1927) has pointed out
most investigations of biological distributions reveal
pattern at some scale.   The approach is supported also
by the work of Taylor, Woiwod and Perry (1978) who
suggested that spatial randomness is highly improbable
because the behavioural responses of living organisms
mediate dispersive processes.

## 1.1  Layout

The text of this account is divided into two main
sections.   The first deals with the zoogeography of
shallow water cumaceans in eastern Tasmania.   The
second section contains an account of cumacean spatial
distribution at the benthic interface and, briefly,
the place of these animals in the water column.

## 1.2  Timing

This project commenced in March, 1977.   The formal
cut-off point for literature survey was June, 1979.   All
literature quoted after that date results from browsing
or the intermission of friendly gatekeepers.

## 1.3  Statement of Intent

During a period of eleven years as a working
naturalist in Tasmania the geographic distribution of
the Tasmanian marine fauna has been of interest.   The
concept of the Maugean marine province (Iredale and
May, 1916) proved a useful working hypothesis if only
because it provided a framework upon which to hang
observed distributions.   This descriptive approach was
emphasized in a paper upon Tasmanian littoral biogeography
(Dartnall, 1974).   Other work which is referred to
later in this text suggested that marine animal
distributions along the east coast of Tasmania were
interrupted by a discontinuity at the approximate
latitude of Maria Is. (c. 42°31'S).   Vernacular evidence
from other working zoologists offered nothing to refute
this view.   It was with some surprise, therefore, to
read the work of King (1972) and to discover that the
distribution of littoral algae did not support the concept
of a Maugean marine province.   Both King and myself
have suggested that marine biogeographic regions should
reflect oceanographic conditions and that investigation
of Maugean distributions might continue profitably
offshore.   This thesis is the result of that suggestion.

The pathways followed during this work are summarized
in a flow diagram following the conclusions.   Logical
pathways are direct but labyrinthine logic plots its own
web.   The actual routes followed are indicated.

## 1.4  Sidelines

Projects often appear to possess destinies peculiarly their own.   This project was no exception and gave birth to an exciting and profitable incursion into fluidmechanics. Some fluidmechanic considerations have crept into the text in spite of my determination to restrict them to Appendices III and IV.

## 2.                    SUMMARY

This thesis contains an account of the distribution patterns of some Cumacea (Crustacea, Peracarida) from high energy, shallow water sands off the east coast of Tasmania. Observations of the beta-diversity of psammophilic Cumacea along the Tasmanian east coast reveal distributional discontinuities at both generic and specific levels. These results contrast with recent work on the distributions of littoral algae for which no discontinuities were found along the coasts of south-eastern Australia. The distributions observed support the older concept of a Maugean marine biogeographic area and match wave energy and water mass distributions around Tasmanian coasts deduced by other workers.

Local distributions of cumaceans from sands at depths between four and 22m of water proved contagious. Laboratory experiments on substrate selection demonstrated that different species have different particle size preferences. However, contagious field distributions governed by sediment size characteristics were not identified. This is explained by the scale of sampling employed which did not identify particle distributions at cumacean sized scales.

Further laboratory experiments led to the conclusion that the contagious distributions of cumaceans that were observed were associated with the proportion of biogenic

carbonate particles in the substrate sands. This conclusion was supported by additional investigation in the field and is explained as a response to the greater surface area and organic content of such particles compared with non-carbonate particles.

The mechanism by which cumaceans of high energy sands congregate in areas of high carbonate content is a two stage feeding process which influences the dispersive movement of the animals. A graphical model was used to demonstrate that successful feeding restricts movement and aids congregation of individuals. Unsuccessful feeding (particle rejection) increases the rate of investigation of interface resources.

It is suggested that selective winnowing of biogenic carbonates in shallow seas causes bands or lenses of high biogenic carbonate concentration to form at the sea bed. Such concentrations of cumaceans which are observed in high carbonate locations in shallow marine sands are, in turn, a reflection of the hydrodynamics of the shallow water interface.

Some evidence is given of differential entry to the water column at night by cumaceans. It is suggested that the water column is employed as a dispersal medium and for reproductive purposes.

An account is given of the development and construction of the air-lift sampler for marine use and also of the modification of a simple permeameter as an experimental tool.

In an appendix essay some simple techniques are
described for the study of the hydrodynamics of benthic
animals.    In the light of current theory which
emphasizes the factors which limit animal distributions,
comment is made upon shear stresses as limiting factors
in aquatic environments.    A paper about boundary layer
control by water pennies (Smith and Dartnall, 1980)
is included as Appendix IV.

THE FIRST PART:  THE LATITUDINAL DISTRIBUTION OF

CUMACEANS ALONG A TASMANIAN EAST COAST TRANSECT

## 3.               ZOOGEOGRAPHY

### 3.1 Introduction

Zoogeography is the study of the distributions of animals. Human geographers mostly confine their studies to a range of orders of magnitude from $10^7$m (approximate diameter of the earth) to about $10^2$m (Haggett, 1972). Pending extra-terrestrial zoology few zoogeographers would deny such an upper limit to their area of interest but their range is wider. Many zoologists would find $10^{-2}$m an appropriate lower boundary but dimensions as small as $10^{-5}$m may interest others. Figure 1 contrasts the range of geographers' and zoogeographers' interests in a scale continuum.

Each animal species occupies a geographic range. That range is an expression of the properties of a species and the constraints that limit the range observed. Ranges may be continuous or more or less disjunct.

The work described in this text is based on the assumption that an animal species occupies a range volume which has dimensions, boundaries and grain. It was assumed also that such dimensions may be measured and that mechanisms which maintain, restrict or expand ranges may be investigated and described. Such assumptions may not be acceptable to some workers. For example, Cox, Healey and Moore (1973) suggest that it is 'impossible' (my emphasis) to distinguish regional biomes in the sea
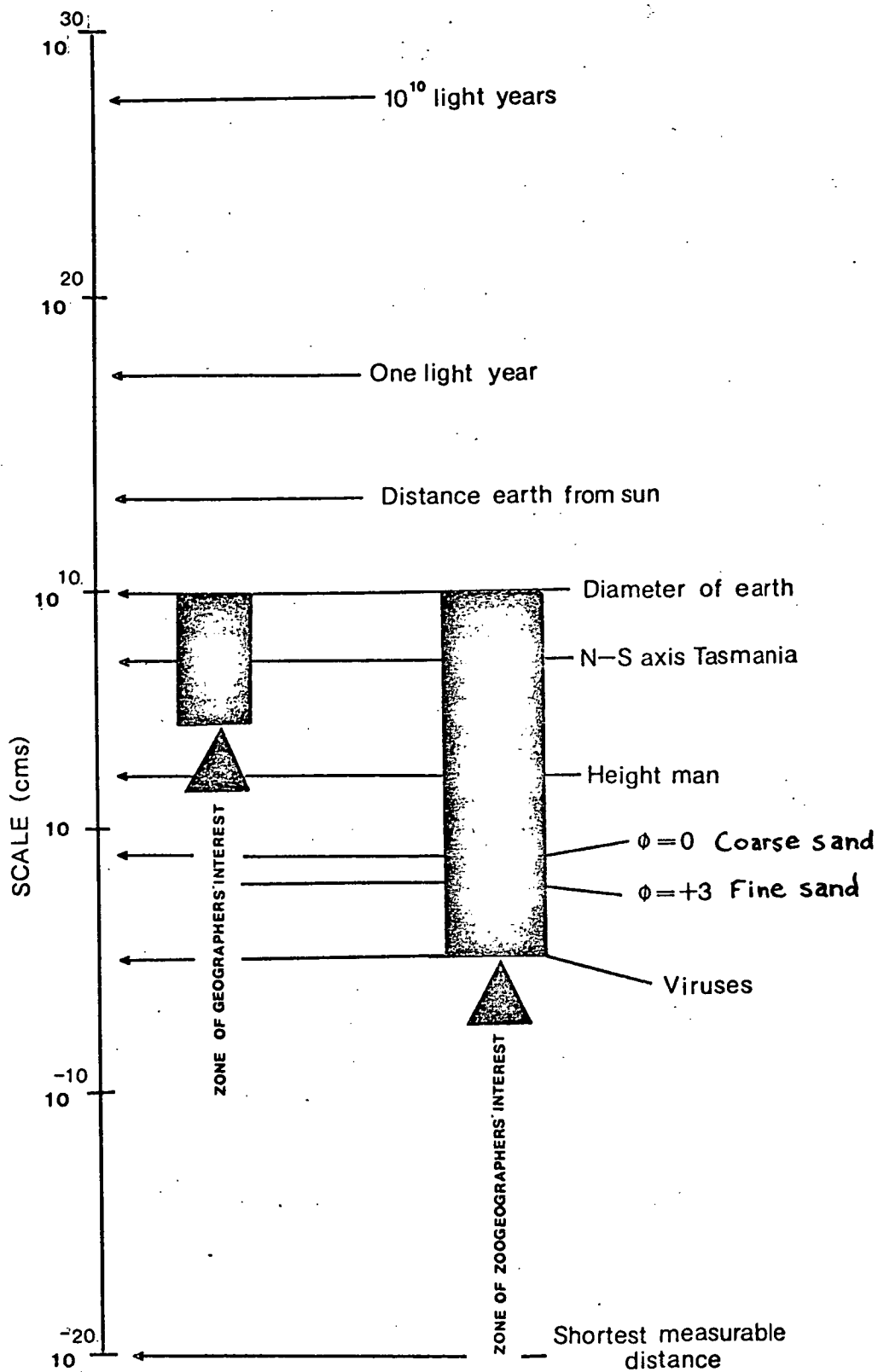
Fig. 1. Zoogeographic study in a scale continuum. Note the larger 'window' of interest of the zoogeographer dictated by the small size and, often, ranges of animals.

because of the uniformity of the marine environment and the ease of distribution of its inhabitants.

## 3.2 Definitions

An elegant definition of zoogeography was offered by Croizat (1972) '......the study of the effects of space and time on the course of organic evolution.'.

Croizat's enthusiastic definition embraces all and contrasts with attitudes which suggest that zoogeography is an exercise in circular reasoning and has little to offer science.

A detailed summary of the phenomena which have interested zoogeographers may be found in Simberloff (1972). The constraints under which zoogeographers labour may include the following:-

(a) Much distributional data do not result from secure sampling. However, one hopes 'that the signal to noise ratio of the data is high enough' (Pielou, 1977).

(b) It is often difficult to determine absolute end points for species ranges and good negative evidence confirming absence is rare. There is also some difficulty in recognising and treating 'absences' and 'zero presence' in distributional data (Michie, 1978).

(c) It is evident that the major biogeographic zones of the world are recognised. The major terrestrial, ecological zones may be distinguished

in terms of distinctive climatic and vegetative
regimes.  The correlation between those zones
and world culture realms is observable (Haggett,
1972) and has implied, perhaps, that little more
remains to be said.

(d)  Zoogeographic practice has often involved
fitting new distributional data to established
zonal schemes.  However, the use of such areal
definitions as models supports this approach
because the support or destruction of such models
allows the construction of hypotheses for experiment.

(e)  The distinction between ecology and zoogeography
often is not clear.  Zoogeography is concerned with
the various faunal areas of the world and the
distributional patterns of animal groups.  Ecological
research is said to be devoted mainly to community
or ecosystem structure (Briggs, 1974).  I consider
the distinctions spurious.  Such an approach is
supported by recent, comparative discussions about
the diversity and structure of tropical and
temperate ecosystems (see, for example, Macarthur,
1972).

## 3.3  Marine zoogeography

A short history of marine zoogeography is given by
Briggs (1974) who recognised three goals of marine
zoogeographic research:

1.  Delineation and characterization of each
distinct faunal area.

2. Attempts to trace the history of distinct faunas.

3. The use of zoogeographic data to augment knowledge about the course of evolution.

To this list one may add:

4. Comparative studies of marine faunal associations, their distributions and the mechanisms that maintain such associations (e.g. Petersen, 1913; Thorson, 1957).

## 3.4 The Tasmanian picture

### 3.4.1 History

Marine research around Tasmania commenced prior to European settlement (1803) with expeditions opportunistically dipping into the marine fauna. The history of marine exploration and collecting, with particular reference to echinoderms, is summarised in Dartnall (1972).

### 3.4.2 Provinces

Delineation of marine zoogeographic provinces in south-eastern Australia commenced when Iredale and May (1916) recognised a distinct molluscan fauna in S.E. Tasmania. The history of the concept of the Maugean province oscillates between recognition of such a provincial unit and the view of those who regarded the Tasmanian marine fauna as an extension, probably depauperate, of a southern Australian fauna (see Bennett and Pope, 1953, 1960; Knox, 1963; Womersley and Edmonds;

1958).

The story is summarized by King (1972) who offered
two conclusions which are relevant here:

(a) Around S.E. Australia, including Tasmania,

a broad overlap exists between cool, temperate

and transitional, warm, temperate elements.

Thus, there is 'little virtue in delimiting

biogeographic provinces'.

(b) King also suggested that marine biogeographic

provinces ought to reflect oceanographic conditions.

Thus, studies on subtidal benthos, nekton and

plankton might be more relevant than intertidal

studies. This approach is supported by the wave

climate approach used by Hayden and Dolan (1975),

particularly along the coasts of the Americas. An

appeal for studies offshore was also made by the

present author (1974). Nyan Taw (unpublished

observations) characterised water masses off the

eastern coast of Tasmania using planktonic indicator

species. Importantly, that work demonstrated

that distinct water bodies do bathe Tasmanian coasts.

3.4.3 Consequences

A further argument for offshore marine zoogeographic
criteria lies in possible changes to the intertidal fauna.
Competitive exclusion by introduced species extending their
range is possible (Dartnall, 1974 , 1979). Supra-littoral
development and industrial and tourist activities at the
littoral fringe may also affect littoral distributions.

Activities that subdivide species ranges may obscure zoogeographic phenomena in the littoral, even if artifically disjunct populations are reproductively robust.

## 3.5 Initial investigation

### 3.5.1 Introduction

This project commenced with the aim of investigating the distribution of shallow water benthos off eastern Tasmania. This interest was initiated by the observation that the east coast of Tasmania is subject to an interchange of identifiable water masses during the year (Rochford, 1975; Nyan Taw, 1975). King's (1972) conclusion that littoral algae show no distributional discontinuity of provincial status, and my own opinion that latitudinal changes in faunal composition might occur in the area, suggested that offshore investigation might be worthwhile. The assumption made was that the zoobenthos of south-eastern Tasmania contained taxa distinct from northern zoobenthos.

### 3.5.2. The habitat

The habitat to be sampled was dictated by latitudinal continuity as far as possible; by accessibility, influence of oceanic conditions and ease of sampling with the boats and gear available. Shallow water, high energy marine sands appeared to satisfy those criteria. A depth limit for sampling of c. 20m was imposed by gear and ease of sampling. Inshore limits were imposed by the seaward edge of the surf zone. All the field work reported
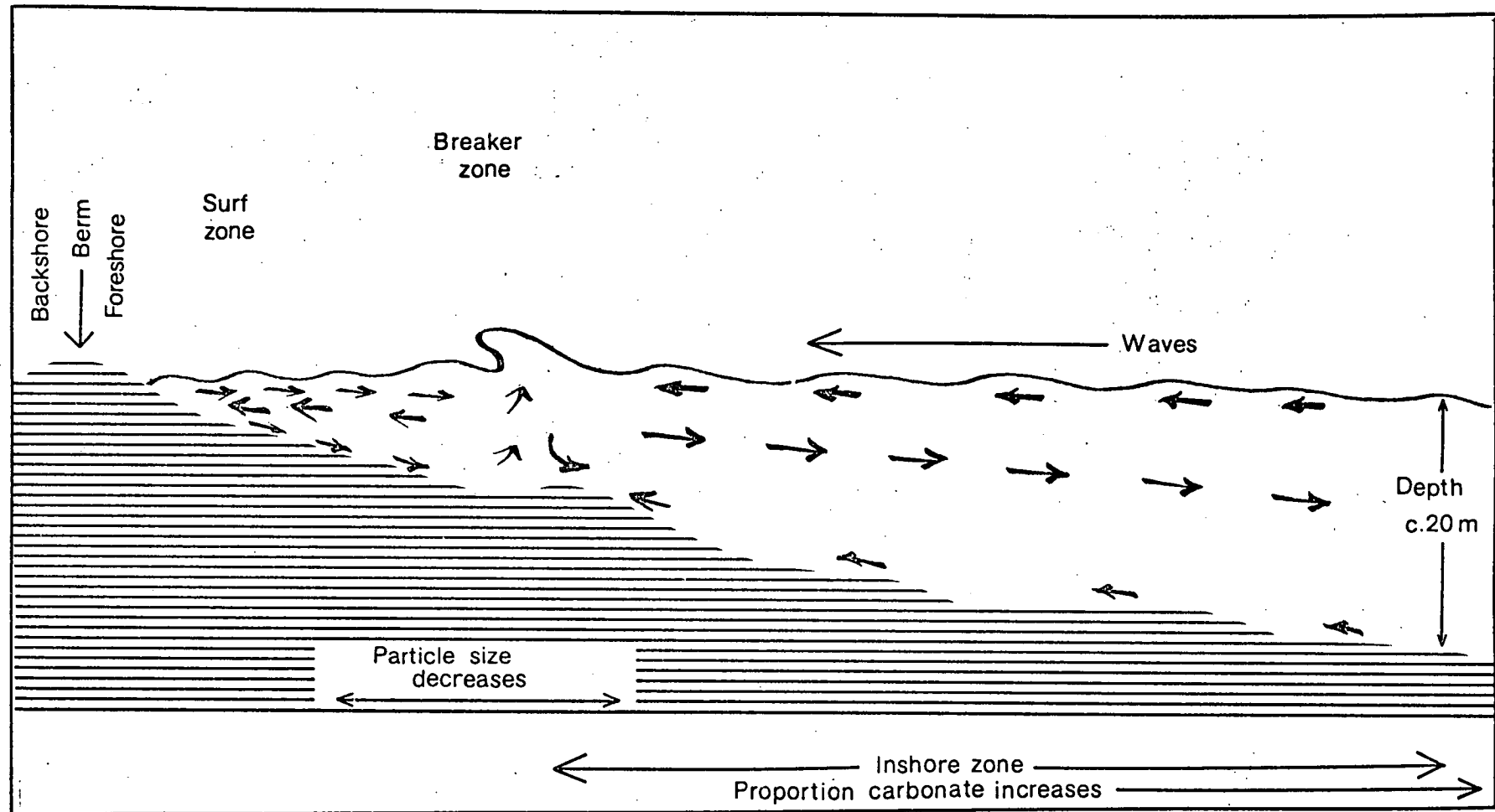
Fig. 2. Diagrammatic representation of shallow, shelf
shore showing areas mentioned in text. Water
movements shown by arrows (after Allen, 1970).

herein refers to samples from a longitudinal transect in the inshore zone (Fig. 2) extending from the Maatsuyker Group of islands in the south to St. Helens in the north.

### 3.5.3 Choice of animal group

The set of animals chosen for study was dictated by available sampling. A good taxonomic literature about the group was necessary because the project was not planned as an exercise in descriptive taxonomy. It was important also that some species, at least, were common enough to provide material for experimental work.

Choice of animal group was made by sampling sands at intervals along the east coast of Tasmania. The F.R.V. Penghana was made available by the Tasmanian Fisheries Development Authority. Samples were taken at eight localities between Fortescue Bay and the Freycinet Peninsula during the Penghana cruise (see Fig. 3.)

Five grab samples were taken at 20m depth by Van Veen grab at each locality. Each sample was sieved through a filter bucket with nominal mesh aperture of 500$\mu$m and the residue preserved.

Approximately one litre of wet sediment was taken from each grab sample. On return to the laboratory the sediments were analysed by sieving following the technique described by Buchanan (1971). Cumulative frequency curves of the composition of sediments from each locality are given in Fig. 4 and the parameters derived from the frequency curves in Table 1.

Fig. 3. Map of the eastern and south-eastern coasts of Tasmania showing sampling locations and geographic localities mentioned in the text.
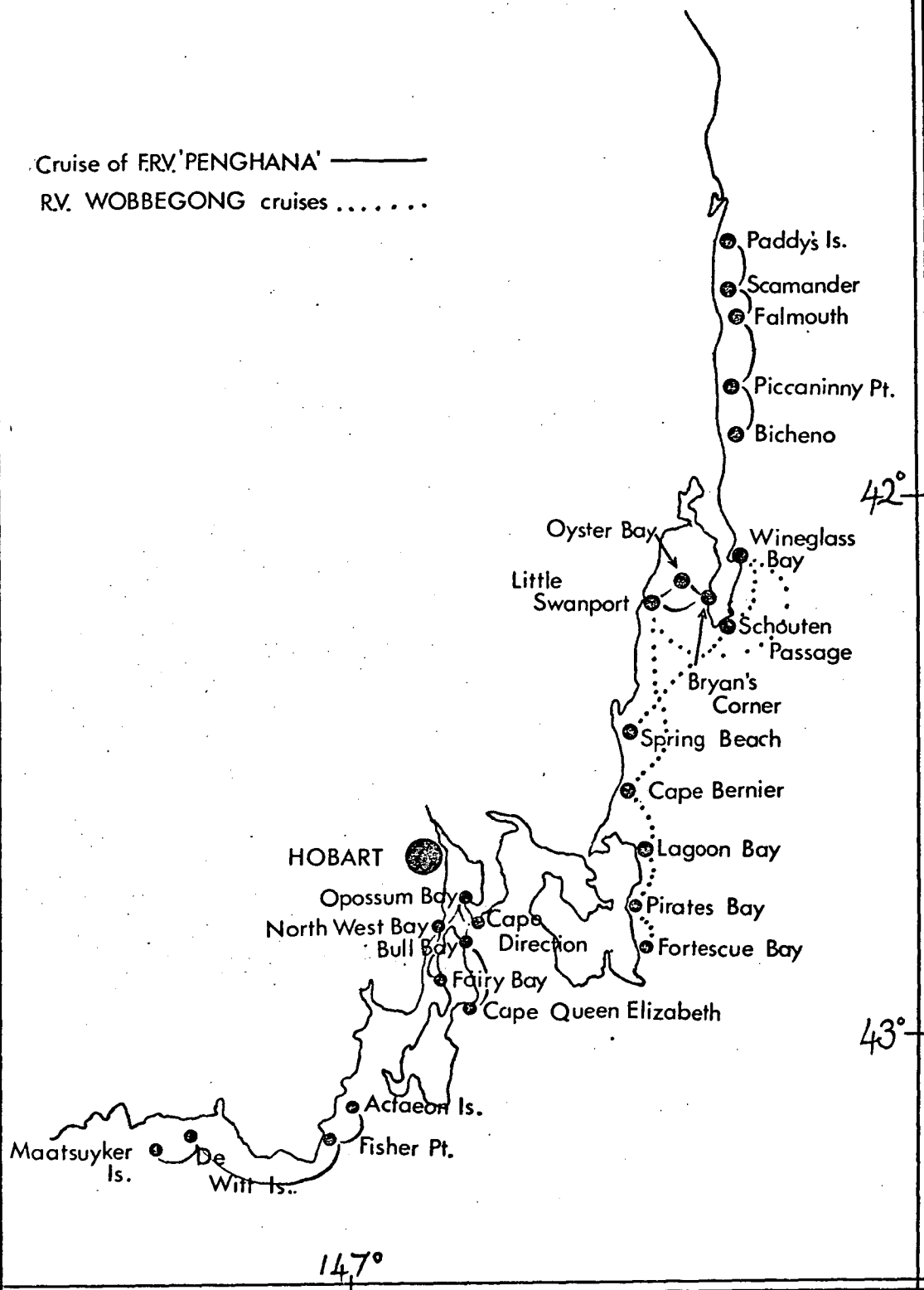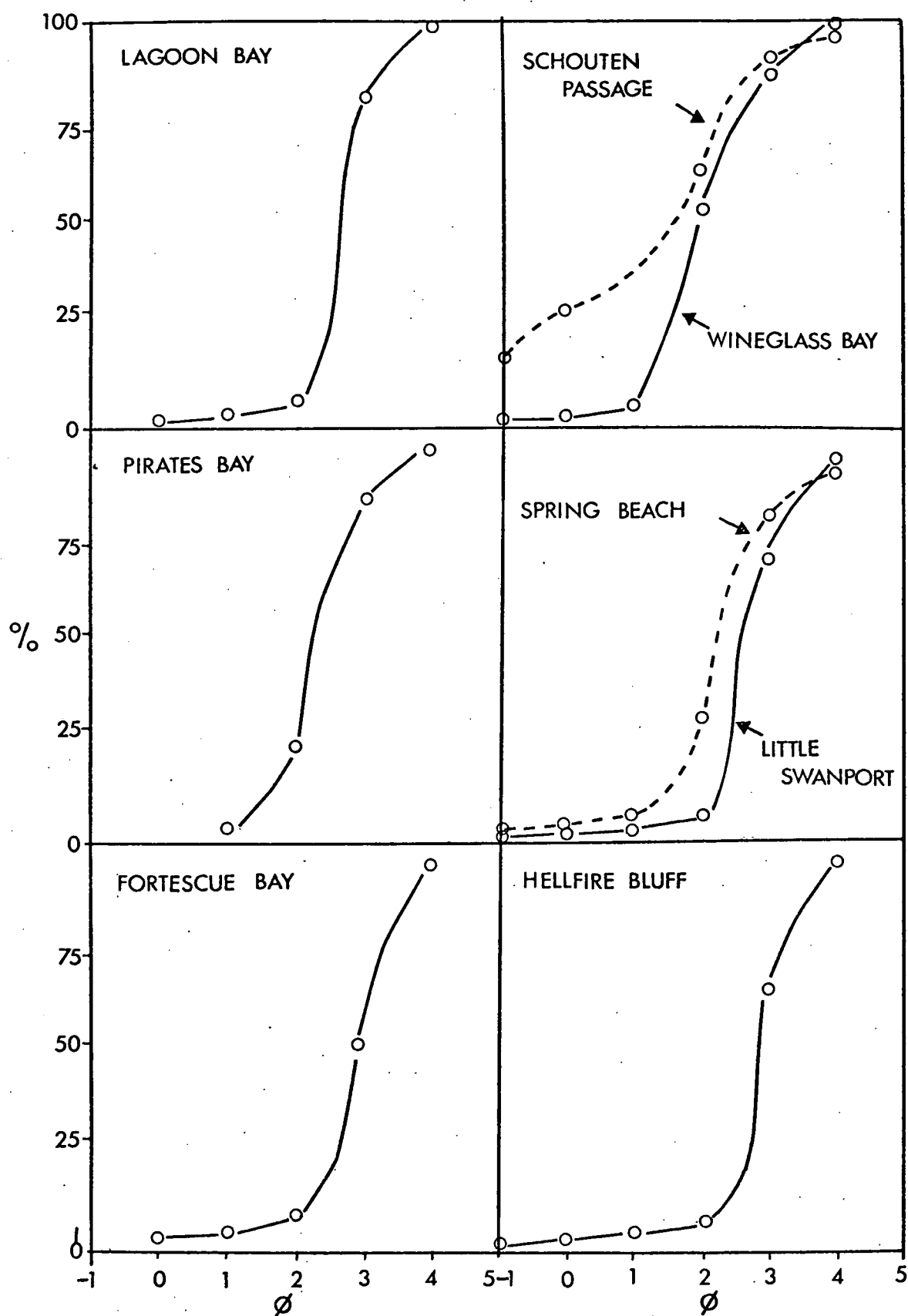
Fig. 4. Cumulative frequency distribution curves
from the analysis of sediment samples from
eight localities.

Table I

Characteristics derived from the size frequency curves (Fig, 4) of sieved sediment samples from eight localities:

| | Md $\emptyset$ | $Q_1$ $\emptyset$ | $Q_3$ $\emptyset$ | QD $\emptyset$ | Skq $\emptyset$ |
|---|---|---|---|---|---|
| Fortescue Bay | 3.0 | 2.8 | 3.3 | 0.25 | +0.05 |
| Pirates Bay | 2.26 | 2.1 | 2.7 | 0.3 | -0.26 |
| Lagoon Bay | 2.66 | 2.5 | 2.9 | 0.2 | +0.04 |
| Hellfire Bluff | 2.9 | 2.76 | 3.13 | 0.185 | +0.045 |
| Off Spring Beach | 2.26 | 1.96 | 2.73 | 0.385 | -0.315 |
| Off Little Swanport | 2.66 | 2.5 | 3.06 | 0.28 | +0.12 |
| Schouten Passage | 1.6 | 1.5 | 2.3 | 0.4 | +0.3 |
| Wineglass Bay | 1.9 | 1.56 | 2.56 | 0.5 | +0.16 |

The stations in Schouten Passage and Wineglass Bay were deleted from further consideration because they contained larger particles (Md $\emptyset$ 1.6 and 1.9 respectively) than the other stations. The adjustment was not unexpected because weather conditions made it impossible to work those two stations offshore. The larger particle fractions are contributions from the Devonian granites of the Freycinet Peninsula.

The faunal samples from the remaining six localities were divided into convenient sorting categories. These categories were then ranked to discover which groups were present most often in the samples (Fig. 5).

Twenty-one sorting groups accounted for the fauna from all of the samples. Fourteen groups were present in less than 50% of the samples and were rejected for study.
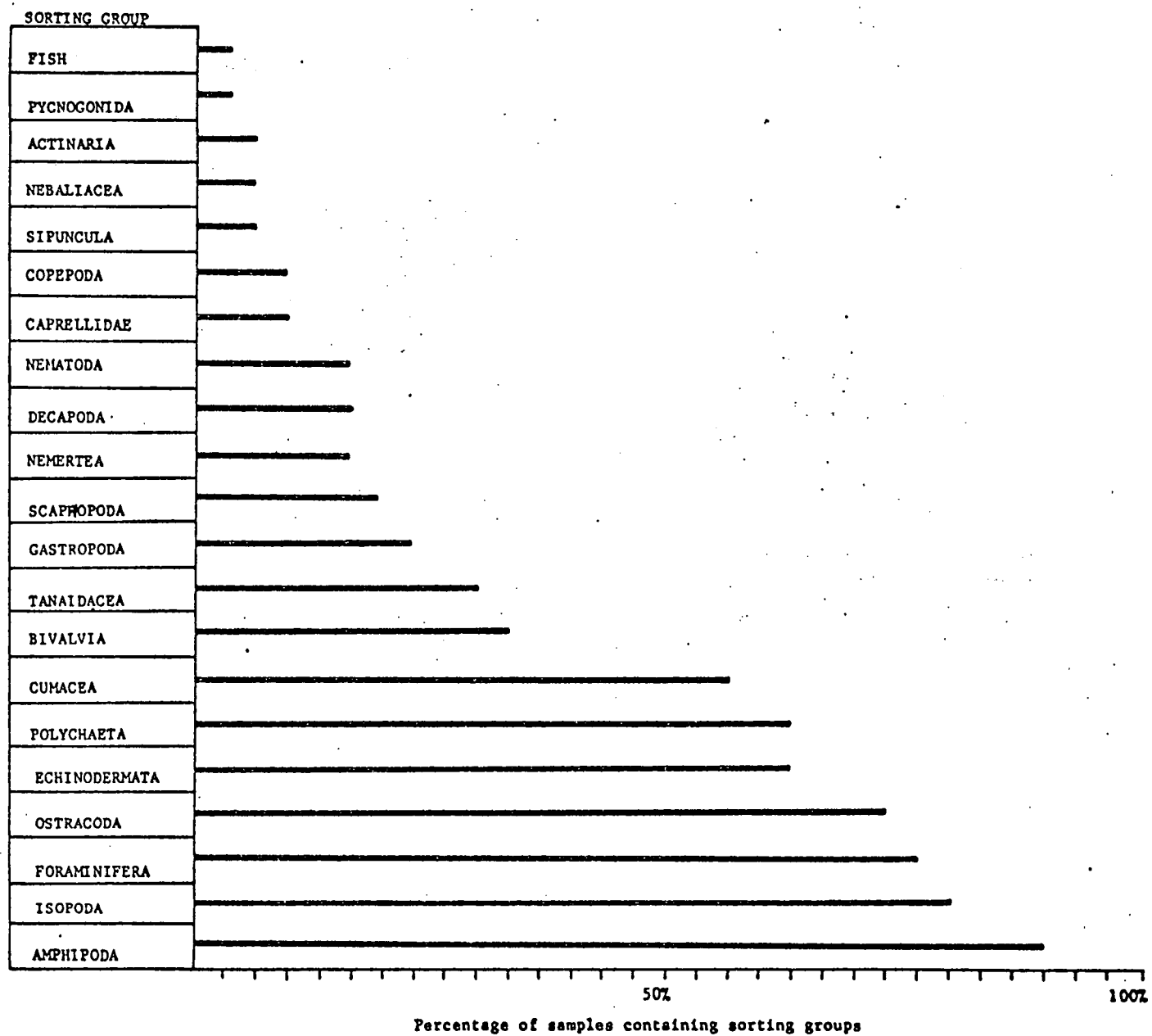
Fig. 5.   Percentage occurrence of sorting groups from thirty benthic samples.

Only seven groups were present in more than 50% of the samples.

Amphipoda were rejected as zoogeographic subjects because the taxonomy of the group is not secure. The Isopoda were rejected similarly. For example, among the Anthuridae determined for me by Dr. G.C.B. Poore only two of seven species were described. A similar situation occurs amongs the Ostracoda collected. Dr. K.G. McKenzie recognised five new species of five recognised genera and one new genus in the samples of ostracods sent to him. McKenzie (1979) has since described the new genus from further specimens obtained during this work.

The Polychaeta were rejected because the taxonomy of the Tasmanian species is poor and the Echinodermata because the majority of occurrences in the samples were contributed by a single species, *Echinocardium cordatum*. Rejection of Foraminifera was based on the difficulty of distinguishing living and recently dead individuals from subfossil specimens (see Arnold, 1974, for commentary).

Cumacea were chosen as the study group.

3.6    Introduction to Cumacea

Cumacea are an order of peracaridan Crustacea whose closest affinities are probably with the Tanaidacea and Isopoda (Jones, 1963). The order is often reported not to have a fossil record but a specimen of *Nannastacus*-like form is reported from the Permian of Germany (Horland

*et al*, 1967).

All known specimens of Cumacea conform to a characteristic shape with an inflated carapace and thoracic somites and a slender elongate abdomen.

Introductory accounts to the group may be found in such works as Fage (1944), Stebbing (1913) and Zimmer (1941) and in more general texts (e.g. Barnes, 1968; Waterman and Chase, 1960). Regional accounts of cumacean faunas include Jones (1963), New Zealand; Day (1975, 1978a, b), South Africa; Kurian (1973), Indian Ocean and Lomakina (1968), Antarctic region.

3.7    Cumacean studies

Cumaceans are poorly studied.    Most publications about Cumacea are taxonomic.    To illustrate the difference between the rates of taxonomic study and investigations of the biology of cumaceans the numbers of new species described and the numbers of papers on other topics were extracted from the issues of the Zoological Record, 1900-1972.    This information expressed as cumulations per decade is expressed in Fig. 6.    In rigorous terms the comparison is invalid unless one assigns relative weights to taxonomic and non-taxonomic endeavour.    This I would not dare.    The important point to note is that non-taxonomic study did not commence until approximately 150 species were known.    The non-taxonomic work curve does not increase its slope until about 500 species were described (the 1960-70 decade).    One may suggest that biological study depends on descriptors.
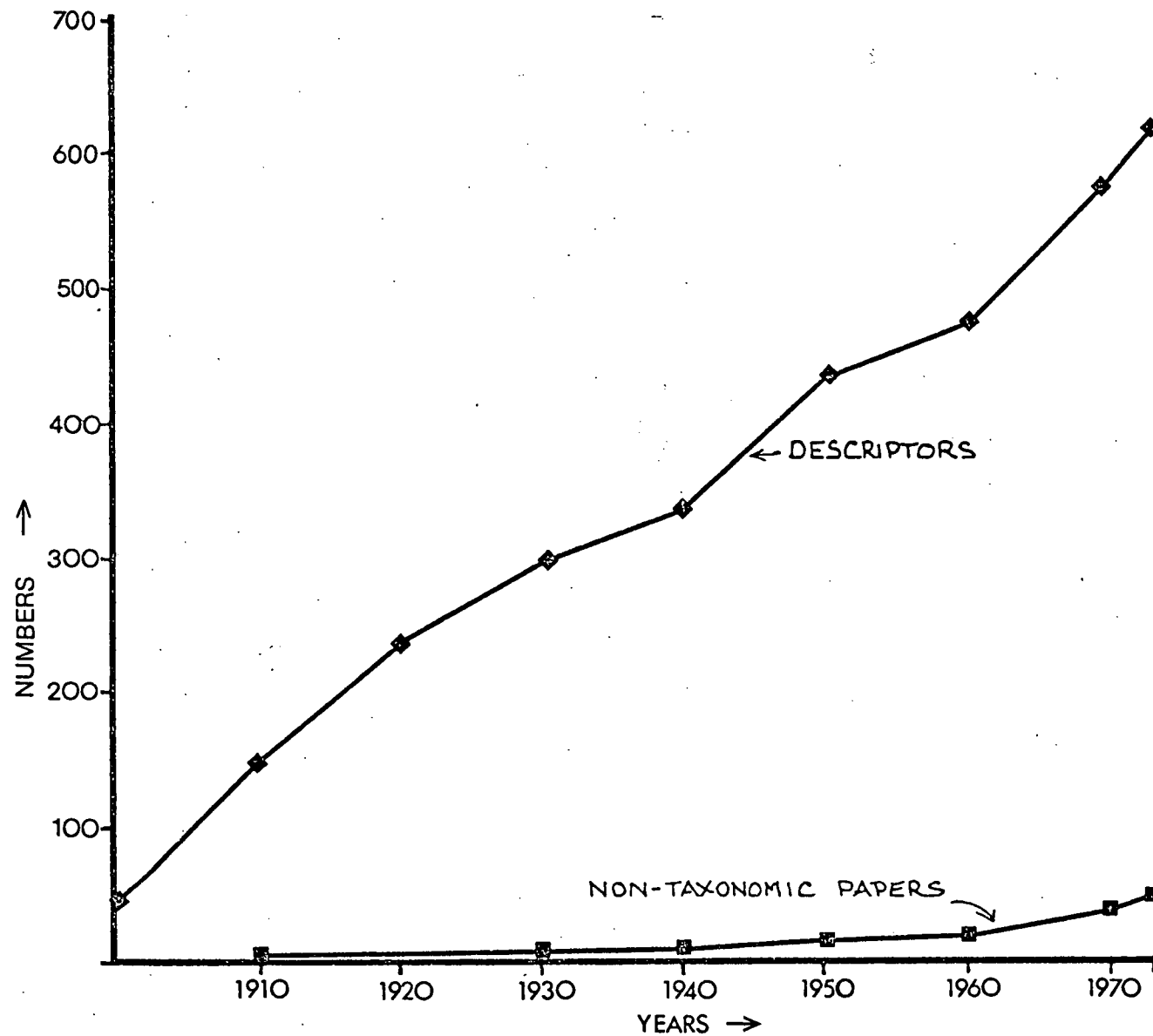
Fig 6.    Cumulative numbers of species of cumaceans described per decade
compared with the cumulative numbers of non-taxonomic papers
about cumaceans.

A selective summary of non-taxonomic works about cumaceans follows:

Oelze (1931) described the anatomy of *Diastylis rathkei*. Fage (1933) commented on the use of low intensity light for trapping Cumacea and (1945) considered the place of some cumaceans in nocturnal plankton. That author also described secondary sexual characteristics in the genus *Iphinoi* (Fage, 1944). Dennell (1934) described the feeding mechanism of *Diastylis bradyi*.

Following the observations of Foxon (1936) on the natural history of sand dwelling cumaceans, a number of papers appeared about Cumacea in their environment. Watkin (1941) wrote on nocturnal tidal migration and Dixon (1944) studied some aspects of the biology of *Cumopsis goodsiri* including observations on other species. Le Sueur who had already (1955) published on the anatomy of *Eocuma dillfusi* later joined with Pike in an examination of the shore zonation of Cumacea in Jersey (Pike and le Sueur, 1958).

Wieser (1956) made the first critical study of substrate choice by cumaceans. Corey (1970a) described the quantitative distribution of three species in Kames Bay, Scotland, and also investigated diurnal vertical migration (Corey, 1970a, b). The biology of *Manocuma stellifera* was reported on by Gnewuch and Croker (1973) and Gladfelter (1975) considered the distribution of some shallow water Cumacea. Corey (1976) resumed her place in the

cumacean time-line with an account of the life history of *Diastylis sculpta*.

The only physiological work apparent to me is that of Stahl (1938) on hormone secretion and control of colour change.

This survey is not exhaustive. Distributional data and environmental information may be extracted from the results of many expeditions and, latterly, a plethora of environmental base-line surveys. Much of this information is useful but correlations may be weak because sampling design is poor for secondary purposes.

3.8    Australian Cumacea

The taxonomic work of Hale spanning twenty-five years (Hale, 1928-1953, see bibliography for details) is the basis for all studies of Australian Cumacea. Since Hale's time, no Australian worker has concentrated on cumacean biology, although species names are included in lists constructed for community studies (e.g. Stephenson, Cook and Newlands, 1978) and impact reports (e.g. Port Philip Survey, 1973). The works of interest are those of Zimmer (1914) who described new material from Western Australia and Foxon (1932) who reported on the Cumacea collected during the Great Barrier Reef Expedition.

3.9    Tasmanian Cumacea

3.9.1  Known species

A list of the Cumacea known from Tasmanian waters

to date follows. The information is dervied from Hale (1928 *et seq*) and a small collection of specimens held in the Tasmanian Museum, Hobart. A few records were also abstracted from the species lists of the Environmental Study of Port Philip Bay (1973).

Annotated list of Tasmanian Cumacea

Family Bodotriidae

*Iphinoe pellucida* Hale, 1944

Tasmanian locality : off Babel Is.

Other localities : all off New South Wales

Depth range : 0-80m

Substrate : coarse sand, mud.

*Leptocuma pulleini* Hale, 1928

Tasmanian localities : this work

Other localities : South Australia, New South Wales and Queensland

Depth range : 2-4m

Substrate : coarse sand.

*Glyphocuma inaequalis* Hale, 1944

Tasmanian locality : off Babel Is.

Other localities : off New South Wales

Depth range : 6-100m

Substrate : coarse sand, sand-mud, mud.

*Glyphocuma serventyi* Hale, 1944

Tasmanian locality : off Cape Barren Is., off Babel Is.

Other localities : off New South Wales

Depth : 64m

Substrate : coarse sand.

*Zenocuma rugosa* Hale, 1944

Tasmanian locality : d'Entrecasteaux Channel

Other locality : New South Wales

Depth range : 30-75m

Substrate : sand, coarse sand.

*Cyclaspis caprella* Hale, 1936

Tasmanian locality : Kettering

Other localities : South Australia

Depth range : 3-6m

Substrate : see text section 7.

*Cycaspis sheardi* Hale, 1944

Tasmanian locality: off Cape Barren Is.

Other localities : South Australia and New South Wales

Depth range : 9-17m

Substrate : ———.

*Cyclaspis tribulis* Hale, 1944

Tasmanian locality : off Cape Barren Is.

Other localities : South Australia and New South Wales

Depth range : 0-70m

Substrate : ———.

*Cyclaspis australis* Sars, 1887

Tasmanian locality : off Babel Is.

Other localities : Victoria, New South Wales

Depth range : 0-100m

Substrate : sand, silt, mud.

Family Nannastacidae

*Nannastacus asper* Hale, 1945

Tasmanian locality : off Cape Barren Is.

Other localities : Western Australia, South

Australia

Depth : 1.8m

Substrate : ————.

*Nannastacus inflatus* Hale, 1945

Tasmanian locality : Fairy Bay, Bruny Is.

Other localities : South Australia, Queensland,

Western Australia

Depth range : 2-7.3m

Substrate : mud, algal epifauna.

*Nannastacus lima* Hale, 1936

Tasmanian locality : Table Bay

Other localities : South Australia

Depth range : ————.

Substrate : ————.

*Campylaspis unisulcata* Hale, 1945

Tasmanian locality : off Babel Is.

Other localities : Western Australia, South

Australia

Depth range : 20m

Substrate : sand.

*Campylaspis thomsoni* Hale, 1945

Tasmanian locality : off Babel Is.

Other localities : New South Wales

Depth range : 40m

Substrate : mud.

*Campylaspis similis* Hale, 1945

Tasmanian locality : off Babel Is.

Other localities : ————

Depth : ————

Substrate : ————.

*Campylaspis latidactyla* Hale, 1945

Tasmanian locality : This work, 3.9.2

Other localities : Queensland

Depth : ————

Substrate : ————.

*Campylaspis roscida* Hale, 1945

Tasmanian locality : off Babel Is.

Other localities : New South Wales

Depth range : 70-100m

Substrate : mud.

Family Diastylidae

*Dimorphostylis subaculeata* Hale, 1945

Tasmanian locality : This work, section 3.9.2

Other localities : ————

Depth range : 6-31m

Substrate : sand.

*Dimorphostylis praecox* Hale, 1945

Tasmanian localities : New South Wales

Depth range : 2-64m

Substrate : sand.

Note:  *D. praecox* as used here is a new combination

raising Hale's subspecies to specific rank

(see 3.9.2).


*Dimorphostylis tasmanica* Hale, 1945

Tasmanian locality : off Babel Is.

Other localities : ―――.

Depth range : ―――.

Substrate : ―――.


*Dimorphostylis cottoni* Hale, 1936

Tasmanian locality : Storm Bay

Other localities : South Australia, New South Wales,

Victoria

Depth range : 9-13m

Substrate : ―――.


*Anchistylis waitei* Hale, 1928

Tasmanian localities : This work, section 4.3

Other localities : South Australia, Victoria

Depth range : 0-22m

Substrate : sand, fine sand.


*Anchistylis similis* Hale, 1945

Tasmanian locality : off St. Helens

Other localities : South Australia, New South Wales

Depth range : 2-9m

Substrate : sand.

*Dicoides fletti* Hale, 1946

Tasmanian localities : Babel Is., this work, section 4.3

Other localities : New South Wales, Victoria

Depth range : 4-80m

Substrate : coarse sand, silt, mud.

*Dicoides brevidactyla* Hale, 1937

Tasmanian localities : this work, section 4.3

Other localities : South Australia, New South Wales

Depth range : 4-70m

Substrate : sand, silt.

3.9.2   Psammophilic cumaceans

Eleven species of Cumacea were obtained from shallow marine sands during this project.

1.   *Leptocuma pulleini* Hale, 1928.

2.   *Cyclaspis caprella* Hale, 1936

3.   *Cyclaspis globosa* Hale, 1944.

Previously recorded by Hale (1944) from off the coast of New South Wales on sand and coarse sand. The records herein constitute the first for Tasmania.

4.   *Cyclaspis* n. sp.

This species belongs to the *exsculpta* group of genus *Cyclaspis*, following Hale (1944).   *Cyclaspis*

n. sp. will be described elsewhere. Voucher material is deposited in the collections of the Tasmanian Museum, Hobart.

5.  *Leucon* n. sp.

Hale (1945b) noted the relative rarity of leuconids amongst the cumacean fauna of Australia and suggested that "the southern waters of Tasmania may produce somewhat different results". This work has not confirmed Hale's suggestion, but as two of the three species described by that author were taken from silt and mud collecting in finer sediments than sands may prove profitable.

*Leucon* n. sp. will be described elsewhere. Voucher material is deposited in the Tasmanian Museum, Hobart.

6.  *Campylaspis unisulcata* Hale, 1945.

7.  *Anchistylis waitei* Hale, 1928.

8.  *Dimorphostylis subaculeata* Hale, 1945.

9.  *Dimorphostylis praecox* Hale, 1945 new combination. The specimens of *D. subaculeata* var. *praecox* collected during this study appear to merit full specific rank. This has been confirmed by scanning electron microscope studies of the two forms which it is intended to publish elsewhere. *D. praecox* will be regarded as a full species throughout this account. However, it must be noted that this action has no taxonomic

significance because this thesis does not
constitute a publication under Article 8 of the
International Code of Zoological Nomenclature (1964).

10.     *Dicoides fletti* Hale, 1946.

11.     *Dicoides brevidactyla* Hale, 1937.

4.      ZOOGEOGRAPHY OF TASMANIAN CUMACEA FROM WELL-
            SORTED, SHALLOW, MARINE SANDS

4.1     Introduction

        Maps are one of the basic tools of the zoogeographer
and repeated mapping of distributions will record temporal
change (Norton, 1978).   Maps have been used to delineate
geographic variation and change at many scales.    Examples
appropriate to this text may be found in Hale (1944) on
the worldwide distribtuion of the species of the Cumacean
genus *Cyclaspis*; circumpolar West Wind Drift distributions
(Fell, 1962); Australian coastal phenomena (Radok, 1976)
and circum-Tasmanian echinoderm ranges (Dartnall, 1980).

4.2     Cumacean presence

        Spot localities of species occurrences (presence)
were plotted on radial maps after the method of Radok
(1976).    The information was taken from samples
collected at the localities plotted on map figure 3.
A common criticism of zoogeographic range maps is that
they collate information collected at different times
and in different ways.    Pielou's (1977) comment applies
here also (3.2).

        The presences reported here were recorded from

METHODS

samples collected by air-lift sampler except for four

stations where records from earlier Van Veen grab

samples were employed.   All the samples were made

within a period of eighteen months, treated by standard

methods and collected by two workers who had standardised

their operations.   The species presences recorded during

this survey are expressed in Fig. 7.

## 4.3    Ranges

### 4.3.1  Species ranges

By inspection of the sheaf of ranges plotted to

the right of Fig. 7 it is apparent that the lengths

and positions of species ranges vary along the eastern

coast of Tasmania.   One may raise the null hypothesis,

$H_o$, that the number of species spans cut by the locality

radii do not vary along the east coast transect.   By

inspection $H_o$ is not supported.   If the numbers of

species spans cut by each locality radius is plotted

(the species plot on the circular graph) it can be seen

that the species richness decreases from north to south;

i.e. from nine species in the north to five species in

the south.

### 4.3.2  Station distinctiveness at species level

$H_o$ = that the dissimilarity or distinctiveness of

neighbouring stations is such that the decrease in species

richness is gradual, without abrupt changes.   In other

words, that King's (1972) concept of gradually depauperate

southern localities holds for cumacean distributions.

Species distinctiveness between each pair of

KEY TO SPECIES

1. C.caprella  2. C.globosa  3. Cyclaspis n.sp.  4. L.pulleini

5. A.waitei  6. C.unisulcata  7. D.subaculeata  8. D.praecox

9. Leucon n.sp  10. D.fletti  11. D.brevidactyla
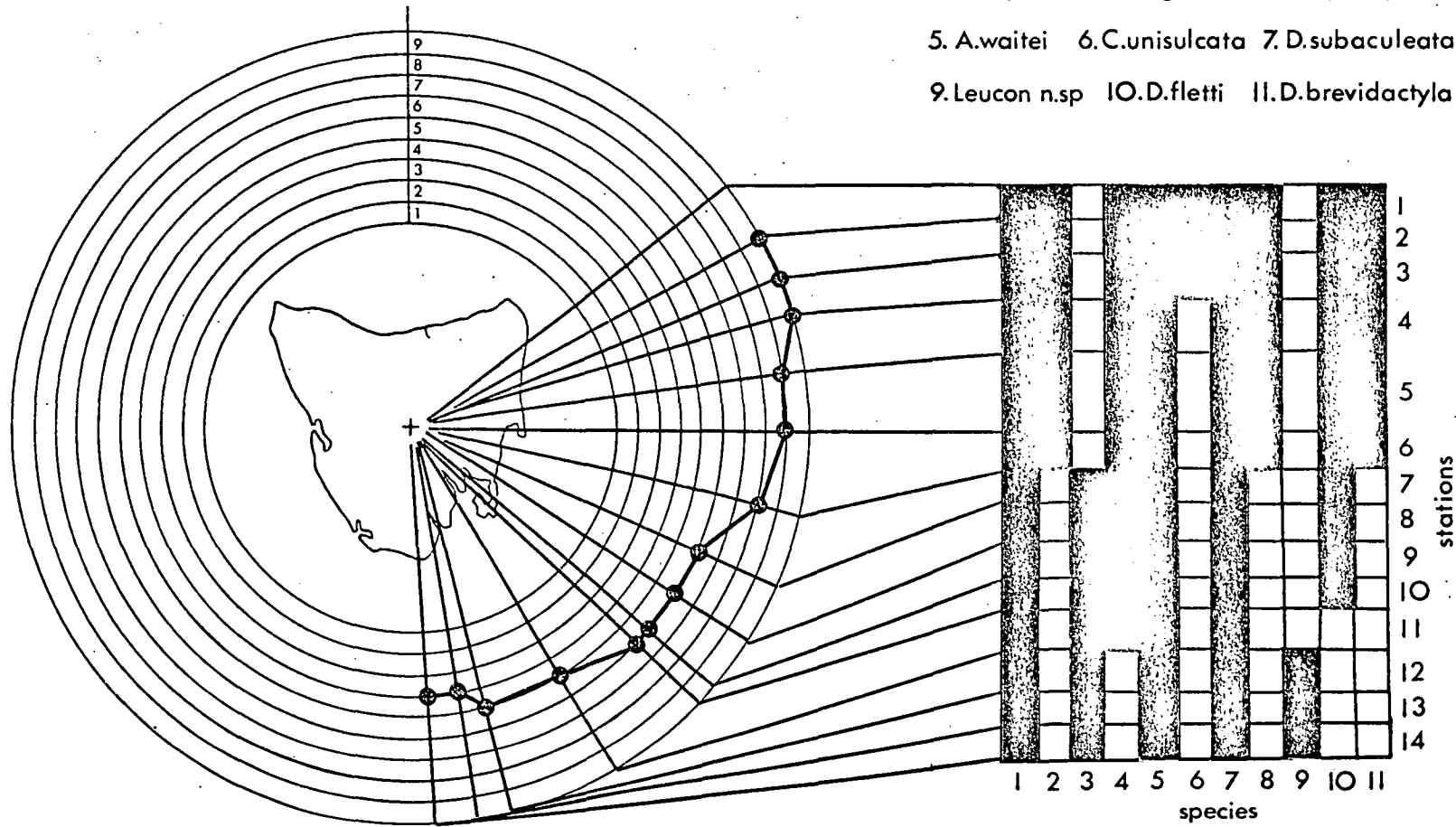
Fig. 7.  Cumacean species presence, derived ranges and species richness.

stations was calculated using the formula of Menzies
*et al* (1973).

$$\text{Distinctiveness} = \frac{T - Tc}{T} \times 100 = \%$$

where T = total number of taxa

present at both

locations

Tc = number of taxa common

to both locations

The results are plotted in Fig. 8.

*upheld*

$H_o$ is not proven.  Three peaks of distinctiveness
are apparent between locations 3/4, 6/7 and 10/11/12/13.
The high level of distinctiveness between localities 6/7
is contributed by the end points of four species spans,
three from the north and one from the south.  It was
considered that the distinctiveness observed was an
artifact of sampling, but random selection of samples
from the latitude of Little Swanport does not alter the
picture.

The sequence of distinctiveness 10/11/12/13
distinguishes all the localities south and west of the
Tasman Peninsula and is discussed later in this account.

4.3.3  Generic distinctiveness

Distinctiveness based on the distribution of
genera along the Tasmanian east coast is plotted in Fig. 9.
Two peaks of distinctiveness are apparent between localities
3 and 4 and between stations 10/11/12/13.  Both peaks
correspond to reductions in the number of genera in the
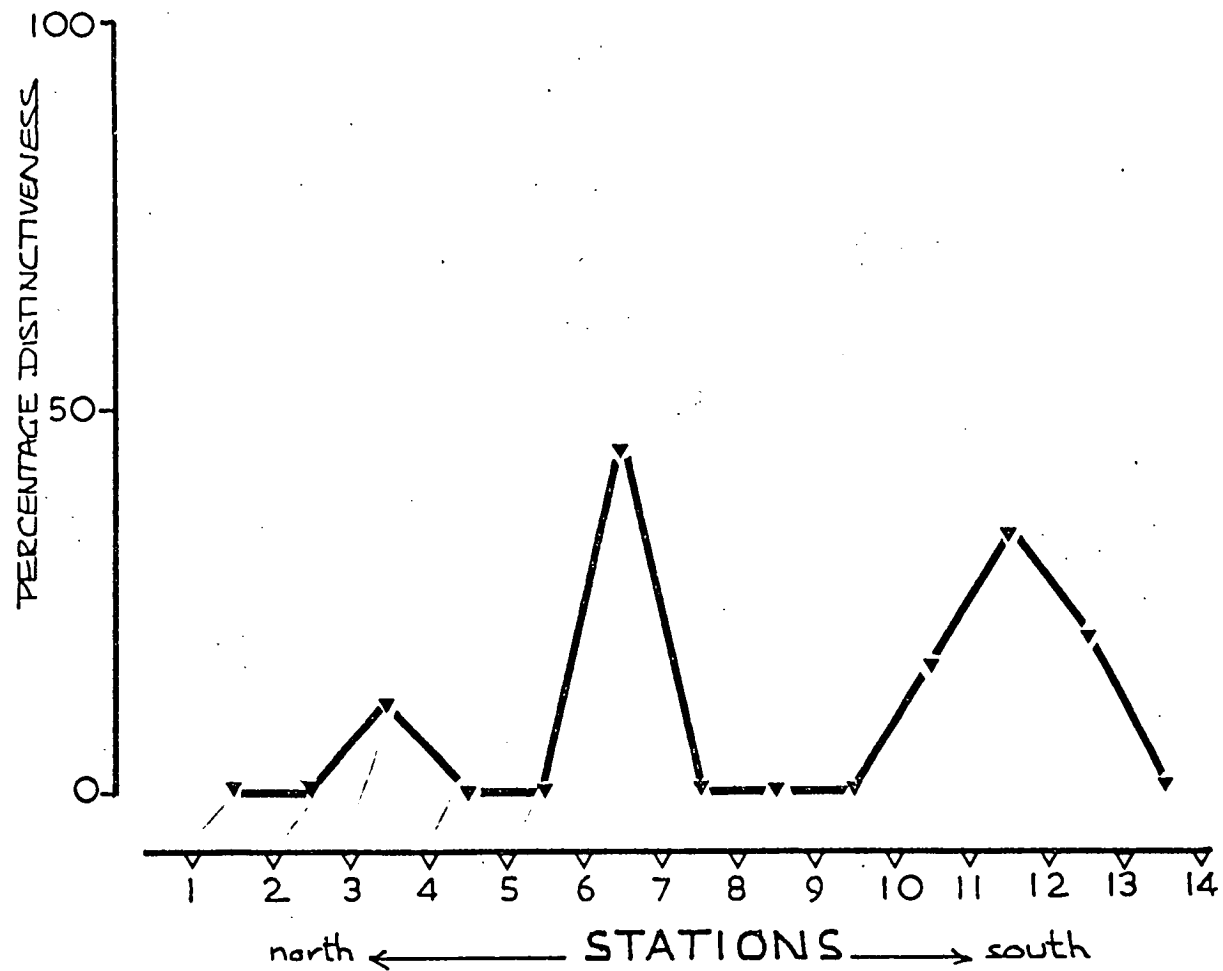
Fig. 8.    Cumacean species    distinctiveness between pairs of
stations along the east coast of Tasmania
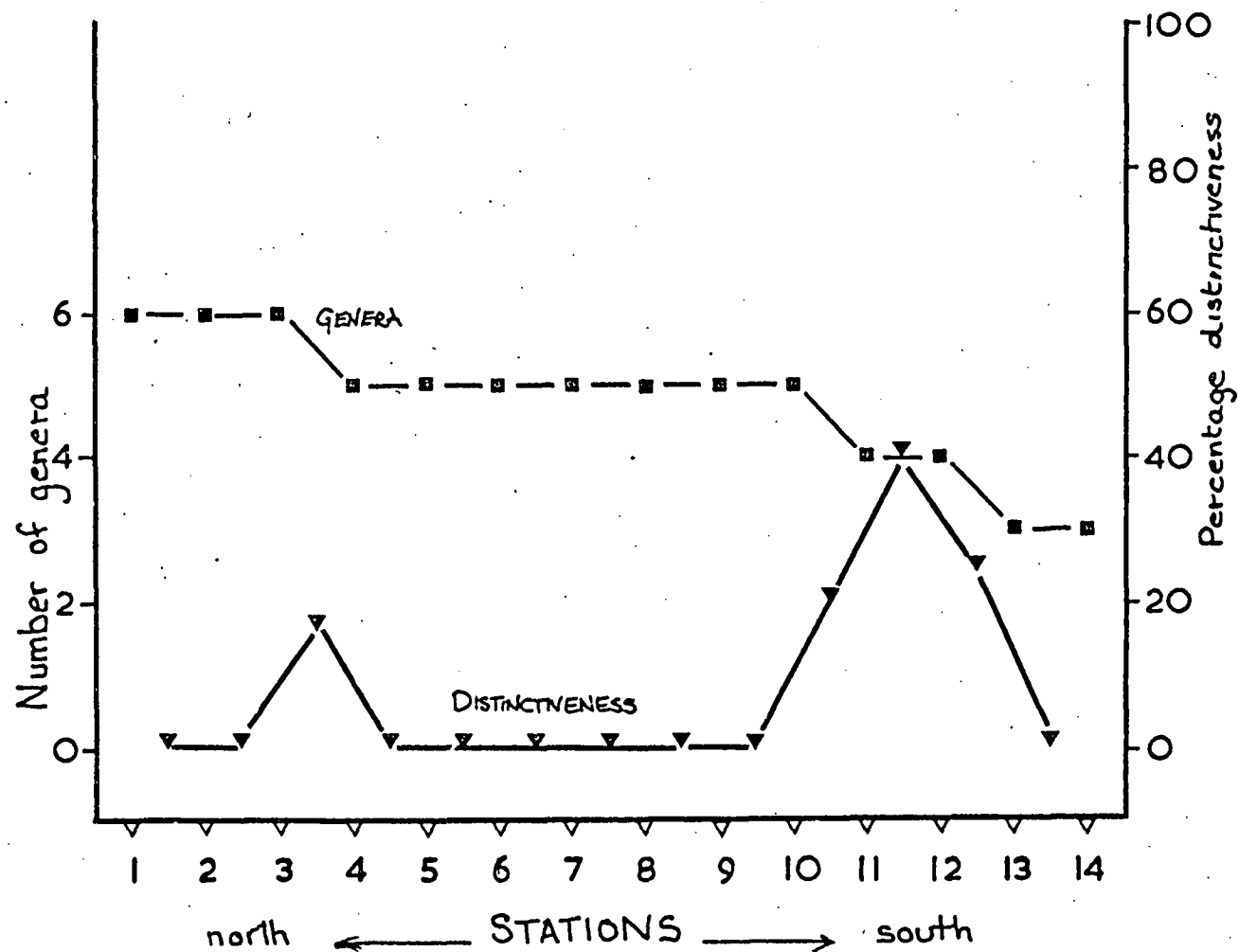
Fig. 9.   Numbers of genera of cumaceans at stations and generic
distinctiveness between stations along a N-S transect,
eastern Tasmania.

sample sets from each locality in spite of the intrusion of genus *Leucon* from the south.

## 4.4    Factors which may control species ranges

### 4.4.1  Introduction

Much zoogeography consists of matching observed ranges to phenomena controlled by the distribution of Coriolis forces around the globe.   This approach is supported by meteorological studies and really consists of correlation between animal distributions and variations in global energy flows.   If energy accumulates in any part of the global system it probably means that an increase in environmental temperature results (Oke, 1978).   Thus temperature regimes are implicated in range maintenance.

In the sea, water bodies are defined by their temperature and salinity characteristics.   The use of indicator species to identify water masses and their distribution is common (e.g. Nyan Taw, 1975).   The assumption made is that a complex of environmental factors is consistent and will be reflected by the fauna of a given regime.   The complex of environmental factors is often lumped under the term "climate" and it is often assumed that the effects of climate may only be indirect.   However, Enright (1976), in an elegant paper, demonstrated that direct effects of climate upon populations can occur.   Thus the biogeographer's dependence upon correlation between climatic variables and the distributional boundaries of species is valid.

Such an assumption has often been made and examples may be found in Bennett and Pope (1953, 1960), Briggs (1974), Dartnall (1974), Knox (1960) and Hayden and Dolan (1975) amongst others.

4.4.2   Distributional oscillations

Global energy distribution is observably not stable.   In some years, for example, water temperatures in the North Pacific Ocean may be as much as $6^{\circ}$C above long term mean temperature (Battan, 1974).   Dzerdzeyevsky (in Rochford, 1973) has argued for global oscillations of atmospheric processes in the order of two years. Rochford (1973) has demonstrated that the transport of subtropical water southward along the east coast of Tasmania varies from year to year with some evidence of two year oscillation.   Namais (in Rochford, 1973) has suggested a mechanism by which atmospheric anomalies may cycle into the oceans and back again to perpetuate ocean anomalies.

If such oscillations do occur distributional boundaries along the east coast of Tasmania may be of two kinds, assuming that they occur at all.   The first kind of boundary is discrete, i.e. of narrow size and is epitomised by the convergences of the oceans.   The second kind of boundary is wide and diffuse being a product of the scale of climatic oscillation.   Such a structure may be indicated by Figures 8 and 9.

Other variables which may affect animal distributions include the scale and persistence of water

bodies. Earlier assumptions, probably more held than real, about the spatial and temporal continuity of water masses in eastern Australian waters have been demolished by studies of the paths of sea buoys tracked by satellite. Mesoscale eddies off eastern Australia persisted for four months (Cresswell and Woods, 1977) and a later eddy persisted for at least one year (Cresswell and Nilsson, 1979). Such eddies extended to 43$^{\circ}$S and 40$^{\circ}$S (see Fig. 10) demonstrating that variable, non-semiannual variations in marine waters may often influence Tasmanian shelf waters.

It is important in any consideration of distributional boundaries, that implied, long-term conclusions are not invalidated by short-term change. The persistence of distributions is an observable phenomenon. Crisp (1965) noted that the distributions of intertidal animals do not vary widely with climatic variations and that severe weather phenomena may cause locally high mortality but do not influence distributions as much as gradual changes in climate.

Two further phenomena may obscure the description of zoogeographic boundaries or, alternatively, help to define such boundaries. Two Tasmanian examples may suffice.

1. The asterinid sea star, *Patiriella brevispina* H.L. Clark has been recorded from low intertidal areas along the northern coasts of Tasmania (Dartnall, 1971). Results of recent

collections have demonstrated that the
distribution of this species extends
southwards but only at sublittoral levels
(Dartnall, 1980).

2.    The sea urchin, *Centrostephanus rodgersii*
(Agassiz) is a distinctive member of the fauna of
the immediate sublittoral of south eastern
Australia but no literature records its presence
from south of Cape Howe (H.L. Clark, 1946).
An account of the discovery of this species in
N.E. Tasmania is in preparation.    The point of
interest here is that none of the specimens
examined from Tasmanian localities so far has been
in reproductive condition.    It remains to be seen
whether the Tasmanian population which probably
originated from an influx of northern larvae,
will become reproductively viable.    The suggestion
made here is that fringe populations of a species
may be able to maintain themselves in fringe
habitats and that such populations may be
identified by their lack of reproductive
competence.

4.4.3    Species richness and distributional change
      If species richness relates to hydrological (= climatic)
change the areas of greatest change off the Tasmanian coast
may be indicated by the rates of decrease of cumacean
species richness southward along that coast.    Such
phenomena have been reported by other authors.    The
observation that if a series of latitudinal boundaries

exists a drop in species diversity takes place as
latitude increases (Briggs, 1974) is supported by the
distribution of cumaceans from eastern Tasmanian benthos.
One striking example, related to the position of the
Subtropical Convergence off New Zealand, was recorded
amongst mesopelagic fishes and crustaceans by Robertson,
Roberts and Wilson (1978).

The diversity of marine climate along the
Tasmanian east coast (i.e. the number of days per
year that a sequence of localities would experience a
given salinity regime) is expressed graphically in Fig.
10.

The area between $41^{\circ}20'S-42^{\circ}27'S$ matches the
northermost dissimilarity peak in Fig. 9. The large
southern dissimilarity peak in that figure is also
matched by those stations south of $43^{\circ}S$ which are influenced
by water of salinity $35^{\circ}/oo$ during the year. The area
between $42^{\circ}27'S$ and $43^{\circ}S$ corresponds to the bank of
null generic distinctiveness between stations 5-10
shown in Fig. 9.

It is also interesting to note that the northern
limit of the area of greatest generic distinctiveness
(station 10 on Fig. 9) matches the northern boundary of
the southern wave energy regime postulated by Davies
(1978) for the east coast of Tasmania (see Fig. 11).

It is suggested that boundaries of greater and
lesser extent do occur between the distributions of benthic
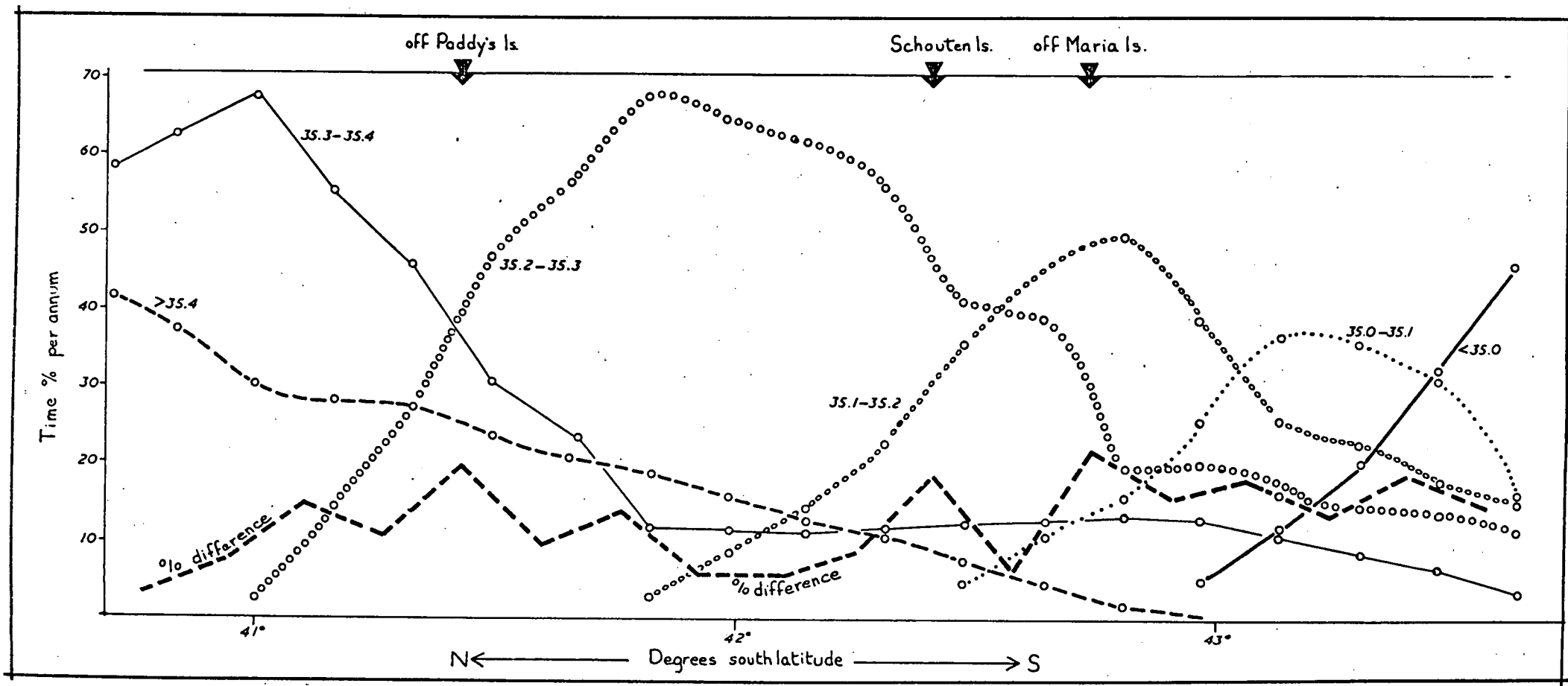
Fig. 10. Per cent time per annum that latitudinal localities are subjected to various salinity regimes. Distinctiveness (as % difference) between stations approximately 10' apart is plotted as a heavily dashed line.

Various landmark localities are indicated along the top edge of the figure.

Data derived from Rochford (1977).
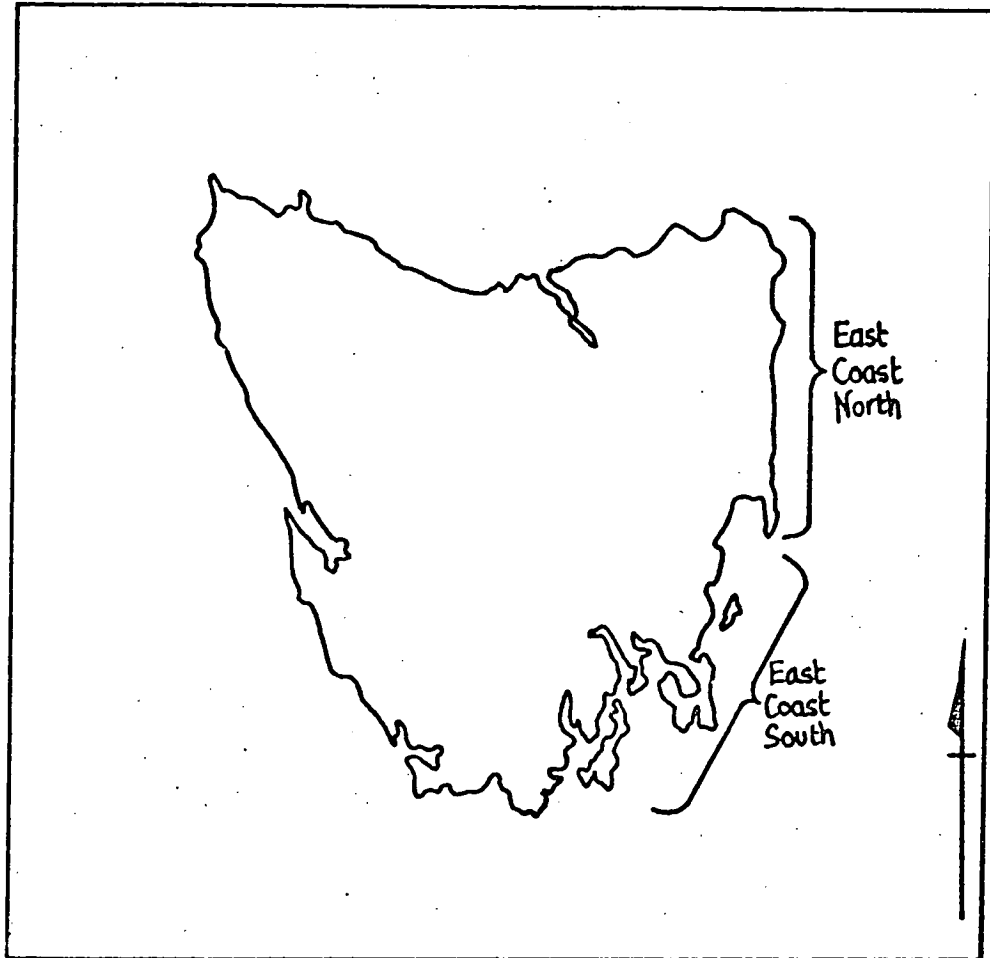
Fig. 11.    Tasmanian coastal wave energy regimes
            (after Davies, 1978).

cumaceans of Tasmanian shallow shelf sands. Whether
the areas are of "provincial" status is discussed in
the next section.

4.5     Biogeographical nomenclature

Two faunal realms are considered to constitute
the marine benthic division; one the photic, phytal
realm; second, the aphotic, aphytal realm.   A faunal
province is a major division of a realm (Menzies,
George and Rowe, 1973).   Those authors suggest that
province distinction may be defined by the rate of change
of genera along a scale thus delimiting the spatial
dimensions of provinces.   For the benthic cumaceans
considered in this study the greatest generic
distinctiveness (4.3.3 and Fig. 9) occurred at two
locations, i.e. between stations 3 and 4 (18%) and
between stations 11 and 12 (40%).

It is suggested that the southern distinctiveness
demonstrated at generic level is a distinct division of
the benthic cumacean fauna of eastern Tasmania.   This
is supported by the division of wave energy regimes
(4.4.3) and the northward extension of water of
subantarctic origin (Fig. 10) along the east coast.
Such a benthic division is also supported by the
distribution of planktonic indicator organisms (Nyan Taw,
unpublished data).

However, it is apparent that patterns and zones
are detectable at virtually any scale chosen by the
worker and may depend on opinion.

Bennett and Pope (1960) sought to define the horizontal distributions of the zone forming organisms of the Tasmanian rocky littoral. They suggested that a marine province, the Maugean, encompasses Tasmanian shores and extends into southern and south-eastern Australia. This level of provinciality has been denied by Womersley and Edmonds (1958) and King (1972). King's conclusions that provincial titles have been used with a number of different meanings is correct. The corollary obtains that provincial nomenclature consists of words alone unless some precise definition is offered. King's final conclusion that a broad overlap between cool temperate and transitional warm temperate elements in S.E. Australia produces a continuum of change with little distinctiveness encourages one to follow his approach and not describe distributional boundaries.

In a survey article (Dartnall, 1974) it was suggested that a true Maugean fauna did not exist because Tasmania did not extend far enough south to include a truly cold temperate faunal contribution. Hidden behind this conclusion was the concept that Pleistocene glaciation and its melt waters would have cooled the waters receiving the contribution of the present Huon and Derwent catchments. Since that time the evidence that wave energy regimes (Davies, 1978) may divide at the Tasman Peninsula and that cold sub-antarctic water may be entrapped within embayments.

by southward moving water of northern origin has made such an historical explanation unnecessary.

As far as psammophilic cumaceans are concerned the distributional evidence (4.4.3), coupled with wave energy regimes and known water body movements, suggests that an identifiable distributional discontinuity does occur.  The evidence of large scale marine climatic studies (Hayden and Dolan, 1975) demonstrates excellent correspondence with faunal distributions already created and it is concluded that a zoogeographic marine boundary exists at about $43^{O}$S off the Tasmanian east coast.  The distinctiveness of fauna either side of this boundary is about 40% for sand dwelling cumaceans.  It remains to be seen if studies on other benthic groups or associations confirm or deny this approach.

4.6     Are biogeographic zones useful tools?

Biogeographic zones are useful tools if they can be used to create testable hypotheses.

Observations that biogeographic zones and marine climates often coincide have been provided by Hayden and Dolan (1975), Horne and Allen (1978) and Valentine (1966) among others.  That the discontinuities between zones may be similar, and thus predictive, was concluded by Horne and Allen (*loc. cit.*).  Because discontinuities are related to marine climates which in turn are a function of global sea-atmosphere interaction the magnitude of different discontinuities may not be the

same because global energy distributions vary around the globe.

It is suggested here than an expression of the magnitude of global marine energy cascades (Oke, 1978) may be used to differentiate the variable compositions of biogeographic zones in a similar manner to the use of distance measurements between sampling stations (see Pielou, 1975).

The work of Petersen (1913) followed by that of Thorson (1957) has expanded the use of empirical indicator communities to a survey tool of great potential for comparative purposes. Work at community level in separate localities has since become common (see Stephenson, 1973). Much of the information garnered appears to offer little in biological terms that could not be inferred by a competent eco-taxonomist. Other criticisms of statistical community studies have been summarised by Peters (1976). Wildish (1977) has also pointed out that the search for an ecological holy-grail has resulted in non-testable tautologies. Whilst recording my support for this approach I must record that Hutchinson (1978) has argued for the value of classifications that, although tautological, allow expression of hypothetic-deductive analyses.

The concept of biogeographic zones provides a framework for the description of mechanisms which may maintain such zones. If geographically separated zones are similar in faunal composition, prediction of detail

from one area to the other may be possible -
Petersen (1913) wrote of the "valuation" of the sea.

Another use for biogeographic zones consists of
temporal comparisons.   Except in exceptional cases
few true fossil associations exist.   Where they do,
direct   comparisons between past and present
associations and their compositions may be made.   Other
fossil associations are the product of larger time
spans than those of modern associations.   It may
be more correct to see many fossil assemblages as the
product of many sequences of community succession.
In order to interpret such stored information we need
to understand the living processes which control assemblages of
organisms and the temporal and physical scales at which they
operate.   Such needs are emphasized by work on spatial
variation (see Thorson (1957), Rhoads and Young (1970),
Poiner (1977)).

5.         CUMACEAN REACTIONS TO SALINITY BOUNDARIES

5.1    Introduction

'Discontinuities in salinity and temperature are
frequent phenomena in natural waters' (Harder, 1968).  If
we accept that water bodies have boundaries and that such
bodies contain distinctive, indicator organisms we may also
postulate that such organisms:

(a)   may detect hydro-chemical boundaries; and

(b)   are more suited to live within a water
      body of given characteristics.

The range within which an animal operates often
is investigated by exposing sets of individuals to
different conditions and recording the survival rate of
that animal under each combination of factors.  The
tolerance and survival technique may be used to define
the parameters of well-being of a species of population
and thus define the attributes of postulate (b).  Such
a technique was not available for this work because it was
not possible to maintain live cumaceans long enough to
acclimate the animals and then run survival experiments.
However, postulate (a) was testable with animals freshly
returned to the laboratory.

All experiments were conducted in daylight in
order to obviate the possibility that responses to
vertical salinity changes differ in cumaceans which
exhibit vertical movements through the water column at
night (see chapter 12).

## 5.2    Method

A small tank was made from clear acrylic sheet
and mounted on a base-board with a levelling screw at each
corner.    Four inlet tubes were inserted in one side of
the tank and four larger drain holes were drilled in the
other side.    The dimensions of the tank are shown in
Fig. 12.

The tank inlets were connected to reservoirs
of sea water by polythene tubing (Fig. 13).    Flow from
each reservoir was controlled by a small tap in each
pipe.    A tank divider constructed from four glass
slides was inserted into the tank dividing it into four
sections.    Sea water was then run from each reservoir
into each section.    The rates of flow and the level of
the base-board were adjusted until all horizontal water
surfaces were level.    The tank divider was then
removed slowly and on some occasions sea water bodies
differing by $1^o$/oo were seen to maintain discrete
boundaries.    This observation was aided by adding
non-toxic food dye to alternate water reservoirs.

The technique is not easy and discrete water flows
are often difficult to maintain.    However, on two
occasions it was possible to move a water body interface
sideways along the tank before mixing took place.    This
was controlled by adjusting the inflow from one
reservoir.    On seven occasions discrete water bodies
were maintained for more than 10 minutes.    Two of the
seven runs held their interface integrity for 15 mins.
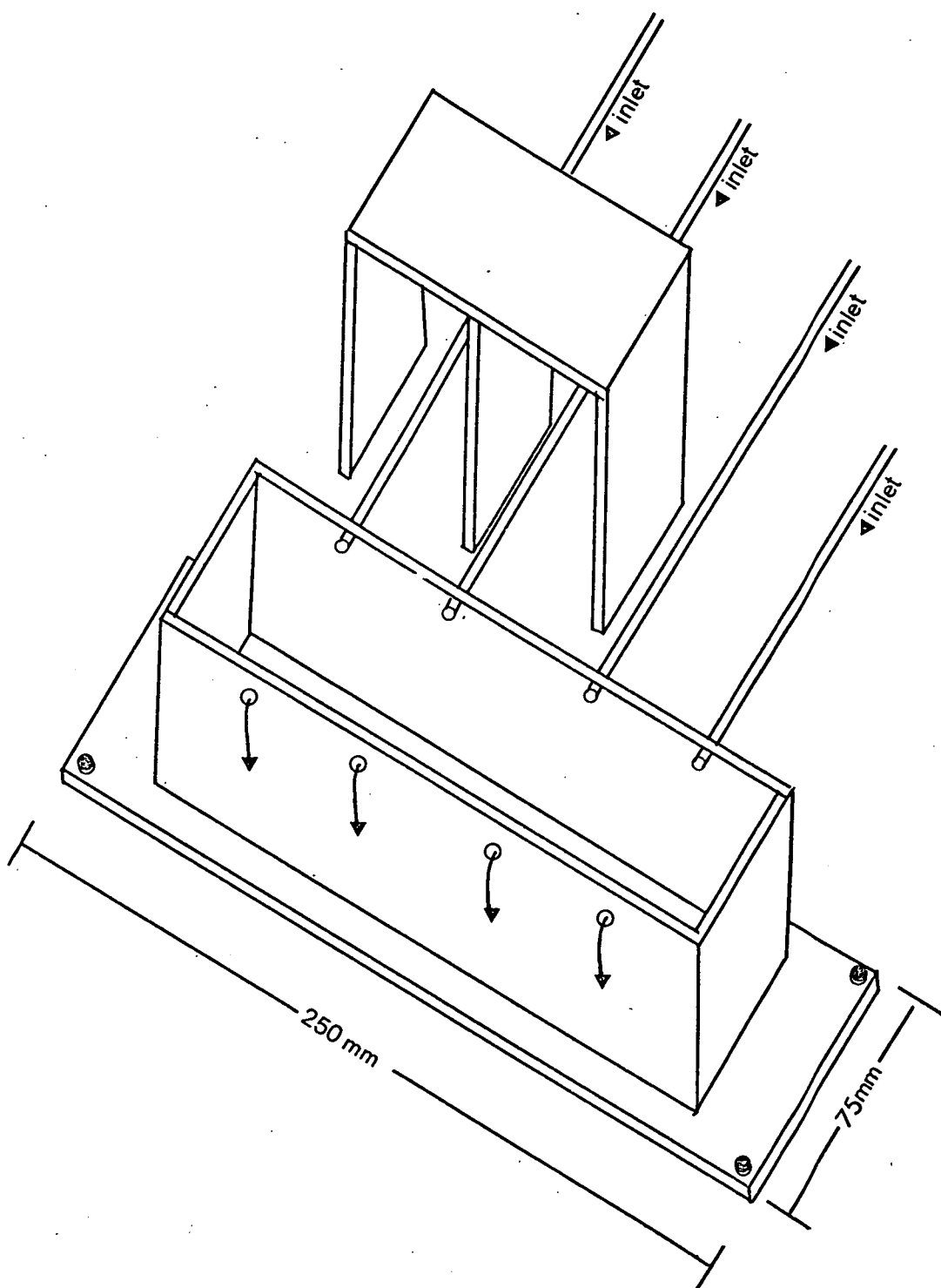
Fig. 12.    Salinity regime test tank (see text for
            details of operation).
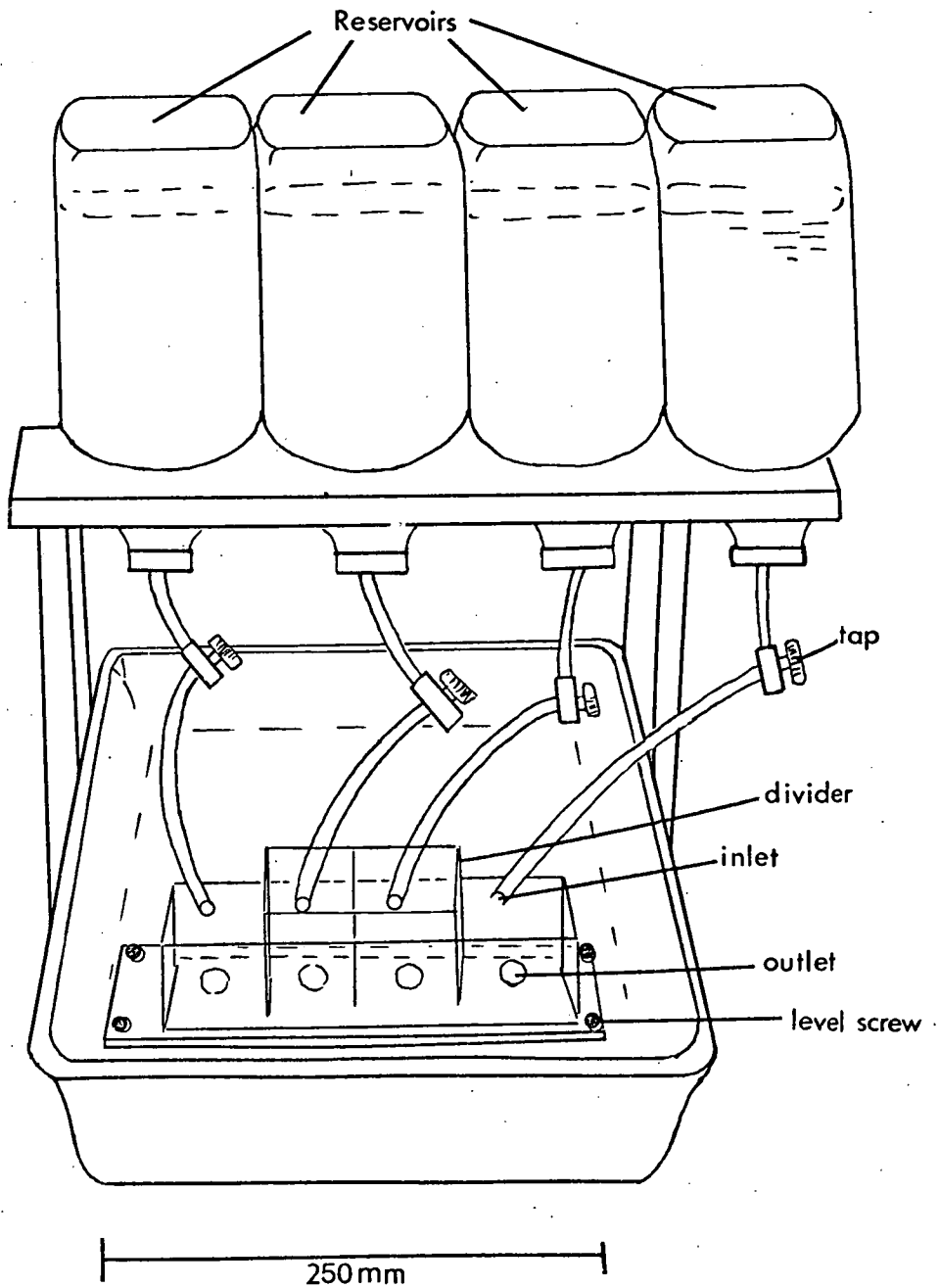
Fig. 13.   Salinity regime test tank with
           tank divider in position (drawn
           from a photograph).

This experimental technique was abandoned when it was found that the nine successful runs amounted to 8% of the total attempts to set up the equipment.

5.3     Experiments

The water bodies eventually used were:

(a)     water from the locality from where the specimens were taken $(34.2^{O}/oo)$;

(b)     water of salinity of $35.4^{O}/oo$ prepared by evaporation from $34.2^{O}/oo$ water. The concentration of water body (b) was chosen because this approximates the concentration of southward reaching water of sub-tropical origin during the Tasmanian summer months.

Both water bodies were maintained at room temperature ($c$. $16^{O}C$) and on each occasion when live specimens were returned to the laboratory one attempted to set up a water body separation experiment.   Equal numbers of cumaceans were added to each water body, their movements were watched closely and counts of numbers in each area were made at five minute intervals. No substrates were added to the tank.

5.4     Results : stable water body experiments

Water boundary collapse indicated by wavy line

*Cyclaspis caprella*

| | | Initial Number | Numbers + 5 mins | Numbers + 10 mins | Numbers + 15 mins | |
|---|---|---|---|---|---|---|
| Run 1 | 34.2 | 25 | 25 | 31 | | }50 |
| | 35.4 | 25 | 25 | 19 | | |
| Run II | 34.2 | 17 | 17 | 18 | | }34 |
| | 35.4 | 17 | 17 | 16 | | |
| Run III | 34.2 | 12 | 12 | 12 | 12 | }24 |
| | 35.4 | 12 | 12 | 12 | 12 | |

*Cyclaspis* n. sp.

| | | Initial Number | Numbers + 5 mins | Numbers + 10 mins | Numbers + 15 mins | |
|---|---|---|---|---|---|---|
| Run IV | 34.2 | 100 | 100 | 117 | | |
| | 35.4 | 100 | 100 | 83 | | |
| Run V | 34.2 | 30 | 29 | 29 | | }60 |
| | 35.4 | 30 | 31 | 31 | | |
| Run VI | 34.2 | 12 | 12 | 12 | 14 | }24 |
| | 35.4 | 12 | 12 | 12 | 10 | |
| Run VII | 34.2 | 24 | 24 | 25 | | }49 |
| | 35.4 | 25 | 25 | 24 | | |

The tank contained no sediment and all the animals were actively leaving the bottom of the tank and swimming into the water column. Animals could be observed to turn back at the salinity interfaces. Six specimens of *C. caprella* (24% of their sample of origin) managed to cross the boundary in run I and 1 specimen crossed in run II.

No specimens crossed the interface in run III.

Greater numbers of *Cyclaspis* n. sp. were available on one occasion and run IV was operated with a high density of animals. In spite of this only 17% of animals apparently chose to leave their original water body. This was a difficult experiment to count and the final score was only achieved by placing a separator across the tank when the salinity interface appeared unstable. Run V was the only occasion when a cumacean crossed from $34^{\circ}$/oo to $35.4^{\circ}$/oo. Two individuals (16%) and 1 individual (4%) crossed the boundary in runs VI and VII.

At this stage it appeared that the experimental technique was not developing into a useful tool. However, before the equipment was rejected it was decided to subject a set of cumaceans to advancing salinity fronts.

5.5      Experiment on advancing fronts

5.5.1    Method

Flows of the two experimental water bodies were initiated with the glass divider in place. Alternate water bodies were identified by adding dye to the water. Cumaceans (*Cyclaspis* n. sp.) were added to the most central $34.2^{\circ}$/oo water in run IX and to the most central $35.4^{\circ}$/oo in run X. The divider was then removed and the flow of the water body without animals was increased. This forced the other water body to contract. At the moment that the interface between the two water bodies appeared

unstable the tank divider was replaced.    The final position of the intact interface was recorded and the numbers of animals in each section of the tank counted.

## 5.5.2    Results
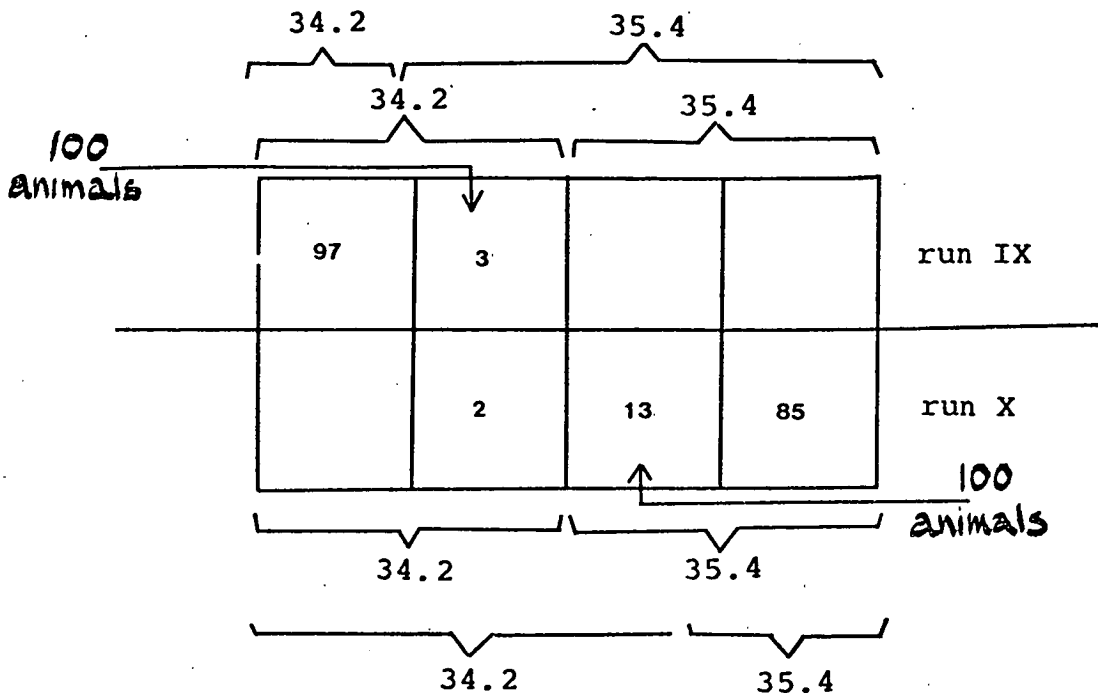


On both occasions the majority of animals inoculated into the inner division of the water body retreated to the most distant division.    In run IX, 3 specimens maintained their original position but finished in 35.4$^{\circ}$/oo water.    In run X, 13 specimens maintained their original position, 85% moved to concentrate in their original salinity and only 2 moved to change position and salinity.

## 5.5.3    Discussion

The results of these simple experiments should be treated as no more than indicators for future

investigation.    However, it does appear that the
cumaceans tested in this way will not, on the whole,
cross salinity interfaces of the order of $1^{o}/oo$.
This conclusion is supported by the evidence of Harder
(1968) who recorded mixed copepods, *Eurytemora hirundo*
and nauplii of *Pollicipes polymerus* reacting to salinity
gradients of $<1^{o}/oo$.    Other, more euryhaline species,
only reacted to salinity gradients of higher
concentration, and it may be that the conclusions drawn
here are only referrable to coastal species or populations.

Run X indicates that the boundary is more
important than the salinity value even though more
animals finished the run in sections of the tank with a
contribution of $34.2^{o}/oo$ water.    That evidence also
supports Harder's (*loc. cit*) suggestions that the
properties of the discontinuity layer between the water
bodies are detected by animals rather than the intrinsic
properties of the water bodies themselves.

THE SECOND PART : CUMACEAN DISTRIBUTION

BETWEEN FOUR AND TWENTY-TWO METRES

6.      THE QUANTITATIVE DISTRIBUTION OF CUMACEANS IN

     SUBLITTORAL SANDS OF LITTLE SWANPORT, EASTERN TASMANIA.

                    The purpose of this part of the project

                    was to investigate the distribution of

                    Tasmanian sublittoral, psammophilic

                    Cumacea in relation to depth, distance

                    offshore and a number of sedimentary

                    parameters.

6.1      Introduction

     Studies upon the quantitative distribution of

cumaceans have been made by Watkin (1942) in Kames Bay,

Scotland; Pike and Le Sueur (1950), Jersey; Clark and

Milne (1955), Kames Bay and White Bay on the Isle of

Cumbrae; Wieser (1956), Californian coast; Barnard and

Given (1961), deep water off the coast of California;

and Corey (1970), littoral and sublittoral Kames Bay.

     This account contains the first quantitative

data about the distribution of some Tasmanian sublittoral

Cumacea.

6.2      Methods

6.2.1      Site and survey

     A survey was made in the bay off Little Swanport

on the east coast of Tasmania at approximately $148^{O}E \times 42^{O}18'S$.

The survey area consisted of a grid of stations, each about

50m apart (Plate 1).   The inshore edge of the survey area

Plate 1: The bay off Little Swanport showing the
positions of survey stations relative to
the coastline.

100METRE
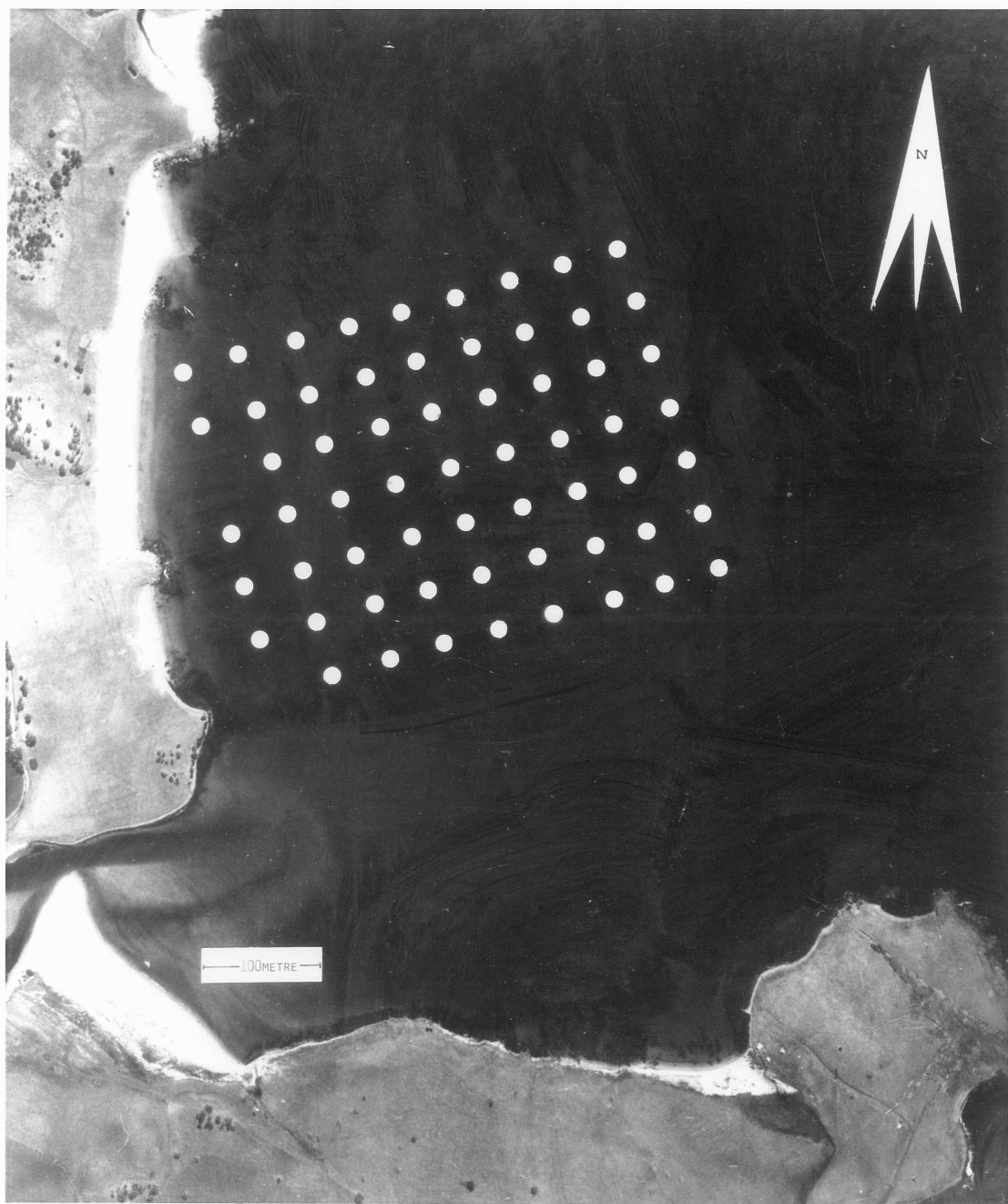
was limited by the depth to which sampling gear could be worked conveniently (*c.* 20m).

The survey grid was planned before working the area. Triple compass sights to conspicuous landmarks were plotted from an aerial photograph of the area (aerial photograph provided by Tasmanian Government Department of Lands and Surveys).

Dan buoys were laid at the most northern and southern of the seaward stations to produce extra sight marks. Compass bearings are a common method of position fixing in inshore water but are usually the least accurate method (Holme, 1971). An attempt to improve the accuracy of position fixing was made by running transits using conspicuous landmarks and the seaward dan buoys when coincidence occurred. Later surveys in this work combined transit approaches with horizontal sextant angles (see Murray (1966), for an explanation of this technique).

6.3      Sampling

6.3.1    Faunal samples

At each station a sample was taken by air-lift sampler (see Appendix I). Faunal samples were filtered, concentrated, labelled and preserved on board (Appendix I).

6.3.2    Sediment samples

Sediment samples were taken at each station using

a Mud Snapper, which is a small, two-jawed grab. In
practice the Mud Snapper was released before the air-
lift sampler was operated because it acted as an anchor.
It was then retrieved when the air-lift samples were
completed. The Mud Snapper was chosen to sample
sublittoral sands because it was one of the few sampling
mechanisms available that consistently took samples
from consolidated sands and was operable from a small boat
with a hand winch. Sediment samples were placed in screw-
capped jars of $c$. 125ml capacity and maintained in
crushed ice in an insulated container.

Salinity and water temperature records were
made at the surface and bottom of each station using a
temperature-salinity meter (Autolab, model 602, accuracy $\pm 0.1°C; \pm 0.03‰$).
Water depth and time of sampling were also recorded.
Depths were later corrected for tidal height using a
nomogram constructed from the tidal data available
(Fig. 14). These corrections were made because if
benthic animals are sensitive to small changes in water
pressure (see Newell, 1976), tidal height changes
may be important in modifying animal distributions at
short intervals (say = 1 hour).

6.4      Onshore treatment

6.4.1    Fauna

On return to the laboratory each sample was
decanted into a petri dish and the contents examined
under a low power dissecting microscope. Cumaceans
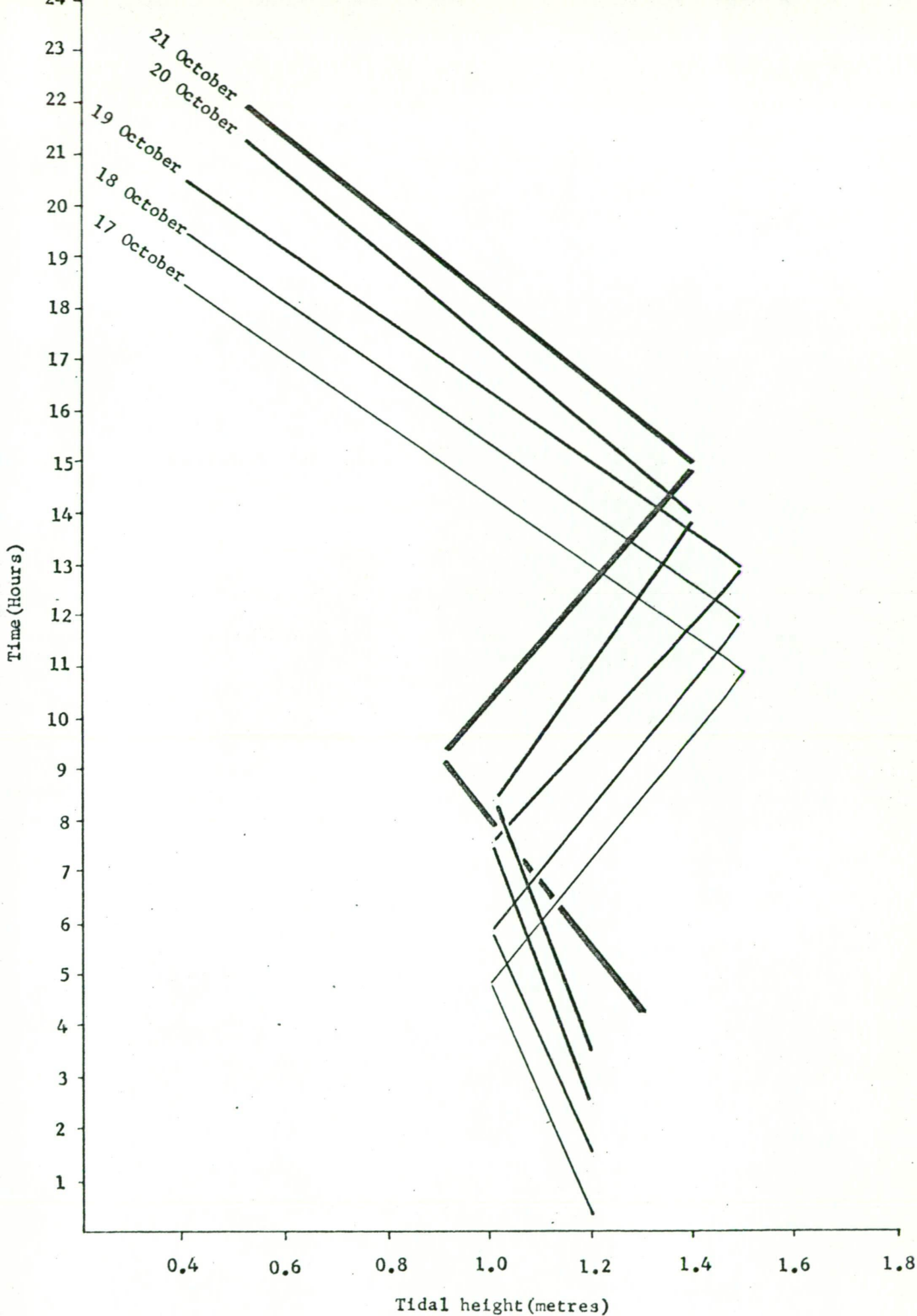
Fig. 14.    Tidal heights, Little Swanport, 17-21
            October, 1977.

were removed, identified (using the keys of Hale, 1928
*et seq.*) and the numbers of each species recorded.

6.4.2    Sediments

On return to the laboratory each sediment sample
was divided into two portions.    One portion was dried
in an oven at 100$^{\circ}$C and passed through a nest of soil
sieves (1000, 500, 250, 125, 63µm mesh) agitated by a
mechanical shaker.

The second portion of each sediment sample was
introduced to the lower arm of a falling head permeameter
(after Webb, 1969) (see also Appendix II).    The number
of consolidation phases were recorded and the permeability
of each sample determined.

6.4.3    Data

The data from the faunal samples are given in
Table III and that from the sedimentary analyses in Table
IV.    (Tables are placed at the end of this chapter.)

The total distribution of cumaceans over the
sampling grid as ranked numbers per sample per station
is shown in Fig. 15.

6.5    On the distribution of cumaceans from Little
        Swanport in relation to water depth above substrate

6.5.1    Total cumaceans

All the sample records were grouped at one metre

KEY
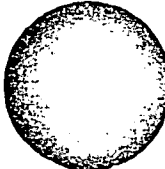


● 1 - 10

● 11 - 20

● 21 - 30

● 31 - 40

● 41 - 50

● 51 - 60
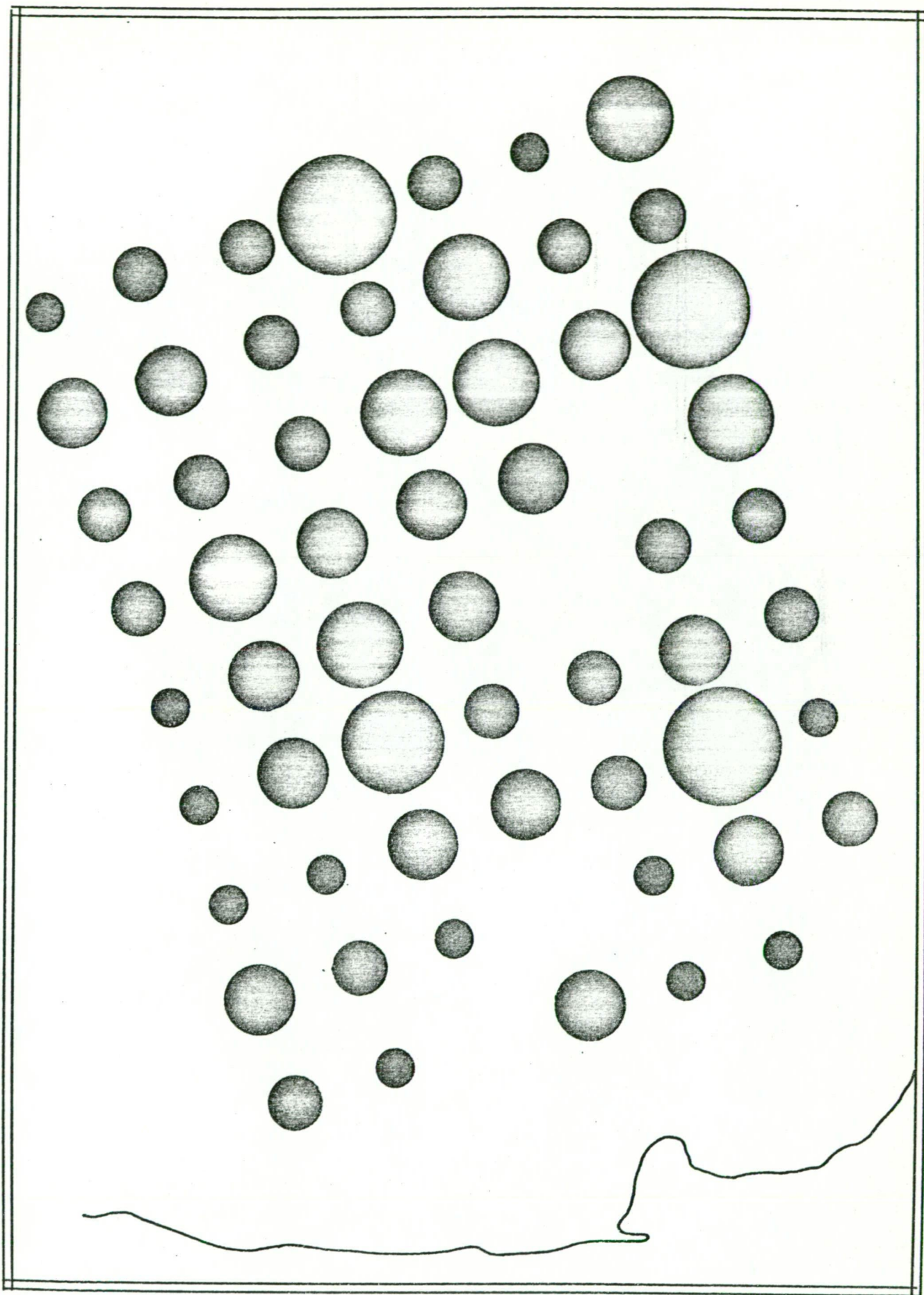
Fig. 15.    All Cumaceans : ranked numbers/sample/
station at Little Swanport.

depth intervals and mean numbers of individuals plotted (Fig. 16).

Ho = that all ranked numbers have an equal probability of occurrence

$x^2$ = 102.66 with 18 df >28.87 (P < 0.05) >34.81 (P < 0.01)

∴ any agreement with a random series is rejected and it is suggested that the ranked figures demonstrate some significant groupings.

6.5.2    The distribution of individual species against depth

6.5.2.1  *Anchistylis waitei* (Fig. 17)

By inspection of the distribution graph it may be seen that no *A. waitei* were recorded at depths < 5 metres.

For depth ranked mean classes,

$x^2$ = 52.72 with 18 df > 28.87 (P < 0.05) >34.81 (P < 0.01)

∴ the observed concentration of this species between 12-17m is not a random phenomenon.

6.5.2.2 *Dimorphostylis subaculeata* (Fig. 18)

No specimens were taken at depths more shallow than 5 metres although I have identified specimens of this species from shallow depths on sheltered sand beaches without a marked surf zone.
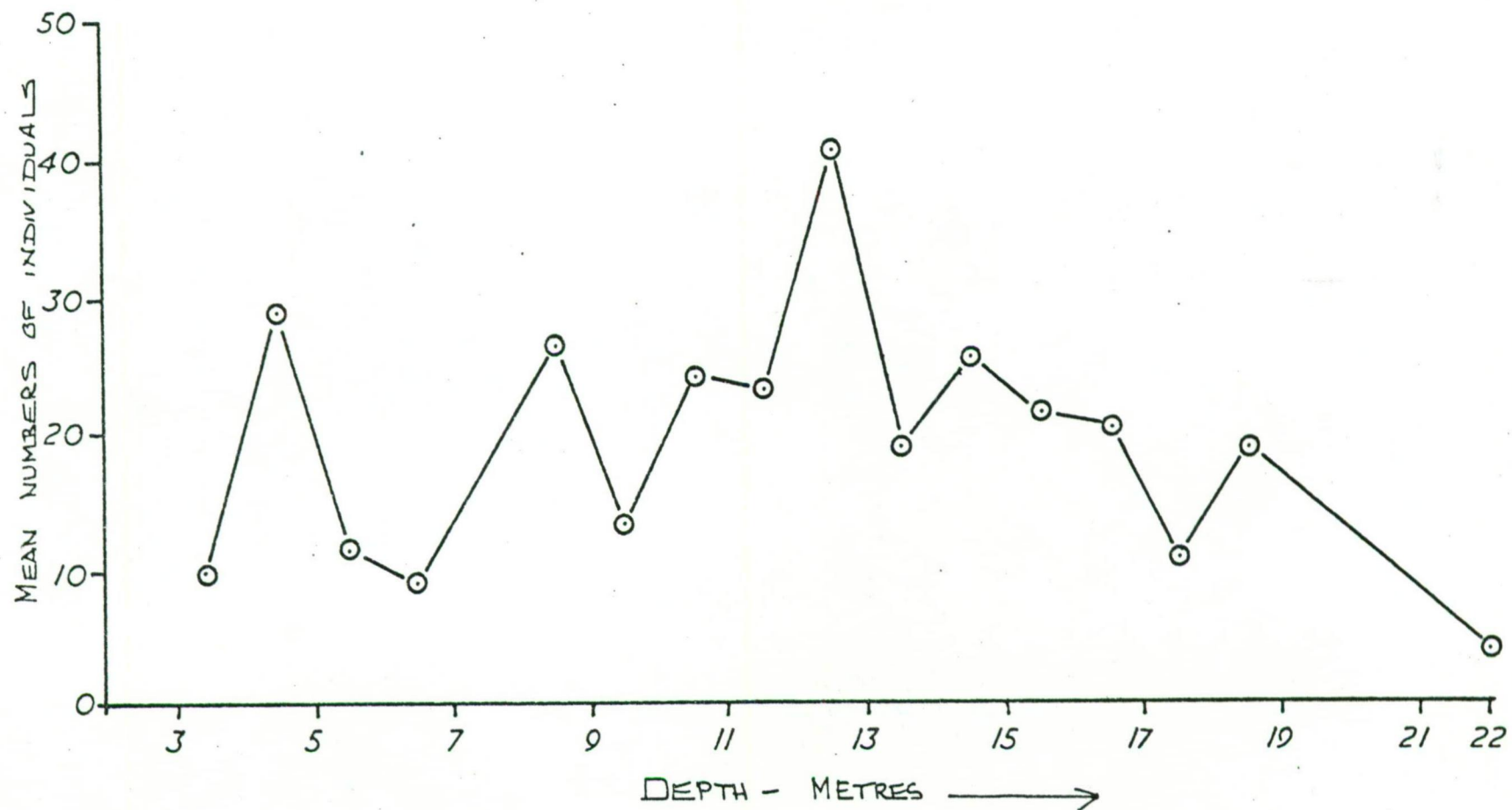
Fig. 16.    Total cumaceans, mean values against depth;
            Little Swanport.
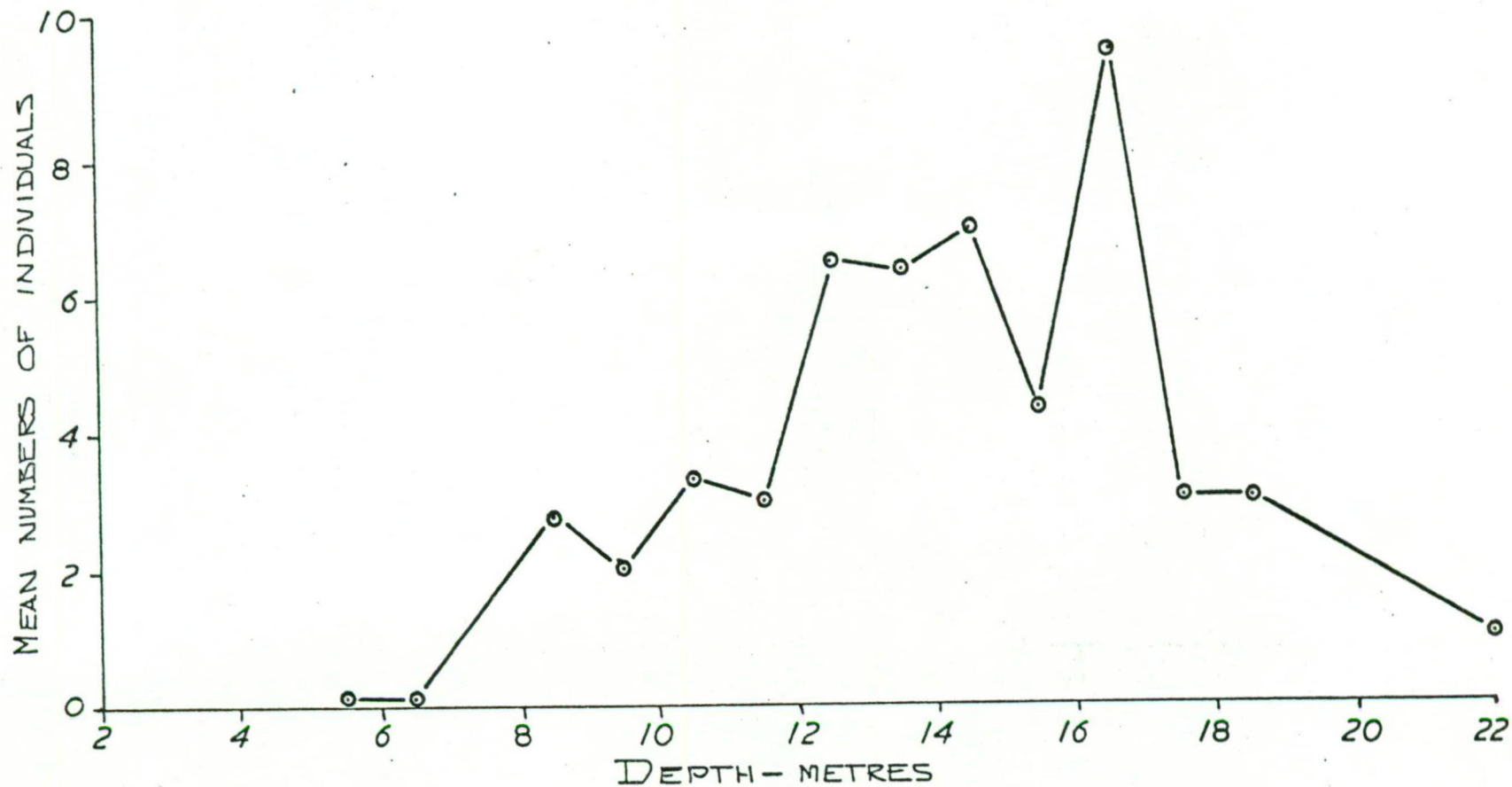
Fig. 17.    *Anchistylis waitei* : ranked mean numbers of
individuals plotted against depth at which
samples were taken.
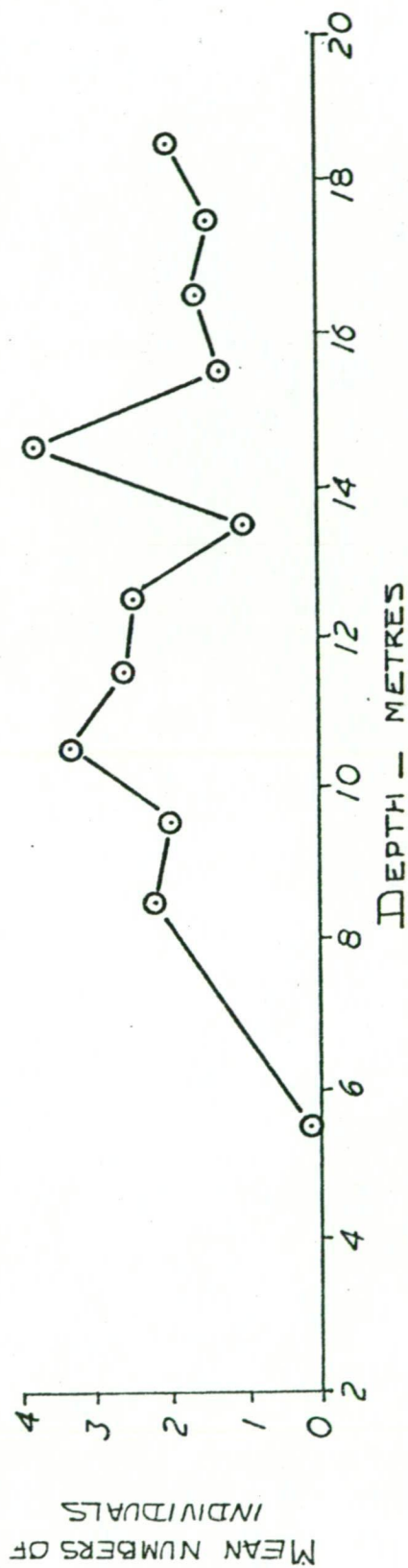
Fig. 18. *Dimorphostylis subaculeata* : ranked mean numbers of individuals against depth.

For depth ranked mean classes,

$$x^2 = 22.0 \text{ with } 18 \text{ df} > 17.34 \ (P < 0.05) < 22.76$$
$$(P > 0.02).$$

Any apparent departure from a random distribution of these samples should be considered carefully.

### 6.5.2.3 *Leptocuma pulleini* (Fig. 19)

By inspection there is an apparent trend for *L. pulleini* to concentrate its distribution at depths between 8-13 metres with lesser numbers ranging to deeper water (sampling depth limit 22m) and towards the surf zone.

$$\text{The } x^2 \text{ value } 123.65 \text{ with } 18 \text{ df} > 28.87 \ (P < 0.05)$$
$$> 34.81 \ (P < 0.01),$$

suggests that the depth classes are clumped.

### 6.5.2.4 *Cyclaspis caprella* (Fig. 20)

*C. caprella* appears to have its major distribution in shallow water tailing off until between 9 and 17 metres only a few individuals are found.

$$x^2 = 90.13 \text{ with } 18 \text{ df} > 34.81 \ (P < 0.01)$$

which supports the observation of this distribution.

### 6.5.2.5 *Dicoides brevidactyla* (Fig. 21)

The distribution of this species in relation to depth is marked on the graph by a relatively high mean value at depth class 4-5m.   The distribution is significantly clumped ($x^2 = 133.70$ with 18 df $> 34.81$ ($P < 0.01$)) but
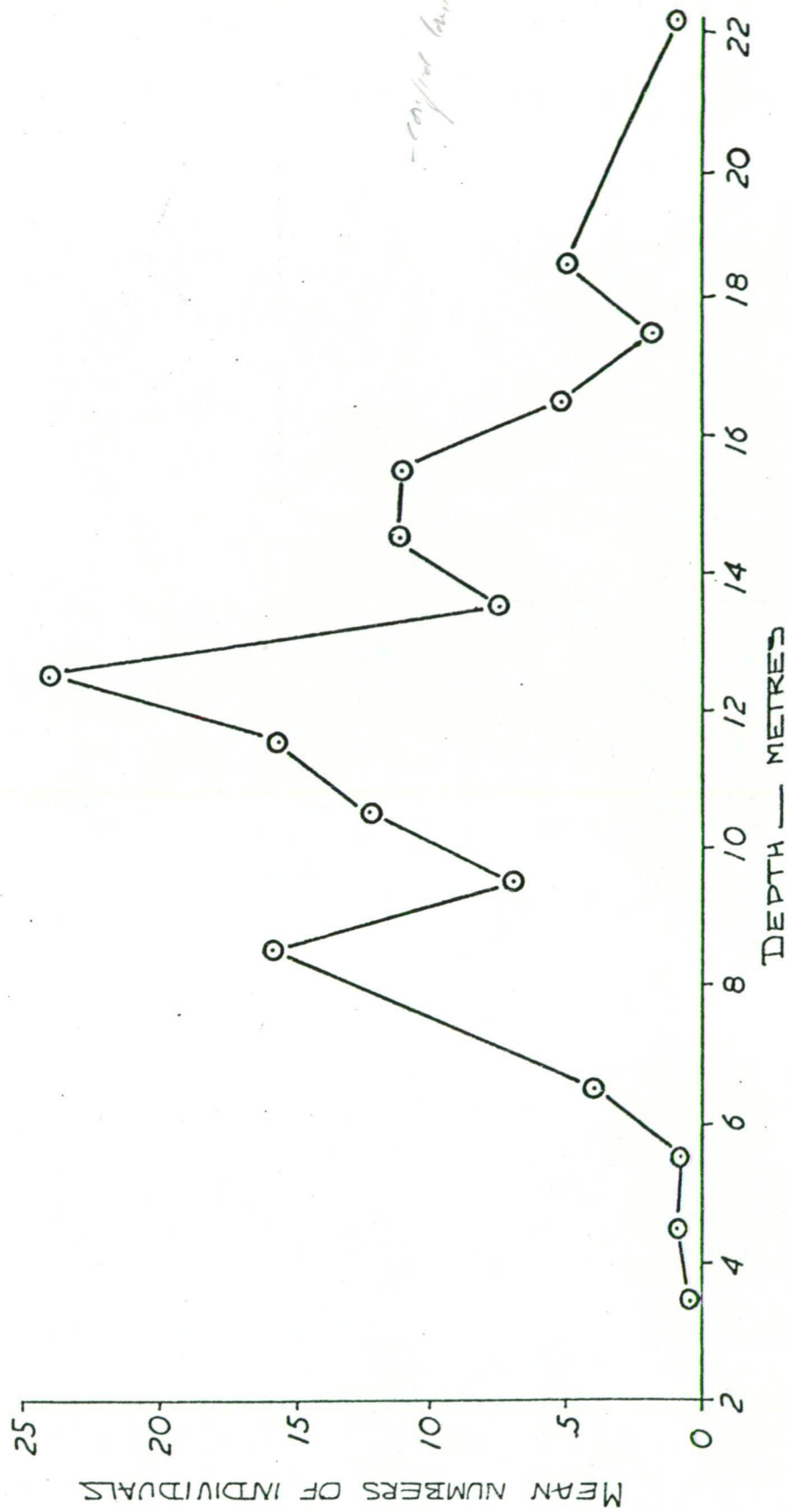
Fig. 19.   *Leptocuma pulleini* : ranked mean numbers of individuals against depth.
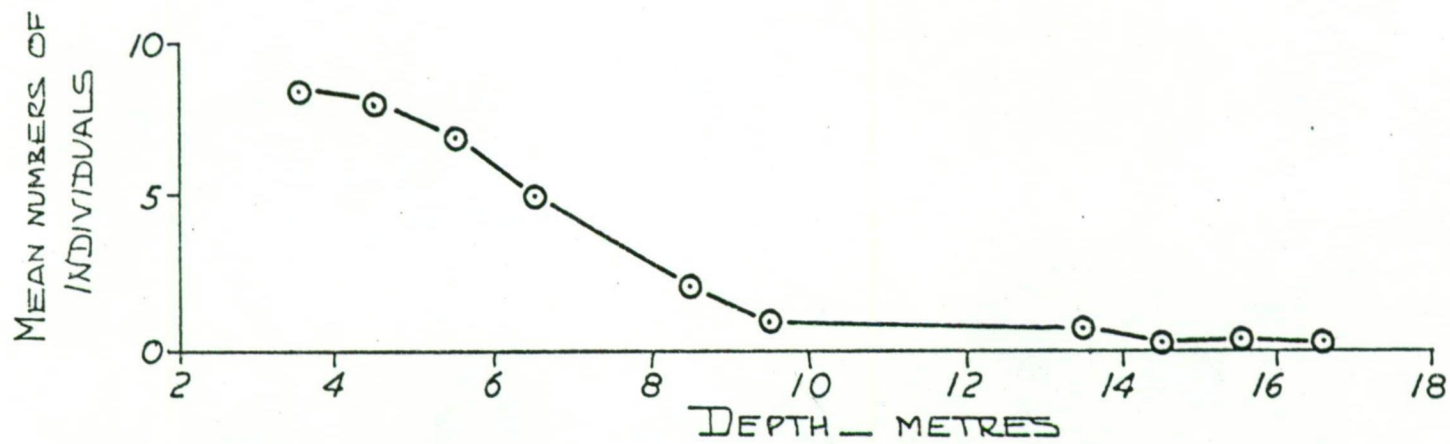
Fig. 20.  *Cyclaspis caprella* : ranked mean numbers of individuals against depth.
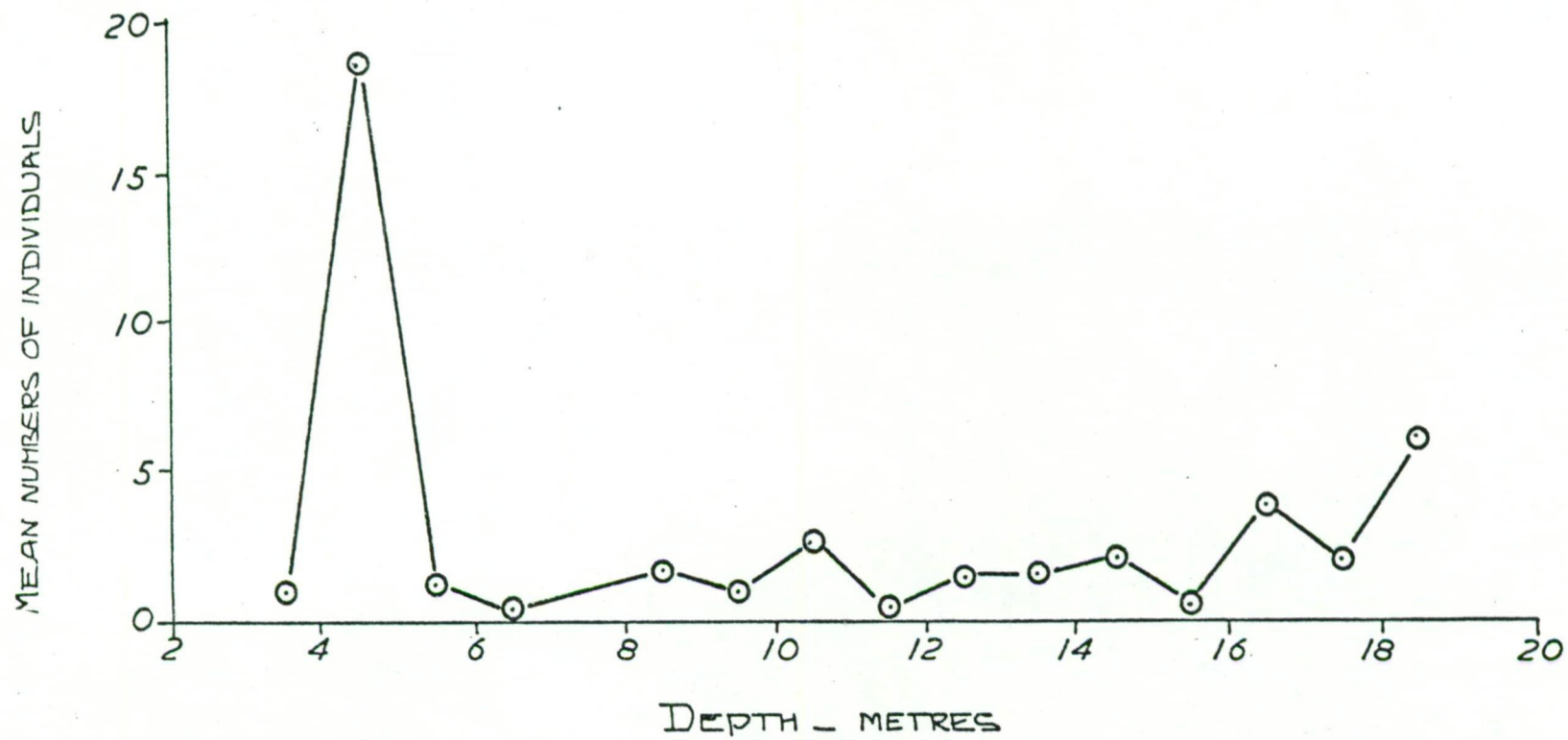
Fig. 21. *Dicoides brevidactyla* : ranked mean numbers of
individuals against depth.

most of this variation was contributed by one station only (E6, with 50 individuals of this species taken in the sample). I have no reasons to explain this aggregation (but see Discussion 11.7).

If the distribution is examined without the contribution of station E6, $x^2 = 23.73$ with 18 df $> 22.76$ (P $< 0.20$) $< 25.99$ (P $> 0.10$) which may indicate that the increase in numbers with increasing depth indicated in the graph is a real phenomenon. At first it was considered that this might reflect an increasing proportion of small sedimentary particles as the water became deeper (i.e. as one moved offshore). The small size of the mouth frame of *D. brevidactyla* may indicate that it feeds upon small particles. As a decrease in grain size seaward of the surf zone is a well recorded phenomenon this appeared a reasonable hypothesis. However, diminution in grain size with increasing depth was not detected in the Swanport samples and no experimental evidence of grain size choice by this species is available as I was unable to return live samples to the laboratory.

6.5.2.6 *Dicoides fletti* (Fig. 22).

*D. fletti* appears to have an inshore limit at the seaward edge of the surf zone (4-5m) and extends seawards at least as far as 22m depth. Peak distributions are found between 12-16m. $x^2 = 29.32$ at 18 df $> 28.87$ (P $< 0.05$) $< 31.53$ (P $> 0.025$). The distribution observed is probably best regarded as random.
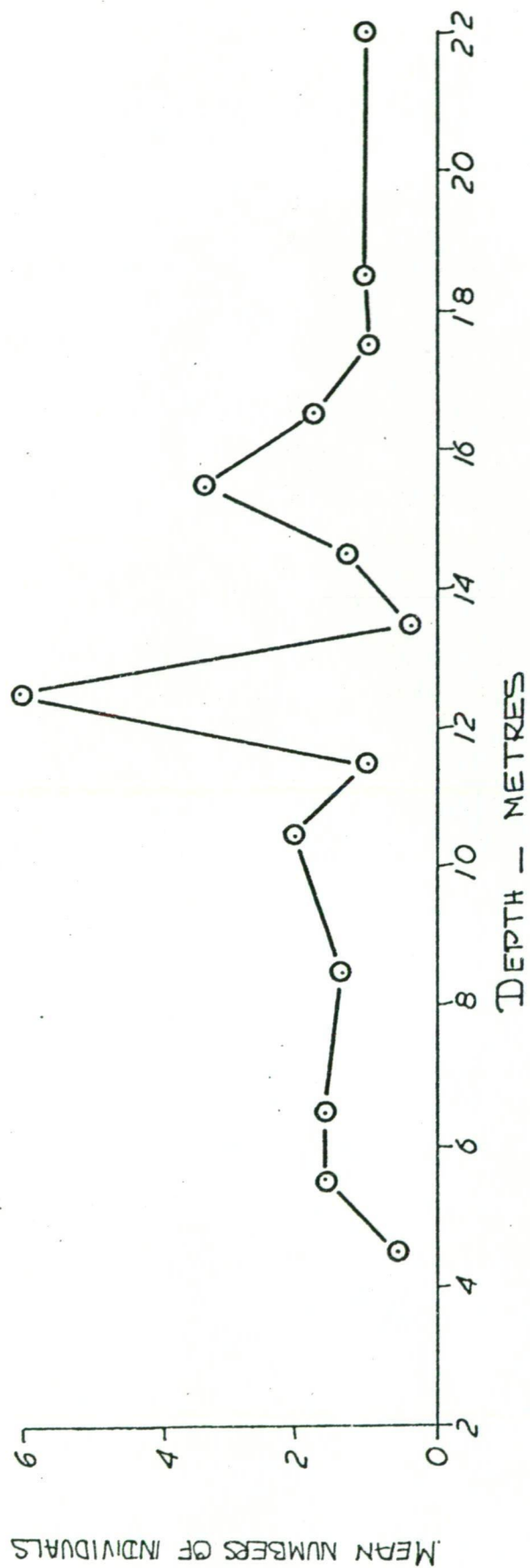
Fig. 22. *Dicoides fletti* : ranked mean numbers of individuals against depth.

6.6    The spatial distribution of Cumacea at Little
       Swanport

6.6.1    All cumaceans

    The numbers of cumaceans at each station were
ranked and plotted (Figure 15). All stations but two
(D4 and H6) contained cumaceans. (N.B. Station 65 was
overlooked; Stations C3 and C7 were rock substrate and
were not sampled.)

    Hypothesis: That the distribution of all cumaceans
    from the Little Swanport samples is random.

    A $x^2$ test for agreement with a Poisson Series was
employed (Elliott, 1977).

|   | C  | D  | E  | F  | G  | H  | J  | K  | M  |
|---|----|----|----|----|----|----|----|----|----|
| 1 | 15 | 21 | 6  | 5  | 9  | 11 | 14 | 22 | 4  |
| 2 | 2  | 3  | 3  | 29 | 24 | 37 | 20 | 26 | 18 |
| 3 | .  | 9  | 17 | 41 | 35 | 22 | 14 | 15 | 11 |
| 4 | 21 | 0  | 18 | 16 | 26 | 22 | 31 | 11 | 53 |
| 5 | 4  | 9  | 12 | 14 | .  | 30 | 29 | 35 | 12 |
| 6 | 5  | 24 | 53 | 18 | 14 | 0  | 29 | 17 | 3  |
| 7 | .  | 14 | 10 | 14 | 13 | 33 | 52 | 17 | 36 |

$n = 60$; $\sum x = 1128$; $\bar{x} = 18.8$; $s^2 = 155.3$

$x^2 = 487.39$; $d = 20.40 > 1.95$ (95%) $> 2.58$ (99%)

$\therefore$ agreement with a Poisson Series is rejected.

    Thus the distribution of all cumaceans at Little
Swanport, as sampled, is probably contagious.

6.6.2    The species

    The counts of each species were isolated from the

total counts.    The general hypothesis employed was that
the distribution of each species of cumacean sampled was
random.

6.6.2.1  *Cyclaspis caprella*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 14 | 16 | 5 | 1 | 0 | 1 | 0 | 1 | 0 |
| 2 | 0 | 10 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| 3 |   | 7 | 5 | 2 | 0 | 0 | 0 | 0 | 0 |
| 4 | 17 | 0 | 15 | 2 | 0 | 3 | 4 | 0 | 0 |
| 5 | 1 | 4 | 5 | 9 |   | 0 | 0 | 0 | 1 |
| 6 | 3 | 13 | 2 | 8 | 0 | 0 | 0 | 0 | 0 |
| 7 |   | 4 | 1 | 1 | 1 | 0 | 0 | 1 | 0 |

n=60; $\{x = 160;$ $\bar{x} = 2.66;$ $s^2 = 16.497$

$x^2 = 365.9;$ $d = 16.24 > 1.96$ (95%) $> 2.58$ (99%)

agreement with a Poisson Series is rejected.

Thus, the distribution of *Cyclaspis caprella*, as
sampled, is probably contagious.

6.6.2.2  *Cyclaspis* n. sp.

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 | 0 | 1 |   | 1 | 1 |
| 3 |   | 0 | 0 | 0 |   |   |   | 1 |   |
| 4 | 0 | 0 |   |   |   |   |   |   |   |
| 5 |   |   |   |   |   |   |   |   | 2 |
| 6 |   |   |   |   |   |   |   |   |   |
| 7 |   |   |   |   |   |   |   |   |   |

n = 60;   x = 6

normal variable, d = -9.248 < 1.96 (95%)

Statistically agreement with a Poisson Series might be accepted.    Commonsense and the knowledge that these individuals are at the northern end of the range of this species rejects such a conclusion as unrealistic.

### 6.6.2.3 *Cyclaspis globosa*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 3 |   | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 4 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 |
| 5 | 0 | 0 | 0 | 0 |   | 1 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 |   | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |

$n = 60$; $\Sigma x = 13$; $\bar{x} = 0.216$; $s^2 = 0.2066$

$x^2 = 56.43$; $d = -0.192 < 1.96$ $(P > 0.05)$

The hypothesis that the distribution of *Cyclaspis globosa* is random is not disproved.

### 6.6.2.4 *Leptocuma pulleini*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 0 | 0 | 3 | 4 | 1 | 3 | 2 | 1 |
| 2 | 0 | 2 | 1 | 17 | 15 | 13 | 2 | 4 | 5 |
| 3 |   | 2 | 9 | 26 | 25 | 10 | 2 | 4 | 1 |
| 4 | 2 | 0 | 0 | 9 | 18 | 12 | 18 | 3 | 13 |
| 5 | 2 | 1 | 1 | 0 |   | 14 | 16 | 11 | 5 |
| 6 | 0 | 3 | 1 | 4 | 5 | 0 | 16 | 7 | 1 |
| 7 |   | 1 | 5 | 9 | 7 | 17 | 32 | 11 | 25 |

$n = 60$; $\Sigma x = 422$; $\bar{x} = 7.033$, $s^2 = 59.2$

$x^2 = 496.79$; $d = 20.70 > 1.96$ (95%) $> 2.58$ (99%)

∴ agreement with a Poisson Series is rejected. Thus, the distribution of the population of *Leptocuma pulleini*, as sampled, is probably contagious.

### 6.6.2.5 *Dimorphostylis subaculeata*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 |   |   |   |   | 2 | 2 |   | 1 |   |
| 2 | 2 |   |   | 3 | 3 | 6 |   | 2 | 2 |
| 3 |   |   |   | 3 | 5 | 3 | 1 | 2 | 2 |
| 4 |   |   | 1 |   | 1 |   | 3 | 1 | 5 |
| 5 |   |   |   |   |   | 4 | 4 | 4 | 1 |
| 6 |   | 3 |   |   | 1 |   | 3 |   |   |
| 7 |   |   |   | 2 | 2 | 6 | 2 | 3 | 2 |

$n = 60$; $\leqslant x = 86$; $\bar{x} = 1.43$; $_s^2 = 46.38$

$_x^2 = 1909.57$; $d = 50.98 > 1.96$ (95%) $> 2.58$ (99%)

∴ agreement with a Poisson Series is rejected. The dispersion of the population of *Dimorphostylis subaculeata*, as sampled, is probably contagious.

### 6.6.2.6 *Anchistylis waitei*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 |   |   |   |   | 1 | 5 | 8 | 11 | 1 |
| 2 |   |   |   | 3 | 4 | 16 | 12 | 16 | 3 |
| 3 |   |   | 1 | 6 | 5 | 7 | 5 | 1 | 4 |
| 4 |   |   |   | 1 | 3 | 4 | 4 | 2 | 25 |
| 5 |   |   |   | 1 |   | 7 | 3 | 15 | 3 |
| 6 |   | 1 |   | 1 | 1 |   | 5 | 8 | 1 |
| 7 |   | 2 |   |   | 2 | 5 | 8 | 2 |   |

$n = 60$; $\leqslant x = 213$, $\bar{x} = 3.55$; $_s^2 = 24.69$

$$x^2 = 410.38; \quad d = 17.83 > 1.96 \ (95\%) > 2.58 \ (99\%)$$

∴ agreement with a Poisson Series is rejected.
The dispersion of the population of *Anchistylis waitei*,
as sampled, is probably contagious.

6.6.2.7 *Dicoides brevidactyla*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 |   | 5 | 1 | 1 |   | 1 | 2 | 7 |   |
| 2 | 1 |   |   | 1 |   |   | 4 | 3 | 6 |
| 3 |   |   |   | 2 |   | 2 | 5 | 6 | 2 |
| 4 |   |   |   | 1 | 1 | 1 | 2 | 4 | 1 |
| 5 |   |   | 6 |   |   | 2 | 3 | 4 |   |
| 6 | 2 | 1 | 50 |   | 3 | 0 | 1 | 1 | 1 |
| 7 |   | 5 | 1 | 1 | 1 | 5 | 2 |   |   |

$$n = 60; \quad \sum x = 148; \quad s^2 = 42.64; \quad \bar{x} = 2.46$$
$$x^2 = 1022.66; \quad d = 34.45 > 1.96 \ (95\%) > 2.58 \ (99\%)$$

∴ agreement with a Poisson Series is rejected.
The dispersion of the population of *Dicoides brevidactyla*,
as sampled, is probably contagious.

6.6.2.8 *Dicoides fletti*

|   | C | D | E | F | G | H | J | K | M |
|---|---|---|---|---|---|---|---|---|---|
| 1 |   |   |   |   | 2 | 1 | 1 |   | 1 |
| 2 |   |   | 1 | 2 | 2 |   | 2 |   | 1 |
| 3 |   |   | 1 | 2 |   |   |   | 1 | 2 |
| 4 | 2 |   | 2 | 2 | 1 | 2 |   |   | 9 |
| 5 | 1 | 4 |   | 4 |   | 2 | 3 | 1 |   |
| 6 |   | 3 |   | 5 | 4 |   | 6 | 1 |   |
| 7 |   | 2 | 3 | 1 |   |   | 7 |   | 8 |

$$n = 60; \; \textstyle\sum x = 91; \; \bar{x} = 1.51; \; s^2 = 4.985$$

$$x^2 = 158.99; \; d = 7.014 > 1.96 \; (95\%) > 2.58 \; (99\%)$$

Therefore agreement with a Poisson Series is rejected. The distribution of the population of *Dicoides fletti*, as sampled, is probably contagious. This interpretation should be accepted with reservations. *D. fletti* is the smallest of the cumaceans studied in this project. Juveniles may pass easily through a sieve of 500 $\mu$m mesh. Adults can manoeuvre through such a mesh. The air-lift sampler probably only samples this species efficiently when the filter head is partially clogged with sediment in the later part of the sampling period.

### 6.6.3    Conclusions

It was concluded from the analysis of the distribution of cumaceans in the benthic samples from Little Swanport that most of the species exhibit contagious distributions. This deduction raised questions about the mechanisms which might cause cumaceans to clump or aggregate.

### 6.7    On the distribution of *Cyclaspis* n. sp. from Bull Bay, Bruny Island

Samples of *Cyclaspis* n. sp. were taken by air-lift sampler along three transects at Bull Bay, North Bruny Island. The position of each station is indicated on Plate 2. Positions were fixed by horizontal sextant readings upon prominent landmarks. Depths were recorded using an echosounder which was operated as each station was

Plate 2.  Bull Bay, North Bruny Island, showing
         the positions of survey stations
         relative to the coastline.

100METRE
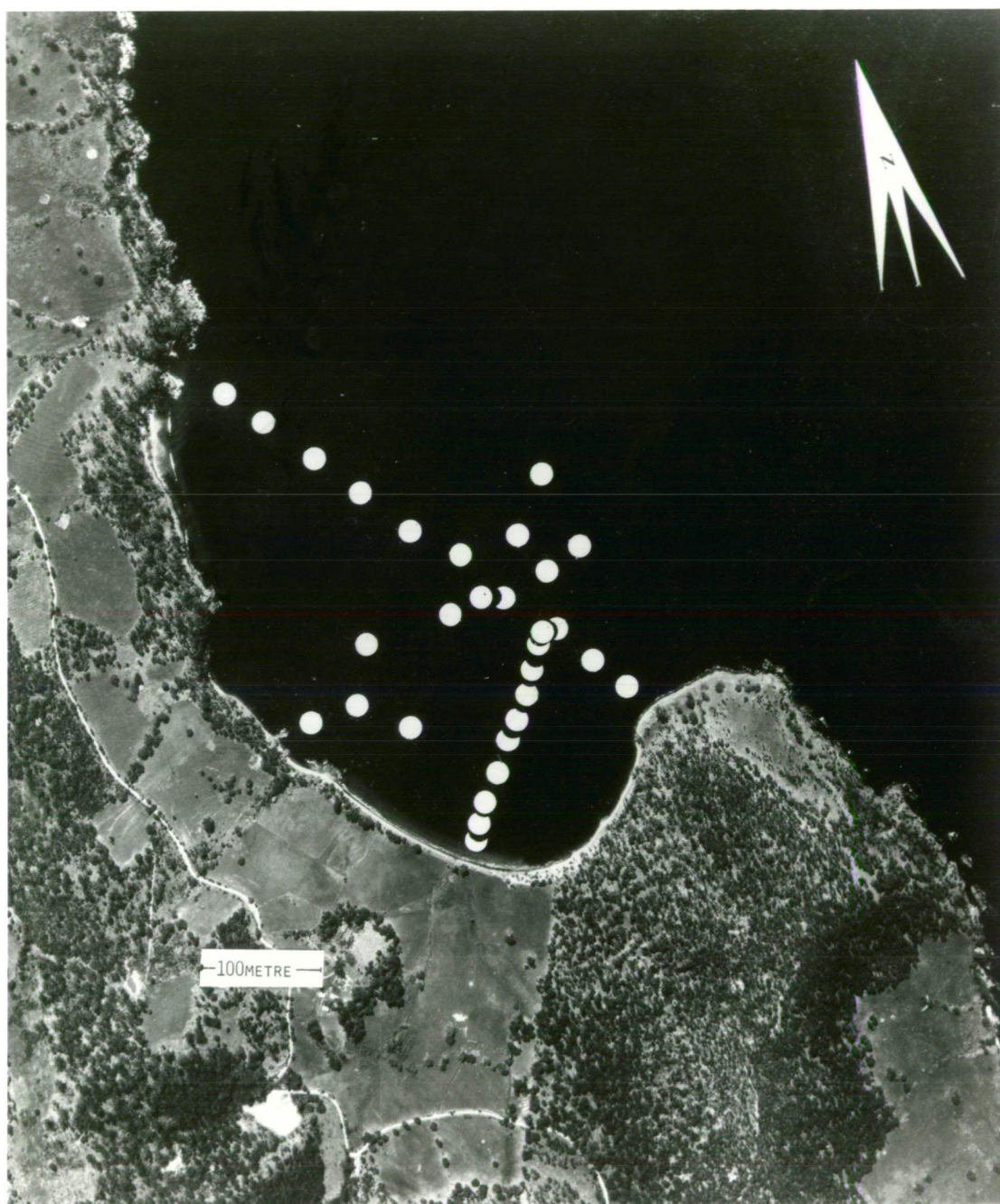
approached. The echosounder scale was calibrated in fathoms and the readings converted to metres.

Numbers of species and individuals of Cumaceans from each station were recorded. Table V (at end of chapter) gives raw data for depth, number of species of cumaceans, numbers of individuals of those species and numbers of individuals of *Cyclaspis* n. sp. at each station.

### 6.7.1 Depth distribution

The data were grouped at one metre depth intervals and the mean values plotted against depth of water (Figure 23).

Individuals of all species and of *Cyclaspis* n. sp. were found throughout the depth range sampled at Bull Bay. The greatest concentrations of individuals were found at depths 12-13m. Apart from a peak at 8-9m (contributed by *Anchistylis waitei* in two samples), the depth distribution of all shallow water cumaceans at Bull Bay follows a similar pattern to that shown by *Cyclaspis* n. sp.

### 6.7.2 Spatial distribution of *Cyclaspis* n. sp. at Bull Bay

The results of the depth distribution analysis for *Cyclaspis* n. sp. suggested that, that species might be aggregated at the scale of sampling.

Ho, that the distribution of *Cyclaspis* n. sp.
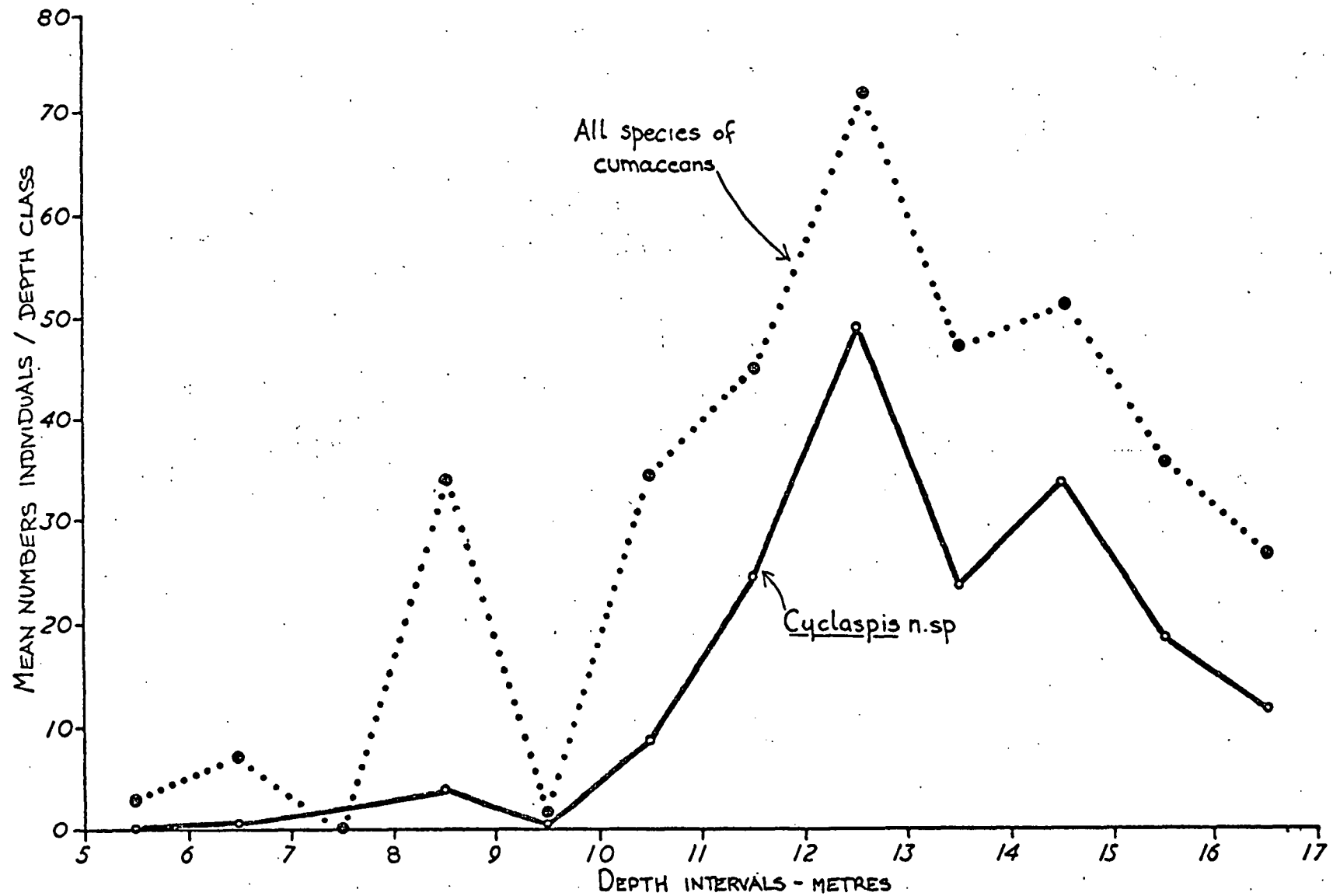
Fig. 23. All cumaceans and *Cyclaspis* n. sp. : ranked mean numbers of individuals plotted against depth at which samples were taken from Bull Bay, Bruny Island.

as sampled at Bull Bay, is random.    Test

for agreement with a Poisson Series:

$x^2$ = 691.7, 29 df $>$ 49.59 (P $<$ 0.01)

agreement with a Poisson Series is rejected.

The dispersion of *Cyclaspis* n. sp. may be considered

contagious.

## 6.8    Conclusions

From the analysis of field samples it was shown

that cumacean species distributions varied with depth of

water over the substrate (6.5) and that, with some

reservations, all spatial dispersions are contagious

(6.6, 6.7).    This is not surprising as it is "increasingly

evident that individuals of any ...... species are seldom,

if ever, randomly dispersed in space" (Cassie, 1962).    For

further comments see Meadows and Campbell (1972), Moritsa

(1959), Parker (1975) and Taylor *et al.* (1978), amongst

others.

## TABLE II

### Station data

### Little Swanport sampling grid, 17-21.x.1977

| Station No. | Date | Time | Uncorrected depth (m) | Corrected depth (m) | Salinity o/oo surface | Salinity o/oo bottom | T °C surface | T °C bottom |
|---|---|---|---|---|---|---|---|---|
| C1 | 17 | 1235 | 5 | 3.75 | 34.4 | 34.4 | 13.3 | 12.8 |
| C2 | 18 | 0925 | 4 | 2.72 | 34.5 | 34.6 | 12.7 | 12.6 |
| C4 | 18 | 0820 | 6.5 | 4.3 | 34.53 | 34.6 | 12.6 | 12.6 |
| C5 | 18 | 0835 | 7 | 5.8 | 34.58 | 34.58 | 12.75 | 12.75 |
| C6 | 18 | 0945 | 4.5 | 3.2 | 34.45 | 44.64 | 12.7 | 12.7 |
| D1 | 17 | 1404 | 7 | 5.25 | 34.6 | 34.5 | 13.2 | 12.8 |
| D2 | 19 | 1115 | 6 | 4.6 | 34.66 | 34.68 | 12.75 | 12.6 |
| D3 | 19 | 1355 | 7 | 5.6 | 34.75 | 34.75 | 12.75 | 12.7 |
| D4 | 19 | 1404 | 6.5 | 5.2 | 34.7 | 34.75 | 12.75 | 12.6 |
| D5 | 18 | 1000 | 7 | 5.7 | 34.53 | 34.53 | 12.7 | 12.7 |
| D6 | 18 | 0853 | 7 | 5.75 | 34.58 | 34.58 | 12.75 | 12.75 |
| D7 | 18 | 1413 | 6.25 | 5.1 | 34.96 | 34.96 | 13.0 | 13.0 |
| E1 | 17 | 1345 | 7 | 5.25 | 34.6 | 34.5 | 13.2 | 12.8 |
| E2 | 19 | 1100 | 8 | 6.7 | 34.68 | 34.7 | 12.8 | 12.6 |
| E3 | 19 | 1348 | 7.5 | 6.1 | 34.62 | 34.7 | 12.8 | 12.7 |
| E4 | 19 | 1412 | 6.5 | 5.2 | 34.65 | 34.65 | 12.75 | 12.75 |
| E5 | 19 | 1417 | 5.5 | 4.2 | 34.7 | 34.7 | 12.7 | 12.7 |
| E6 | 18 | 1430 | 6 | 4.9 | 34.96 | 34.96 | 13.0 | 13.0 |
| E7 | 18 | 1405 | 8 | 6.8 | 34.82 | 34.98 | 13.0 | 13.2 |
| F1 | 17 | 1417 | 7 | 6 | 34.45 | 34.41 | 13.4 | 12.8 |
| F2 | 19 | 1054 | 10 | 8.7 | 34.68 | 34.68 | 12.9 | 12.7 |
| F3 | 19 | 1340 | 13 | 11.6 | 34.62 | 34.62 | 12.9 | 12.7 |
| F4 | 18 | 1015 | 9.5 | 8.1 | 34.4 | 34.58 | 12.7 | 12.7 |

| Station No. | Date | Time | Uncorrected depth (m) | Corrected depth (m) | Salinity o/oo surface | Salinity o/oo bottom | T °C surface | T °C bottom |
|---|---|---|---|---|---|---|---|---|
| F5 | 19 | 1415 | 6.75 | 5.5 | 34.7 | 34.7 | 12.7 | 12.7 |
| F6 | 18 | 0902 | 8 | 6.7 | 34.5 | 34.63 | 12.7 | 12.7 |
| F7 | 18 | 1357 | 9.5 | 8.3 | 35.0 | 35.0 | 13.0 | 13.0 |
| G1 | 17 | 1445 | 7 | 6 | 34.35 | 34.43 | 13.2 | 12.8 |
| G2 | 19 | 1045 | 12 | 10.7 | 34.58 | 34.62 | 12.75 | 12.7 |
| G3 | 19 | 1335 | 13 | 11.6 | 34.58 | 34.62 | 12.9 | 12.7 |
| G4 | 19 | 1134 | 13 | 11.6 | 34.65 | 34.72 | 12.9 | 12.7 |
| G5 | | | | | | | | |
| G6 | 19 | 1008 | 12.0 | 10.8 | 34.9 | 34.9 | 12.6 | 12.5 |
| G7 | 18 | 1350 | 10.5 | 9.3 | 34.85 | 34.92 | 13.0 | 13.2 |
| H1 | 17 | 1455 | 16 | 15.1 | 34.38 | 34.45 | 13.2 | 12.75 |
| H2 | 19 | 0845 | 14.5 | 13.4 | 34.88 | 34.98 | 12.8 | 12.7 |
| H3 | 19 | 1327 | 14.5 | 13.1 | 34.58 | 34.58 | 13.0 | 12.7 |
| H4 | 19 | 1125 | 15 | 13.6 | 34.65 | 34.65 | 13.1 | 12.7 |
| H5 | 19 | 1151 | 15.5 | 14.1 | 34.76 | 34.72 | 12.9 | 12.6 |
| H6 | 19 | 0955 | 15 | 13.8 | 34.91 | 34.98 | 12.75 | 12.7 |
| H7 | 18 | 1340 | 12 | 10.8 | 34.82 | 34.82 | 13.1 | 13.25 |
| J1 | 17 | 1548 | 17.5 | 16.8 | 34.38 | 34.5 | 12.8 | 12.75 |
| J2 | 19 | 0900 | 17.5 | 16.4 | 34.88 | 35.0 | 12.9 | 12.7 |
| J3 | 19 | 0835 | 15.0 | 13.9 | 34.89 | 34.98 | 12.7 | 12.7 |
| J4 | 18 | 1035 | 9.5 | 8.14 | 34.4 | 34.58 | 12.7 | 12.7 |
| J5 | 19 | 1144 | 16 | 14.6 | 34.78 | 34.78 | 12.9 | 12.6 |
| J6 | 19 | 0950 | 14 | 12.8 | 34.8 | 35.2 | 12.7 | 12.7 |
| J7 | 18 | 1330 | 14 | 12.8 | 34.48 | 34.82 | 13.2 | 13.2 |
| K1 | 17 | 1515 | 17.5 | 16.65 | 34.27 | 34.4 | 13.2 | 12.75 |
| K2 | 19 | 0825 | 15.5 | 14.4 | 34.82 | 34.96 | 12.7 | 12.7 |
| K3 | 19 | 0910 | 18.0 | 16.8 | 34.95 | 35.0 | 12.7 | 12.6 |
| K4 | 19 | 0920 | 18.5 | 17.3 | 34.98 | 35.2 | 12.8 | 12.6 |

| Station No. | Date | Time | Uncorrected depth (m) | Corrected depth (m) | Salinity o/oo surface | Salinity o/oo bottom | T °C surface | T °C bottom |
|---|---|---|---|---|---|---|---|---|
| K5 | 19 | 0930 | 17.5 | 16.3 | 35.1 | 35.1 | 12.75 | 12.6 |
| K6 | 19 | 0936 | 16.5 | 15.3 | 34.9 | 35.2 | 13.0 | 12.6 |
| K7 | 18 | 1315 | 16 | 14.7 | 34.75 | 34.81 | 13.0 | 13.0 |
| M1 | 17 | 1205 | 23 | 21.7 | 34.25 | 34.4 | 13.2 | 12.7 |
| M2 | 18 | 1140 | 20 | 18.5 | 34.52 | 34.52 | 12.5 | 12.5 |
| M3 | 18 | 1130 | 18.5 | 17 | 34.52 | 34.52 | 12.6 | 12.5 |
| M4 | 18 | 1300 | 17.5 | 16.2 | 34.55 | 35.28 | 12.75 | 12.5 |
| M5 | 18 | 1115 | 18 | 16.56 | 34.52 | 34.52 | 12.6 | 12.5 |
| M6 | 18 | 1055 | 18 | 16.6 | 34.52 | 34.6 | 12.7 | 12.4 |
| M7 | 18 | 0715 | 17 | 15.9 | 34.55 | 34.55 | 12.5 | 12.5 |

Table III

Cumacean sampling : Raw data

Locality : Off Little Swanport, East Coast, Tasmania

Dates of Sampling : 17-21.x.1977

| Station No. | *Leptocuma pulleini* | *Cyclaspis caprella* | *Cyclaspis globosa* | *Dicoides fletti* | *Dicoides brevidactyla* | *Anchistylis waitei* | *Dimorphostylis subaculeata* | *Cyclaspis n. sp.* | Total number Cumaceans |
|---|---|---|---|---|---|---|---|---|---|
| C1 | 1 | 14 | – | – | – | – | – | – | 15 |
| C2 | – | – | – | – | 1 | – | 2 | – | 3 |
| C3 | | | | | | | | | |
| C4 | 2 | 17 | – | 2 | – | – | – | – | 21 |
| C5 | 2 | 1 | – | 1 | – | – | – | – | 4 |
| C6 | – | 3 | – | – | 2 | – | – | – | 5 |
| D1 | – | 16 | – | – | 5 | – | – | – | 21 |
| D2 | 2 | 10 | – | – | – | – | – | – | 12 |
| D3 | 2 | 7 | – | – | – | – | – | – | 9 |
| D4 | – | – | – | – | – | – | – | – | 0 |
| D5 | 1 | 4 | – | 4 | – | – | – | – | 9 |
| D6 | 3 | 13 | – | 3 | 1 | 1 | 3 | – | 24 |
| D7 | 1 | 4 | – | 2 | 5 | 2 | – | – | 14 |
| E1 | – | 5 | – | – | 1 | – | – | – | 6 |
| E2 | 1 | 1 | – | 1 | 1 | – | – | – | 3 |
| E3 | 9 | 5 | 1 | 1 | – | 1 | – | – | 17 |
| E4 | – | 15 | – | 2 | – | – | 1 | – | 18 |
| E5 | 1 | 5 | – | – | 6 | – | – | – | 12 |
| E6 | 1 | 2 | – | – | 50 | – | – | – | 53 |
| E7 | 5 | 1 | – | 3 | 1 | – | – | – | 10 |
| F1 | 3 | 1 | – | – | 1 | – | – | – | 5 |
| F2 | 17 | 2 | 1 | 2 | 1 | 3 | 3 | – | 29 |
| F3 | 26 | 2 | – | 2 | 2 | 6 | 3 | – | 41 |
| F4 | 9 | 2 | 1 | 2 | 1 | 1 | – | – | 16 |

| Station No. | Leptocuma pulleini | Cyclaspis caprella | Cyclaspis globosa | Dicoides fletti | Dicoides brevidactyla | Anchistylis waitei | Dimorphostylis subaculeata | Cyclaspis n. sp. | Total number Cumaceans |
|---|---|---|---|---|---|---|---|---|---|
| F5 | – | 9 | – | 4 | – | 1 | – | – | 14 |
| F6 | 4 | 8 | – | 5 | – | 1 | – | – | 18 |
| F7 | 9 | 1 | – | 1 | 1 | – | 2 | – | 14 |
| G1 | 4 | – | – | 2 | – | 1 | 2 | – | 9 |
| G2 | 15 | – | – | 2 | – | 4 | 3 | – | 24 |
| G3 | 25 | – | – | – | – | 5 | 5 | – | 35 |
| G4 | 18 | – | 2 | 1 | 1 | 3 | 1 | – | 26 |
| G5 | | | | | | | | | |
| G6 | 5 | – | – | 4 | 3 | 1 | 1 | – | 14 |
| G7 | 7 | 1 | – | – | 1 | 2 | 2 | – | 13 |
| H1 | 1 | 1 | – | 1 | 1 | 5 | 2 | – | 11 |
| H2 | 13 | – | 1 | – | – | 16 | 6 | 1 | 37 |
| H3 | 10 | – | – | – | 2 | 7 | 3 | – | 22 |
| H4 | 12 | 3 | – | 2 | 1 | 4 | – | – | 22 |
| H5 | 14 | – | 1 | 2 | 2 | 7 | 4 | – | 30 |
| H6 | | | | | | | | | |
| H7 | 17 | – | – | – | 5 | 5 | 6 | – | 33 |
| J1 | 3 | – | – | 1 | 2 | 8 | – | – | 14 |
| J2 | 2 | – | – | 2 | 4 | 12 | – | – | 20 |
| J3 | 2 | – | 1 | 5 | 5 | 1 | – | – | 14 |
| J4 | 18 | 4 | – | – | 2 | 4 | 3 | – | 31 |
| J5 | 16 | – | – | 3 | 3 | 3 | 4 | – | 29 |
| J6 | 16 | – | – | 5 | 1 | 5 | 3 | – | 30 |
| J7 | 32 | – | 1 | 7 | 2 | 8 | 2 | – | 52 |
| K1 | 2 | 1 | – | – | 7 | 11 | 1 | – | 22 |
| K2 | 4 | – | – | – | 3 | 16 | 2 | 1 | 26 |
| K3 | 4 | – | – | 1 | 6 | 1 | 2 | 1 | 11 |

| Station No. | *Leptocuma pulleini* | *Cyclaspis caprella* | *Cyclaspis globosa* | *Dicoides fletti* | *Dicoides brevidactyla* | *Anchistylis waitei* | *Dimorphostylis subaculeata* | *Cyclaspis n. sp.* | Total number Cumaceans |
|---|---|---|---|---|---|---|---|---|---|
| K4 | 3 | – | 1 | – | 4 | 2 | 1 | – | 11 |
| K5 | 11 | – | – | 1 | 4 | 15 | 4 | – | 35 |
| K6 | 7 | – | – | 1 | 1 | 8 | – | – | 17 |
| K7 | 11 | 1 | 1 | – | – | 2 | 3 | – | 18 |
| M1 | 1 | – | 1 | 1 | – | 1 | – | – | 4 |
| M2 | 5 | – | – | 1 | 6 | 3 | 2 | 1 | 18 |
| M3 | 1 | – | – | 2 | 2 | 4 | 2 | – | 11 |
| M4 | 13 | – | – | 9 | 1 | 25 | 5 | – | 53 |
| M5 | 5 | 1 | – | – | – | 3 | 1 | 2 | 12 |
| M6 | 1 | – | – | – | 1 | 1 | – | – | 3 |
| M7 | 25 | – | 1 | 8 | – | – | 2 | – | 36 |

## Table IV

Some characteristics of sediments sampled at Little Swanport

| Station | Md Ø | Sd Ø | Packing phases | % $<63\mu$m |
|---------|------|------|----------------|-------------|
| C1 | 2.4 | 0.7 | 3 | 3.1 |
| C2 | 2.5 | 0.3 | 2 | 3.0 |
| C4 | 3.33 | 0.9 | 2 | 2.6 |
| C5 | 3.23 | 0.85 | 2 | 2.78 |
| C6 | 2.5 | 0.3 | 2 | 2.86 |
| D1 | 2.4 | 0.8 | 2 | 2.9 |
| D2 | 2.9 | 2.5 | 2 | 2.8 |
| D3 | 3.1 | 2.8 | 2 | 3.8 |
| D4 | 3.3 | 0.8 | 2 | 2.6 |
| D5 | 3.0 | 1.0 | 2 | 4.76 |
| D6 | 2.0 | 1.2 | 2 | 3.2 |
| D7 | 3.0 | 0.4 | 2 | 0 |
| E1 | 2.5 | 0.3 | 2 | 2.63 |
| E2 | 2.6 | 0.3 | 2 | 2.6 |
| E3 | 2.5 | 0.32 | 2 | 2.7 |
| E4 | 2.5 | 0.2 | 2 | 2.9 |
| E5 | 2.26 | 0.3 | 2 | 2.9 |
| E6 | | NO SAMPLE | | |
| E7 | 2.3 | 0.32 | 2 | 2.0 |
| F1 | 2.66 | 0.2 | 2 | 4.0 |
| F2 | 2.7 | 0.28 | 2 | 2.9 |
| F3 | 3.0 | 2.8 | 2 | 3.3 |
| F4 | 3.1 | 0.8 | 2 | 2.5 |
| F5 | 3.1 | 0.8 | 2 | 2.6 |
| F6 | 2.6 | 0.25 | 2 | 3.0 |

| Station | Md ∅ | Sd ∅ | Packing phases | % < 63μm |
|---------|------|------|----------------|----------|
| F7 | 2.9 | 0.3 | 2 | 2.27 |
| G1 | 2.5 | 0.2 | 2 | - |
| G2 | 2.48 | 0.28 | 2 | 2.9 |
| G3 | 3.0 | 0.18 | 2 | 4.0 |
| G4 | 2.5 | 0.2 | 2 | 0.8 |
| G6 | 2.5 | 0.2 | 2 | 1.2 |
| G7 | 2.5 | 0.2 | 2 | - |
| H1 | 3.2 | 0.25 | 2 | 2.9 |
| H2 | 2.8 | 0.18 | 2 | 1.9 |
| H3 | 2.8 | 0.3 | 2 | 4.0 |
| H4 | 2.8 | 0.28 | 2 | 4.18 |
| H5 | 2.8 | 0.25 | 2 | 2.39 |
| H6 | 3.2 | 0.3 | 3 | 2.32 |
| H7 | 2.8 | 0.9 | 2 | 2.3 |
| J1 | 3 | 2.5 | 2 | 0 |
| J2 | 2.4 | 0.3 | 2 | 0.8 |
| J3 | 2.5 | 0.25 | 2 | 1.4 |
| J4 | 2.2 | 0.2 | 2 | 0.5 |
| J5 | 2.4 | 0.18 | 2 | 0.5 |
| J6 | 2.5 | 0.2 | 1 | 1.7 |
| J7 | 2.6 | 0.28 | 2 | 3.4 |
| K1 | 2.8 | 0.8 | 2 | 4.0 |
| K2 | 2.8 | 0.28 | 2 | 2.7 |
| K3 | 2.8 | 0.3 | 2 | 1.98 |
| K4 | 2.6 | 0.2 | 2 | 3.04 |
| K5 | 2.8 | 0.2 | 2 | 2.89 |

| Station | Md $\emptyset$ | Sd $\emptyset$ | Packing phases | $\% <63\mu m$ |
|---------|------|------|------|------|
| K6 | 2.65 | 0.2 | 2 | 0.2 |
| K7 | 3.1 | 0.35 | 2 | 0.5 |
| M1 | 2.66 | 0.28 | 2 | – |
| M2 | 3.2 | 0.3 | 2 | 2.6 |
| M3 | 3.2 | 0.31 | 2 | 3.8 |
| M4 | | NO SAMPLE | | |
| M5 | 3.2 | 0.3 | 2 | 4.55 |
| M6 | 2.8 | 0.8 | 2 | 4.76 |
| M7 | 2.2 | 0.3 | 2 | 3.7 |

Table V

Bull Bay, Bruny Island.    5.5., 6.1 and 13.1.1978.    Station
data, numbers of species and individuals of all Cumaceans
       and numbers of individuals of *Cyclaspis* n. sp.

| Station No. | Depth m | No. species of Cumaceans | No. of individuals | No. individuals *Cyclaspis* n.sp. |
|---|---|---|---|---|
| C1 | 6.4 | 2 | 3 | 0 |
| C2 | 8.2 | 5 | 34 | 2 |
| C3 | 9.7 | 3 | 3 | 1 |
| C4 | 10.9 | 5 | 21 | 6 |
| C5 | 11.9 | 4 | 41 | 27 |
| C6 | 13.1 | 4 | 44 | 29 |
| C7 | 13.4 | 5 | 50 | 30 |
| C8 | 14.0 | 3 | 78 | 56 |
| C9 | 14.6 | 5 | 61 | 44 |
| C10 | 14.19 | 4 | 54 | 36 |
| 2A | 5.5 | 2 | 3 | 0 |
| 2B | 9.5 | 0 | 0 | 0 |
| 2C | 10.34 | 3 | 54 | 0 |
| 2D | 11.6 | 5 | 31 | 5 |
| 2E | 12.4 | 3 | 35 | 1 |
| 2F | 13.1 | 4 | 49 | 13 |
| 2G | 14.0 | 3 | 22 | 16 |
| 2I | 15.8 | 5 | 36 | 19 |
| 2J | 16.1 | 4 | 27 | 12 |
| 1A | 6.4 | 5 | 11 | 1 |
| 1B | 10.6 | 4 | 9 | 6 |
| 1C | 11.9 | 5 | 54 | 36 |
| 1D | 12.4 | 5 | 61 | 43 |
| 1E | 12.8 | 5 | 50 | 38 |
| 1F | 12.8 | 5 | 105 | 88 |

| Station No. | Depth m | No. species of Cumaceans | No. of individuals | No. individuals *Cyclaspis* n.sp. |
|---|---|---|---|---|
| 1G | 12.2 | 5 | 106 | 77 |
| 1H | 11.6 | 4 | 54 | 29 |
| 1I | 10.4 | 5 | 51 | 23 |
| 1J | 8.52 | 4 | 34 | 6 |

7.    EXPERIMENTS ON SUBSTRATE SELECTION BY CUMACEA

7.1    Introduction

Investigation of the presence of cumaceans at Little Swanport site against the sedimentary parameters measured produced meaninglessly high correlations.  For example, correlation with the number of packing phases of the sands was necessarily high - most were two phase sands.    Therefore it was decided to give the animals a choice of a variety of sediments   ᵔᵔ  by means of free choice experiments.

Free choice experiments to test substrate selection by marine invertebrates have been used by a number of workers (e.g. Meadows, 1964; Gray, 1967; Wieser, 1956; Williams, 1958; further references in Gray, 1974). Free choice experiments depend on the observation that animals might alight upon a substrate at random. Cumaceans, for example, then either nestle or swim off. Attractive sites eventually acquire greater numbers of animals than unattractive sites.

Meadows and Campbell (1972) have suggested that habitat selection, i.e. free choice, largely determines the local distribution of animals.

Moore (1975) has criticised this approach, largely by reiterating Thorson's statement that animals are not given a free choice in the sea.    Some of Moore's criticism may be removed by disregarding the specialist evidence provided by the settling larvae of non-motile adults and by not providing unrealistic choices in one's experiments.

7.2     Materials and methods

The cumaceans tested in the experiments which follow
were *Cyclaspis caprella*, *Cyclaspis* n. sp., *Leptocuma*
*pulleini* and *Anchistylis waitei*.    Specimens of *Cyclaspis*
n. sp. for experimental work were obtained from Bull Bay,
Bruny Island.    Specimens of the other species were
obtained from three localities:- Bull Bay (*A. waitei*).
North-West Bay (*C. caprella*) and Little Swanport Bay
(*L. pulleini*, *C. caprella*, *A. waitei*).    The localities
are shown on map Figure 3.    Most specimens were taken
with an air-lift sampler, but *C. caprella* from North-West
Bay was also taken using a D-net (base opening 0.5m,
nominal mesh 500$\mu$m) with runners, towed from a dinghy.

On return to the laboratory, the catch was
decanted into shallow, white trays and cumaceans removed
with a wide-ended pipette.

Each experiment was set up using a 5 x 5 choice
tank containing 25 sample trays.    The dimensions are
shown in Figure 24.    Five sample trays were filled with
each sediment grade.    Each set of five trays was
allocated a sediment grade by reference to a table of random
numbers.    The trays were then placed in the choice tank
in a Latin square arrangement dictated by the
randomisation of a transformation set (Cochran and Cox,
1957).

The experimental substrate is divided, in this
technique, into $\underline{k}$ row blocks and $\underline{k}$ column blocks (in the

25mm

2.5mm external dimension

inlet

125 mm internal dimension
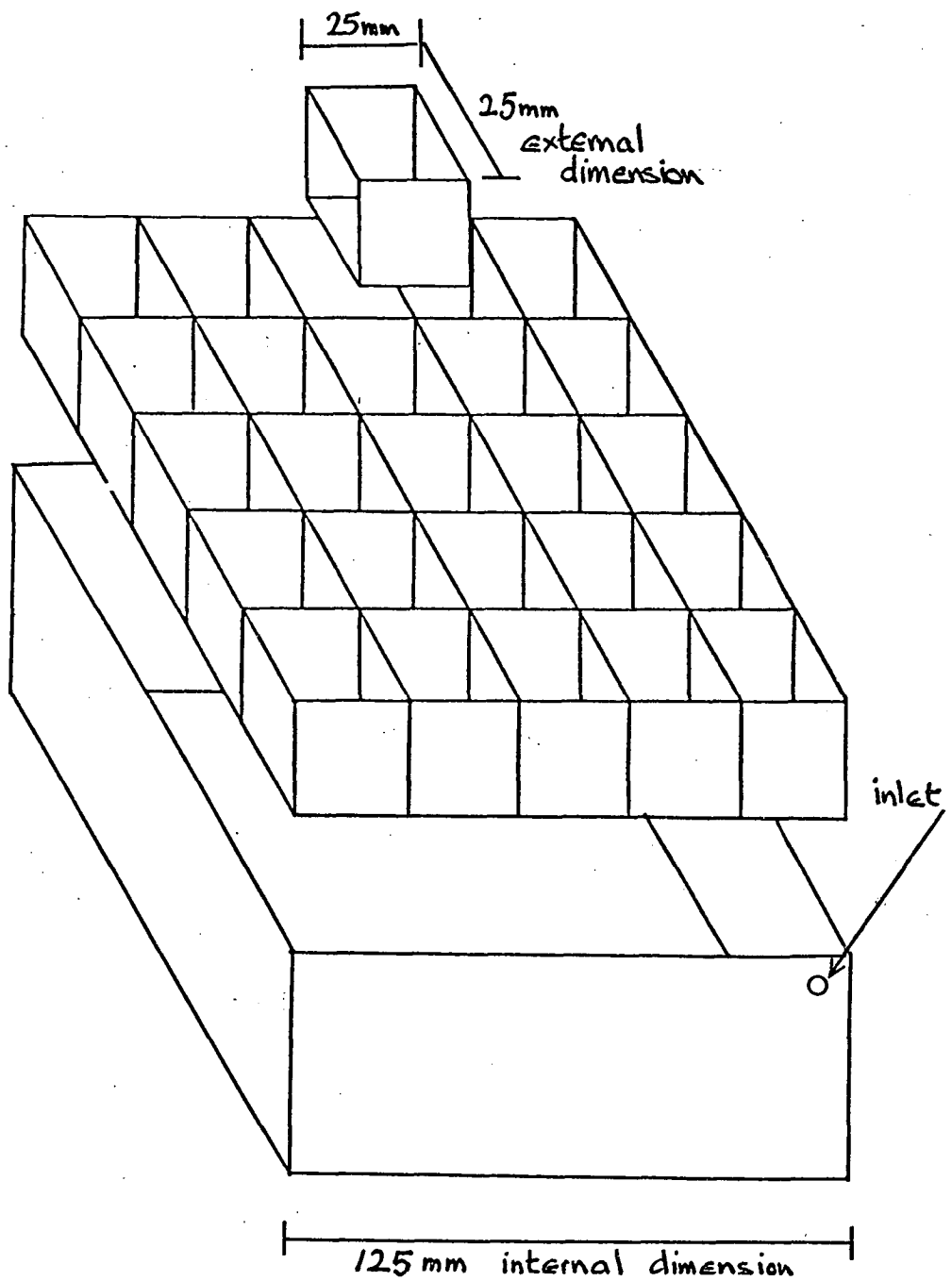
Fig. 24.  5 x 5 choice tank and sample trays.

experiments described here, 5 x 5). Each level of
treatment (i.e. sediment grade) is replicated only once
in a row or a column. In such an experiment the
arrangement is based on a transformation set that
occurs once, and only once, in each column and row.
It is necessary that each treatment not retain
its position in the sampling matrix in repeated
experiments. Latin square transformation sets may
be selected from standard texts (e.g. Cochran and
Cox, *loc cit.*) and the allocation of sample grades to
the set made by reference to a table of random numbers.
The rows of the set then may be randomised and the
columns treated similarly. Such a procedure
satisfies the requirements of the anova that non-random
arrangements of treatments, effects and positions are
least imposed by experiment.

After the sample trays were placed in position a
sheet of paper was placed over the trays and the tank
filled with sea water. Cumaceans were added to the water
column and the paper removed. The paper served two
purposes. Firstly it prevented disturbance and mixing
of the sediment samples when sea water was added to the
tank. Secondly, its removal aided dispersal of the test
cumaceans through the water column. This technique was
an attempt to reduce refugee choice resulting from
artificial clumping in the small inoculation volume.
"Refugee choice" describes a propensity to settle in a
location dictated by experimental inoculation. This is
an observation, not a definition, because no experiments

were considered at the time to test the observations further.

The test tank was covered with a lightproof box and left overnight. All experiments were concluded between 0900 and 1000 hours.

The sample trays in the choice tank are the lids of small acrylic boxes sold in toyshops as containers for specimens. A small hole was drilled in the base of each box. At the end of each experiment each base, now a lid, was placed over each sample tray to trap both sediment and animals. The boxes were removed from the tank and the contents washed into a beaker with 70% ethyl alcohol to immobilise the specimens. The contents of the beaker were strained through a mesh of nominal size 100$\mu$m. The damp mixture of animals and sediment was added to saturated sugar solution. When most of the sediment particles had settled out the sugar solution was strained (again through 100$\mu$m mesh). The filtrate of animals and some sediment was then washed into a petri dish and the numbers of animals counted and recorded.

The results were analysed by analysis of variance of the Latin square followed by comparison of sediment yields using Duncan's New Multiple Range Test (Senter, 1969). The calculations were executed by hand in the early stages of this work and later using a standard statistical programme package prepared for a Hewlett-Packard 9825A desktop calculator.

7.3     Choice of method

Many choice experiments are designed to test preference between two treatments.    An example is the work of Deans, Anderson and Meadows (1977) who tested the response of the amphipod, *Corophium volutator*, to irradiated and untreated whole sediments.    Such an approach is appropriate when alternative decisions are important to the investigation and were employed later in this work.

Multiple choice experiments are more complex, more likely to be dominated by experimental error and may be misleading when interactions are present (Scheffé, 1959).    Latin square design appeared appropriate for experimental tests on cumaceans (see Moroney (1965) for an introduction to the technique and analysis of variance and Cochran and Cox (1957) and Scheffé, *loc. cit.*, for further refinements).

A similar approach has been used by many other workers.    A particularly elegant marine example was that used by Crisp (1976) who employed a 3 x 3 Latin square design in an experiment to test choice of settlement sites by barnacle cyprid larvae.

7.4     The experimental substrates

When this series of experiments was initiated it was not apparent that any of the species in the two main study areas were distributed according to characteristics of the sediments.

The bulk experimental substrate used throughout

this work consisted of sand from Little Swanport Bay.
The sand was collected by a diver who scraped a large
sample of sediment from the surface of the sea bed to an
approximate depth of 40mm.   On return to the
laboratory bulk substrate was separated into convenient
fractions through a nest of soil sieves shaken by a
mechanised sieve shaker.   Sieving was continued until
adequate amounts of the following fractions were obtained.

Sediment grades for experimental work separated
from bulk Little Swanport sand

| Size range   m | Phi = $\emptyset$ size | Treatment numbers |
|---|---|---|
| 1000-500 | +1 | 1 |
| 500-250 | +2 | II |
| 250-125 | +3 | III |
| 125-63 | +4 | IV |
| <63* | +4 | V |

*The final isolate of sediment V (fines, <63 m) was made
by settlement from a suspension.

7.5      Experiments to test whether four species of
         cumaceans prefer one or more sediment grades.

7.5.1    Presentation
         The results of each experiment are presented as
follows.   The counts are listed first, arranged as in
the Latin square.   Secondly, the treatment (sediments)
totals are given.   Thirdly, a table of analysis of

variance is presented. Fourth, a pictorial representation of the choices made is shown in control chart format (Moroney, 1965).

7.5.2.

7.5.2.1 Expt. 1.

To test whether *Cyclaspis* n. sp. "preferred" one or more sediment grades.

Results

| II | III | IV | I | V | |
|---|---|---|---|---|---|
| 0 | 3 | 4 | 0 | 0 | 7 |
| IV | I | V | III | II | |
| 7 | 1 | 1 | 7 | 2 | 18 |
| V | II | I | IV | III | |
| 0 | 1 | 3 | 5 | 7 | 16 |
| I | V | III | II | IV | |
| 3 | 1 | 14 | 3 | 6 | 27 |
| III | IV | II | V | I | |
| 24 | 8 | 2 | 3 | 1 | 38 |
| Totals 34 | 14 | 24 | 18 | 16 | 106 = T = Number of Animals |

Treatment totals (sediments)

| I | II | III | IV | V |
|---|---|---|---|---|
| 8 | 8 | 55 | 30 | 5 |

Correction factor, $\dfrac{T^2}{N} = \dfrac{106^2}{25} = 449.44$

Table of Analysis of Variance

| Source | Sum of Squares | df | Variance estimate |
|--------|----------------|-----|-------------------|
| Rows | 110.96 | 4 | 27.74 |
| Columns | 52.16 | 4 | 13.04 |
| Sediments | 366.16 | 4 | 91.54 |
| Residual | 139.28 | 12 | 11.6 |
| Totals | 688.56 | 24 | |

Inspection of the Analysis of Variance table reveals that the variance estimate contributed by sediments is significantly greater than that contributed by all other components. The F ratio, sediments/residual = 7.89 (4,12 d.f) > 3.26 (5%), > 5.41 (1%).
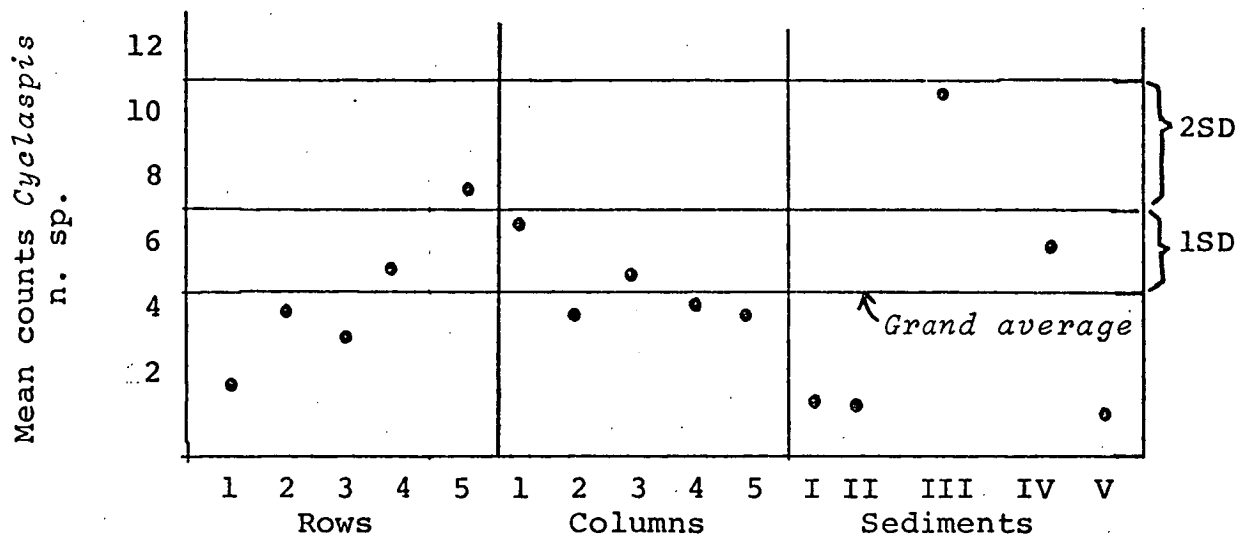


Control chart for row, column and sediment mean counts.

$$SD = \sqrt{\text{residual variance}} = 3.4$$

The main contribution to the sediment variance was made by sediment III.

Ho, that no sediment grade will be chosen in preference to another is not supported. It appears, from this experiment, that *Cyclaspis* n. sp. chose a substrate of 250-125μm grade the values for this grade differing significantly at $P < 0.05$ from all other sediments (Duncan's New Multiple Range Test).

### 7.5.2.2 Expt. 2.

To test whether *Leptocuma pulleini* "preferred" one or more of five sediment grades

Results

| V | I | I | III | IV | |
|---|---|---|-----|----|---|
| 1 | 0 | 2 | 1 | 0 | 4 |

| II | III | IV | I | V | |
|----|-----|----|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 1 |

| IV | II | I | V | III | |
|----|----|---|---|-----|---|
| 0 | 12 | I | 0 | 2 | 15 |

| I | V | III | IV | II | |
|---|---|-----|----|----|---|
| 0 | 0 | 2 | 0 | 10 | 12 |

| III | IV | V | II | I | |
|-----|----|---|----|---|---|
| 1 | 0 | 0 | 4 | 0 | 5 |

| Totals | 4 | 12 | 5 | 5 | 12 | 37 = T = Number of animals |

Treatment totals (sediments)

| I | II | III | IV | V |
|---|----|-----|----|---|
| 1 | 29 | 6 | 0 | 1 |

Correction factor, $\dfrac{T}{N} = \dfrac{37^2}{25} = 54.76$

Table of Analysis Variance

| Source | Sum of Squares | df | Variance estimate |
|--------|----------------|-----|-------------------|
| Rows | 27.44 | 4 | 6.86 |
| Columns | 16.04 | 4 | 4.01 |
| Sediments | 121.04 | 4 | 30.26. |
| Residual | 47.72 | 12 | 3.97 |
| Total | 212.23 | 24 | |

Inspection of the Analysis of Variance table shows
that the variance estimate for sediments exceeds that for
column, row or residual variance.   The F ratio sediment:
residual is 7.6 with 4 and 12 df respectively.   This
value significantly exceeds the 1% and 5% values of the
F-distribution.

The results are partitioned in the control diagram
below
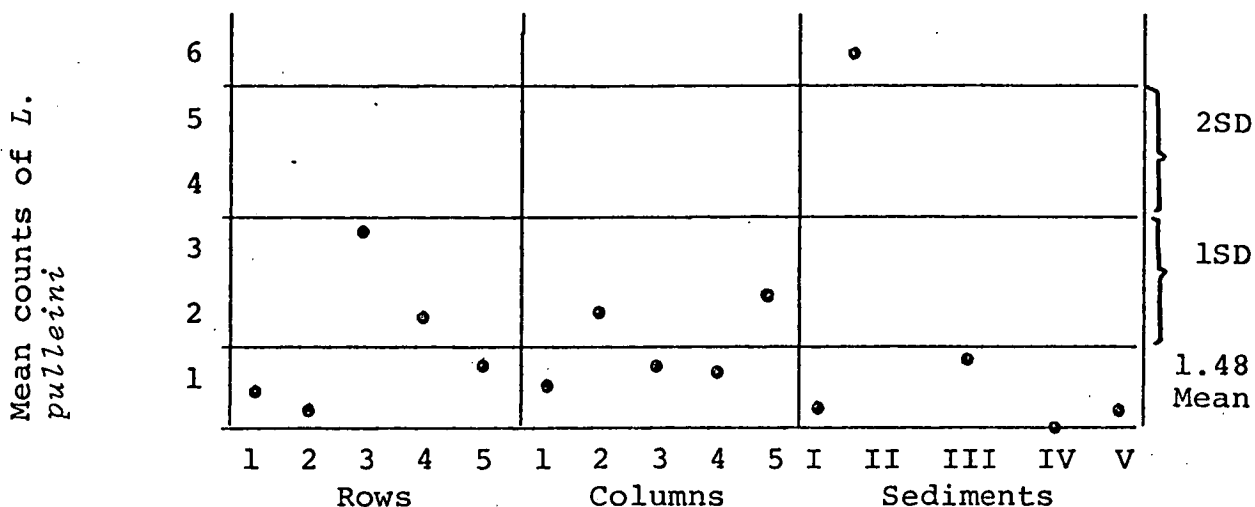


Control chart diagram for row, column and sediment

counts.

SD = 1.99

The main contribution to sediment variance was made by sediment II with 78% of yield differing significantly at $P < 0.05$ (Duncan's test).

Ho is not supported.    It appears that *Leptocuma pulleini* "prefers" a substrate of 500-250$\mu$mgrade.

7.5.2.3  Expt. 3.

To test whether *Cyclaspis caprella* "prefers" one or more of five sediment grades.

Results

| I | II | III | IV | V | |
|---|---|---|---|---|---|
| 0 | 1 | 1 | 5 | 0 | 7 |

| IV | V | I | II | III | |
|---|---|---|---|---|---|
| 1 | 0 | 1 | 3 | 17 | 22 |

| II | III | IV | V | I | |
|---|---|---|---|---|---|
| 1 | 12 | 8 | 0 | 1 | 22 |

| V | I | II | III | IV | |
|---|---|---|---|---|---|
| 1 | 0 | 3 | 22 | 4 | |

| III | IV | V | I | II | |
|---|---|---|---|---|---|
| 10 | 7 | 0 | 1 | 0 | 18 |

| | totals | 13 | 20 | 13 | 31 | 22 | 99 = T = Number of animals |
|---|---|---|---|---|---|---|---|

Treatment of totals (sediments)

| I | II | III | IV | V |
|---|---|---|---|---|
| 3 | 8 | 62 | 25 | 1 |

Correction factor, $\dfrac{T^2}{N} = \dfrac{99^2}{25} = 392.04$

Table of Analysis of Variance

| Source | Sum of Squares | df | Variance estimate |
|--------|---------------|-----|-------------------|
| Rows | 56.16 | 4 | 14.04 |
| Columns | 44.56 | 4 | 11.14 |
| Sediments | 516.56 | 4 | 129.14 |
| Residual | 187.68 | 12 | 15.64 |
| Total | 804.96 | 24 | |

Inspection of the Analysis of Variance table suggests that the greater variance estimate was contributed by sediments. $F = 8.25 > 5.41$ (significant at 1% with 4 and 12 df) $\therefore$ Ho, rejected.
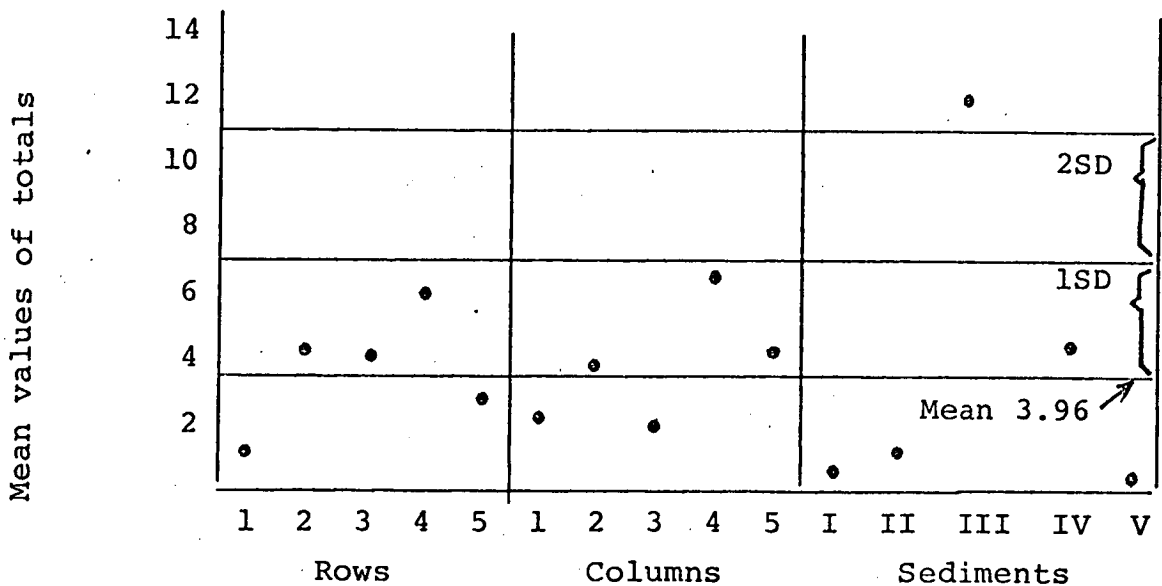


Control chart diagram for row, column and sediment mean counts.

SD = 3.95.

Ho, that no sediment is preferred is not proven.

Testing for shortest significant ranges by Duncan's test showed that both sediment grades III and IV differ

significantly (P < 0.05) from the other grades but the difference between grades III and IV is not significant. It is concluded that *Cyclaspis caprella* 'prefers' sediment in the range 250 < 125 > 63 µm.

### 7.5.2.4 Exp. 4.

To test whether *Anchistylis waitei* "prefers" one or more sediment grades. (This experiment repeated an earlier experiment which was dominated by a row effect.)

Results

| I | II | III | IV | V | |
|---|----|-----|----|---|---|
| 0 | 0 | 0 | 7 | 3 | 10 |

| IV | V | I | II | III | |
|----|---|---|----|-----|---|
| 10 | 3 | 0 | 0 | 1 | 14 |

| II | III | IV | V | I | |
|----|-----|----|---|---|---|
| 0 | 7 | 4 | 2 | 1 | 14 |

| V | I | II | III | IV | |
|---|---|----|-----|----|---|
| 5 | 1 | 0 | 0 | II | 17 |

| III | IV | V | I | II | |
|-----|----|---|---|----|---|
| 7 | 12 | 1 | 0 | 0 | 20 |

| Totals | 22 | 23 | 5 | 9 | 16 | 75 = T = Number of animals |

Treatment totals (sediments)

| I | II | III | IV | V |
|---|----|-----|----|---|
| 2 | 0 | 15 | 44 | 14 |

Correction factor $= \dfrac{T^2}{N} = \dfrac{75^2}{25} = 225$

Table of Analysis of Variance

| Source | Sum of Squares | df | Variance estimate |
|--------|----------------|-----|-------------------|
| Rows | 11.2 | 4 | 2.8 |
| Columns | 50 | 4 | 12.5 |
| Sediments | 247.2 | 4 | 61.8 |
| Residual | 45.6 | 12 | 3.8 |
| Total | 354 | 24 | |

Inspection of the Analysis of Variance table suggests that the greatest variance estimate was contributed by sediments (F = 16.26; 4, 12df > 5.41. Therefore, significant at 1% level).
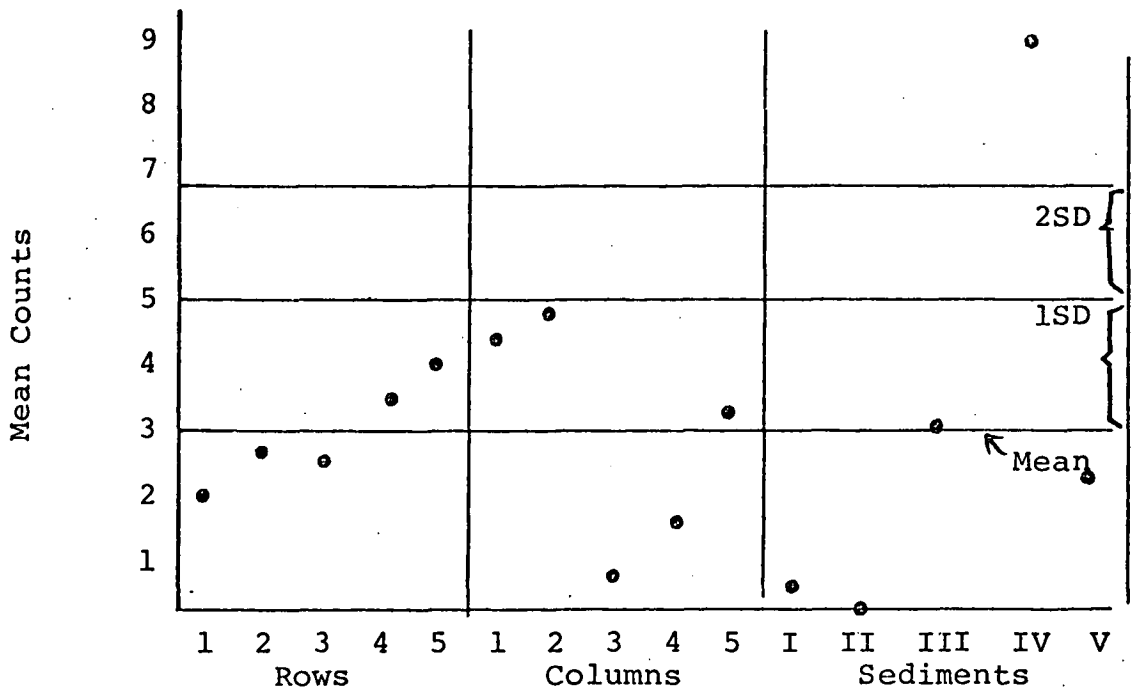


Control chart diagram for row, column and sediment mean counts.

SD = 1.94.

Ho, that no sediment is preferred to any other is not proven. *Anchistylis waitei* prefers sediment grade IV

(125-63$\mu$). By Duncan's test the counts associated with sediment grade IV are significant at P<0.05.

### 7.5.3 Commentary

It appeared from the experiments just described, that the four cumacean species studied did choose between five sediment grades isolated from a natural sediment. However, in the habitat at least two of those grades are only present in relatively small amounts. Unless the sea bed is composed of homogeneous patches of substrate similar to such artificial fractions it is unlikely that choice would occur so clearly. It is most probable, and this is borne out by the sediment analyses from both Little Swanport and Bull Bay, that well sorted sands are dominated by one or two grades of particles. The characteristics of the sands vary, therefore, in the proportions of other particles which may be of importance to the animals in their habitat.

The next stage in this experimental series included a test to see whether cumaceans will select between natural "whole-grain" sediment and fractions derived from that sediment.

### 7.6 Experiments to test choice by cumaceans between whole sediments and fractions of that sediment

### 7.6.1 Preparation of whole sediment and fractions

A sample of wet Little Swanport sand was divided into two. One subsample was placed in a bucket with sea water and aerated for three days. The other subsample

was sieved gently in a tank of sea water and the
fractions left to mature for three days in an attempt
to produce fractions incubated in the same manner as
the subsample of whole sand.

The grades prepared are listed below.   They are
numbered to distinguish them from the sand grades
prepared for experiments 1-6 although they were derived
from the same bulk sample.

VI      Whole sand
VII  ·  500-250 $\mu$
VIII    250-125 $\mu$
IX      125-63 $\mu$
X       < 63 $\mu$

7.6.2   Exp. 7

To test whether *Cyclaspis caprella* "preferred"
whole sand to any of four size grades isolated from the
same sand sample.   The results of experiment 3 suggested
that sediment VIII might be preferred.   However, whole
sand contained *c*. 65% of that grade and if it were
preferred one might suggest that preference of habitat
is not only determined by the median diameter of the
sand but by other properties.   An alternative explanation
for such a choice might be that whole sand is so
dominated by sediment VIII that cumaceans do not
distinguish between whole sand and its major percentile.

Results

| VI | VII | VIII | IX | X | |
|----|-----|------|-----|-----|-----|
| 12 | 1 | 4 | 0 | 0 | 17 |

| IX | X | VI | VII | VIII | |
|---|---|---|---|---|---|
| 0 | 1 | 32 | 1 | 2 | 36 |

| VII | VIII | IX | X | VI | |
|---|---|---|---|---|---|
| 1 | 7 | 0 | 0 | 19 | 27 |

| X | VI | VII | VIII | IX | |
|---|---|---|---|---|---|
| 0 | 6 | 0 | 0 | 0 | 6 |

| VIII | IX | X | VI | VII | |
|---|---|---|---|---|---|
| 3 | 0 | 0 | 9 | 3 | 15 |

| Totals | 16 | 15 | 36 | 10 | 24 | 101 = T = Number of animals |
|---|---|---|---|---|---|---|

Treatment totals (sediments)

| VI | VII | VIII | IX | X |
|---|---|---|---|---|
| 78 | 10 | 16 | 0 | 1 |

Correction factor $= \dfrac{T^2}{N} = \dfrac{101^2}{25} = 408.04$

Table of Analysis of Variance

| Source | Sum of Squares | df | Variance estimate |
|---|---|---|---|
| Rows | 106.96 | 4 | 26.74 |
| Columns | 82.56 | 4 | 20.64 |
| Sediments | 880.16 | 4 | 220.04 |
| Residual | 259.28 | 12 | 21.6 |
| Total | 1328.96 | 24 | |

Inspection of the Analysis of Variance table demonstrates a major contribution to the variance estimate by sediments. $F = 10.18 > 5.41$ at 1% with 4 and 12 df.
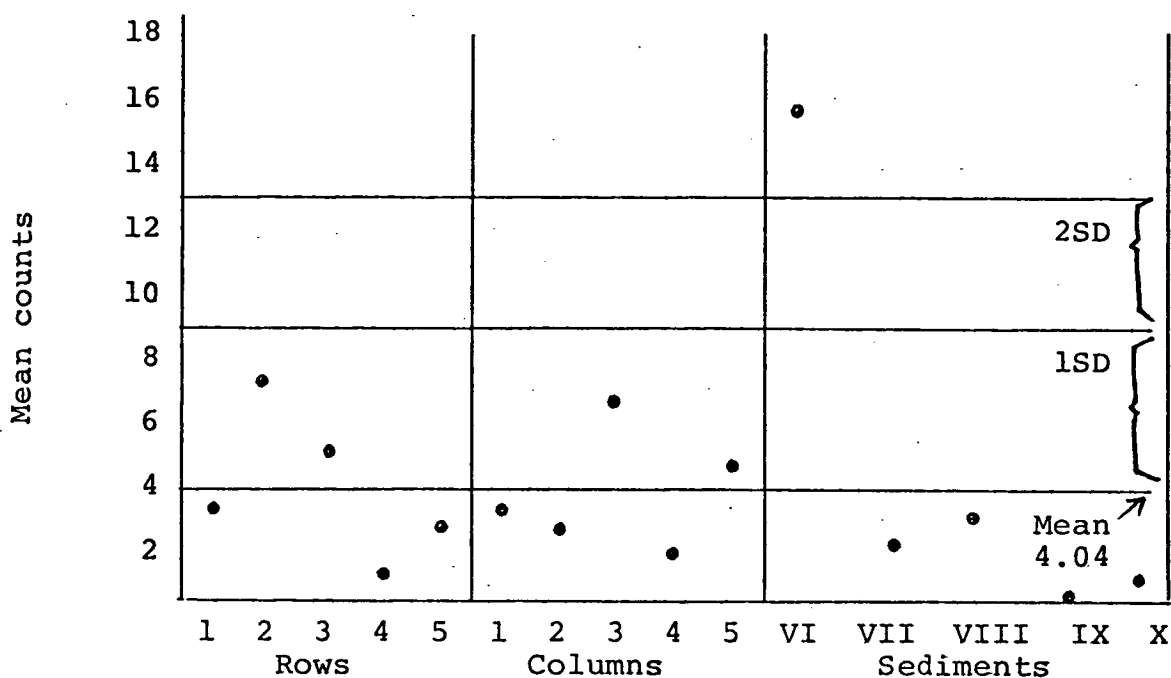
Diagram of row, column and sediment mean counts.

SD = 4.64.

Ho, that no choice would be made was rejected.
*Cyclaspis caprella* chose whole sediment in preference to
sediment grades all other values being rejected at
P < 0.01 (Duncan's test).

7.6.3    Experiments 8, 9, 10

The experiment was repeated using the three other
cumacean species available.    The results are tabulated
below (Table VI).    No significant choice between sediment
grades and whole sediment was demonstrated for *Cyclaspis*
n. sp. and *Leptocuma pulleini*.    *Anchistylis waitei*,
however, chose whole sediment in preference to sediment grades
but demonstrated preference for grade 125-63µm in earlier
experiments (7.5.2.4 and Table VII).

Table VI

Analysis of Variation;  Latin square design

| Experiment number Species No. of animals | Source | Sum of Squares | df | Variance estimates | F  Ratio treatments | Sign. at 1% | Sign. at 5% |
|---|---|---|---|---|---|---|---|
| Expt. 8 *Cyclaspis* n. sp. | Rows | 14.56 | 4 | 3.64 | | | |
| | Columns | 43.76 | 4 | 10.94 | | | |
| | Sediments | 64.96 | 4 | 16.24 | 2.77 | NS | NS |
| 60 | Residual | 70.48 | 12 | 5.87 | | | |
| | Total | 193.76 | 24 | | | | |
| Expt. 9 *Leptocuma pulleini* | Rows | 22 | 4 | 5.5 | | | |
| | Columns | 10 | 4 | 2.5 | | | |
| | Sediments | 37.2 | 4 | 9.3 | | | |
| 40 | Residual | 40.8 | 12 | 3.4 | 2.7 | NS | NS |
| | Total | 110 | 24 | | | | |
| Expt. 10 *Anchistylis waitei* | Rows | 9.60 | 4 | 2.4 | | | |
| | Columns | 46.40 | 4 | 11.6 | | | |
| | Sediments | 117.60 | 4 | 29.4 | 21.45 | ** | * |
| 75 | Residual | 16.40 | 12 | 1.37 | See Table VII | | |
| | Total | 190 | 24 | | | | |

7.6.4     Cumacean grain size preferences

Wieser (1959) demonstrated that the cumaceans of
Puget Sound exhibited preference for fine substrates, most
species preferring particles < 200 $\mu$m in diameter.   In an
earlier study that author had shown (Wieser, 1956) that
*Cumella vulgaris* may act as a sand grain scraper operating
upon particles between 500-150 $\mu$m.

Parker (1975) showed that two species of cumaceans
from the Hadley Harbour complex inhabited sands of
different median diameter.   *Leucon americanus* was found
in sandy-silts and silts of median diameter 89.5 $\mu$m.
*Oxyurostylis smithi* was found at stations characterised by
higher currents and sands of median diameter 175 $\mu$m.

The species upon which it was possible to carry
out experiments in this study "preferred" particles of
different sorting grades (summarised in Table VII).

Table VII

Preferred grades of substrate by cumaceans in choice experiments

| Species | Grade ($\mu$m) |
| --- | --- |
| *Cyclaspis caprella* | 250-125-63 |
| *Cyclaspis* | 250-125 |
| *Leptocuma pulleini* | 500-250 |
| *Anchistylis waitei* | 125-63 |

However, particle size preference is not the only
part of the story.

7.6.5     Factors modifying particle size preference

Most animals which manipulate particles to obtain

their food shows preferences for particles which they can handle efficiently. The constraints upon this situation may be: (a) mechanical, and (b) the level of metabolic success.

Mechanical constraints are imposed upon particle manipulating cumaceans by the dimensions of the particles available and also by the dimensions of the nest of maxillipedes which processes the particle after acceptance (see Chapter 11). A similar conclusion was drawn by Wieser (1956).

The level of metabolic success depends upon the structure and content of the particles which are manipulated by cumaceans. Some aspects of this phenomenon are also treated in Chapter 11.

## 8. SEDIMENT DEPTH SELECTION EXPERIMENTS WITH THREE SPECIES OF CUMACEA

The cumaceans studied during this project are essentially animals of open interfaces (Anderson and Meadows, 1978). The aim of the simple experiments which follow was to decide whether cumaceans burrow and, if so, to what depth. If extrapolation of the results to the real world is attempted it must be remembered that real sediments are heterogeneous where one constituent may surround another.

8.1 Experimental substrates

Isolated from bulk Little Swanport sand.

| Substrate Number | Particle size range ($\mu$m) |
|:---:|:---:|
| I | 1000-500 |
| II | 500-250 |
| III | 250-125 |
| IV | 125-63 |
| V | $<63$ |

8.2 Experimental animals : *Cyclaspis caprella*
*Cyclaspis* n. sp.
*Leptocuma pulleini*

8.3 Method

A small subsample of each experimental substrate was dried, soaked in non-toxic enamel paint and allowed to dry again. Each sample was then ground in a mortar and pestle and sieved to isolate coloured components which matched the size ranges of the experimental substrates.

Both experimental substrates and coloured indicator sands were washed with sea water and maintained (aerated and submerged) until animals were available for experiment.

Circular museum jars (height 250mm, diameter 100mm) were then loaded with 9mm thick layers of experimental substrate separated by 1mm layers of indicator sand. A different colour indicator was used for each layer. The sand column was filled with sea water and cumaceans were added to the water column. Twenty specimens were used in each experiment.

The jars were left for 24 hours and then each layer of sediment was siphoned off through a sieve of mesh 125μm. The numbers of cumaceans in each layer were counted and the presence of indicator sands within each layer noted.

8.4     10mm interval experiments : results (Table VIII)

Table VIII

Depths at which cumaceans were found in experimental sand columns.   + = present; movement of coloured sand grains is indicated by the arrow. The base of the arrow stands at the original level of indicator sand.

| species | L. pulleini | | | | | Cyclaspis n.sp. | | | | | C. caprella | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Substrates | I | II | III | IV | V | I | II | III | IV | V | I | II | III | IV | V |
| 0.10 | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| 11.20 | | | | | | + | | | | | + | + | | | |
| 21.30 | | | | | | | | | | | | | | | |
| 31.40 | | | | | | | | | | | | | | | |
| 41.50 | | | | | | | | | | | | | | | |

Depth intervals mm

In each of these experiments animals were found in the upper layer of each sediment column. Two species only

penetrated the next deeper substrate layer and only one
species disturbed the second indicator layer.  It was
also observed that most individuals were visible at
the sediment water interface or that their position
just below the sediment surface could be detected.

It was concluded from these data that

(a) the cumaceans studied do not burrow to a
depth > 20mm in such substrates

(b) the technique, which withdrew animals from
each 10mm layer, would obscure any differential
distribution within these layers.

8.5      5mm interval experiments : results

The experiments were repeated with sediment columns
20mm high and with indicator sands at 5mm intervals.

The results are presented in Table IX.
Depth ranges at which cumaceans were found in experimental
sand columns.

Conventions as Table VIII.

| Species | *L. pulleini* | | | | | *Cyclaspis* n.sp. | | | | | *C. caprella* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Substrates | I | II | III | IV | V | I | II | III | IV | V | I | II | III | IV | V |
| 0-5 | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| 6-10 | | | | | | | | | | | | | | | |
| 11-15 | | | | | | | | | | | | | | | |
| 16-20 | | | | | | | | | | | | | | | |

(Depth intervals mm)

8.6      Discussion

The results of these experiments suggested that cumaceans do not burrow to any great depth, and indicated that cumaceans may burrow more deeply in deeper sands.

8.7    Experiments to test the relationship between burrowing and substrate depth.

A further series of experiments was conducted to investigate whether cumaceans burrow more often in deeper sediments.    The technique employed by Meadows (1964) was adopted for these experiments.

8.7.1    Materials and methods

Circular plastic trays divided into four quadrants by acrylic partitions were used for each experiment. Each quadrant was filled with molten paraffin wax in such a way that the upper level in each quadrant was a known distance from the top edge of the partitions.    Each experiment was conducted using well mixed, wet, aerated, shallow water sand from Little Swanport.    Wet sediment was added to each tray until it was level with the top of the partitions and sea water was added to the trays. Twenty specimens of a cumacean species were added to each tray for each experiment.    Each tray was surrounded by either a tube or thick card or a section of drainpipe to exclude stray light and was illuminated from above by a 20 w. globe.    The experiments were set up during the afternoon of one day and concluded at 0900 hours the next day.    Experiments ran between 12-18 hours.

8.7.2    Results

The pooled results from the replicate runs for each species (expressed as percentages for each sediment depth) are presented in Table X. The results are presented in this manner because no significant differences were detected between trials for each species.

Table X

% animals in each depth of sediment

| species | Sediment depth mm | | | | No. of trials |
| | 1mm | 2mm | 5mm | 10mm | Total No. of animals |
|---|---|---|---|---|---|
| C. caprella | 5.0 | 26.4 | 30 | 33.6 | 7<br>140 |
| Cyclaspis n.sp. | 2.7 | 49.3 | 19.4 | 28.6 | 8<br>154 |
| L. pulleini | 0 | 38.4 | 56.6 | 5.0 | 4<br>80 |

## 8.7.3    Discussion

This technique is easier to operate than the layered indicator sand used earlier (8.4, 8.5).

Of the three species tested in this manner, only *Leptocuma pulleini* did not burrow in the most shallow layer of sand. It is suggested that such a thin layer of sediment is inadequate for feeding and burrowing. Whether the animal detects and avoids a hard substrate under thin sediment or detects an appropriate depth of substrate remains problematical.

Both of the smaller species were taken in small numbers in sediments of 1mm depth. All of the species were taken in deeper sediments although there is no evidence from these experiments that they burrowed more

deeply in deeper sediments.

From the results of this series of experiments I conclude, tentatively, that sand dwelling cumaceans generally do not burrow to any great depth.   I conclude that they constrain their benthic activities to the uppermost 10mm of sediment and that they prefer sedimentary layers which are not very shallow and do not overlie hard surfaces.

Observations of cumaceans in tanks and in observation chambers (Fig. 25) confirm that cumaceans do not burrow deeply in sands but nestle in the surface layers of sediment.   These observations support those of Corey (1970) who suggested that the upper 3mm of sands acted to determine the distribution of cumaceans in her survey.   That author also stated that "..... cumaceans burrow into the surface few millimetres of the sea bottom.....".   A similar conclusion was drawn for sediment-living ostracods except in sediments with very large interstitial spaces (Williams, 1969).

acrylic insert

glass
slides

25 mm

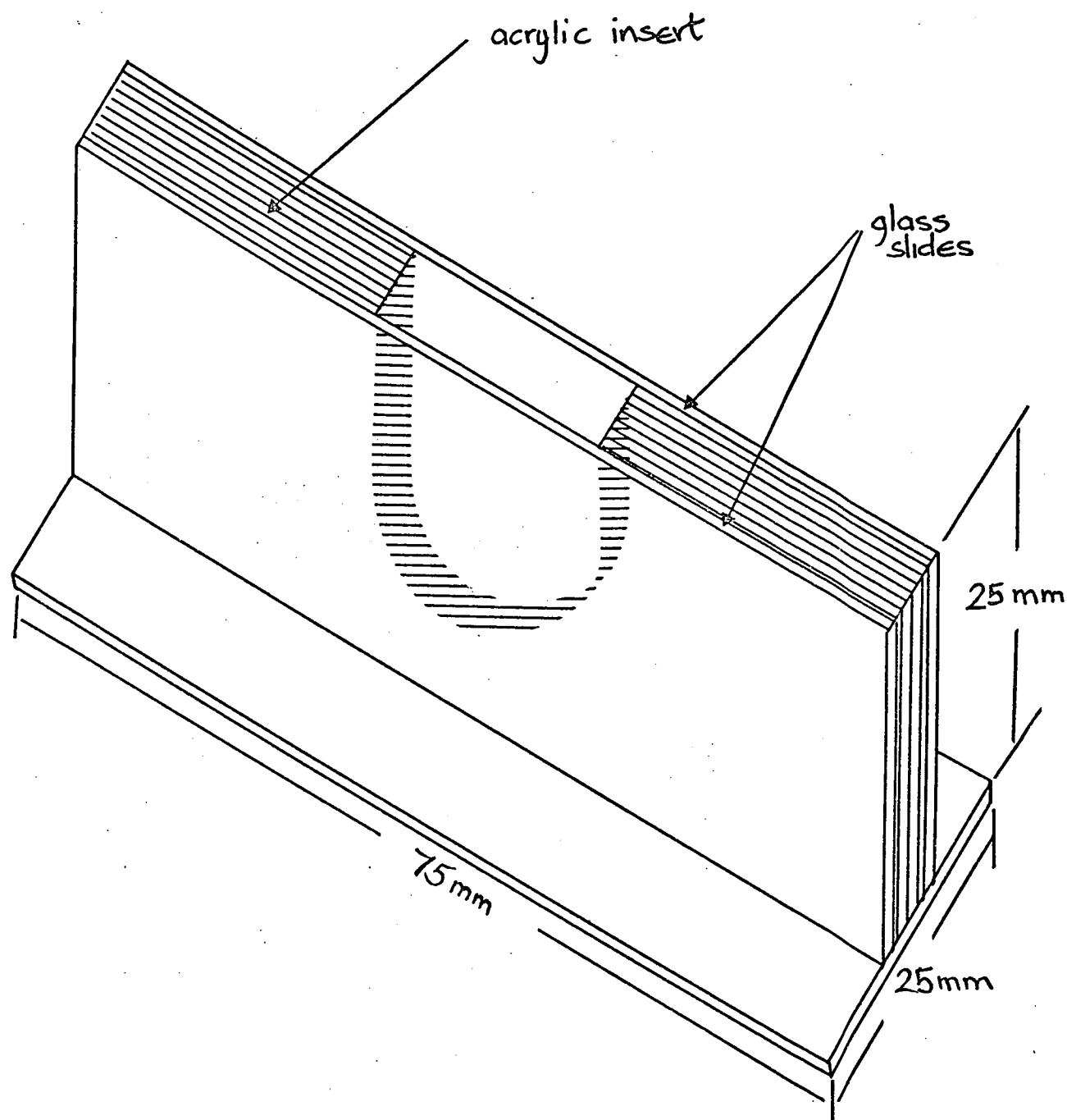75 mm

25 mm

Fig. 25.   Observation chamber used to watch
           cumaceans at a sediment-water
           interface.   The chamber was observed
           through a binocular microscope tilted
           so that the light path was horizontal.

9. SEDIMENT MODIFICATION BY CUMACEANS

9.1    Introduction

Psammophilic cumacea are deposit feeders and mine organic particles from sands. Such "biological bulldozers" (Thayer, 1979) may exclude suspension feeding forms by bioturbation (trophic group amensalism of Rhoads, 1974). One result of bioturbation by benthic animals is fluidizing of mud substrata. A further aspect of such activities is permeability change by substrate modification. Irrigation of marine sands has been observed (Webb and Theodor, 1968). Observations by the present author of cumaceans handling particles suggested that surface sediment permeability of benthic sands might be changed by such activities. This idea was tested by the experiements which follow.

9.2    Methods

Ten sediment samples were placed in permeameter extension tubes to a depth of 10cm. The extension tubes and their sediments were then immersed in a tank of running sea water and left for one week. Permeability of each sample was then measured. (For details of construction and operation of permeameter and the use of permeameter extension tubes see Appendix II).

Ten cumaceans (*Cyclaspis caprella*, ♂♂ and ♀♀) were added to each of five samples and five samples were retained as controls. All samples were maintained in sea water for a further week. Permeameter readings were taken of all the samples at intervals through that week.

9.3     Results

The results are presented in Figure 26.  For the purpose of these experiments permeability change was expressed as absolute time, in seconds, for water to pass through the sediment on different occasions.  One cumacean sample is not plotted because it was dropped when fitting the extension tube to the permeameter.  "Caprella" sample 4 reached a high level of permeability and then the experiment was terminated because the animals died.  "Caprella" sample 3 was terminated at day 6 because the animals were found dead on that day.  Control 4 plots off the figure because it was decided to consider any sediment that did not complete its test run within 1000 seconds as impermeable.

9.4     Discussion

It can be seen that there is a tendency for control sediments without microfauna, to decrease permeability, i.e. increased percolation time.  In samples with cumaceans present there is a trend toward increased permeability, i.e. decreased percolation time.  This observation may be explained by (a) mining or bulldozing of the sediment, and (b) the reduction of organic layers upon particle surfaces by the feeding action of the cumaceans.

9.5     Sediment interactions by ostracods

When examining samples of sand-living benthos it was observed that one of the animals commonly encountered was an ostracod, *Tasmanocypris dartnalli* McKenzie, 1979. As that species moved through the sediment, it was seen to drag a mucus string which became entangled amongst sediment particles.  A series of control sediments and sediments
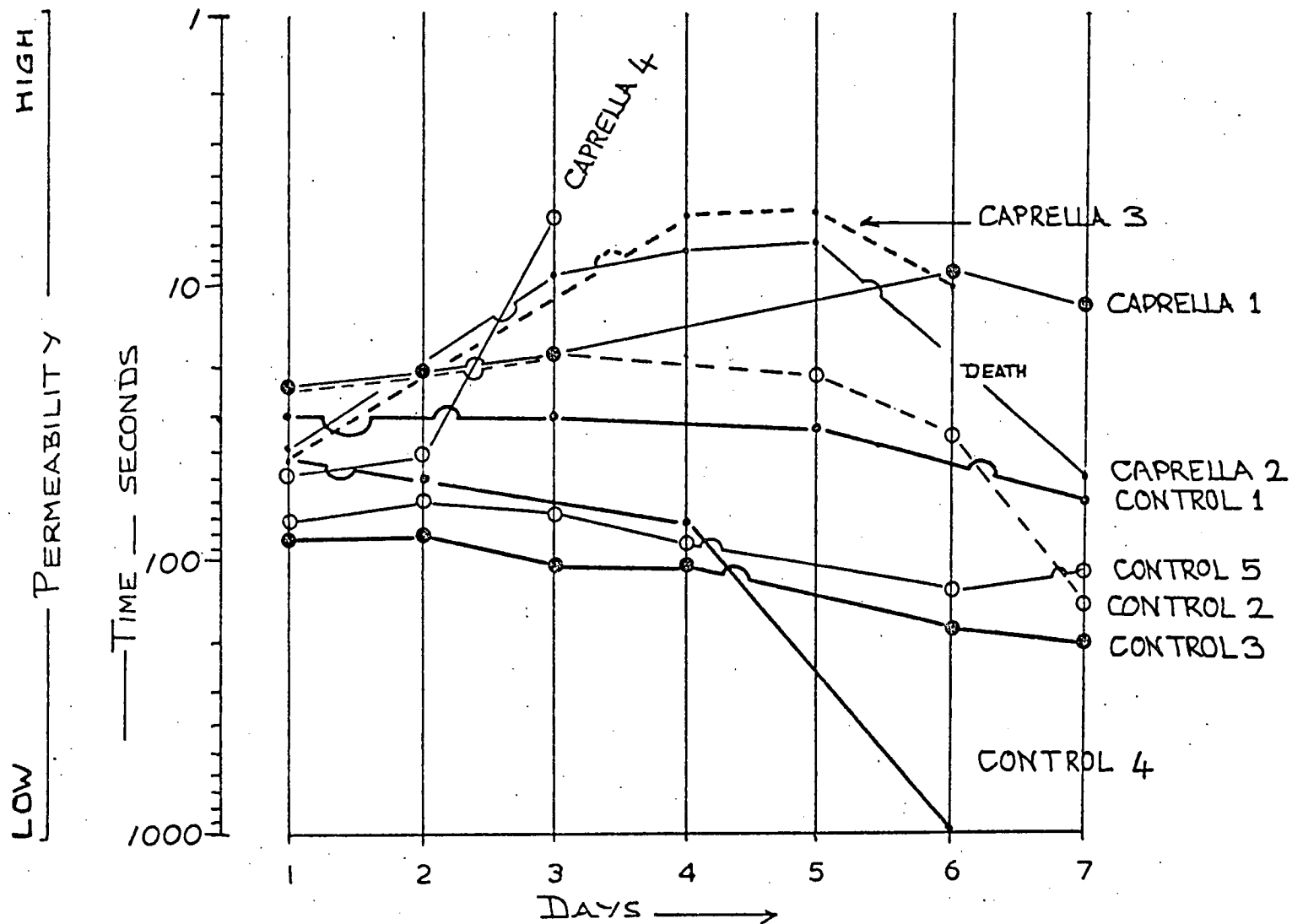
Fig. 26. Permeability history of sediment samples with and without cumaceans. Note inverted left-hand axis. Permeability increases upwards on the figure.

with ten ostracods were set up in a similar manner to the
cumacean series described above.    The results of the ostracod
series are shown in Fig. 27.

## 9.5.1  Results

All the sediments decreased permeability throughout this
series except for Ostracod 1 which had increased permeability
by day 3, and controls 3 and 5 which initially lost permea-
bility but gained on the 6th and 5th days of observation
respectively.    Amongst the ostracod samples, 1, 4, and 5,
clearly had lost permeability, i.e. gained percolation time
by the end of the experimental run.

## 9.5.2  Discussion

It is suggested that the agglutinating effects of
mucus strings may act to glue particles together and block
interstices when animals such as *T. dartnalli* are present.  A
second explanation for decreased permeability in this
experimental situation may be that the ostracods' faeces and
mucus strings offer a suitable substrate for increased bacterial
growth which closes the interstitial spaces of the sediment.

## 9.6    Sediment interactions by cumaceans and ostracods

One further experimental series was run because I
considered that if cumaceans increase sediment permeability and
ostracods decrease sediment permeability there would be a
point at which their effects would balance in mixed populations.

## 9.6.1  Method

To test this suggestion sediment samples were incubated
in running sea water as before and then samples of ostracods
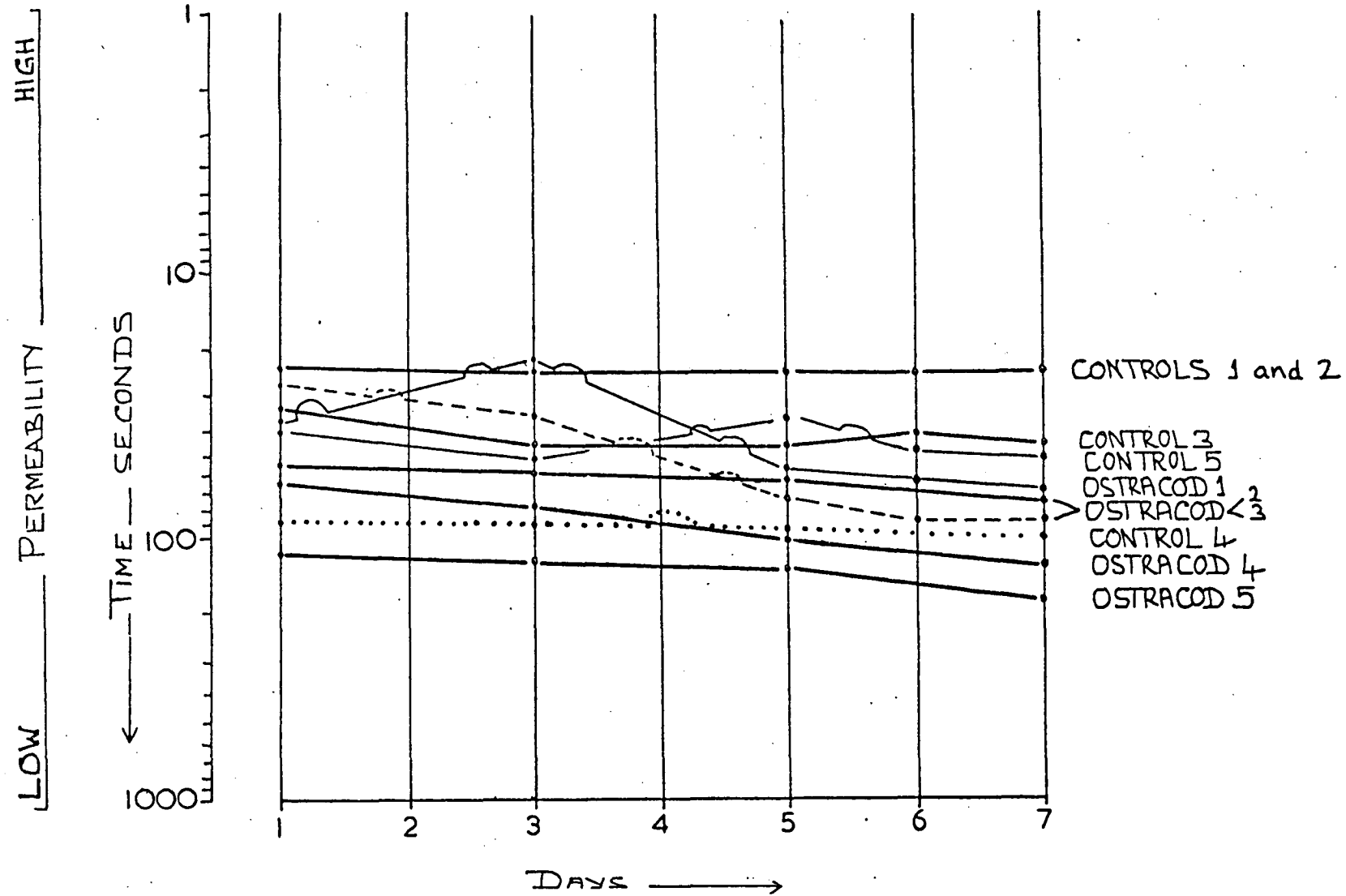
Fig. 27.    Permeability history of sediment samples with and without ostracods.    Note inverted
left-hand axis.    Permeability increases upwards on the figure.

and cumaceans in different proportions were added to each
sample.

The animal samples were made up as shown in Table XI.

TABLE   XI

Numbers of *Cyclaspis caprella* and *Tasmanocypris dartnalli* used
for permeability interaction experiments.

| Sample No. | Number of cumaceans | Number of ostracods |
|:---:|:---:|:---:|
| 1 | 10 | 0 |
| 2 | 8 | 2 |
| 3 | 7 | 3 |
| 4 | 6 | 4 |
| 5 | 5 | 5 |
| 6 | 4 | 6 |
| 7 | 3 | 7 |
| 8 | 2 | 8 |
| 9 | 0 | 10 |

9.6.2   Results

The results of the sediment permeability runs are
shown graphically in Fig.28.

Sample 1.   Cumaceans 10 : Ostracods 0.   Permeability
increased but the run was discontinued after day 4
because the animals died.

Sample 2.   C 8 : O 2.   Permeability increased.

Sample 3.   C 7 : O 3.   Permeability was apparently
steady between days 2 and 3.   The cumaceans were found
dead on day 5, and permeability decreased dramatically
to day 7.
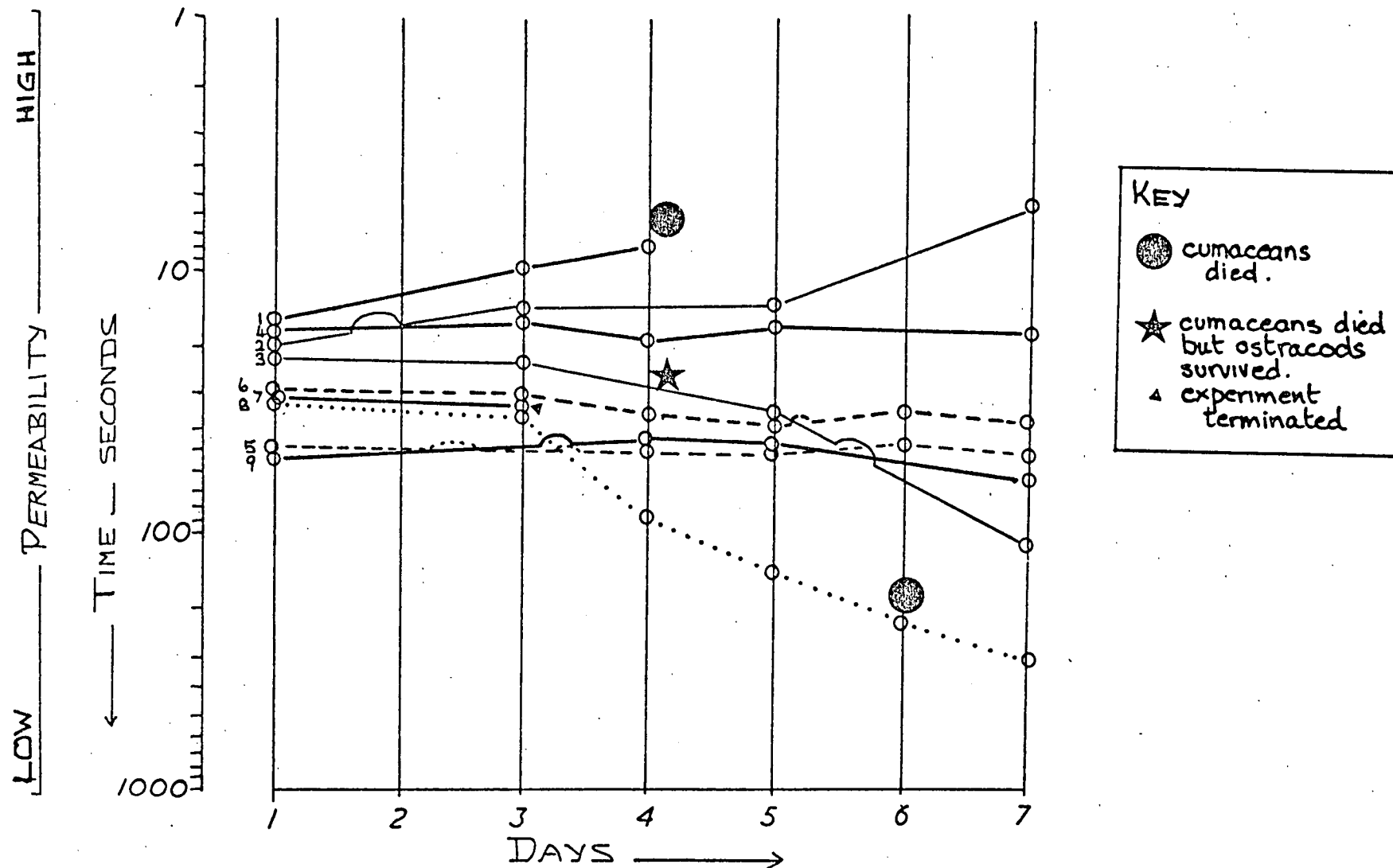
Fig. 28.  Permeability history of sediment samples inoculated with combinations
of ostracods and cumaceans.

Sample 4.   C 6 : 0 4.   Permeability varied but finished at approximately the same level on day 7.

Sample 5.   C 5 : 0 5.   Permeability varied but finished at about the same level on day 7.

Sample 6.   C 4 : 0 6.   As 4 and 5.

Sample 7.   C 3 : 0 7.   The run on this sample was terminated after day 3.

Sample 8.   C 2 : 0 8.   Permeability decreased after day 3.

The cumaceans were found dead on day 6 and permeability had decreased further by day 7.

Sample 9.   C 0 : 0 10.   Permeability did not vary greatly.

## 9.6.3 Conclusions

I have not analysed these results further because I feel that the experimental design must be improved.   Such improvements could be made if information about the rates of ingestion and feeding efficiency of benthic animals were obtained.   The experiments do show that a simple permeameter technique is useful to investigate aspects of animal-sediment interaction.

The results indicate that one species of cumacean, *Cyclaspis caprella*,  is able to increase the permeability of the sands which it exploits.   This may be due to removal of organic layers from particle surfaces or mechanical separation of the sedimentary fabric during the feeding and burrowing process.

## 9.7     Tanaid-sediment interaction

9.7.1   One further experiment was carried out on one sediment sample.   A small sample of sand was sieved and the sieved grade between 0.125-0.250$\mu$m was isolated and its permeability recorded.   The sediment was then salted with biogenic carbonate fragments collected when isolating fauna from other sediment samples using a saturated sugar solution.   The mixed sample was then placed in the permeameter and the permeability recorded again.   A large sample of an unidentified tubicolous tanaid which incorporates shell fragments in its case was available.   About 100 animals were induced to leave their tubes by squeezing the end ⟨...⟩ and the naked animals placed on the carbonate-modified sediment.   After two days most of the tanaids had constructed new cases and the permeability of the sample was recorded.   The animals were removed and the proportion of carbonate particles remaining was recorded.

9.7.2   Results

### TABLE   XII

Permeability (time) and proportion of carbonates of sand

exposed to tanaid activity

| Sand | % Carbonate v/v | Permeability time (secs)* (mean of three readings) |
|---|---|---|
| 0.125-0.250 $\mu$m | 0 | 91 |
| Sand + Carbonate | 44% | 47.3 |
| Sand + Carbonate + Tanaids | 21% | 82 |

### 9.7.3 Conclusion

It may be concluded that animals such as tanaids which selectively remove particles from a sediment fabric modify the physical properties of those sands.

### 9.8 Discussion

This work indicates that the effects of benthic faunas upon their substrates may be marked. The tentative conclusions to be drawn are:-

1. That particle handling cumaceans may increase sediment permeability.

2. The one ostracod species studied may decrease sediment permeability.

3. That animals such as tubicolous tanaids which remove part of the sedimentary fabric may modify the permeability of a sediment.

These conclusions are not unexpected. Webb (1969) suggested that lancelets may modify sands by sorting grains by their own activities. Animals such as cumaceans which exploit benthic patches may exhaust such patches in a short time leaving a modified patch suitable for exploitation by other animals in the community. The inhabitants of finer sediments tend to build relatively permanent tubes and burrows and remain static for long periods. The surface fauna of well-sorted sands is mobile and any spot on the shallow sand sea-bed will be successively occupied by opportunistic niche-gatherers which have exhausted their previous locality. This is a reasonable reaction to a high energy sand-water interface where the action of sorting ensures that a habitat may always be present but not always in the same place.

This work needs extension and refinement in the future until a flow chart of animal-sand structure-permeability relations and successions can be constructed.    One way to investigate this would be to monitor sediment hydraulics and faunal change through time in small areas of shallow water sands.

10.                DIFFERENTIAL CHOICE OF "IDENTICAL" SEDIMENTS

10.1    Introduction

Cumaceans sampled at Little Swanport and Bull Bay
possess contagious distributions and differential offshore
distributions (Sections 6.5, 6.6, 6.7).   It has been shown,
in laboratory experiments, that cumaceans prefer sediments with
grains of a given size range (Section 7).   It has also been
shown that cumaceans apparently chose whole sediments rather
than their preferred size fraction alone (Section 7.6).

It was apparent that the cumacean distribution
observed could not be explained on the basis of these data
alone.   Inspection of the results of choice experiments
suggested that choice of a sediment in a Latin  square design
was dominated by choice of some of the experimental subsamples.
The test sediments from Experiment 2 (Section 7.5.3.2) had been
retained.   The five subsamples of sediment II were examined
to ascertain whether they were identical or not.

10.2    Method

10.2.1  Sieve separation

Each subsample was dry sieved and broken down into
one-quarter phi units in an attempt to identify a different
distribution of particles within the 500-250$\mu$m grade.   The
distributions were virtually identical (Figure 29).

10.2.2  Settlement separation

To speed sand analysis and in an attempt to describe
samples by the behaviour of their constituent particles in an
aqueous medium, a settlement tube was constructed (after
Emery, 1938).   To calibrate the operation of the settlement
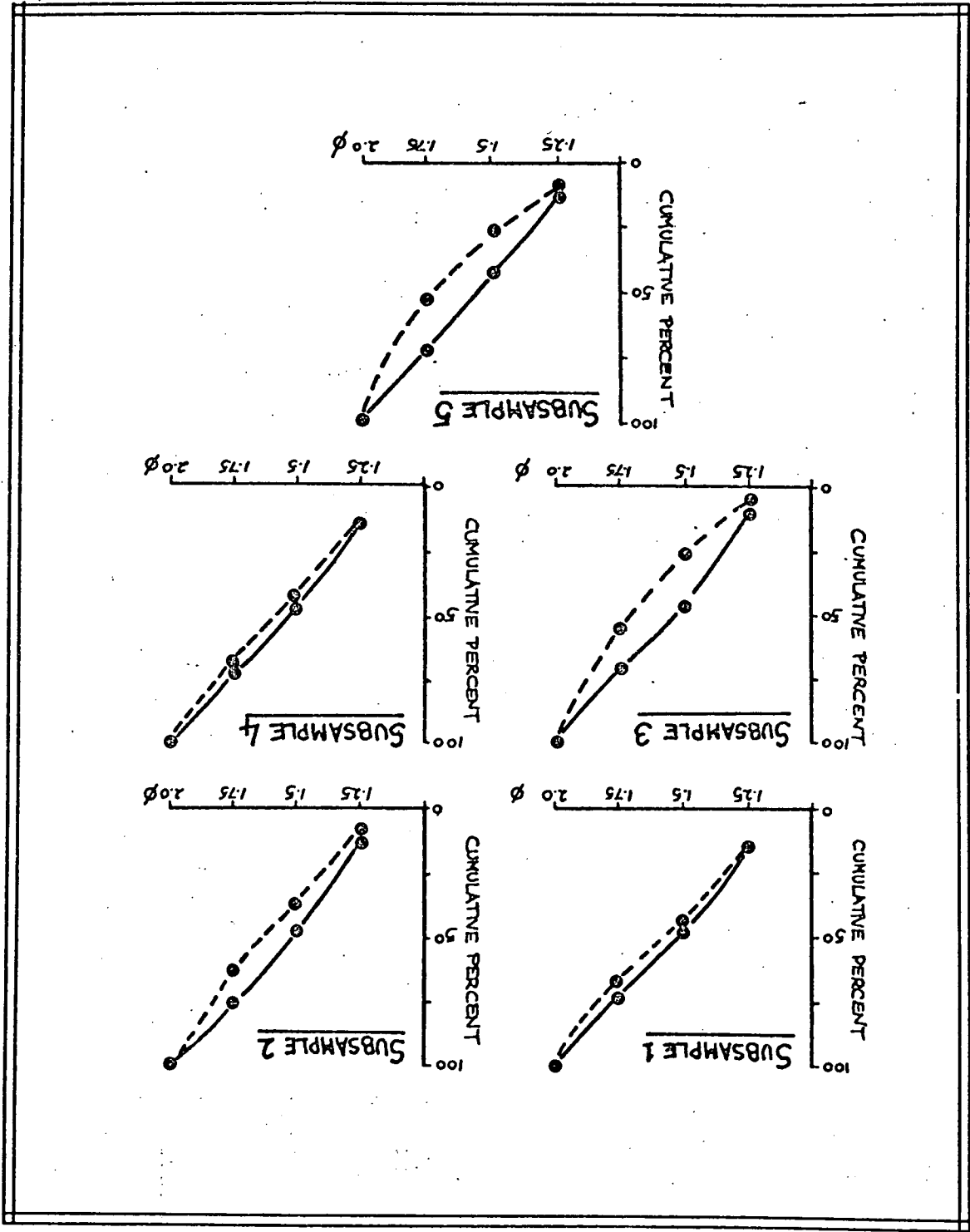
Fig. 29. Comparative particle size distributions of apparently identical sediment subsamples between 500 and 250 μm grade.

tube, accurately sieved fractions were needed. The fractions examined above (10.2.1) were still available. When the results of drop-tube analysis were plotted beside the curves obtained from the sieved series differences were apparent (Fig.29).

It can be seen that the subsamples of sediment grade II were very similar in composition by sieve analysis. The plots of data obtained by settlement tube differed from the sieve data. All variation was towards the smaller fractions of the sediment. The observation could be explained if a proportion of the particles sized by sieving behaved as if they were of smaller size in the settlement tube. This would occur if particles of similar size were of lower effective density.

Microscopic examination of the sediments suggested that carbonate fragments of biogenic origin contributed the predominant fraction with densities less than quartz particles (Plate 3). Simple acid treatment was employed to remove carbonates from the sand samples. The results are shown in Table XIII.

TABLE XIII

% carbonates, acid-leached from sand samples

| Subsample | % carbonate |
|---|---|
| 1 | 7.5 |
| 2 | 26.0 |
| 3 | 40.0 |
| 4 | 6.5 |
| 5 | 38.5 |

1000-500 μm
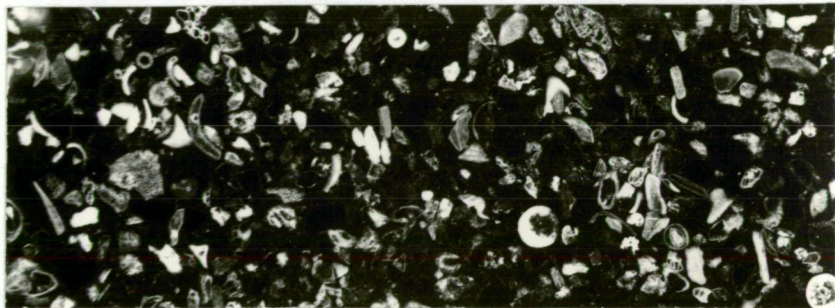
500-250 μm
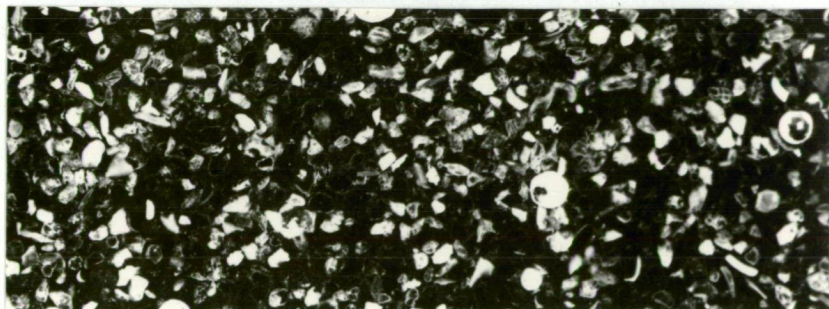
250-125 μm
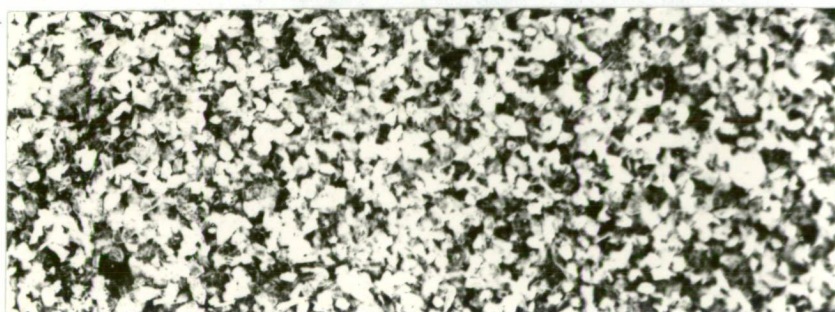
125-63 μm

Plate 3.    Resin embedded sections of sieved grades of Little
            Swanport sands.  The pictures were obtained by
            placing the sections in the negative carrier of a
            photographic enlarger.

It can then be suggested that sediments with carbonate fractions were more attractive to cumaceans than carbonate-less sediments.

10.3 To determine whether cumaceans distinguish between whole sediments and sediments without biogenic carbonates.

10.3.1 Methods

Whole sand from Little Swanport was divided into two lots. Lot 1 was treated with dilute hydrochloric acid until no obvious carbonates were present and effervescent bubbles were no longer produced. Both lots (1 and 2) were then washed with distilled water on two occasions on three succesive days. Both samples were then washed with sea water and maintained for seven days in aerated sea water.

Simple 2 x 2 choice trays were set up with whole sediment in two sections and modified sediments in the two remaining sections. Two species of cumaceans, *Cyclaspis caprella* and *Cyclaspis* n. sp. were available at the time. Four choice trays were set up for each species and fifty animals were introduced to each tray. The trays were covered to exclude light and left overnight. The following morning the sea water overlying the sediment was removed quickly from each tray using a large bulb pipette. Each sediment sample was then decanted into a petri dish and the numbers of individuals counted.

10.3.2 Results

The results are given in Table XIV.

TABLE XIV

(a) *Cyclaspis caprella*

| Experiment | % animals in sediment without carbonate | % animals in whole sediment | Total no. animals |
|---|---|---|---|
| 1 | 11 | 39 | 50 |
| 2 | 17 | 33 | 50 |
| 3 | 23 | 27 | 50 |
| Totals | 51 | 99 | 150 |

$x^2$ = 6.529, 2 df $>$5.02 (P $<$ 0.025) $<$6.63 (P $>$0.01)

(b) *Cyclaspis* n. sp.

| Experiment | % animals in sediment without carbonate | % animals in whole sediment | Total no. animals |
|---|---|---|---|
| 4 | 21 | 29 | 50 |
| 5 | 8 | 42 | 50 |
| 6 | 19 | 31 | 50 |
| Totals | 48 | 102 | 150 |

= 103.86, 2 df $>$ 9.21 (P $<$ 0.01)

Experiment 2 is responsible for the low chi-square value of the C. *caprella* series because the observed and expected values of the contingency table happen to coincide. In spite of this, Ho, that the proportions in both groups of samples is the same, is rejected.

## 10.3.3  Discussion

The results of the simple experiments described above suggested that cumaceans may prefer whole carbonate sands. As a next stage it was decided to investigate the presence and abundance of cumaceans in the field in relation to the proportion of carbonate present.

## 10.4  The quantitative distribution of Cumaceans at Little Swanport in relation to the proportion of biogenic carbonates in bottom sediments.

### 10.4.1  Introduction

The main field site, the bay off Little Swanport, was visited on 15-16.xi.1978.  A transect line was contemplated running approximately ENE from the northern point of the Little Swanport estuary.  No great accuracy was required for position fixing although horizontal sextant sights were taken to prominent landmarks for each station.  The ten stations are shown on Figure 30.  At each station a sediment sample was taken by Mud Snapper (see Section 6.3.2) and a faunal sample with air-lift sampler.  The water depth at each station was also recorded.  Samples of sediment were returned to the laboratory in a cool, insulated container.  Faunal samples were concentrated and preserved as described earlier in this account (6.3.1).

### 10.4.2  Carbonate content of sediments

On return to the laboratory each sediment sample was divided into two portions and each portion was air-dried and weighed.  One sample was then treated with dilute HCl until no further reaction was observed.  The sample was then dried

Fig. 30. Little Swanport Bay showing the positions of the
ten stations    (see Section 10.4.1.).

in an oven at c. 100°C and the sample weighed again. The difference between initial and acid-treated weights was taken as a measure of carbonate content.

TABLE XV

Carbonate content of Little Swanport sands

| Station | Water depth (m) | % carbonate |
| --- | --- | --- |
| 1 | 5.6 | 4.25 |
| 2 | 5.75 | 3.55 |
| 3 | 5.0 | 0.91 |
| 4 | 6.3 | 3.39 |
| 5 | 11.3 | 6.73 |
| 6 | 13.1 | 4.29 |
| 7 | 12.9 | 8.34 |
| 8 | 14.7 | 27.5 |
| 9 | 16.6 | 12.53 |
| 10 | 15.9 | 15.29 |

10.4.3 Faunal composition

The faunal samples were then sorted for numbers and species of cumaceans. In order to remove any chance of subjective bias between station numbers, known carbonate concentration and cumacean abundances, the sample jars were jumbled on a tray and substitute station numbers applied to each jar by reference to a table of random numbers. The numbers were replaced when the columns of data were complete.

The counts of each sample were continued until cumaceans were difficult to find - then a further 15 minute search was conducted.

The results of the faunal counts are given in Table XVI.

### TABLE XVI

#### Numbers of cumaceans at ten stations off Little Swanport

| Random station number | *Leptocuma pulleini* | *Cyclaspis caprella* | *Dicoides fletti* | *Dicoides brevidactyla* | *Anchistylis waitei* | *Dimorphostylis subaculeata* | Total number Cumaceans | True station number |
|---|---|---|---|---|---|---|---|---|
| 30 | – | 14 | – | – | – | – | 14 | 1 |
| 84 | – | 2 | – | 50 | – | – | 52 | 9 |
| 66 | 8 | 2 | – | 4 | 17 | 1 | 32 | 7 |
| 72 | 1 | – | – | 10 | 5 | – | 16 | 6 |
| 02 | 24 | 9 | 5 | 15 | – | 1 | 54 | 8 |
| 70 | 9 | 6 | 1 | 1 | – | – | 17 | 2 |
| 09 | 11 | 2 | – | 2 | 3 | – | 18 | 5 |
| 74 | 25 | 2 | 4 | 16 | 22 | 1 | 70 | 10 |
| 94 | 1 | 12 | – | 1 | – | – | 14 | 4 |
| 12 | 5 | – | – | – | – | 1 | 6 | 3 |
| $x^2$ | 105.27 | 44.8 | 32.00 | 209.19 | 124.67 | NS | 42.72 | |
| df | 9 | 9 | 9 | 9 | 9 | | 4 | |

$x^2$ values at the base of the table are tests for contagious distributions. All are significant being $> 21.67$ $(P < 0.01)$. $x^2$ for total cumaceans is calculated for ranked mean numbers of individuals. The departure from randomness is significant being 13.28 $(P < 0.01)$.

The results from this field experiment are presented graphically (see Figures 31-33).

10.4.4     Results

10.4.4.1  Numbers of individuals/species (Fig. 31)

Throughout the samples there was a tendency for numbers of species and individuals to increase together. By inspection of the figure where the stations are identified it can be seen that there is some correspondence between this relationship and increasing water depth.

10.4.4.2  Numbers of individuals/% carbonate (Fig. 32)

It can be seen that there is a tendency for cumacean numbers to increase in proportion to the percentage of carbonate in the sediment. Following angular transformation of the data $r = 0.832$. In other words, there is a tendency for an increase in individual animal numbers in these samples with increase in sediment carbonate content.

10.4.4.3  % carbonate/water depth (Fig. 33)

Following angular transformation of the data the relationship between biogenic carbonates and water depth may be expressed by the correlation coefficient $r = 0.87$. This

Stations identified by
numbers beside the points
plotted.
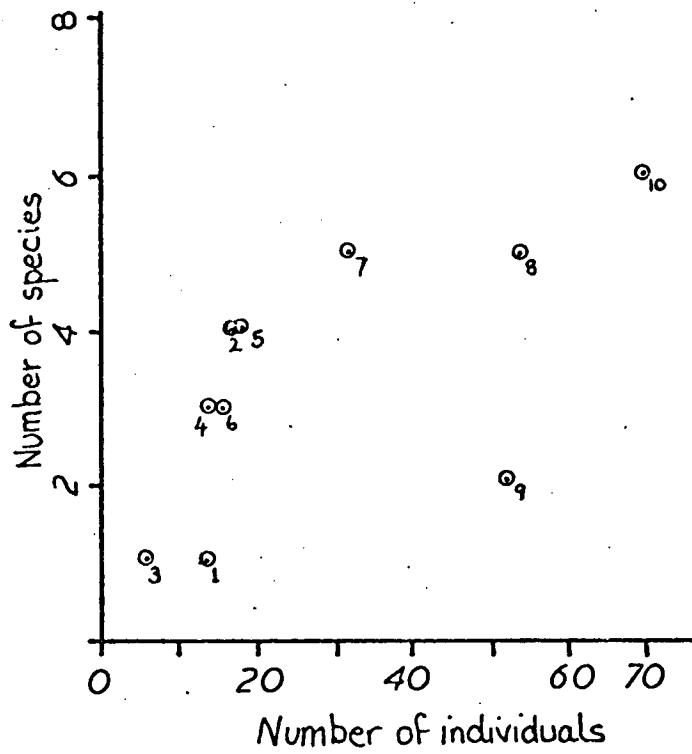


Fig. 31.    Relationship between numbers of individuals and
            numbers of species in ten samples from
            Little Swanport.
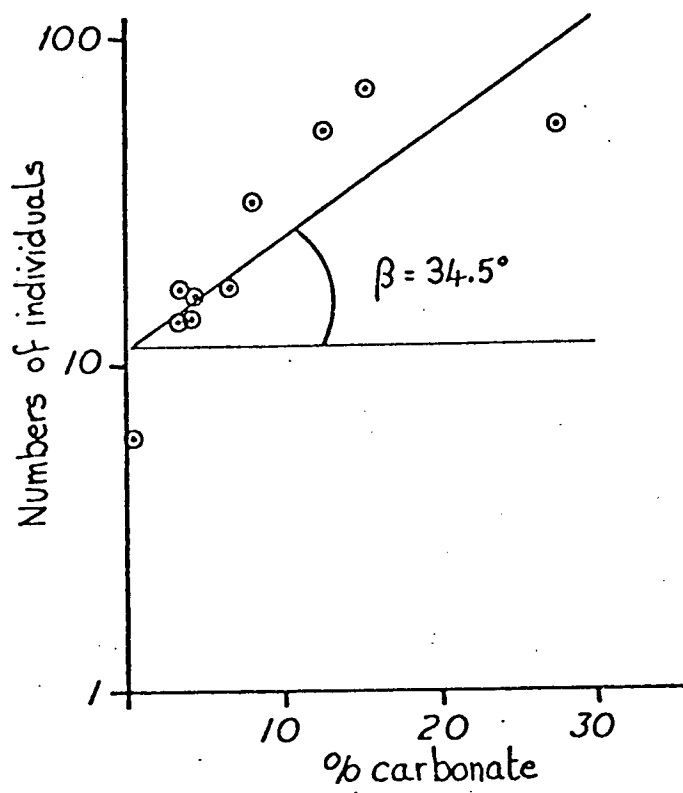
Fig. 32    Relationship between numbers of individuals of
cumaceans and percentage of biogenic carbonates.
r = 0.832,8df > 0.805(P<0.005)< 0.872(P>0.001)
following angular transformation of data.
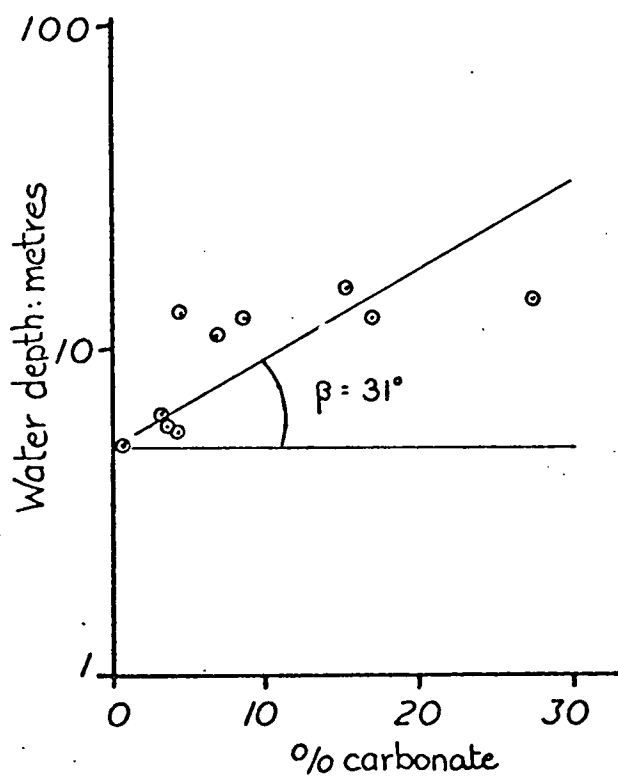
Fig. 33    Relationship between water depth over the sediment
           and the percentage of carbonate in the sediment.
           r=0.87,8df > 0.805(P<0.005)≾ 0.872(P≯0.001)
           following angular transformation of data.

suggests that the carbonate content is also related to water depth in some way.

## 10.4.4.4   Cumaceans/depth/carbonate

The previous results suggest that the observed correspondence between cumacean individuals and carbonate content and that between cumaceans and water depth might be related in some way.

The measured attributes of each station were ranked and the rankings   tested by coefficient of concordance W. viz:

| Station | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| No. of Cumaceans | 2.5 | 5 | 1 | 2.5 | 6 | 4 | 7 | 9 | 8 | 10 |
| Water depth | 2 | 3 | 1 | 4 | 5 | 7 | 6 | 8 | 10 | 9 |
| % carbonate | 4 | 2 | 1 | 3 | 6 | 5 | 7 | 10 | 8 | 9 |
| Rank totals | 8.5 | 10 | 3 | 9.5 | 17 | 16 | 20 | 27 | 26 | 28 |

$n = 10$, $m = 3$   expected rank value to support $H_o = 16.5$

Coefficient of concordance, $W = 0.925$ which with a continuity correction $= 0.924$

$F = 24.315$ $(8, 16 d.f)$ $> 3.89$ $(1\%)$.

On the basis of this analysis it appears that the correspondence of factors at each station was not fortuitous. This point is discussed later (section 11.7).

## 10.4.5   Discussion

The results of the carbonate choice experiments and the tentative correspondence between biogenic carbonate concentrations and cumacean numbers in the field needed

explanation.  Cumaceans are able to make choices about their
substrate.  They are mobile.  They may move short distances in
the sediment.  They may swim above the benthic interface.  They
may also employ the water column as a dispersal route.

Each of these mechanisms may be used to explain how
dispersal occurs.  However, an explanation was still required
for the contagious distributions observed in high carbonate
sediments both in laboratory and field.

11.      OBSERVATIONS OF PARTICLE MANIPULATION BY CUMACEANS

11.1      Introduction

This section of this account considers particle handling
by cumaceans followed by a discussion of the implications of
the mechanisms involved.

11.2      Observations

When cumaceans are placed in a dish of sea water with
the bottom covered by a layer of sediment they eventually nestle
into the epistratal layer and commence to  manipulate particles.

Particle manipulation proceeds in a formal sequence.
The observations offered here are a synthesis of observations
of individuals of *Cyclaspis caprella*, *Cyclaspis*  n. sp. and
*Leptocuma pulleini*.

Such cumaceans reach forward with the first peraeopods
and draw sedimentary particles towards the mouth frame where
each particle is manipulated upwards by the combined movements
of the first peraeopods and the third maxillipeds.   Particles
which are too large to fit within the manipulatory mechanism
are rejected before they reach the mouth frame.   This part of
the mechanism may explain the size range dependence of cumaceans
in particle choice experiments.   Wieser (1956) suggested
that a similar mechanism mediates the manipulation of larger
sizes of particles by  *Cumella vulgaris*.

Particles which fit the peraeopod-third maxilliped
manipulators are conveyed upwards until they reach the level

of the basal segments of the first antennae.    At this level

the particle stops moving and is retained for a short period.

At this point in the sequence alternative pathways

may be followed.

1.  Rejection.    Particles may be rejected either by

allowing them to fall backwards and sideways over

the pseudocarapace or by flicking them backwards

and upwards over the animals.

2.  Acceptance.    If a particle is not rejected it

is allowed to pass downwards over the mouth frame

until it is picked up again by the third maxillipeds.

At this point the maxilliped nest opens out and the

particle is manipulated and rotated against

the armature of the maxillipeds until the particle

is cleaned of material clinging to it.    The

particle is then raised and rejected.

This two stage process of particle choice-rejection,

particle processing-rejection has not been reported before as

far as I am aware.    The observations reported above raised a

further question.    The two stage sequence of particle manipu-

lation is mediated by a rejection or acceptance mechanism.

The site which operates this mechanism is located at the stage

when the particle stops moving, i.e. between the bases of the

first antennae.    Scanning electron microscope investigation

of the site revealed a perforated plate on the inner surface

of the second segment of the first antenna in *Cyclaspis caprella*

(Plate 4).    Successful preparations were not achieved for

other species but it is suggested that a similar site may be
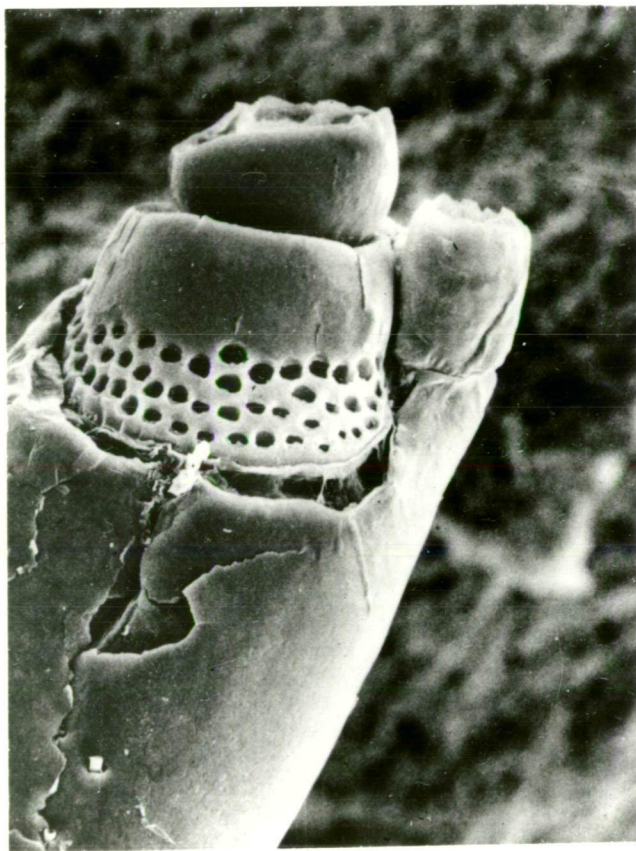
Plate 4    Perforated plate on second segment of
           first antenna of *Cyclaspis caprella*

present.     This note is inserted here as a pointer to future

work.

11.3     The consequences of one pass (rejection) and two pass
(acceptance) manipulation in cumaceans.

Single pass, rejection sequences of particle manipu-
lation in psammophilic cumaceans last about one second.   If an

animal maintains this mechanism without processing any particles

further, an excavation is made in the sand in front of the

animal to the limits of bulldozing efficiency in about 120 secs.

The process may take longer if particle manipulation is not

continuous.   When the forward excavation is complete the animal

reacts in either of two ways.   One, by moving forward to the

forward face of the excavation, or secondly, by leaving the

substrate and landing in another spot.   Whichever response is

initiated a cumacean in an area which provides a poor response

to first stage choices may move its position in the substrate

after intervals as short as two minutes.

If cumaceans take particles which are accepted for

the second phase of the manipulation sequence the timing of the

operation changes.   Particle rotation and cleaning may be

observed by coating particles or dyeing particles which already

possess organic coatings.   Individuals of *Cyclaspis caprella*

offered particles which entered the second phase spent as long

as 77 seconds processing particles (100 observations;   range,

55-77 secs;     $\bar{x}$, 60.25 secs;         s.d. , 19.01).

For the purposes of this argument we will take the duration

of the second phase as 60 seconds.   We will also accept that

feeding animals move to another site when 100 particles have been processed. When these assumptions are made we can construct a simple model to predict the effects of cumacean choice operations (Figure 34).

It can be seen that a cumacean rejecting particles continuously (i.e. feeding unsuccessfully) will exhaust its immediate feeding site in about 100 seconds. A cumacean feeding continuously and operating according to our assumptions will only have handled 1.66 particle operations in the same time.

If we assume that cumaceans change feeding site after every century of operations a continuously rejecting individual will have changed its feeding site sixty times before the individual which is feeding continuously needs to move. If we offer our model a set of particles which initiates 50% acceptances and 50% rejections, 100 particles will be handled in 3050 seconds by which time our continuously rejecting individual will have moved 30 times.

The model postulates animals making 50% successful feeding choice of available particles and remaining on site for periods of up to one hour. It also postulates animals rejecting particles of little food value and moving site at intervals of about one minute.

The conclusion to be drawn is that animals meeting particles of adequate food value remain on site for relatively long periods. Animals rejecting particles from unacceptable sands move on to new sites. The only mechanism which will
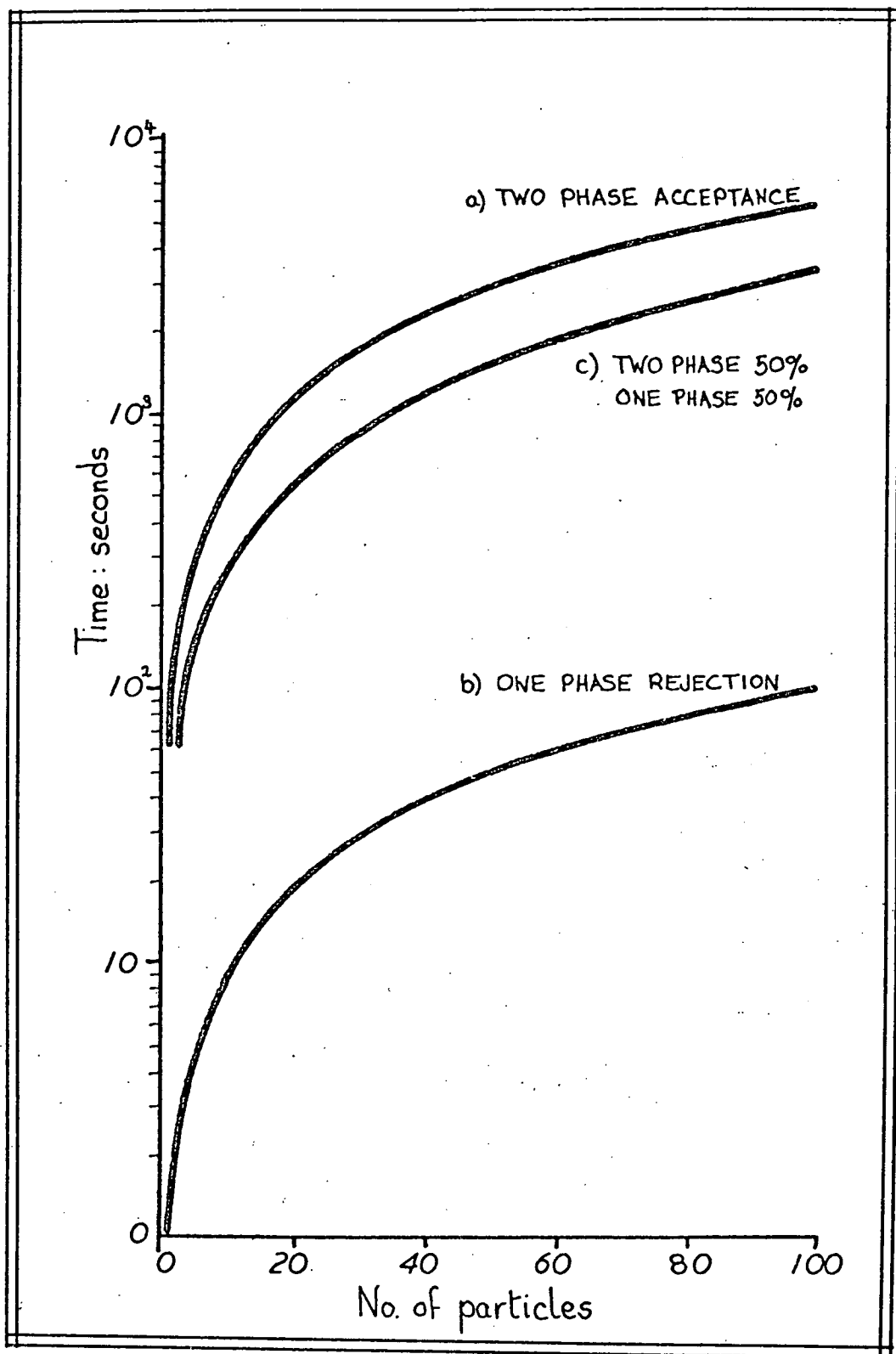
Fig. 34    Graphical model indicating the rates at which feeding
           site exhaustion would be achieved by cumaceans,
           a)   accepting all particles and manipulating each
                one for 60 seconds;
           b)   rejecting all particles;
           c)   accepting 50% of particles for 60 seconds each
                and rejecting 50% of particles for 1 second each.

stop movement is an increase in the number of successful

manipulations.

It was suggested that carbonate particles modified

sediments in some manner so that

(a) feeding cumaceans were able to remain at one feeding site

for long periods, and

(b) that cumaceans congregated in such areas.

11.4 An investigation of some properties of biogenic

carbonate particles.

In Tasmanian shallow water marine sands, biogenic

carbonates are contributed by the tests of Foraminifera,

fragments of bryozoan skeletons, mollusc shells, echinoderm

tests and echinoderm spines. Most particles are broken, some

are naturally reticulate. Other particles are secondarily

modified by sponge or algal burrows.

It is suggested that biogenic carbonate fragments

provide particles of high surface area relative to the quartz

particles of sands. Such an increase in surface area might

provide a substrate carrying a greater amount of organic matter

than particles of more simple outline. This approach was

encouraged after listening to a lecture by Dr. K. Mann on the

sequence of breakdown of leaves of *Spartina* and *Zostera* in

northern America. The observation of importance was that

smaller particles possess relatively greater surface areas

than larger particles. The consequence of importance that

followed was that smaller particles carried more organic matter upon their surfaces than larger particles.

High energy sands in eastern Tasmania possess low levels of fine particles. Most Little Swanport sands, for example, have less than 4% of particles finer than 63 $\mu$m. Thus, cumaceans would have few fine particles available even if they were able to handle them. Dixon (1947) has suggested that some cumaceans can inhabit fine sediments and possess filter sieves on the basis of the third maxillipeds to filter particles. I have no evidence of filter feeding amongst Tasmanian psammophilic Cumacea and must suggest that maxilliped sieves in the species studied may only clear the inhalent respiratory current of particles.

Wieser (1956) suggested that *Cumella vulgaris* acted as a deposit feeder in fine sediments ($<$150 $\mu$m) and as a particle manipulator (epistratal feeder) in coarser sediments.

High surface area carbonates of biogenic origin would provide more substrate area for epipsammic films than quartz particles. It was decided to investigate: (a) the surface area of sand particles; and (b) the respiratory activity of sand particles as a measure of the amount of organic matter contributed by epipsammic layers of bacteria and other organisms.

11.5      On the surface areas of sand particles.

11.5.1    Method and materials.

Sand from Little Swanport was sieved into phi-fractions.

Each fraction was then hand-picked to provide 100 particles each of mineral (mostly quartz) and biogenic carbonate particles. Each sample was air-dried and treated with 10% $H_2O_2$ overnight to destroy organic matter. The samples were then washed three times with distilled water and air-dried again.

15.1.1.1 EGME technique

The surface areas of the samples were determined by the method of Heilman, Carter and Gonzalez (1965) where adsorption of ethylene glycol monoethyl ether (EGME) upon particulate surfaces provides a measure of surface area. Further details of the method may be found in that paper.

The samples were dried to contant weight over $P_2O_5$ in an evacuated desiccator. Each sample was then mixed with EGME to form a slurry which was then placed in a desiccator over $CaCl_2$ for 30 minutes. The desiccator was then evacuated. Each sample was weighed twice daily until a constant weight was attained.

The total surface area for each sample was calculated by dividing the grams of EGME retained per gram of sediment by $0.000286g/m^2$ (being the weight of a monomolecular layer of EGME over a surface of a square metre).

11.5.1.2 Results

The results are expressed in Table XVII and the derived value of one-hundredth of total surface area (i.e. surface area of an average grain of sediment) is plotted in Figure 35.

## TABLE XVII

Surface areas of mineral and carbonate sand particles of four size grades determined by the EGME method

| Constituent grade | Replicates | Surface area $m^2$ x $10^{-5}$/ 100 particles |
|---|---|---|
| mineral 1000-500 µm | 1 | 2.30 |
| | 2 | 0.76 |
| | 3 | 1.05 |
| 1000-500 µm carbonate | 1 | 28.6 |
| | 2 | 1.43 |
| | 3 | 1.30 |
| mineral 500-250 µm | 1 | 1.71 |
| | 2 | 1.82 |
| | 3 | 3.2 |
| 500-250 µm carbonate | 1 | 22.47 |
| | 2 | 12.20 |
| | 3 | 2.73 |
| mineral 250-125 µm | 1 | 2.26 |
| | 2 | 2.47 |
| | 3 | 2.3 |
| 250-125 µm carbonate | 1 | 2.25 |
| | 2 | 3.90 |
| | | 7.00 |
| mineral 125-63 µm | 1 | 0.79 |
| | 2 | 1.68 |
| | 3 | 0.82 |
| 125-63 µm carbonate | 1 | 1.50 |
| | 2 | 1.52 |
| | 3 | 12.35 |

Testing for equal variances between carbonate and mineral particles gives an F statistic = 1975.99 which with 11 df in both denominator and numerator exceeds tabulated values at all
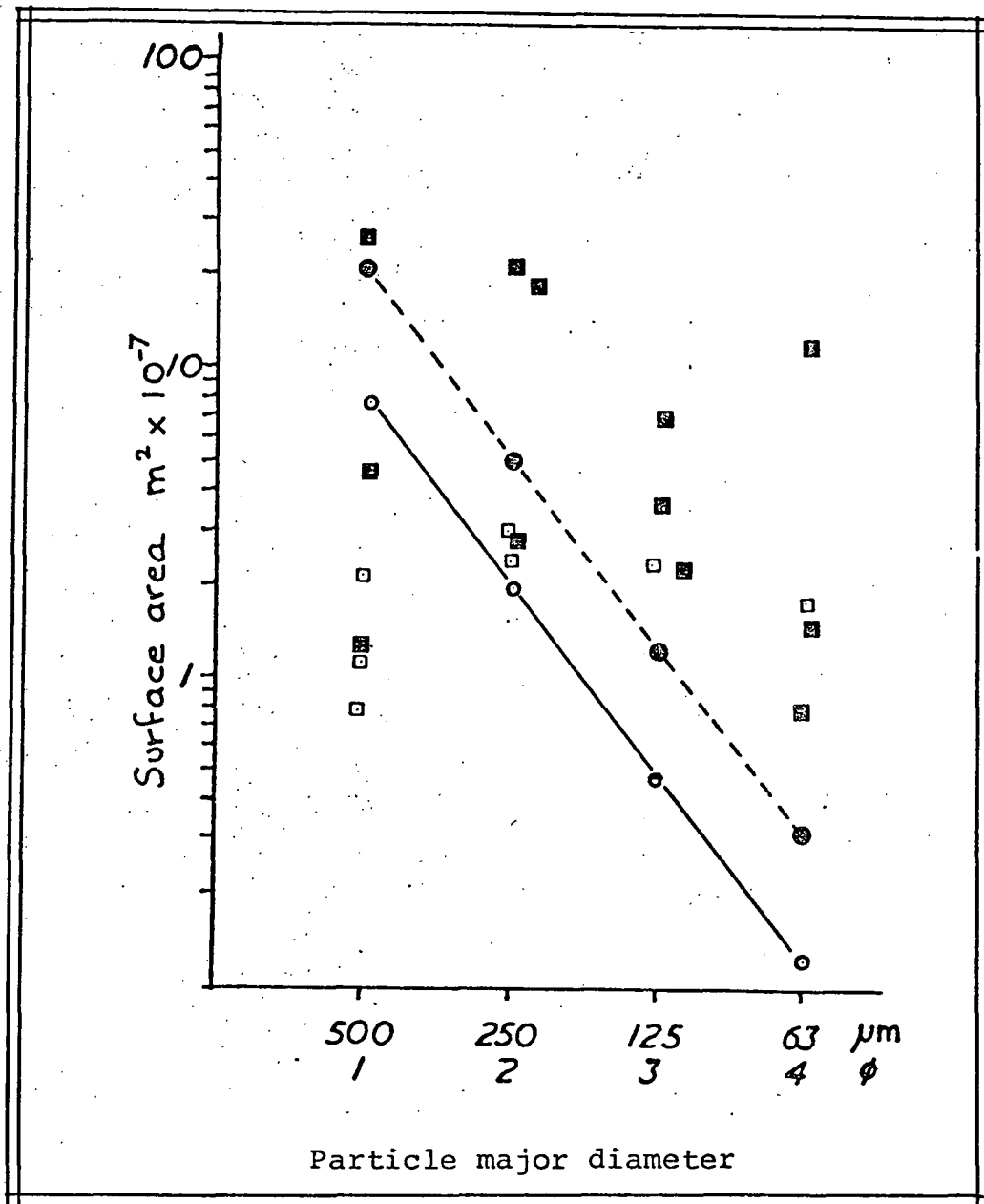
Fig. 35. Calculated surface areas of spheres and cubes and
determined surface areas of four size grades of
mineral and carbonate sand particles from Little
Swanport sands.

levels.    The difference between the surface areas of carbonate

and mineral particles is significant and was confirmed by a

subsequent t-test comparing means, using Bessel's correction

for small samples;    t = 73.8,22 df, ( $>$ 3.792, P $<$ 0.001).

11.5.2    Discussion

It has been demonstrated that biogenic carbonate

particles in sands possessed greater surface areas than mineral

particles.    The next step was to investigate whether such

particles actually carry more organic material that may be

attractive to Cumaceans.

11.6    On the oxygen uptake of sands.

11.6.1    Recitative

It has been shown that carbonate sands are more

attractive to cumaceans than sands without carbonate particles

(section 10.3).    It has been shown that biogenic carbonate

particles possess greater surface areas than non-eroded mineral

particles in sands.

If biogenic carbonates carry more epipsammic organic

material particles such particles probably will (a) prove more

attractive to Cumaceans and/or (b) occupy feeding activities for

longer (see section 11.3).    If the organic surface layers are

composed of heterotrophic bacteria, algae and diatoms the levels

of respiratory rates of carbonate sediments should be higher

than those of mineral sands.    This approach is supported by

the evidence that microorganisms are distributed in patches over

the surfaces of sand grains (Meadows and Anderson, 1966, 1968;

Anderson and Meadows, 1978).    However, detrital particles in

marine sediments may have higher densities of investing micro-

organisms (Fenchel, 1972; Hargrave, 1976).

Meadows and Anderson (1968) have shown also that the microtopography of sand grains plays a large part in the placement of colonies of microorganisms on sand grains. Sand grains which were agitated, simulating the movement of cohesionless sands under stress, were abraded and microorganisms were limited to hollows on the sand grains.

Carbonate particles of biogenic origin have greater surface areas and more varied topography. Echinoderm fragments are primarily reticulate for example. Secondarily increased topography by the action of boring organisms has been observed in molluscan shell fragments by this author. Similar observations were made by Davies (1979) in nearshore sands off the coast of New South Wales. The holes and pits are attributed to the activities of boring algae and sponges. The foraminiferan content of sands may be high in some localities (Kukal, 1971; Murray, 1973). Dead tests and fragments of foraminiferan tests may possess greater surface areas than solid grains and possess a primary complex topography.

To investigate the hypothesis that biogenic carbonate particles carry more respiratory substrate than mineral sand particles the following experiment was conducted.

11.6.2    Materials

Little Swanport sand was sieved into phi-fractions. Each fraction was divided into two parts. One part was treated with dilute HCl until visible reaction ceased. Both parts were

treated with 4% $H_2O_2$ for 24 hrs to remove organic material from the particles. Both parts were washed with distilled water on three occasions over a 24 hour period and then washed a further three times with sea water. All the samples (4 size ranges, with and without carbonates = 8) were placed in jars of sea water, immersed in an aquarium of flowing sea water and left for ten days to develop new organic colonies. Each sample was then divested of two subsamples (total = 8 x 2 = 16) for experimental use.

11.6.3    Method

The apparatus used for this experiment was a Gilson differential respirometer (see Umbreit, Burris and Stauffer, 1972, for method of operation). Rate of oxygen uptake was taken as a measure of the activity of epipsammic organisms in the samples. $CO_2$ produced during respiration was absorbed by an alkali trap (10% KOH). This series of determinations was run in a constant temperature room at $15^{\circ}C$ and the shaking mechanism was adjusted to $c.$ 50 oscillations per minute to reduce abrasion between the experimental particles. Manometer microlitre readings were converted to standard temperature and pressure. The results of the respirometer determinations are shown in Figure 36. Details of the sediments employed are presented in Table XVIII along with determinations of the proportion of organic matter present in each sample. Organic matter was determined by ignition in a muffle furnace at $c.$ $450^{\circ}C$. It should be noted that only twelve of the samples survived the treatment because of a series of experimental errors that will not be divulged here.
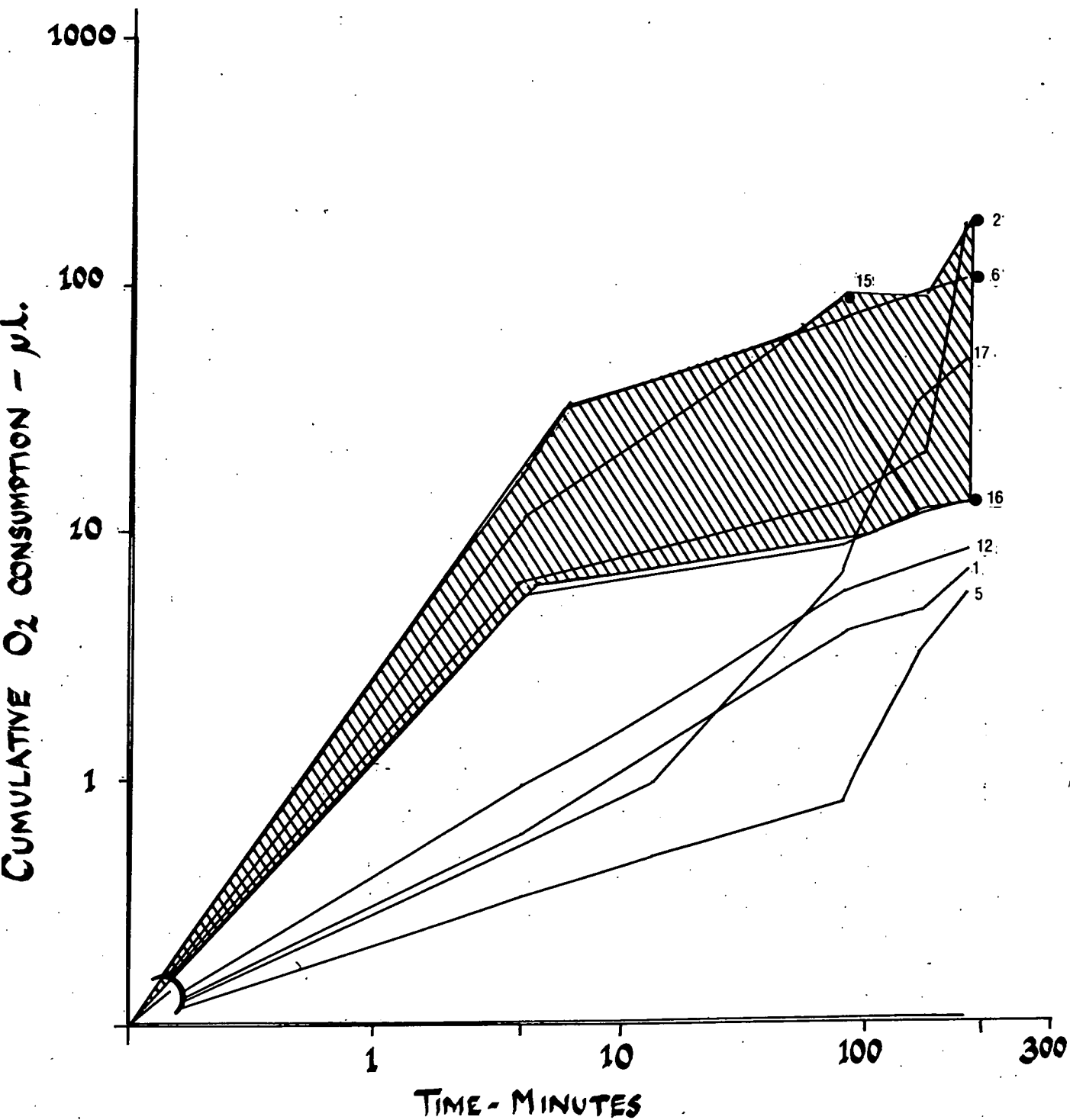
Fig. 36    Cumulative O$_2$ consumption by selected sediments over
a four hour period.    Carbonate sediments are marked (●)
and the area of activity of such sediments is shown on
the overlay.
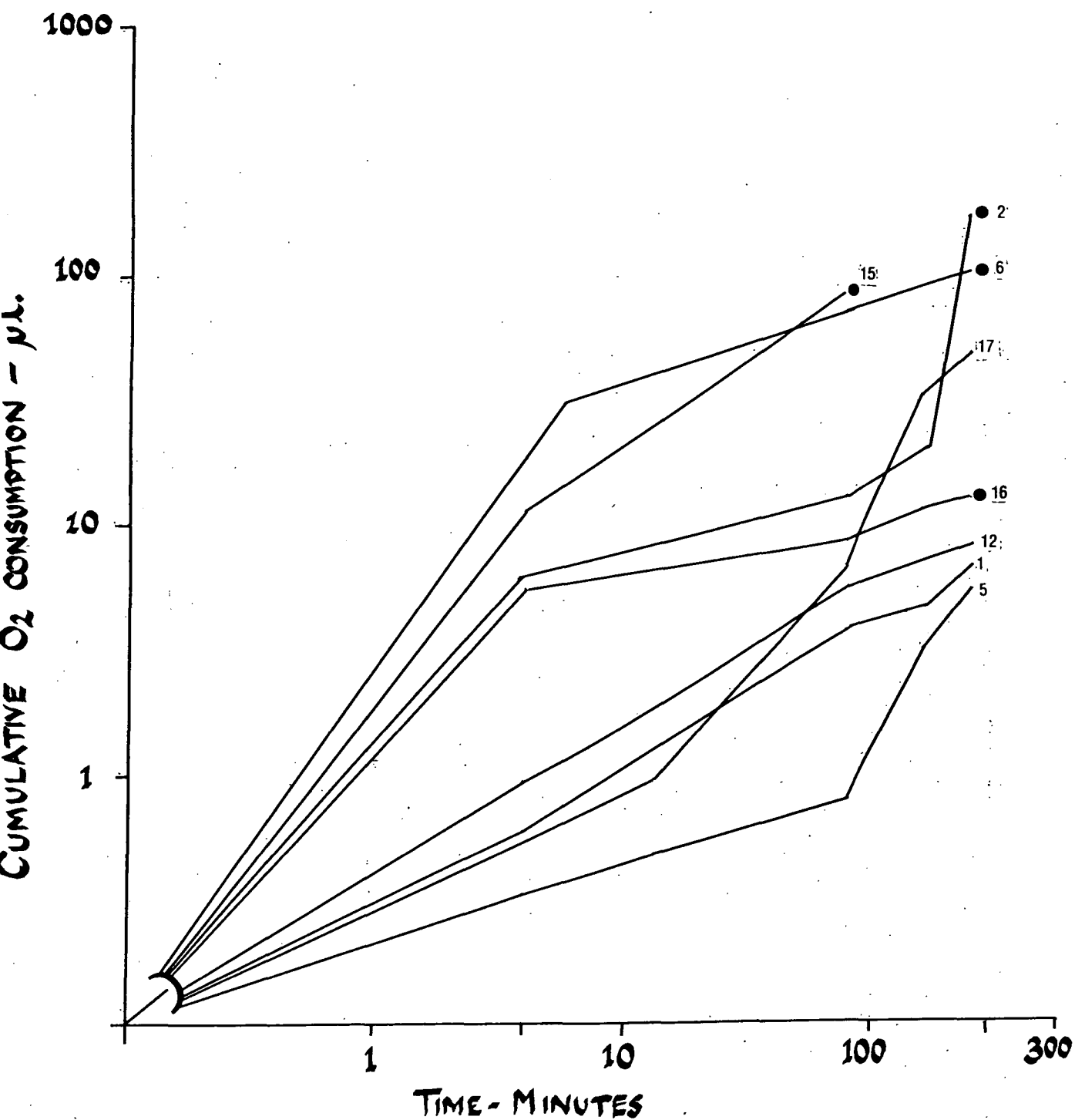
Fig. 36 Cumulative O₂ consumption by selected sediments over
a four hour period. Carbonate sediments are marked (●)
and the area of activity of such sediments is shown on
the overlay.

## TABLE XVIII

Particle samples used for $O_2$ uptake : carbonate content and % organic matter

| | Sample | Air dried weight gms | % carbonate | % organics |
|---|---|---|---|---|
| 1. | 1000-500 μm mineral | 2.72 | 0* | 1.47 |
| 2. | 1000-500 μm + carbonate | 0.60 | 7.2 | 11.66 |
| 3. | 250-125 μm mineral | 0.54 | 0* | 11.0 |
| 5. | 500-250 μm mineral | 1.15 | 0* | 15.6 |
| 6. | 250-125 μm + carbonate | 1.91 | 7.3 | 17.80 |
| 7. | 125-63 μm mineral | 2.32 | 0* | 49.13 |
| 9. | 125-63 μm mineral | 2.36 | 0* | 33.89 |
| 12. | 600-250 μm mineral | 0.85 | 0* | 1.17 |
| 13. | 500-250 μm carbonate | 1.08 | 1.2 | 27.7 |
| 15. | 250-125 μm + carbonate | 0.75 | 22.0 | 53.3 |
| 16. | 1000-500 μm + carbonate | 1.72 | 2.40 | 2.32 |
| 17. | 500-250 μm mineral | 2.62 | 0* | 31.0 |

* Carbonates removed by acid treatment (see section 11.6.2)

11.6.4   Results

Of the twelve samples, oxygen uptake rates were indicated to be higher in samples 6 and 15, both of which were sands with carbonates present.   Sample 15 did not survive to complete the experimental period.   The results are not conclusive but do indicate that carbonate sands may carry more heterotrophic organisms than non-carbonate sands.

When the respirometer experiment was concluded the samples were analysed by drying, weighing, firing and reweighing to gain some estimate of organic content.

11.7   Discussion

It is apparent that much cumacean activity is mediated by the nature of the particles in epistratal habitats.   This worker has not investigated their possible role as filter feeders but has concentrated upon particle manipulations and choice.   This approach may not offer a complete picture. For example, on two occasions cumaceans (an individual of *Leptoouma pulleini* and another of *Dimorphostylis subaculeata*) were observed to remove flocculent material from the boundary layer by reaching upwards into the near water column.   This may be an important method of feeding for inhabitants of high energy irrigated sands.   Alldredge (1979) considers that flocculent aggregates (marine snow) serve as a major source of vertical flux to the benthos.   Such aggregates which may range in size from 1mm to tens of millimetres (Shanks and Trent, 1979) are probably rich food sources because they adsorb nutritionally valuable substances and may maintain internal

populations of marine bacteria which favour eutrophic conditions and are rare in relatively oligotrophic marine waters (Alldredge, 1979).

Observations of floc manipulation may also alter our approach to sediment size specificity on the part of psammophilic cumaceans. Flexible masses, such as marine snow, are often larger than inflexible particles. Manipulation of a flexible mass as large as a solid particle which would be rejected, is easier because of the nature of the floc which only needs abrasive breakdown to make its constituents available. Large solid particles which may be rejected because of their size would be uneconomical to handle because their food value is low. Recent work demonstrates that ampharetid worms can distinguish between particles of different specific gravity (Self and Jumars, 1978). It may be that particulates of economical interest to cumaceans are distinguished by lower densities. The hypothesis is reasonable when one considers relative densities of particulates available to cumaceans (Table XIX).

The use of microbial organic material from sediment particles as a food source for sedimentary feeders is well documented (e.g. Fenchel, 1970; Fenchel and Kofoed, 1976; Anderson and Meadows, 1978). Theory suggests that particle size selection will be found among deposit feeders (Taghon et al., 1978). Such selection has been demonstrated in this work. Given certain constraints more organic epigrowth may be ingested relative to the volume of sediment processed if smaller particles are ingested (Hargrave, 1972; Dale, 1974).

If small particles, say < 63μm, are in short supply as in many high energy sands or are not available to an animal because there are limits to small particle manipulation, any phenomenon which increases the organic content of a particle will be important.

TABLE XIX

Examples of densities of natural sand
particulates and experimental ballotini

| Type of particle | Density g.cm$^{-3}$ | Source |
|---|---|---|
| Glass beads | | |
| Type 1 | 2.99 | Self and Jumars, 1978 |
| Type 2 | 3.99 | |
| Quartz particles | 2.65 | Weast, 1978 |
| Granite | 2.64-2.76 | Walton Smith, 1974 |
| Marine snow | 1.02549 | Alldredge, 1979 |
| Mud pellet | 1.83 | Fisher, Pickral and Odum, 1979 |

Biogenic carbonate particles are suggested here as an efficient source of organic material to the benthos of high energy sands. This occurs because surface area is relatively high per volume of particle. Two other factors may make choice of carbonate particles an efficient one. Carbonates may apparently scavenge organic compounds from sea water (Suess, 1968). Such scavenging may be an active physico-chemical process not just heterotrophic build-up. Carbonate particles of lower

specific gravity than the mineral matrix of their host sands may winnow out selectively under the shear stresses exerted on the sea bed (Miller and Komar, 1977). Such processes may provide locally high carbonate concentrations in benthic sediments with consequent high, available organic content. Such concentration in shallow water seas may provide sites where behaviourally mediated concentrations of mobile, particle-manipulating benthos will occur.

Davies (1974) has suggested that for any given particle size, bottom slope and wave environment, there is a line seawards of which particles tend to move out and landward of which particles will tend to move in. Where, as is usual, a range of particle sizes occurs this mechanism will provide a null point zone. The offshore distrubutions of cumaceans described earlier in this account may be directed in part by the selective winnowing of carbonates either side of the null point zone. Davies (1974) recorded that off St. Helens there is a clear break at c. 20m below which sands become very different and much richer in carbonate.

Winnowing of biogenic carbonates towards the surf zone may explain one food source for *Cyclaspis caprella* which appears to be more numerous in shallow water. The quantitative increase in animals with depth may also be explained either by selective winnowing of carbonates to produce locally high carbonate lenses or by local relative enrichment in areas of low hydrodynamic stress. In the latter case wave energy would dilute the surrounding sand matrix whilst concentrating areas of deposition.

It is clear that an extension of this work into the surf zone and into deeper water would be rewarding to clarify the idea that local carbonate concentrations directed by wave regimes are directly related to the quantitative distribution of deposit feeding benthos.

Self and Jumars (1978) demonstrated that spionid worms may distinguish between particles of different surface texture. One may suggest that such a mechanism may operate among particle manipulating cumaceans. Confirmation that the antennal organ, implicated as a choice site in *Cyclaspis caprella,* has particular sensory functions, awaits a sensory physiologist. Cumacean appendages and other body surfaces are bedecked with structures that may be sensillae. The sensillae of the first pair of walking legs may also be involved in textural discrimination. Cumaceans landing from the water column upon unsuitable substrates (e.g. *Leptocuma pulleini* and *Cyclaspis caprella* upon mud) lower an undercarriage of walking legs to the substrate. Very quick rejection is often observed and similar mechanisms may operate at the level of individual particles.

12.                    CUMACEANS IN THE WATER COLUMN

Introduction

Most cumaceans are inhabitants of the superficial layers of benthic particulate substrates.    It is evident that some species are present in the water column for some of the time (Fage, 1933;  Hale, 1953;  Wieser, 1956).   It is also evident that the sex ratios of cumaceans taken from the water column by various means are skewed in favour of males, whereas samples taken from the substrate are often dominated by females.

The occurrence of vertical migration by planktonic crustaceans is well established (Longhurst, 1967).    It is also documented that inshore marine plankton often includes benthic species which move into the water column (Hobson and Chess, 1976). Colman and Segrove (1955), for example, demonstrated that nocturnal plankton catches in shallow water often contained immigrants from below tide marks.

A number of hypotheses have been suggested to account for vertical movements of benthic animals which include:-
(a)   avoidance of nocturnal predators at the benthic interface
(b)   reproductive strategies
(c)   dispersal strategies.

This part of the project was planned to answer a number of simple questions.
1.   Do benthic cumaceans enter the water column at night?
2.   Are the reported biased sex ratios of samples of Cumacea caught by light trap an artefact of trapping?

12.1     An investigation of cumaceans in the water column.

12.1.1    Methods

Both benthic sands and the water column above the sands at Little Swanport were sampled for cumaceans. Bottom samples were taken by air-lift sampler. The water column was sampled by plankton net hauled at the surface and obliquely from bottom to surface.

Sampling was carried out over two days and two nights. The first night was cloudy with no visible moonlight. The second night was moonlit. Samples from both air-lift sampler and the plankton net were concentrated, labelled and preserved for later examination. On return to the laboratory the samples were sorted. All cumaceans were removed, counted, identified and sexed. Often males and females are intermediate between the juvenile, manca release stage and full adulthood and are difficult to determine. The term "subadult" is used throughout this text.

12.1.2    Results

The raw results are presented in Tables XX-XXII. N.B. No cumaceans were taken in plankton nets during the day. Investigation at Bull Bay, Bruny Island, at a later date showed that no cumaceans were taken from the water column during daylight hours (all samples taken between 1000 and 1400 hours). One worker obtained *Cyclaspis cottoni* Hale in night plankton hauls between Betsey Island and South Arm (J. Palmer, *pers. comm.*). No specimens of that species were detected in underlying benthos by the author.

TABLE XX

Benthic samples : Little Swanport
Numbers of individuals

M = male; F = female;
S = subadult

| Species | "Sex" | Day 1 Sample | | | | Day 2 Sample | | | | Night 1 Sample | | | | Night 2 Sample | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 9 | 10 | 11 | 12 | 5 | 6 | 7 | 8 | 13 | 14 | 15 | 16 |
| *Leptocuma pulleini* | M | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | F | 3 | 18 | 11 | 3 | 8 | 1 | 2 | 0 | 22 | 3 | 0 | 17 | 0 | 12 | 0 | 4 |
| | S | 2 | 6 | 0 | 0 | 0 | 22 | 19 | 0 | 0 | 2 | 12 | 0 | 0 | 42 | 0 | 17 |
| *Cyclaspis caprella* | M | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| | F | 11 | 16 | 3 | 2 | 0 | 23 | 12 | 17 | 3 | 14 | 14 | 1 | 3 | 2 | 7 | 5 |
| | S | 17 | 0 | 0 | 7 | 0 | 0 | 19 | 0 | 0 | 0 | 1 | 20 | 0 | 22 | 0 | 0 |
| *Anchistylis waitei* | M | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | F | 27 | 17 | 9 | 0 | 7 | 3 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| | S | 2 | 12 | 0 | 17 | 13 | 27 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dimorphostylis subaculeata* | M | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | F | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| | S | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 |
| *Dicoides fletti* | M | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 6 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| | F | 0 | 22 | 0 | 0 | 0 | 12 | 0 | 17 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| | S | 17 | 4 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicoides brevidactyla* | M | 7 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| | F | 41 | 0 | 0 | 0 | 0 | 0 | 27 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 3 | 0 |
| | S | 0 | 0 | 2 | 10 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

b.

# TABLE XXI

## Plankton net : Little Swanport
### Surface and oblique hauls.   Numbers of individuals

| Sample | "Sex" | Dark | | | | Moonlit | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Night 1 Surface | | Night 1 Oblique | | Night 2 Surface | | Night 2 Oblique | |
| *Leptocuma pulleini* | M | 2 | 1 | 8 | 4 | 2 | 21 | 0 | 4 |
| | F | 1 | 19 | 118 | 35 | 43 | 62 | 9 | 72 |
| | S | 13 | 7 | 70 | 11 | 53 | 213 | 21 | 18 |
| *Cyclaspis caprella* | M | 1 | 4 | 33 | 5 | 10 | 17 | 0 | 1 |
| | F | 2 | 8 | 328 | 49 | 36 | 30 | 2 | 2 |
| | S | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Anchistylis waitei* | M | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 0 |
| | F | 0 | 0 | 2 | 3 | 1 | 0 | 0 | 0 |
| | S | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dimorphostylis subaculeata* | M | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| | F | 0 | 13 | 5 | 1 | 2 | 8 | 2 | 13 |
| | S | 1 | 0 | 6 | 0 | 2 | 0 | 0 | 2 |
| *Dicoides fletti* | M | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| | S | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicoides brevidactyla* | M | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| | F | 0 | 1 | 5 | 0 | 0 | 0 | 0 | 0 |
| | S | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

M = male;   F = female;   S = subadult

TABLE XXII

Sex ratios of samples of Cumaceans taken from the benthos and the water column.

1 = ratio ♂ : ♀;   2 = ratio ♂ : ♀ and subadults

| Species | | Benthos<br>Days 1 + 2<br>pooled | Benthos<br>Nights 1 + 2<br>pooled | Dark<br>Water column<br>Oblique | Dark<br>Water column<br>Surface | Moonlit<br>Water column<br>Oblique | Moonlit<br>Water column<br>Surface |
|---|---|---|---|---|---|---|---|
| *Leptocuma pulleini* | 1 | 1 : 23 | 1 : 88 | 1 : 12.7 | 1 : 6.6 | 1 : 20.2 | 1 : 4.5 |
|  | 2 | 1 : 47.5 | 1 : 161 | 1 : 19.5 | 1 : 13.3 | 1 : 30 | 1 : 16.1 |
| *Cyclaspis caprella* | 1 | 1 : 9.3 | 1 : 24.5 | 1 : 9.9 | 1 : 2 | 1 : 4 | 1 : 2.4 |
|  | 2 | 1 : 14.1 | 1 : 46 | 1 : 9.9 | - | - | - |
| *Anchistylis waitei* | 1 | 1 : 23.6 | - | 1 : 1.6 | - | - | 2 : 1 |
|  | 2 | 1 : 48 | - | - | - | - | - |
| *Dimorphostylis subaculeata* | 1 | 1 : 5 | 1 : 2 | 1 : 3 | 1 : 6.5 | 1 : 7.5 | 1 : 5 |
|  | 2 | 1 : 6 | 1 : 4 | 1 : 6 | 1 : 7 | 1 : 8.5 | 1 : 7 |
| *Dicoides fletti* | 1 | 1 : 17 | 1 : 2 | 1 : 1 | - | - | - |
|  | 2 | 1 : 24.6 | 1 : 9.5 | - | - | - | - |
| *Dicoides brevidactyla* | 1 | 1 : 5.2 | 1 : 16.5 | - | - | - | - |
|  | 2 | 1 : 6.8 | - | - | - | - | - |

12.1.3 Analysis and commentary

The presence of cumaceans in the water column was proven. The presence of *Dicoides fletti* rests upon a total of four specimens which may have been collected by the net at the start of an oblique haul and *Dicoides brevidactyla* was not captured by plankton net. It is suggested that these species may not have entered the water column.

I must accept that *Anchistylis waitei* enters the water column because it was found at the surface on moonlit night 2. Again small numbers are involved which contrasts markedly with the magnitude of the benthic samples of this species.

Analysis

The raw data for catches of *Leptocuma pulleini* were pooled and arranged in a 6 x 3 contingency table (Table XXIII). The null hypothesis was that the proportions of sexed adults and subadults is the same in each set of samples. The cell values of the contingency table indicate that all classes of *L. pulleini* are more likely to be found at the water surface on moonlit nights. The greatest departures from expected values are shown by females and subadults in the water column on both dark and moonlit nights and at the surface on moonlit nights. It appears from these data that *L. pulleini* does enter the water column, that all groups are more likely to be found at the surface on moonlit nights and that the females and subadults may enter the water column on most nights. It may be that the males preferentially enter the surface layers on moonlit nights.

TABLE XXIII

Total catches of *Leptocuma pulleini* from day and night benthos
and moonlit and dark water column and water surface.    Pooled
data from Tables XX  and XXI

|  | Male | Female | Subadults | Total |
|---|---|---|---|---|
| Dark night surface | 3 (1.86) 0.69 | 20 (19.2) 0.03 | 20 (21.9) 0.16 | 43 |
| Dark night water column | 12 (10.6) 0.18 | 153 (109.9) 16.1 | 81 (125.4) 15.7 | 246 |
| Moonlit surface | 23 (17.1) 2.04 | 105 (176.1) 28.7 | 266 (200.8) 21.2 | 394 |
| Moonlit water column | 4 (5.3) 0.32 | 81 (55.4) 11.8 | 39 (63.2) 9.3 | 124 |
| Day benthos | 2 (4.2) 1.2 | 46 (43.8) 0.1 | 49 (49.4) 0.003 | 97 |
| Night benthos | 1 (0.59) 0.28 | 58 (58.9) 0.014 | 73 (67.3) 0.48 | 132 |
| Total | 45 | 463 | 528 | 1036 |

Numbers in parentheses are expected values.

The lowest figures in each set are the cell values for
$x^2$ analysis.

Total $x^2$ = 108.29 with 10 df (highly significant).

A similar exercise conducted with the data for *Cyclaspis caprella* (Table XXIV) suggests that males of that species enter the water column on both moonlit and dark nights and are more likely not to be present in the water column on moonlit nights.

I do not wish to subject these data to further analysis because they only represent a few samples from one period of 48 hours. It must remain for another worker to investigate the phenomenon of nocturnal migration of cumaceans from the benthos and to investigate whether seasonal variations occur.

*Leptocuma pulleini* was sampled from a population where females exceed males by at least 23 : 1. The proportion of males in the water column was greater rising to *c*.18% of the sample of that species on the moonlit night.

*Cyclaspis caprella* again showed a predominance of females in the benthos but the proportion of males increased to about 30% on both nights. Female dominance in the benthos with lesser dominance in the water column is exhibited by the other species. Although the observation is based on three specimens only it is interesting to note that *Anchistylis waitei* was the only species where males dominated the population, *sic volo sic jubeo*!

Subadults of two species also enter the water column. The presence of subadult *Cyclaspis caprella* is

TABLE XXIV

Total catches of *Cyclaspis caprella* from day and night benthos
and moonlit and dark water column and water surface.    Pooled

data from Tables   XX and XXI

|                           | Male   | Female   | Subadults | Total |
|---------------------------|--------|----------|-----------|-------|
| Dark night<br>surface     | 5<br>(1.4)<br>9.26 | 10<br>(11.8)<br>0.27 | 0<br>(1.8)<br>1.8 | 15 |
| Dark night<br>water column | 38<br>(39)<br>0.026 | 377<br>(328.9)<br>7.03 | 2<br>(49.1)<br>45.2 | 417 |
| Moonlit<br>surface        | 17<br>(7.8)<br>10.9 | 66<br>(65.5)<br>0.004 | 0<br>(9.8)<br>9.8 | 83 |
| Moonlit<br>water column   | 1<br>(0.5)<br>0.5 | 4<br>(3.9)<br>0.0026 | 0<br>(0.6)<br>0.6 | 5 |
| Day<br>benthos            | 9<br>(12.7)<br>1.1 | 84<br>(107.3)<br>5.06 | 43<br>(16)<br>45.6 | 136 |
| Night<br>benthos          | 2<br>(8.8)<br>5.3 | 49<br>(74.1)<br>8.5 | 43<br>(11.1)<br>91.7 | 94 |
| Total                     | 70 | 590 | 88 | 748 |

Numbers in parentheses are expected values.

The lowest figures in each set are the cell values for
$x^2$ analysis.

Total $x^2$ = 242.7 with 10 df $>$ 23.21 ($p \leq 0.01$).

Therefore association is highly significant.

Therefore hypothesis of no association is rejected.

recorded from an oblique haul and reservations about such records were recorded earlier in this account.

12.1.4    Discussion

Cumaceans may enter the water column for the reasons following:

1.   Avoidance of nocturnal benthic predators.

2.   As a dispersal mechanism allowing exploitation of areas beyond the range of daily swimming.

3.   For reproductive purposes.

This latter purpose may be achieved in two ways:

a.   Males may enter the water column as a reproductive dispersal strategy. This might be appropriate when population sex ratios are biased towards females. Nocturnal redispersal may be an economical method of spreading male favours.

b.   Males may enter the water column to await females who are prepared to mate. Concentration of males at the sea surface cannot be greater than at the benthic interface. The important mechanism may be that only prepared females enter this dimension of the cumacean realm. Such a mechanism may also explain the presence of juveniles (subadults) in the surface layers.

A combination of reasons 2 and 3 may provide a more realistic hypothesis. If males enter the water column and are then redispersed by waves and currents mating may take place

at the new location. If males, precopulatory females and subadults mate in the water column dispersion of fertilised females would ensure successful colonisation of any empty area. Further work is required on this aspect of cumacean biology.

13.                           CONCLUSIONS

    This project was planned as, or, more honestly,
grew into, an investigation into mechanisms which limit the
distributions of psammophilic Cumacea.

    It has been demonstrated:-

13.1

    I.    That the cumaceans studied are unwilling to
    cross boundaries between water bodies differing
    in salinity at a scale of $1^{o}/oo$.
    II.   That most of the cumacean species studied
    from shallow water offshore sands exhibited
    contagious distributions at the scale of sampling
    employed.
    III.  That distributions apparently related to
    the depth of water over the substrate are, in
    fact, related to the presence of biogenic carbonate
    fragments which are selectively winnowed from
    offshore sands by water action and then redeposited
    in concentrated patches on the sea bed.
    IV.   That cumaceans feed by cleaning organic
    matter off particles employing a mechanism which
    is two stage; involving, firstly, selection,
    examination and choice, followed by particle
    manipulation.
    V.    That cumaceans concentrate in carbonate
    sands by a behavioural mechanism mediated by
    the two stage feeding process.

VI.   That particle-handling Cumacea may modify the permeability of interface sands by their feeding activities.

VII.   That some cumaceans, at least, enter the water column at night and that the proportions of males, females and subadults vary between the benthos, the water column and the surface.   Also that the distributions of cumaceans in the water column vary on dark and moonlit nights.

I also conclude (the evidence is presented in Appendix III):-

VIII. That hydrodynamic shear stresses at the benthic interface affect the stability of non-cohesive sands before they affect the cumaceans living in the sand.

IX.   That cumaceans are sensitive to water velocities and, by a behavioural mechanism, increase their effective densities when a critical velocity is reached which enables them to drop out of the water column under stressed conditions.

My conclusions support the concept of multiple limiting factors introduced by Wildish (1977).   However, I would modify that author's insistence upon water speed as a limiting factor for benthic animals.   Limiting shear stresses are more realistic expressions of the dynamics of moving water upon substrates whether they be animal surfaces or sediment-water interfaces.

I reject the concept of microenvironments raised by Anderson and Meadows (1978). It is no other than an expression of axes of multidimensional niches and does not aid investigation.

13.2    Discussion

The observed correspondence between cumacean distributions and concentrations of biogenic carbonates supports the concept that major wave climates and faunal distributions correspond. The carbonate concentrations demonstrated are a function of hydrodynamic forces dictated by wind-wave regimes. The cumaceans studied during this project are geographically limited by water body limits; by the effect of hydrodynamic sorting upon an heterogeneous substrate and by feeding behaviour which causes the animals to congregate in areas of sediment created by such sorting. Cumaceans may employ the water column for dispersal of precopulatory females and subadult females but are able to maintain their commitment to a given habitat by removing themselves from the water column if critical water velocities are attained. These considerations add up to a mechanism that maintains habitat, allows dispersal within it and limits geographic range.

King's (1972) comment with regard to the bio-geography of marine algae in S.E. Australia, that their distribution

> "is best explained as a biotic continuum with cooler water affinities becoming more evident in S. Tasmania",

is not supported.   The presence of northern and southern
species of cumaceans which are distributed differentially
along the Tasmanian east coast does not demonstrate a
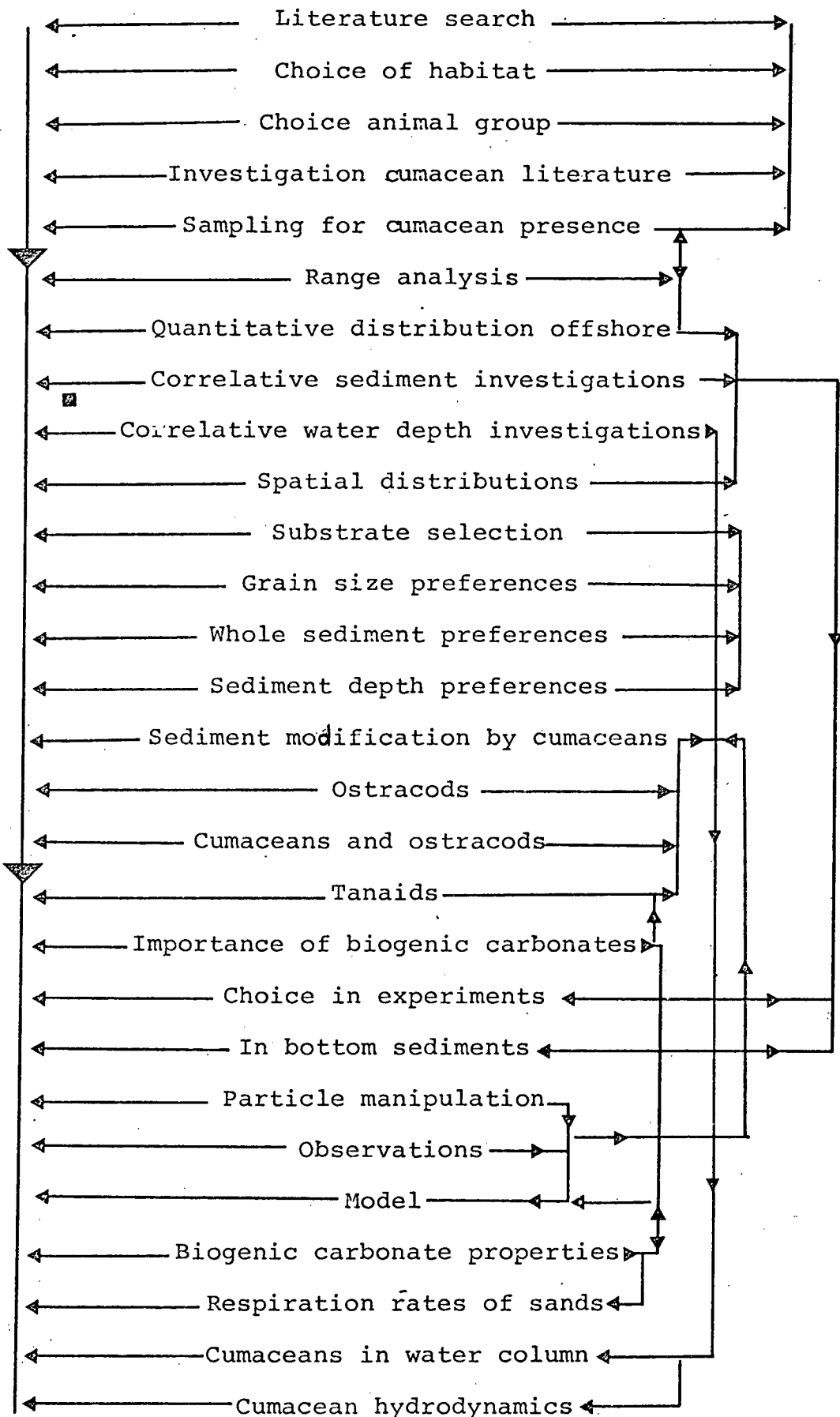continuum but the meeting of two biotic regimes.

Also the assortment of species of psammophilic
Cumacea found at successive localities along the Tasmanian
east coast is not a continuum.   The numbers of species and
genera become less as one travels southwards but measures of
distinctiveness between localities demonstrate discontinuities
north of Maria Island and south of the Tasman Peninsula.
I consider that the northern discontinuity reflects the
variable penetration southward of northern water during the
year.   The southern, Tasman, discontinuity is more extensive
and matches the wave energy regimes offered by Davies (1978).

If this supposition is correct the discontinuities
in the distribution of littoral flora attributed by King (1972)
to breaks in the littoral habitat may, in fact, reflect
wave climates.   The adage that the land adapts to the sea,
not the sea to the land, may explain the mechanical breaks
in habitat continuity.

# INVESTIGATIVE FLOW DIAGRAM

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APPENDIX I

THE T.F.T. AIR-LIFT SAMPLER

# THE T.F.T. AIR-LIFT SAMPLER

## 1.    Summary

This essay contains an account of the choice, construction and use of an air-lift sampler for sublittoral benthic fauna. Some comments are given on possible development of this kind of sampler.

## 2.    Contents

## 3.    Introduction

The design of ship-borne samplers is dictated primarily by the kind of boat available.  Early in this project benthic samples were taken using a chain-rigged van Veen grab slung over a stern gallows and hauled by an hydraulic winch.

This method of sampling was inappropriate during later cruises because the boat available was not equipped with a winch to haul a heavy grab nor robust enough to withstand the impacts which are inevitable when landing such a grab in choppy weather.

A colleague was using an air-lift sampler with some success to sample the benthos of a freshwater river (Norris, 1979).  Air-lift samplers use air under pressure to lift substratum and animals from the bottom into a collecting net or filter.  The design available was based on that of Pearson *et al.*(1973)

with some modifications for use on irregular rocky bottoms.

It was decided to investigate the use of an air-lift sampler to obtain samples of the fauna of shallow water marine sands. Preliminary trails with Norris' machine were successful and a version was constructed for marine use.

The design constraints were:-

a) The sampler should be light enough to haul by hand and to bring aboard without damage to vessel and personnel.

b) The sampler should sample an adequate area.

c) The sampler should be stable when on the sea bed.

d) The mechanism should be simple and constructed from available materials.

e) The machine should sieve efficiently.

f) A diver should not be needed to operate the sampler.

Delle Croce and Chiarabini (1971) used an air-lift pipe to sample mid-water and bottom organisms which were collected in a net. The total length of lift pipe was 8.5m and the apparatus weighed 160kg. Such a device was too heavy for small boat operation and the sampling depth was limited. Mackey (1972) used an air-lift to transport sediment and other material up a pipe 3m long to a net bag above water. Pearson *et al.* (1973) air-lifted samples from a square aluminium hood to a net filter at the U-shaped apex of the lift tube. Both of those machines operate in limited depths (0.2-4.0m) but the limitations are imposed by the method of operation not the efficacy of the air-lift machine.

Emig (1977) published an account of an air-lift sampler similar to the one described hereafter. The lift pipe of the *"aspirateur sous-marins"* was connected to the work boat and sieving and processing of samples was carried out at the surface.

The sampler weighs about 15kg.  Another advantage is that it
is possible to acquire all the material removed from the bottom
by the sampler.

4.   The T.F.T. sampler

The sampler developed for use in this work uses an air-lift
mechanism and is constructed of easily available components.
The code initials of its designation are an affectionate
vernacular.

The T.F.T. (see sectional drawings for details, Figs. 11,
12) consists of a sampling hood, a lift tube, a filter head
and a set of air jets.

The sampling hood is a recycled industrial lampshade of
370mm diameter which is made of mild steel and is stove enamelled.
An early version used an alloy lampshade which soon became
fatigued and cracked.

The hood is joined to a length of plastic drain pipe (700 mm
long x 60mm diameter) which is connected at its upper end to
the angled face of a plastic sewer reduction junction (150 > 50mm)
which forms the filter head.  The open top of the filter head
is covered with nylon neeting (500$\mu$m mesh) protected by bronze
mesh (nominally 1.0mm).  The filter meshes are retained by a
ring of plastic pipe split on one side and clamped by attaching
the ends of a divided worm drive hose clip to the cut ends of
the pipe section.  Four ports (c. 60mm diameter) were cut in
the sides of the filter head and covered with mesh held in
place by retaining rings cut from scraps of plastic pipe of
appropriate curvature.  The side ports were  included to
release pressure if the filter top became clogged.

The nose of the filter head of the T.F.T. was constructed

to hold a polythene bag to retain the sample. However, the bags available could not withstand the weight of the sample and the water in the filter head. A screw cap modified from the ring of a domestic U-bend junction was added to the nose and the sample retained in the filter head thereafter.

T.F.T. was weighted to reduce its buoyancy and lower the centre of gravity of the machine. Concentric lengths of mild steel pipe which were a sliding fit over the lift tube and each other were placed at the junction of hood and lift tube. Some trial and error tests were needed to find an appropriate weight, but T.F.T. weighed 8kg at maturity.

The air jets are lengths of copper tubing (30mm x 4mm I.D.) brazed to a ring of copper tubing (10mm I.D.) which is strengthened by a cross strut of the same tubing. The arrangement of jets and the position of the jets in relation to the hood is shown in Figs. 11 and 1 2. A further length of 10mm I.D. tube leads from the jet ring, through the hood and terminates in a pressure hose connector. The junction between hood and pipe is closed with a rubber grommet and the air pipe is clamped beside the lift tube by a worm drive hose clip surrounding both.

Plate 11 shows the T.F.T., its compressor and pressure hose.

5.　Submarine action of the T.F.T.

In operation 100m of pressure hose is connected between the T.F.T. and a hookah compressor on the boat deck. The hose is lashed to the handle which projects above the filter head. This ensures the security of the sampler and that T.F.T. approaches the bottom suspended beneath the hose. When sampler, hose and compressor are linked and the compressor is running
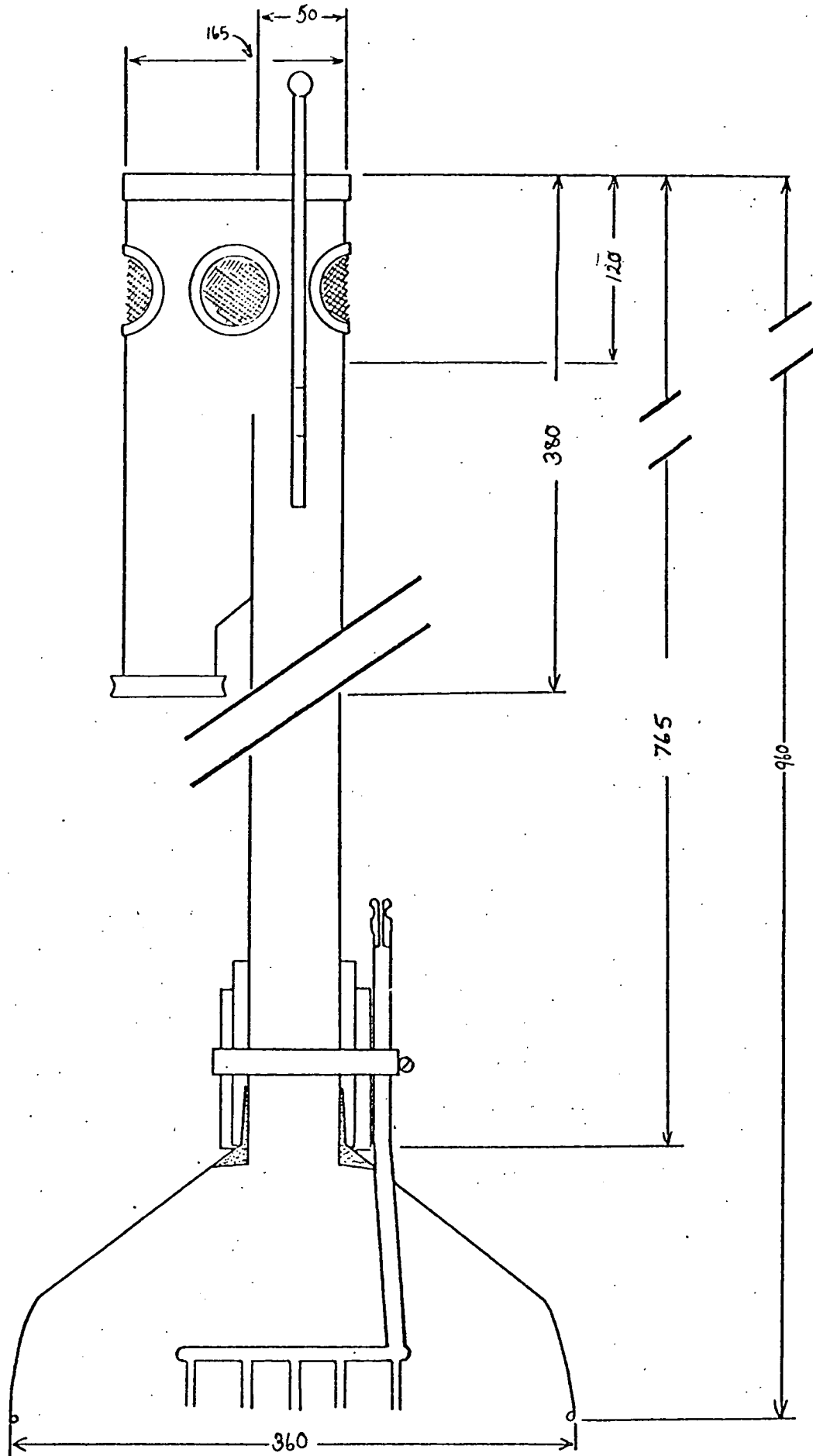
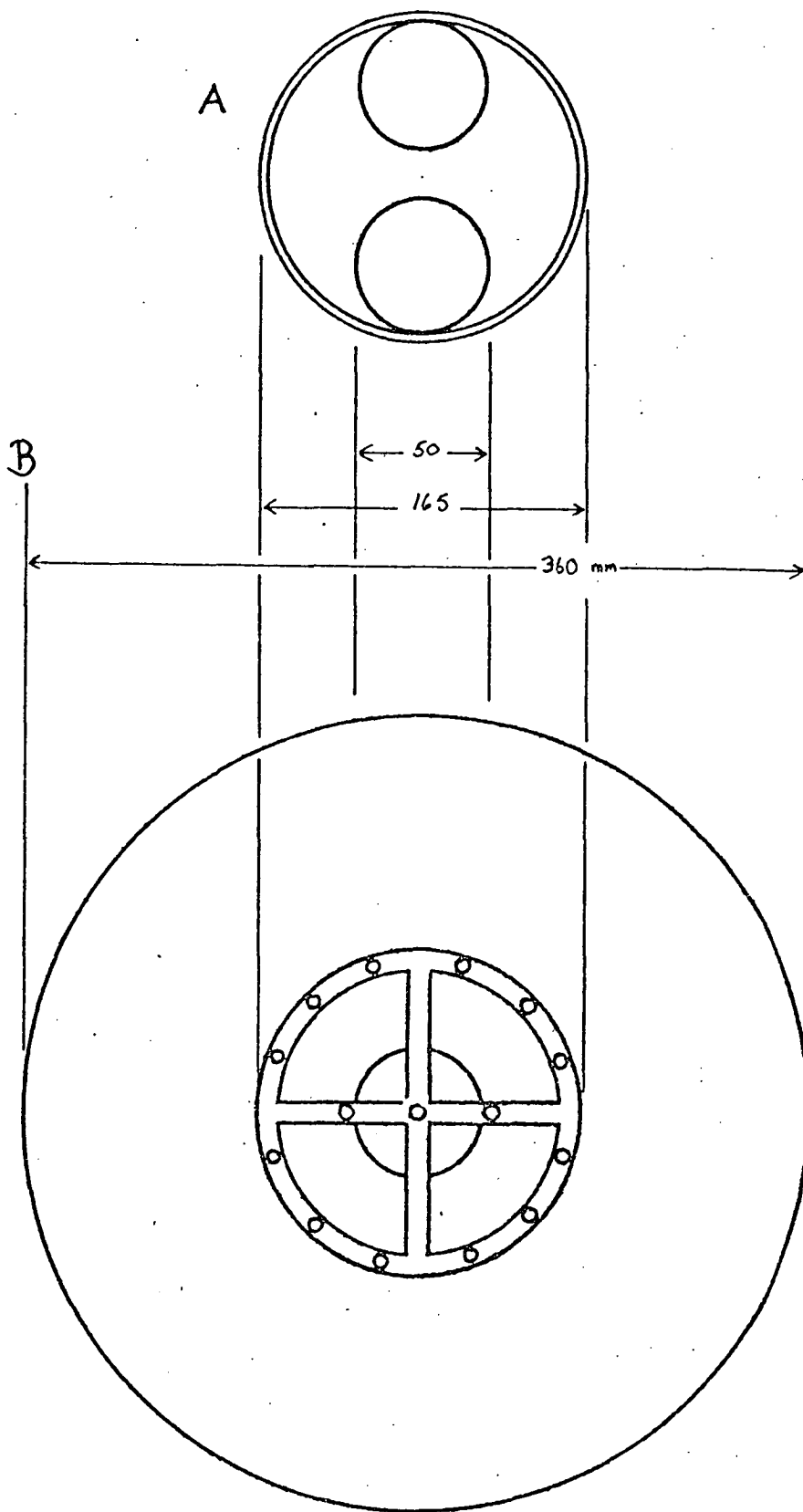Fig 11.   Air lift sampler, sectional diagram side view.

Fig. 12. Air lift sampler, sectional drawing. Horizontal sections (a) through filter head, (b) through sampling hood.
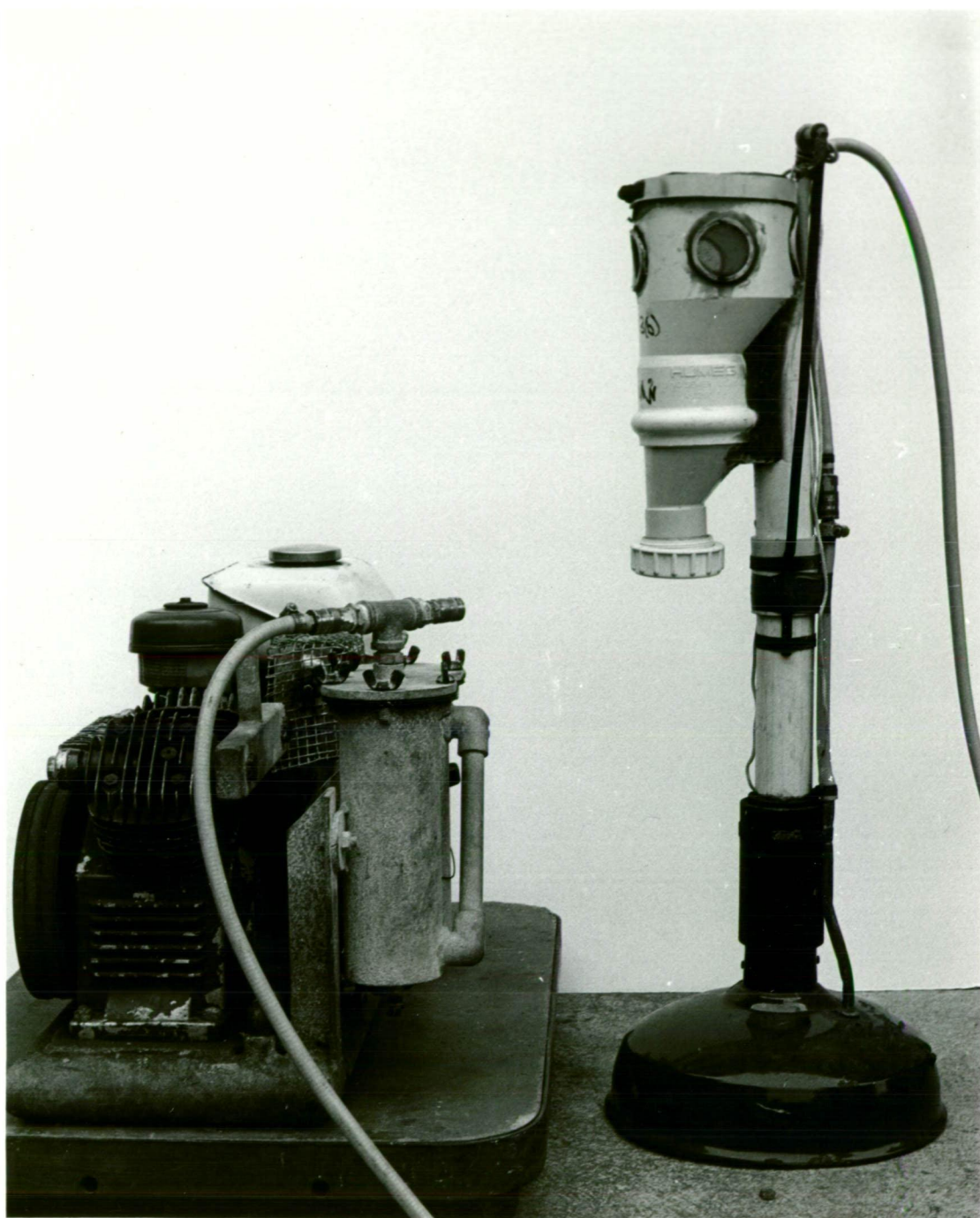
Plate 11.   T.F.T. sampler, compressor and pressure hose

Plate 12.   T.F.T. sampler at sand-water interface

T.F.T. is lowered overboard and the air hose is paid out
until the sampler reaches bottom.  Extra hose is then paid
out to maintain the hydrostatic lift of the air filled hose
above the sampler.  A taut hose may pull the sampler over in
spite of its Kelly-like behaviour.  In operation the filter
head is full of air and T.F.T. has been observed to regain
the vertical from a list of approximately 45$^{\circ}$. When the
sampling period is complete T.F.T. is hauled to the surface
using the pressure hose as a cable.

Two points should be made here.

1.  An air hose used in this manner should never be
used for diving operations and should be appropriately
and clearly marked to distinguish it from diving hoses.

2.  T.F.T. must be hauled to the surface with the
compressor running.  This stops loss of mobile fauna
back down the lift tube and retains the sample if the
machine tips over during ascent.

Diver observation, for which I am indebted to Mr. R.B. Mawbey,
and observation in clear shallow water, has shown that an air-
lift sampler such as T.F.T. is stable on the bottom.  The
length of lift tube is not important to the action of the air-
lift but a long tube increases the leverage exerted by the
filter head if the sampler tips over.

In operation the sampler stands on the open hood which
descends into the substrate as sampling proceeds (see Plate 12).
In sands of Md $\phi$ + 2 T.F.T. descends approximately 100mm into
the substrate in 2 minutes. The volume sampled probably is not
that of a cylinder with vertical walls.  Water is drawn into
the sampler around the edges of the hood and the volume sampled
includes the edges of the substrate surrounding the hood.

This is shown in Plate 12. The reader should also note that a mound of sediment appears in the centre of the sample area. The air jets carried on the cross pieces of the jet ring were included to stir and suspended sediment from the centre of the sample area. It is not clear whether the sediment mound is unsampled volume from the centre or a contribution from the edges of the sample. As early observations indicated that the upper 10mm of sediment were entirely removed from the sampling area the characteristics of deeper sampling were not investigated further. It is apparent, however, that the parameters of deeper sampling change throughout penetration.

6. On board sample treatment

On deck the material sampled was washed from the nose of the filter into a standard soil sieve of $250\mu$m mesh. The sieve was then capped with a wide mouthed plastic funnel modified at its narrow end to receive a specimen tube. Sieve and funnel were then inverted and the sample washed into the specimen tube. Excess water was drained through a filter of $100\mu$m in the neck of the funnel. The filter apparatus and on-deck sequence of operations are illustrated in Fig. 13.

Samples were labelled on board using pre-prepared metal labels stamped with numbers. Throughout the project such labels were used only once and were not returned to the field kit. The contents of the specimen tubes were preserved by addition of 40% formaldehyde to attain a final concentration of 4% formalin.

7. Efficiency of T.F.T. sampler

Sampling efficiency is a loose term which encompasses the functional aspects of a sampler's performance as well as its ability to capture and retain fauna in numbers and proportions
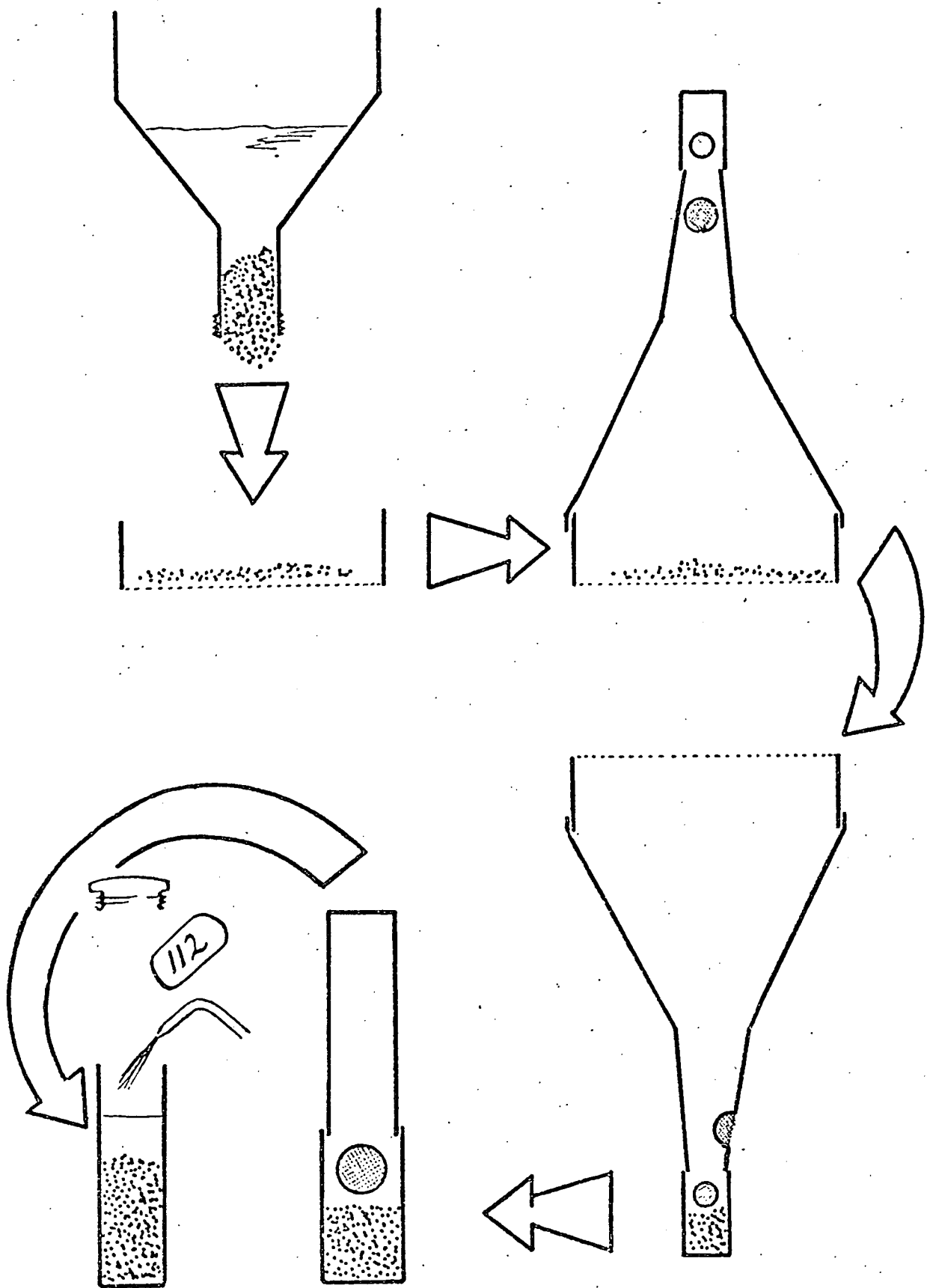
Fig. 1 3. Filtration and concentration sequence for
air lift samples

that reflect the true situation at the sea bed.  Further
comments may be found in Holme and McIntyre (1971).

The first requirement of a benthic sampler is that it
reach the bottom oriented to perform its task. T.F.T. has
operated well in this respect and has only reached the sea
bed on its side on seven of 228 drops (*c*. 3%).  The seventh
failure was caused by an un-nautical lashing releasing the
air hose from the sampler handle.

It is appropriate to mention here that most single samples
were taken from an unanchored vessel.  Using a standard sampling
time of 2 minutes, working to a depth of 20m, and dropping
the sampler upwind of the vessel, it was possible to complete
a sample before the air hose was paid out completely.

Samples at greater depths were taken using extra lengths
of hose.

One of the constraints attending dropped grabs is that
the "bow" wave preceding their arrival at bottom disturbs both
surface layers and mobile fauna.  T.F.T. disturbs the entire
sample and if sedimentary or structural characteristics are
important it is an inappropriate sampler.  However, T.F.T.
is operating before it reaches bottom and appears an appropriate
tool to sample the fauna of marine, high energy sand
interfaces.  Such fauna may be very mobile and escape a
descending bow-wave.

Efficiency of capture may be defined as the ratio of the
numbers of animals collected to the numbers present *in situ*.
In this project the animals of interest are interface nestlers
(see Chapter 8).  It was suggested that a van Veen grab would
not sample this fauna as efficiently as an air-lift sampler
grab. The figures comparing the numbers of individuals and

species of cumaceans taken by these two machines are given
in Appendix Table I.

APPENDIX TABLE I

|  | No. of Species | Total Specimens | No. of Samples | Specimens: Sample | Sample: Species |
|---|---|---|---|---|---|
| van Veen grab | 8 | 393 | 32 | 12.3:1 | 4 :1 |
| T.F.T. | 11 | 1114 | 120 | 9.28:1 | 10.9:1 |
| Totals | 19 | 1507 | 152 | 9.9:1 | 13.8:1 |

It can be seen that the T.F.T. catches more species of
cumaceans but used more samples to acquire them, and that the
van Veen grab acquired more specimens per sample. However, the
data are not strictly comparable because the samples were taken
on different occasions. The T.F.T. data are a meld of one Swanport
grid series, the van Veen samples are from 5 localities on 3
separate days.

Air-lift samplers are not efficient samplers of attached
infauna such as tubicolous polychaetes (see Plate 12.) and fast
burrowing infauna which may leave the area before lower levels of
the sediment are sampled. Such observations suggest that grabs
are more efficient samplers of whole in-benthos whilst air-lift
samplers are better samplers of mobile, interface fauna.

Air-lift samplers have advantages over other apparatus. Light
in weight and with no submarine moving parts they are useful
for small boat operation. All the ship-board and sampling
activities are sequential and the apparatus may be operated by
one man. Air-lift samplers are useful for qualitative collecting
because the specimens are obtained in good condition, and with

some appreciation of their mode of action, such samplers may be used on most substrates.

A bibliography of air-lift samplers may be found in Elliott and Tuller (1978).

8. Further development

Further development of air-lift samplers is possible. Emig (1977) surrounded the hood of his machine with a cylinder which restructed the sampling area and constructed vents in the hood surface to counter-balance the suction effect. I take this to mean that Emig's "*aspirateur sous-marins*" only sampled surface-living benthic fauna.

A number of diver operated air-lift samplers have been used. Barnett and Hardy (1967) used air-lift to remove material from a sampling cylinder pushed into sand and a similar machine, which included a self-contained air supply, was employed by Keegan and Könnecker (1973). A Barnett and Hardy-type sampler was used by Hiscock and Hoare (1973) to remove the contents of benthic quadrats.

Most diver-operated samplers are used as vacuum cleaners for an area or volume defined by a quadrat frame or sampling tube. Apart from those examples mentioned above, Zoutendyk (1971) used a diver-operated air-lift pump to sample infratidal rock communities and this sampler was modified by Christie and Allen (1972) for use on soft substrates. Apart from T.F.T. and Emig's machine the only other sampler which enclosed its sampling area is the "Gismo" of Kritzler *et al*. (1974) which samples an area of $0.063m^2$ but whose sample contents are sieved on board and which requires at least a diver and boatman during operation.

A possible development is to mount an air-lift sampler on a towed sled capturing the sample between strips of filter cloth as plankton is held in a continuous plankton recorder (Hardy, 1956). The longitudinal dimensions of faunal distributions along a towed transect would be recoverable from such a continuous filter record even though the spatial organisation within each sampling unit would be destroyed by filtration.

## 9. Discussion

In this project diver involvement was not possible and also is inefficient when speedy samples are required. T.F.T. has now been worked down to 30m from a small boat in a range of conditions. Its advantages include its low weight, lack of moving submarine parts, ease of construction and quality of specimens obtained. Its disadvantages include the fact that all its sampling is a function of sediment structure, faunal mobility and time. Thus it is difficult to compare infaunal samples from different substrates. Also the structure of the benthic sample is not preserved for examination.

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APPENDIX II


CONSTRUCTION AND USE OF A SIMPLE FALLING HEAD PERMEAMETER

# CONSTRUCTION AND USE OF A SIMPLE FALLING HEAD PERMEAMETER

## 1. Summary

This account describes the modification of a falling head permeameter for experimental use.

## 2. Contents

3. Construction

4. Comments

5. References

## 3. Construction

A simple falling head permeameter was constructed from acrylic tubing after the design of Webb (1969). The dimensions and form of the apparatus are shown in appendix figure 1. The version used during this work (particularly that described in section 9) differs from Webb's apparatus in two ways.

1. The rubber bung closing the top of the lower limb of the permeameter was bored to hold a glass stopcock which made is easier to fill the apparatus with water without trapping air bubbles or disturbing the sediment sample.

2. The lower end of the lower limb of the apparatus was strengthened with a projecting plastic ring which was an interference fit for short extension tubes. Stainless steel mesh was glued across the lower end of each extension tube (Figure 11.1.). This adapter allowed experimental substrates to be transferred to the permeameter without disturbing their structure (see 9.2 *et seq.*). By adding a perforated cap to the upper end of the adapter tube samples plus fauna could be maintained as "microenvironments" in the aquaria of a recirculating seawater system.

10mm
50mm

extension tube

mesh
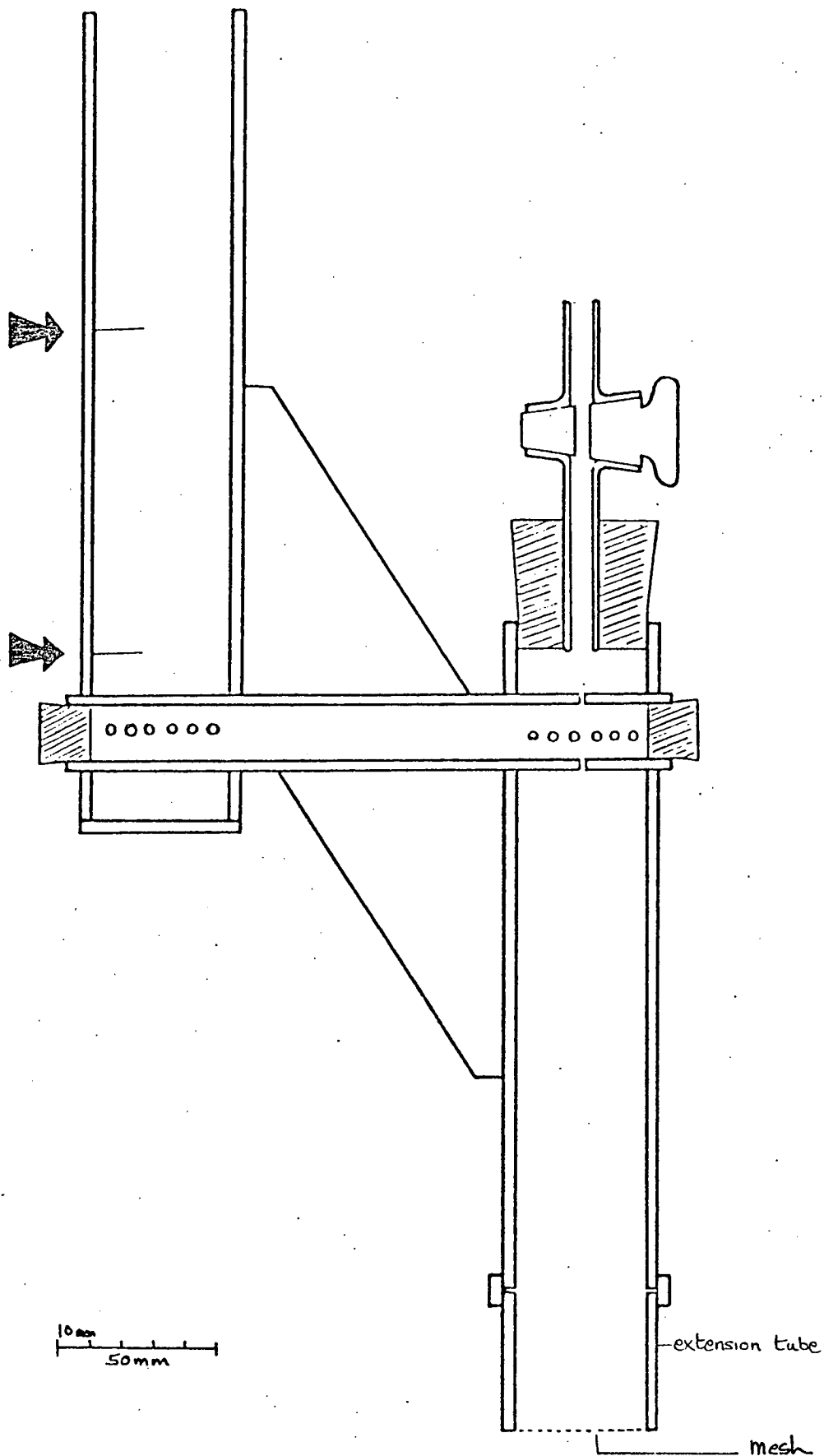
Fig 111.  Permeameter, sectional diagram side view

4.   Comments

The technique of operation and details of calculation of drainage factor and porosity are provided by Webb (1969). Another approach and another technique are given by Buchanan (1971). It is well to record here that reproducible results depend on reproducible operator technique and that test runs should be repeated until consistent results are obtained.

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# APPENDIX III

## SIMPLE TECHNIQUES FOR INVESTIGATION OF FLOW AND HYDRODYNAMIC FORCES

Much of this work was carried out in cooperation with Mrs. J. Smith who is also co-author of the paper submitted as Appendix Iv.

CONTENTS

## 1. Introduction

Benthic animal distributions are governed by a complex of interactive physical and biotic factors. In the search for integrative expressions of animal diversity workers have used mathematical concepts of distribution and information theory (for references see Clifford and Stephenson, 1975 and Pielou, 1969). A number of workers have criticised the use of such concepts as diversity, succession and stability-time relationships (see Abele and Walters, 1979,; Hurlbert, 1971; Peters, 1976).

In reaction many workers have retreated to the basic biology of the experimental scientist from which synthetic theory is built on blocks of experimental evidence. One result of this approach has been the theory of multiple limiting factors enunciated by Wildish (1977). The theory states that:-

"Sublittoral macrofaunal community composition, biomass and productivity are controlled by multiple interactive physical and biotic factors."

Among the major physical factors are salinity, temperature, oxygen availability, sediments, water-sediment exchange phenomena and water speed. It is with the latter that we are concerned here.

## 2. Basic fluid mechanics

Whenever a fluid impinges upon a surface of different characteristics an interaction occurs.

The time period of such interaction in shallow seas ranges from 12 hours (approximate duration of tidal cycles) to shorter events in the order of seconds (oscillating ripple flows and shear stress bursts) and to longer events such as wind induced wave action and climatic adjustments of water bodies.
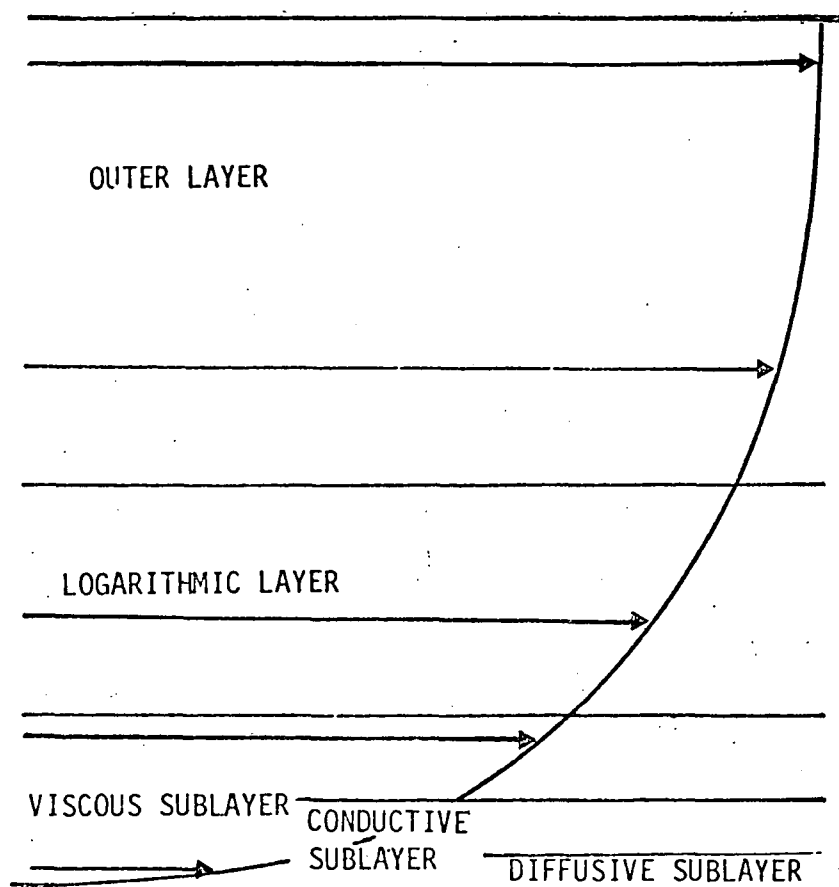
OUTER LAYER

LOGARITHMIC LAYER

VISCOUS SUBLAYER
CONDUCTIVE SUBLAYER
DIFFUSIVE SUBLAYER

Fig. 111. Velocity profile at the benthic interface

Most sea water is in motion. The movement is induced by lunar gravity forces, winds and density differences between and within bodies of water. Water movement around the globe is mediated by Corioli's effects and the presence of land masses in the current streams. Moving water influences the substrate and the substrate the water above it. Assuming an impermeable, flat, smooth sea bed overlain by moving water, frictional forces at the interface will negate velocity. The effect of the sea bed becomes less marked as the distance above the interface increases. The relationship between velocity and distance above the interface is not linear and the velocity profile is of logarithmic form (see Appendix Figure 1, modified after Wimbush, 1976).

In theory and under some controlled experimental conditions, the flow of water above an interface will initially show laminar characteristics. Laminar flows possess streamlines which are linear, remain discrete and do not diverge to mix with neighbouring parallel streamlines. Laminar regimes are simple to comprehend and measure and in many experimental situations one attempts to produce laminar conditions for that reason.

In the imperfect real world laminar flow rarely exists and given time and distance most flows develop turbulence. Turbulent conditions are characterised by random fluctuations of velocity (i.e. speed and direction) even though a mean velocity may be measurable.

The theory of flow phenomena is treated exhaustively in many texts. The reader is referred to Bradshaw (1970), Duncan,Thom

and Young (1960), Mehaute (1976), Schlichting (1960) and Walz (1969).   Two concepts are of importance to the biologist and will be dealt with here.

## 2.1   Reynold's Numbers

Reynold's number is a ratio expressing the relationship between inertial and viscous forces which act upon a fluid.

Reynold's number, $R_e$ is defined by

$$R_e = UL/v$$

where U = mean velocity

   L = a characteristic length dimension

   v = kinematic velocity

Many investigations have shown that flows are definitely laminar, or viscous, when $R_e < 500$ and turbulent when $R_e > 2000$.

Reynold's numbers are non-dimensional.   Thus investigations at one Reynold's number are comparable with similar or different Reynold's regimes.   This is important because the ratio is derived from an expression which has a length, a size, component.   Unless a dimension is included we cannot discuss constructively the effects of water speeds in nature. In general terms we can discuss life at high or low $R_e$.   If an animal is small enough few natural flows will be of adequate velocity to raise $R_e$ above 500, let alone 2000, and life at low $R_e$ is life within the constraints of a viscous environment (see Colinvaux, 1979, for comments).

Reynold's dimensions are also important because we can calculate them for animals at a range of velocities.   One may then test animals in flow tanks to see whether they diverge from their expected Reynold's criteria, in what manner, and for what purpose.

## 2.2  Boundary Layers

A boundary layer may be described "as a layer of tired fluid" (Duncan, Thom and Young, 1960) which is retarded by friction at a surface.   Such a layer has given up some of its momentum relative to the surface to balance the frictional drag of the body.

Boundary layers are detectable by measurements of velocity or temperature flux (Wimbush, 1976) or by flow visualisation (see section 4 and Appendix IV).   As far as this essay is concerned boundary layers are of importance to benthic animals in two ways.

a)  Many benthic animals live within the boundary layer of the water column and must either avoid its constraints or oppose them.

b)  Benthic animals living in water flows will possess boundary layers of their own which impose conditions separate from the interface environment of the abiotic habitat.

In shallow waters over non-cohesive substrates the benthic boundary layer is the site where energy is given up. This is nowhere more apparent than over well sorted sands where high energy release sorts particles, initiates and maintains ripples of various wavelengths, winnows particles selectively and determines the behaviour of its inhabitants. The benthic boundary layer is the site where shear forces act upon bodies which may need to resort to mechanisms such as anchors, guyropes or streamlining to  maintain position in the habitat.
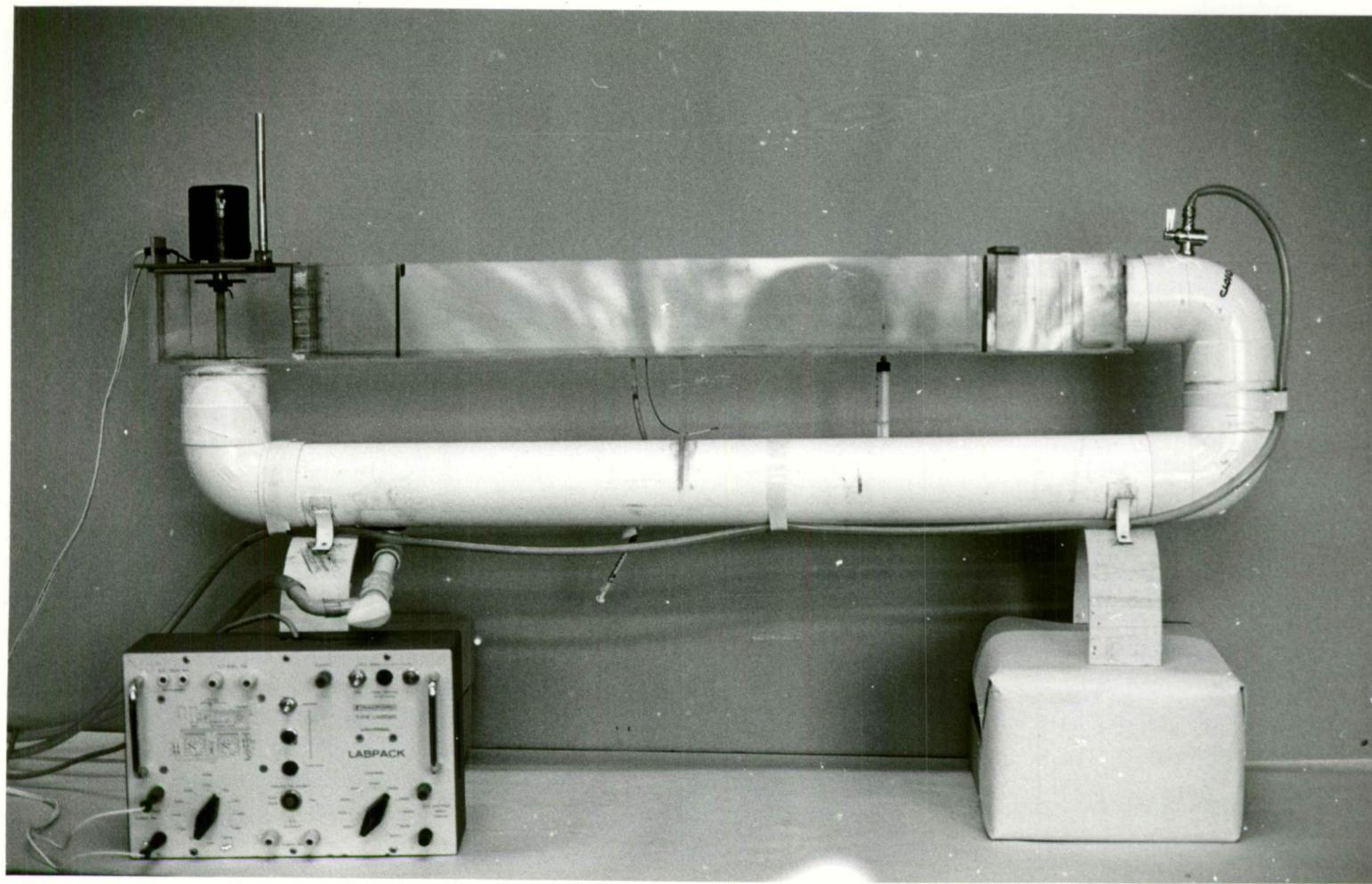
Plate III1.    Vertical recirculating flow tank (after Vogel and La Barbera, 1978).
A D.C. electric motor drives a propeller which circulates water
through the lower passage of the tank to enter the open-topped glass
portion of the flume at the right-hand end of the picture. Motor speed
is controlled by the variable voltage source shown bottom left.

Further comment upon boundary layers is made later in this study (Appendix IV). For further reference the reader may apply to the following authors: to Tokaty (1971) for history and background with particular reference to Russian work; to Walz (1969) for a treatment of boundary layers of both flow and temperature; to McCave (1976) who conceals, under one editorial hat, a series of symposium papers and working group reports treating the benthic boundary layer from a variety of points of view. A further important reference is that of Oke (1978) whose treatment of energy cascades and boundary layer climates is refreshing even tho' his fluid is air.

## 3. Techniques for the investigation of flow

In order to investigate flow phenomena one must employ techniques which produce flow regimes in a reproducible manner. Having achieved such regimes one must use techniques to describe and measure the phenomena observed.

## 3.1 Flow tanks

The theory of flow tanks, tow tanks and flumes is treated extensively in hydrodynamic literature. Access to such information may be through a basic text (e.g. Bradshaw, 1970) or review journals (e.g. Applied Mechanics Reviews, Journal of Scientific Instruments, Annual Review of Fluid Mechanics).

During this work two simple flow tanks were used.

## 3.1.a The classical racecourse

A recirculating tank of "classical racecourse" form (Buchanan, 1964) was constructed from marine plywood. The water was driven by a water wheel set in one of the straight sides. The water wheel was driven by a small motor (24 v.D.C.)

the speed of which was controlled by a wire wound variable
resistance.    The apparatus differs little from Buchanan's
(1964) model and is not illustrated here.

### 3.1.b   Small flow tank

The racecourse design is bulky, takes up much space
in a small laboratory and is laborious to empty and refill.

A small vertical, recirculating flow tank was built
after the design of Vogel and La Barbera (1978).    For details
of construction the reader should refer to that paper.
Our version is illustrated in Appendix Plate III*1*.

### 3.1.c   Tow tanks

More power is needed to drive fluid past a stationary
object than to drive that object through the fluid.    Thus it
is sometimes appropriate to reverse the roles of subject and
fluid by towing the object through the water.    Any mechanism
which will carry an object and appropriate recording apparatus
at a constant velocity may be employed.    We have used model
cars with low friction bearings towed along wooden tracks and
an overhead model railway line with fibre strain gauges
attached to model rail bogies.

Movement was imparted to the bogies by winding a tow
line on the drive shaft of a small D.C. motor which was used
as a capstan winch.

### 4.    Visualisation of flow

If particles or dyes are introduced to fluid flows
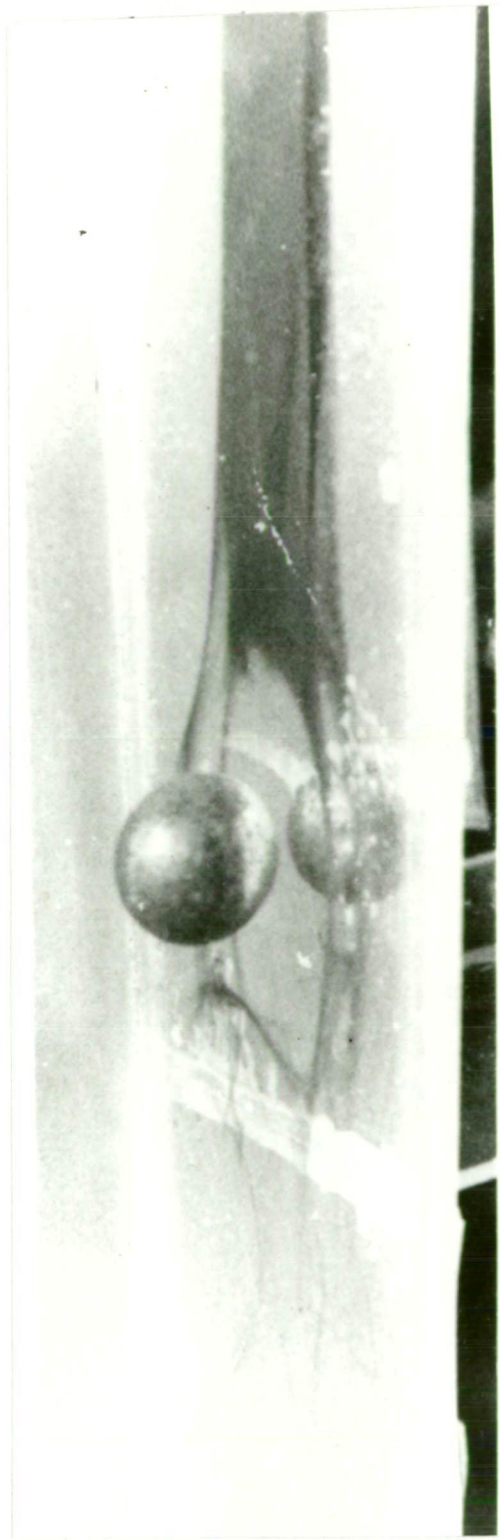streamlines and filament lines may be detected.

Plate 1112.    Indian ink visualisation around a sphere

In most biological work with live animals it is important that the tracers employed are not toxic. We have used, with some success, diluted Indian ink, blue writing ink, non-toxic food dyes and milk (the latter after Crisp and Southward, 1956). An example of Indian ink visualisation is given in Appendix Plate III 2 and the Plates of Appendix IV.

Particle paths, which are the loci of fluid particles, may be shown up by time exposure photographs. Finely divided aluminium powder is an appropriate tracer for this technique. Particle paths during a photographic exposure at one-250th sec are demonstrated in Appendix Plate III 3.

5. Flow, ripples and cumaceans

The classical racecourse flume bedded with Little Swanport sand was filled with sea water and the paddle accelerated until sand particles commenced to move at the interface. The mean velocity of the tank was then recorded either by (a) timing the path of a dye packet, or (b) by timing the path of a polystyrene bead equipped with a glass fibre keel.

Two indicators were employed to reset the flow of the tank to predetermined levels. Firstly the rheostat setting which controlled the water wheel motor. Secondly the position against a quadrant scale of a pointer which moved against a weak spring as the flowing water impinged upon its submerged end. This simple water vane was constructed from milk straws and components from gimbal levers as used in kymograph apparatus.

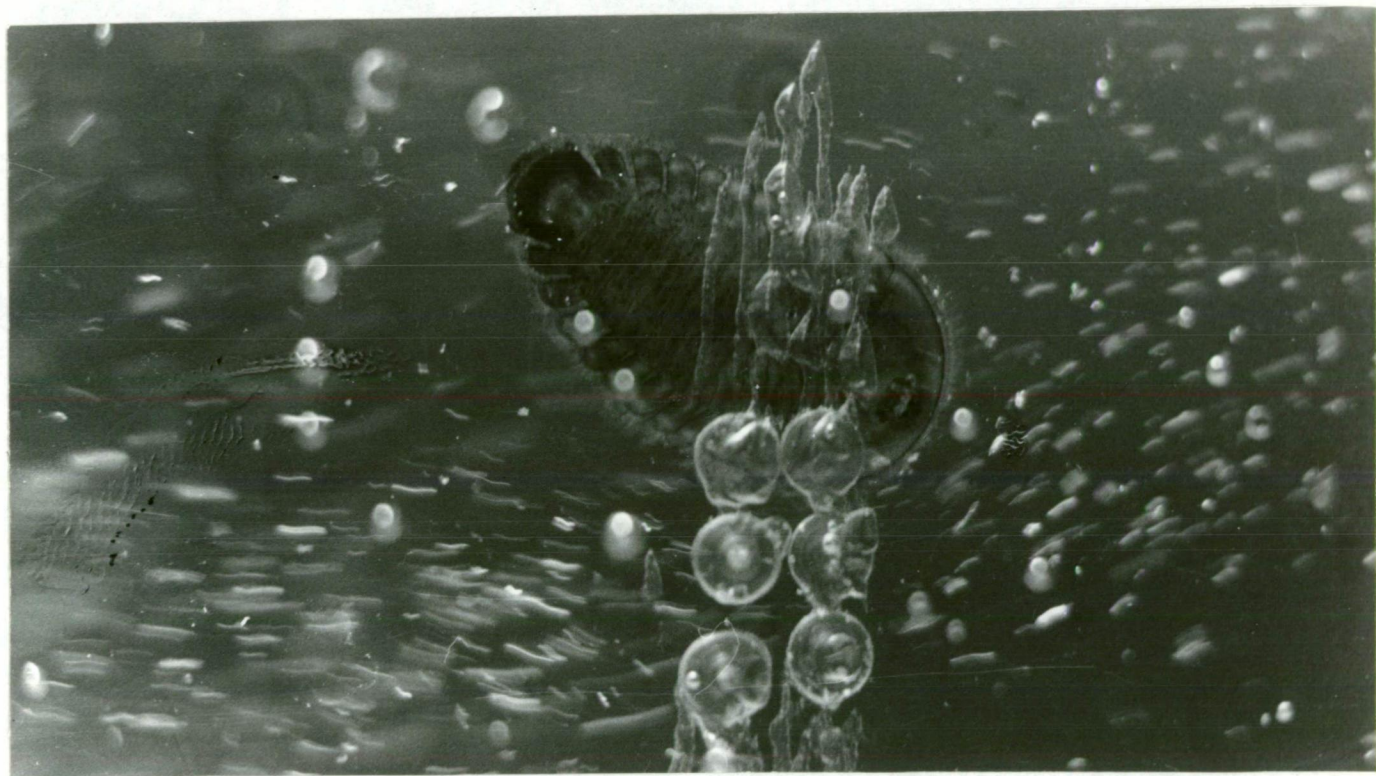Two kinds of experiment were carried out using this apparatus.

Plate III3.   Particle paths of aluminium powder.
             Exposure 1/250s.
             (*Sclerocyphon aquaticus*, ventral view
             of live larva.  Scratches on the acrylic
             substrate provide attachment points for
             the larva.)

## 5.1 Cumacean washout velocities

Having established the velocities at which the substrate commenced to move, cumaceans were added to the tank. A fine net screen was constructed to fit across the channel downstream of the experimental sea bed. The speed of the driven water wheel was then increased by small increments. Each increment was arbitrary, being tenths of the distance of travel of the rheostat switch. Each switched increment was maintained for 5 minutes. At the end of each flow period the screen was removed from the tank and the numbers of cumaceans caught at that speed were recorded.

The numbers of cumaceans of three species washed out from sands during runs of increasing velocity regimes are shown in Appendix Figure III 2. The sand shift point is indicated and the point at which the water column carried suspended particles throughout its depth.

The results show that few cumaceans were caught at velocities less than increments 5 (mean main stream speed $c.5 \times 10^{-2}$ m.s.$^{-1}$). It is suggested that the low levels recorded result from the exploratory activity of cumaceans leaving the boundary layer of the flume and travelling with the main stream.

At speeds > increment five the proportion of cumaceans caught upon the screens rose rapidly and for both species of *Cyclaspis* the ratio of specimens introduced to the substrate and specimens washed out is nearly unity. However, individuals of *Cyclaspis caprella* appear to be washed out at higher velocities. This may be due to two factors:

(1) *Cyclaspis* n. sp. is a smaller animal and may find it more difficult to regain the benthic interface after washout.

(2) *Cyclaspis caprella* appears to be an inhabitant of high energy surf and back surf zones (see main text) and may be adapted better to recovering habitat. Certainly surf amphipods such as species of *Exoediceros* are speedy burrowers after they have been dislodged by wave action. A similar conclusion was drawn by Withers and Thorp (1978) who suggested that where organisms were frequently washed out by wave action (i.e. where effective shear stresses were excessive) the ability of small crustaceans and polychaetes to rapidly re-enter the sediment becomes especially advantageous.

Individuals of *Leptocuma pulleini* were taken from the screens at higher washout levels than the other two species. However, only 52% of the animals added to the flume were recovered during the experiment. This may indicate:

(a) that this species, the largest of the three, nestles more deeply (see main text) and (b) that the greater span of the extended pereiopods acting as guyropes anchors that species more securely in the substrate.

## 5.2   Discussion

Washout velocities for animals may differ from critical current velocities causing erosion of sedimentary particles. In these simple flume experiments particle saltation was first observed at velocity increment 3 ($c$. $3 \times 10^{-2}$ m.s.$^{-1}$) and the water column carried suspended particles throughout its depth by increment 5. It is apparent (Figure 2) that erosion of particles occurred before most cumaceans were captured upon the screens of the flume.
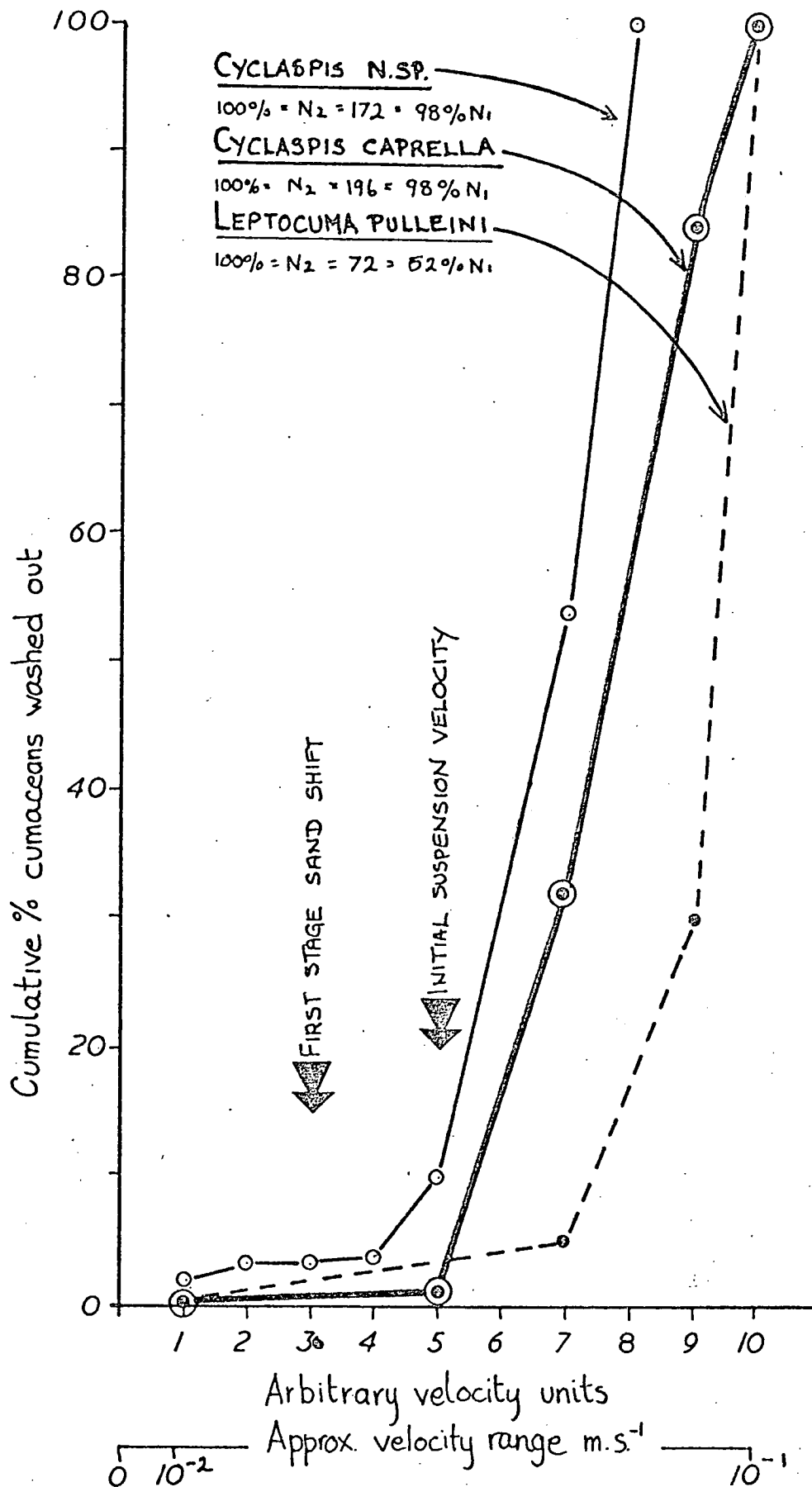
Fig 1112. Cumulative percentage washout for three species
of cumaceans from Little Swanport sand.
N1 = No. cumaceans added to flume
N2 = Total cumaceans retained on screen

One may postulate two hypotheses to explain this phenomenon.

A.    That by behavioural adjustment (i.e. by adjusting the animals' own position in the eroding bed), cumaceans may remove themselves from critical stress regimes.

B.    That cumaceans are less susceptible to shear stresses.  (For further comments see section 7).

6.    Cumacean position and sand ripples

One of the disadvantages of a flume driven by a water wheel, especially when screens are employed to catch suspended material and animals, is that oscillating regimes are produced. These are caused by the widely separated paddle vanes of the water wheel and build up and release of hydrostatic heads behind screens.

In practice such hydraulic oscillation may be employed to produce rippled sand beds.  Ripples were of interest in this work because the sea bed in the main study area (Little Swanport) was rippled throughout (clear water and diver observation).  It is apparent that ripple formation and the mechanics of separated flows is a complex situation (see Williams and Kemp, 1972) although recent work has described some of the mechanisms (Koneko and Honji, 1977).

In this work the presence of ripples was of interest because ripples provide two phenomena where low stresses may occur.  Oscillating flows may never be anything but laminar because their duration is too short for turbulence to develop thus isolating interface fauna from turbulent stresses.

Ripples possess lee and stoss faces (see Allen, 1970;  Hollister *et al.*, in McCave (ed.) 1976) which may offer different sedimentary constitutions and different dimensions of hydraulic stress.

It was decided to investigate the position of cumaceans in relation to sand ripples.

## 6.1  Method

A layer of experimental sand was laid in one straight channel of the flume to a depth of 20mm.  The sand had been washed in sea water and aerated for 24 hours before use.  When constructing the artificial bed, layers of sand particles about 1.0mm. thick were laid down in succession in order to maintain some horizontal homogeneity.

The water in the tank was circulated at speed increment 1 (*c.* $10^{-2}$ m.s.$^{-1}$) and specimens  of *Cyclaspis caprella* (N = 200) were introduced to the tank.  After one hour the position of visible cumaceans (detected by particle movement and the excavated depression in front of the animal) was recorded with reference to an overlay grid.
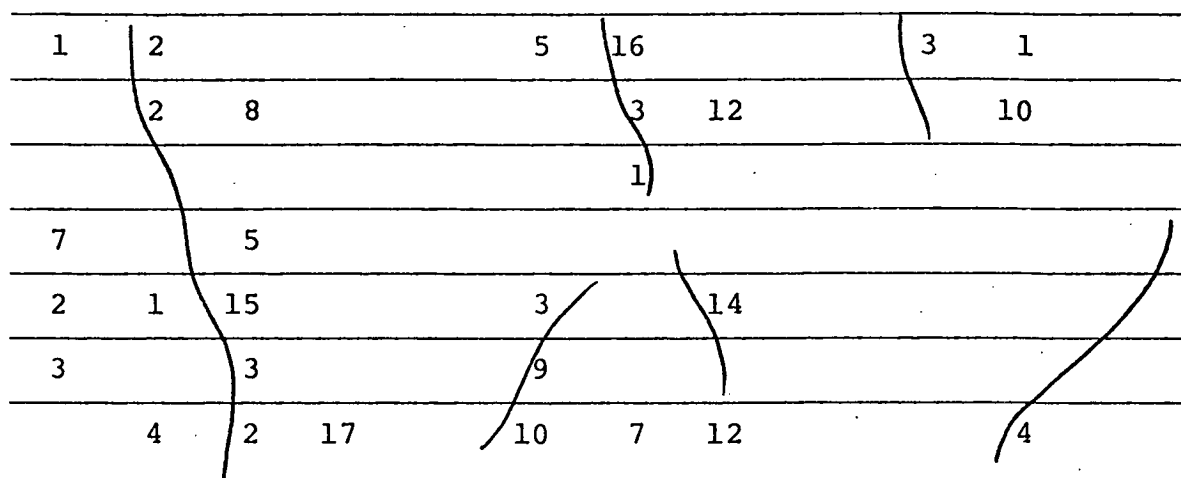
The water speed was then increased to switch-increment three and a net screen introduced to the tank.  The flow regime was maintained for one hour and the position of detectable cumaceans again recorded and the position of ripple crests was recorded.

The ripple structure which eventually resulted is shown in Appendix Plate III.4.  The results of the experiment are expressed in Figure III 3.

Figure III 3 Numbers and positions of cumaceans on plain bed
and rippled beds.

N1 = initial inoculation of cumaceans;

N2 = number cumaceans detected.

Plain bed : velocity $c.10^{-2}$ m.s.$^{-1}$

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | | | 5 | 4 | 1 | | 3 | | | | |
| 5 | | 2 | 4 | 5 | | | | | 2 | 3 | |
| 4 | | 2 | 6 | 4 | 5 | | 2 | | 1 | | |
| 4 | | | | | | | | 5 | | | 4 |
| | | 6 | | | | 5 | | 3 | 5 | 2 | |
| | 6 | | 2 | | | 3 | | | 5 | | |
| 4 | | 2 | 3 | 3 | | | | | 8 | 5 | 2 |

Time : Zero

N1 200

N2 139

$x^2 = 231.50$

83 df $> 135.46$

(P $< 0.01$)

Rippled bed I:  velocity $c$. $3 \times 10^{-2}$ m.s.$^{-1}$

| 1 | 2 | | 5 | 16 | | 3 | 1 |
|---|---|---|---|----|---|---|---|
| | 2 | 8 | | 3 | 12 | | 10 |
| | | | | 1 | | | |
| 7 | | 5 | | | | | |
| 2 | 1 | 15 | 3 | | 14 | | |
| 3 | | 3 | 9 | | | | |
| | 4 | 2 | 17 | 10 | 7 | 12 | 4 |

Time to + 1 hr

    N1 200

    N2 182

    $x^2 = 664.58$

    83 df $> 134.46$

    ($P < 0.01$)


Rippled bed II:  velocity $c$. $3 \times 10^{-2}$ m.s.$^{-1}$

| | | | | | 15 |
|---|---|---|---|---|----|
| | | 12 | | | 3 |
| | 1 | 9 | | | |
| 4 | 3 | 3 | | | |
| 16 | 3 | | 7 | 4 | 2 | 4 |
| 1 | 2 | 10 | 2 | 7 | 3 | 1 |
| | 4 | 6 | 4 | 12 | |
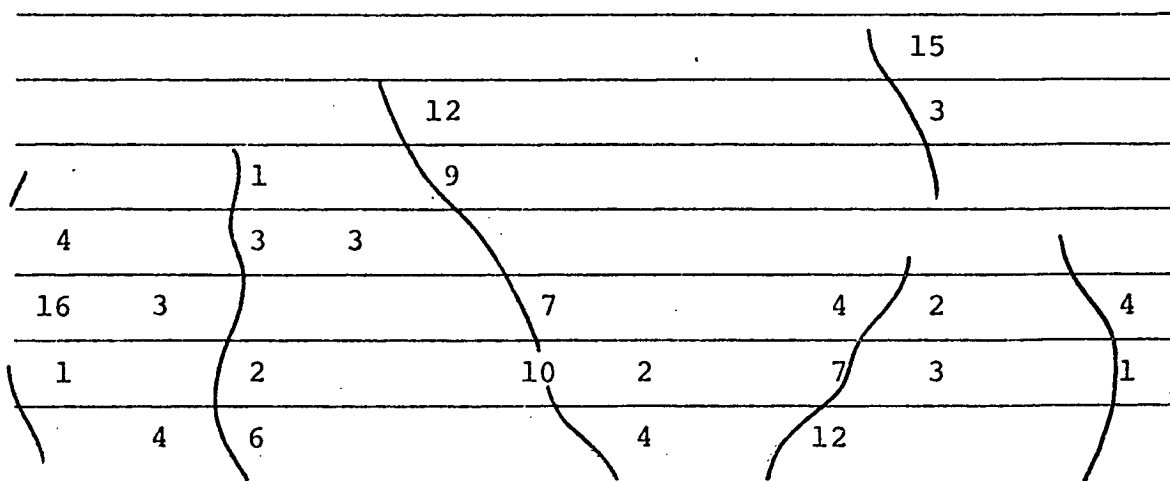
Time to + 2 hr.

    N1 200    N2 138

    $x^2 = 587.99$

    83 df $> 134.46$

    ($P < 0.01$)        &longrightarrow;    Current direction

Plate 1114.    Ripple structure at flow tank interface.

## 6.2    Discussion

The conclusions drawn from this experiment are that in a unidirectional flow over a rippled bed of sand of wavelength between 70-175mm cumaceans will congregate on the downstream side of the ripple.  As the ripples advance cumaceans will shift to regain this position.  It should also be noted that biogenic carbonates winnowed from the sand concentrate in the lee trough of ripples.   This phenomenon is visible in Plate III4.   Commentary about cumacean aggregations and biogenic carbonate concentrations may be found in the main text of this thesis.

## 7.    Drag forces upon cumaceans

Cumaceans which enter the water column are subject to tital streams, swash currents and local turbulence.  It has been suggested earlier in this account (Chapter 12) that cumaceans may employ the water column for dispersal.  When cumaceans leave the benthic boundary layer they lose the protection of that layer but expose themselves to the stresses of the water column.

Cumaceans were placed in the simple flow tank described earlier (3.1.b) and flow visualisation by dye injection was attempted.   Live specimens in sand offered little information other than that they were contained within the boundary layer of the flow.   In other words the phenomenon observed was that of the substrate boundary layer.

It was difficult to restrain cumaceans in the water column and apparent that the magnitude of flow modification

observed was a function of the restraining apparatus rather than the animal. Preserved, and dried and gold plated animals were eventually available. Animals were air dried from alcoholic solution, coated with gold in a sputter coater and attached to a fine glass thread made by drawing out glass rod in a gas flame.

The thread was attached to the parallel linkage of a force balance (Figure III4) and the cumacean specimens subjected to increasing flow regimes.

The results are expressed in Figure III5. The investigation was exploratory and would not be written here except that I cannot explain the phenomenon observed. Drag forces measured at increasing velocities for two species of cumacean were small until stream velocities in the region of $3.0-3.6 \times 10^{-2}$ m.s.$^{-1}$ were attained. After this point the drag on both animals increased markedly. It was not possible to extrapolate these observations to higher velocities because the motor employed to drive the water in the tank would not work any faster.

Live specimens of *Cyclaspis caprella* were then placed in the flow tank at night and encouraged to remain in the water column by lighting the tank from above with a small hand torch. The cumaceans were then observed as the tank velocity was raised by as many small steps as possible. Combinations of multiple step switching for the motor and banks of milk straw collimators which could be removed separately allowed about thirty velocity steps through a velocity range 0-0.4m
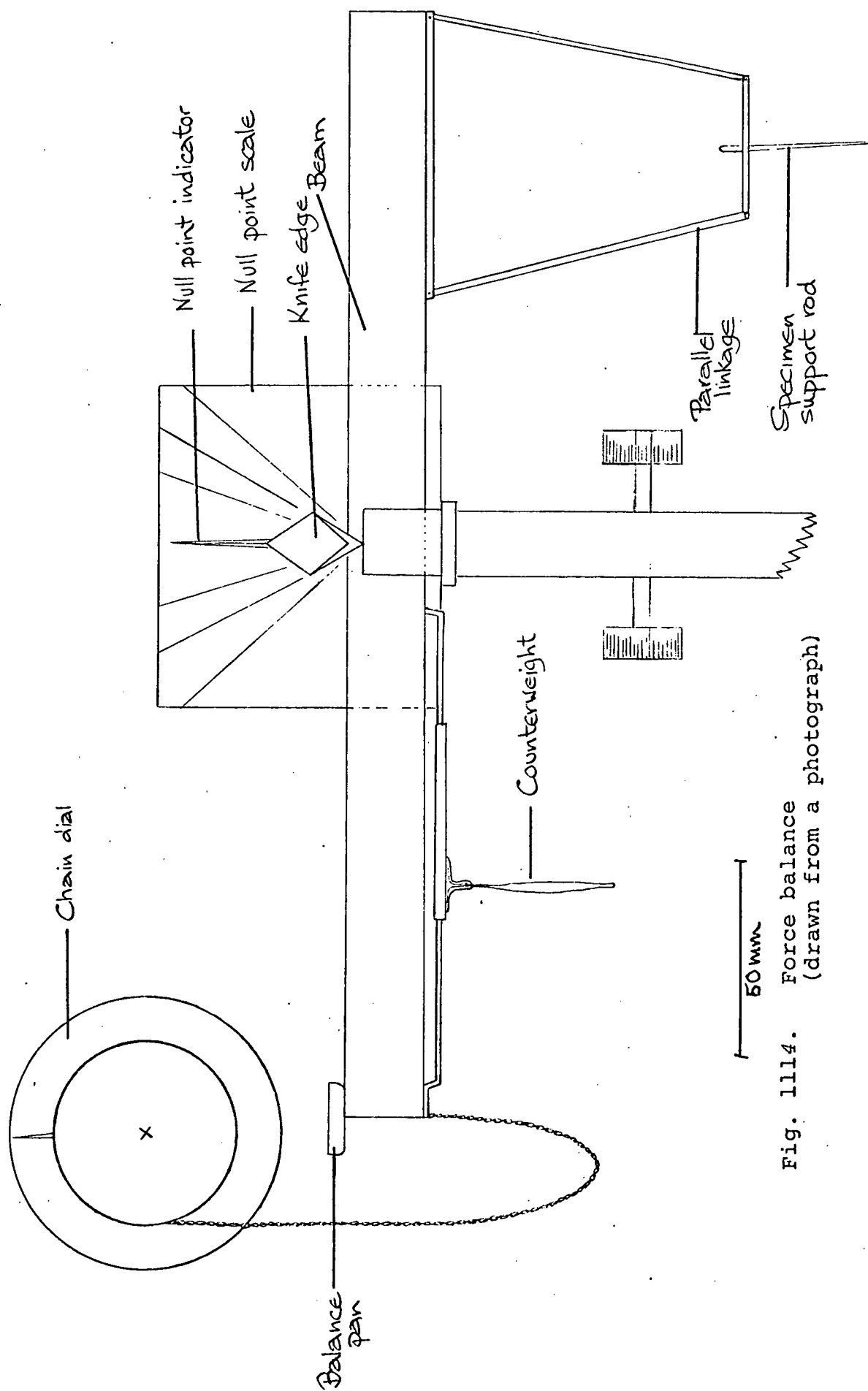
Chain dial

Null point indicator

Null point scale

Knife edge

Beam

Parallel linkage

Specimen support rod

Counterweight

Balance pan

50 mm

Fig. 1114. Force balance
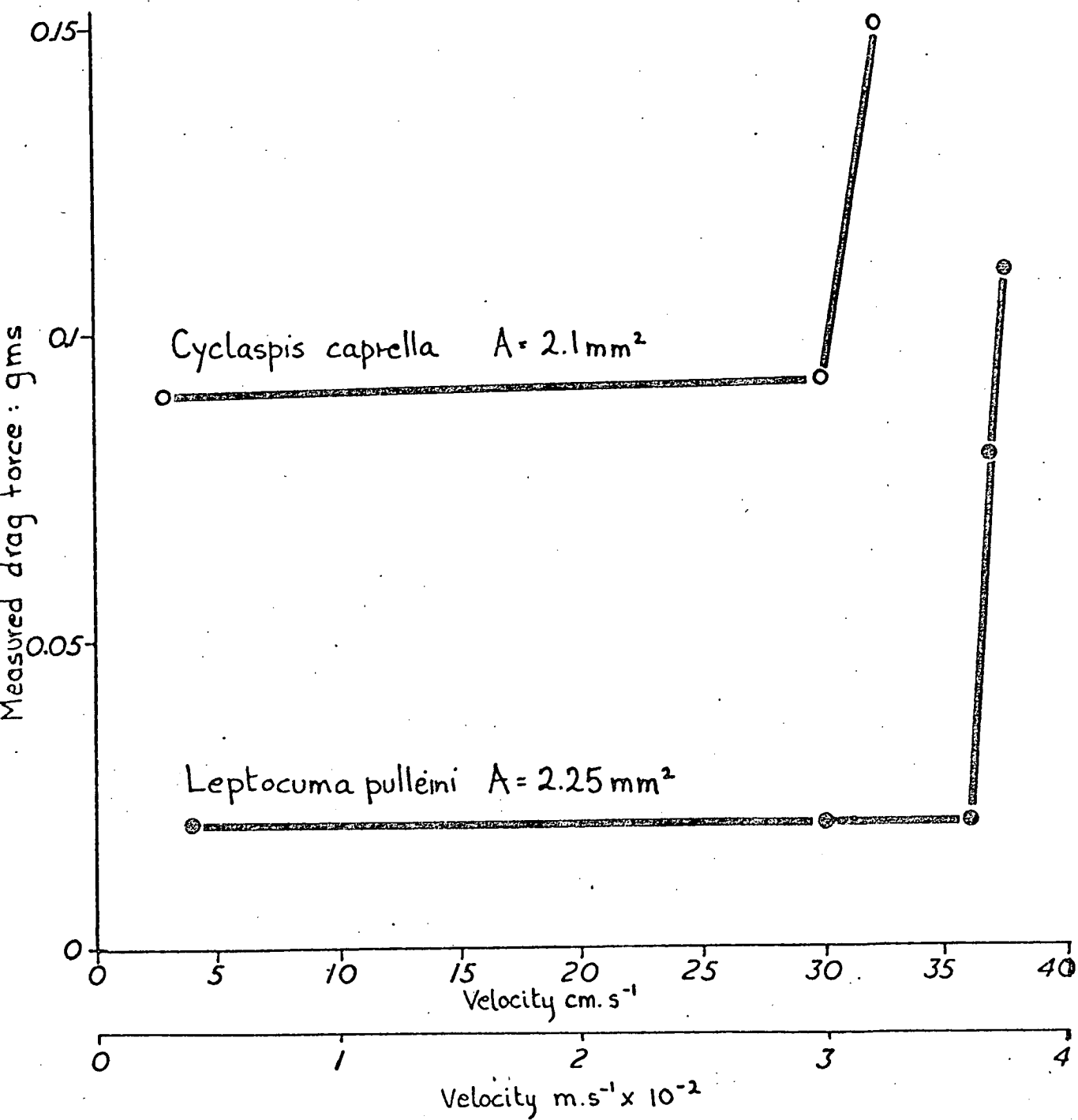(drawn from a photograph)

Fig. III5.   Total drag forces recorded at increasing
velocities for specimens of two species of
cumaceans.

sec $^{-1}$. At low speeds cumaceans were observed throughout
the water column. At velocities greater than 2.5 x $10^{-2}$m.s.$^{-1}$
individuals were seen to stop swimming, fold the peraeopods in
under the body and fold the tail over the back of the carapace.
The tail folding action is a flicking action which projects
the animal backwards and slightly downwards. The animal
then falls freely until the laminar layer at the sand substrate
is attained. The tail and peraeopods are then extended and
the animal lands ten-square.

It can be seen from these observations that cumaceans
may be able to detect drag forces and avoid them by a
behavioural mechanism. This evidence suggests that cumaceans
may be able to avoid being swept away from an area if they so
desire or may be able to leave the water column where they
require having employed horizontal currents for dispersal
(cf. Colman and Segrove, 1955).

It is apparent from these observations that investigation
of diel movement of cumaceans in the water column must take
account of relative water velocities and shear velocities
over substrates. Further development of hot bead thermistor
velocimeters within the Zoology Department of the University
of Tasmania may make this possible in the near future.

8.    Miscellanea

It is apparent that visualisation of flow phenomena is
an heuristic technique.

Three observations of interest have been made during
this work and are reported here. They were initiated because

many surface living aquatic animals maintain position by not allowing shear stresses to overturn them. Mytilids retain position with byssus threads as do other bivalve molluscs. Glued adhesion to the substrate is common amongst barnacles and tubicolous polychaetes. Gastropod molluscs can oppose lift forces effectively by means of an adhesive foot and oppose impact forces by dividing and deflecting water masses (e.g. the patelliform shell).

The gliding foot is not a good mechanism for opposing horizontally applied forces and a number of mechanisms are employed to diminish fluid forces which may overcome sliding friction. Three are described here based on observations made in a flow tank with Indian ink used for visualisation.

## 8.1    Streamlining (Figure III6)

One of the common pleurobranchomorph molluscs of south eastern Australia is the side-gilled slug, *Pleurobranchaea maculata* (Quoy and Gaimard) which is found in a range of habitats from mud to well sorted sand substrates. When *P. maculata* is placed in unidirectional flows it is apparent that it is a well streamlined animal. Placed obliquely to the flow direction it is able to maintain the integrity of its streamline by local modification of body form. In contrast to the water pennies described in Appendix IV *P. maculata* controls its boundary layer by modifying its shape rather than by suction through slots. The magnitude of the boundary layer tempts one to suggest that surface mucus acts to reduce shear stresses upon the body surface also. This is of further interest when one recalls that polymers employed to reduce drag in fluids are molecules of high molecular weight (Berman, 1978).
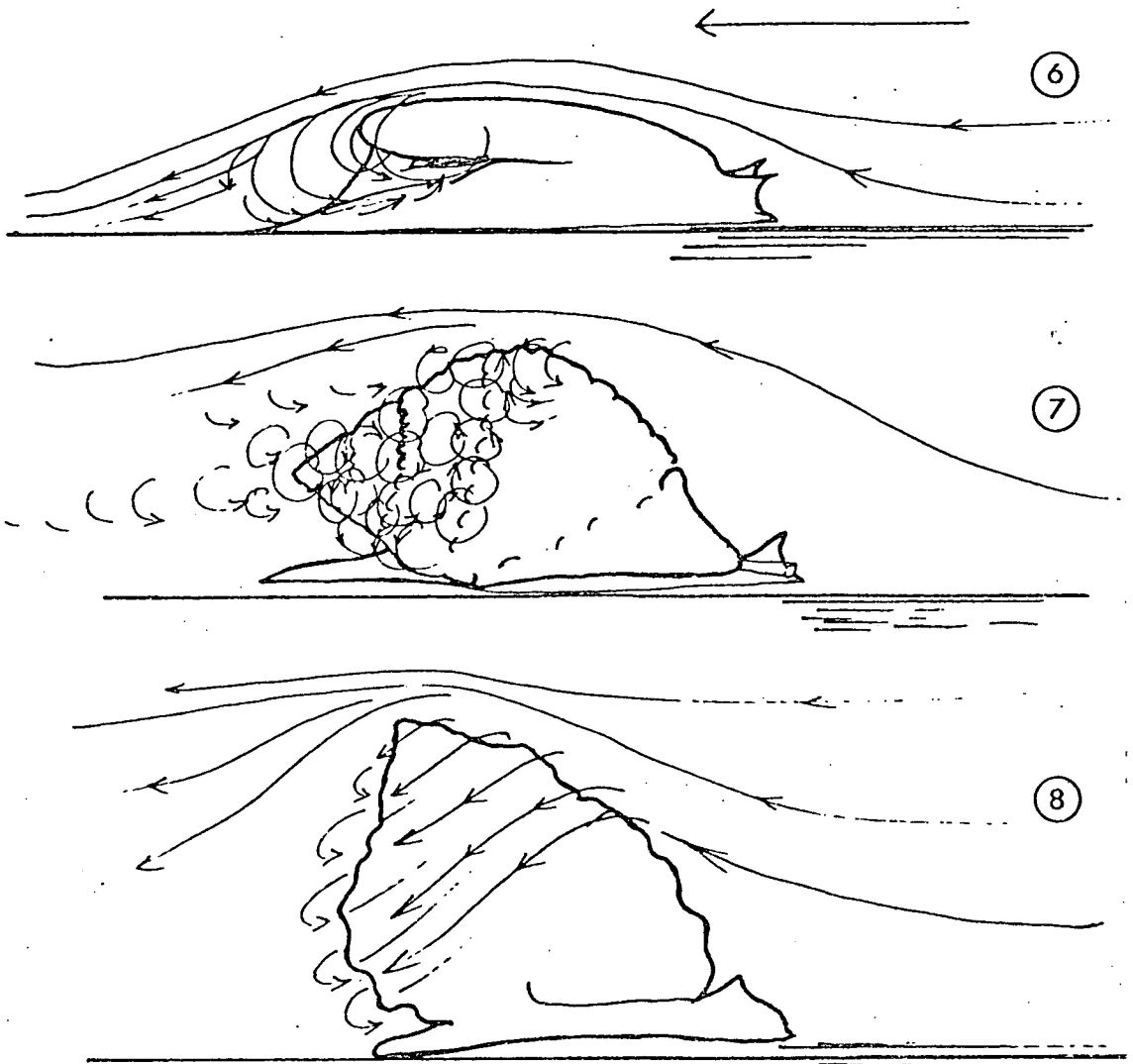
Fig 111 6    Diagram showing stream lines around an individual of
             *Pleurobranchaea maculata* .  Velocity $c.3 \times 10^{-2}$m.s.$^{-1}$
             Derived from photographs.

Fig. 111 7   Diagram showing turbulent diffusion eddies around the
             shell of *Parcanassa pauperata* .  Velocity $c.\ 4 \times 10^{-2}$m.s.
             The diagram is a representation of visual observations.

Fig. 111 8   Diagram showing spiral structure of streamlines around
             a specimen of *Austrocochlea constricta*. Velocity $c.$
             $4 \times 10^{-2}$m.s.$^{-1}$.  The diagram is a representation of
             visual observations.

It is apparent that *P. maculata* is totally enclosed within a controlled boundary layer. In order to overcome boundary layer constraints such as enforced diffusive exchange of respiratory and waste molecules, a secondary turbulent stream is created. The gill on the right hand side is overlain by a mantle flap which acts as a hydrodynamic spoiler. The spoiler flap reverses the direction of boundary layer flow and produces a controlled vortex over the gill which must aid respiratory exchange. It is also tempting to suggest that the gill flap also acts to delay separation of the boundary layer streamlines. The respiratory vortex observed is powerful and the effect extends beyond the animal's tail. Dye introduced aft of the animal is carried forward to the gill region at stream velocities $5 \times 10^{-2} m.s.^{-1}$.

## 8.2   Turbulent diffusion (Figure III7)

A number of intertidal and sublittoral gastropod molluscs possess shell sculpture composed of granular projections. This is particularly apparent for the nassid, *Parcanassa pauperata* (Lamarck) and the muricid, *Dicathais textilosa* (Lamarck) although many lack distinctly nodulose sculpture.

When specimens of these species are placed in turbulent flows of *c.* $4 \times 10^{-2} m.s^{-1}$ instead of observing the gradual development of a turbulent boundary layer with a single distinctive separation point, separation occurs at each nodule of the shell sculpture. Visualisation shows this as a complex sequence of small eddies generated by each nodule.

It is apparent from the visualisation experiments that sculptural nodules on the shells of these species are not immersed within a laminar sublayer and the shells are therefore not hydraulically smooth. It is suggested that such nodules act to diffuse stress energies by breaking down the main stream boundary layer into smaller random packets and delaying separation.

8.3    Turbulent diffusion by spiral sculpture (Figure III*8*)

Many gastropod molluscs possess shell sculpture composed of spiral grooves or ridges which parallel the whorls of the shell. An example from the Tasmanian littoral is the trochid, *Austrocochlea constricta* (Lamarck). Placed in flows similar to those described above, visualisation demonstrates a spiral and outwardly diffusing boundary layer. It is suggested here that this is a mechanism for spinning shear stress energies off the shell and maintaining a stable boundary layer around the shell by delaying turbulent separation.

8.4    Discussion

These examples have been included to demonstrate the value of simple visualisation experiments with live animals. Vogel and La Barbera (1978), and references therein, have demonstrated this with experiments on live sponges and fossil animals. It is to be expected that aquatic animals have adapted to constraints peculiar to their way of life, most particularly those of overcoming the difficulties imposed by diffusion processes within non-turbulent boundary layers. Most hydrodynamic literature depends on the application and refinement of empirical relationships. As the hydraulic evolution of animals can be no less idiosyncratic than the

evolution of other mechanisms it may be expected that biological studies will extend the empiricism of the pure mechanic.


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APPENDIX IV


BOUNDARY LAYER CONTROL BY WATER PENNIES

(COLEOPTERA: PSEPHENIDAE)


*Aquatic Insects*,   1980.

# Aquatic Insects

## International Journal
## of Freshwater Entomology

# Boundary Layer Control by
# Water Pennies (Coleoptera: Psephenidae)

by

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ABSTRACT

Evidence is given that larvae of Psephenidae control their boundary layer by suction and that it is an active compensating process.

The Psephenidae are a small coleopteran family recorded from Europe, North and South America, Africa, India, S.E. Asia and Australia (Hinton, 1955). The larvae, commonly known as water pennies, (Fig. 1) are well known members of the freshwater benthos, possessing a characteristic dorso-ventrally flattened body. They are found clinging to rocks in rivers and streams with flow regimes that are fast and turbulent for at least part of the year. It has been suggested (Hynes, 1970; Bayly and Williams, 1973) that the flattened form of psephenid larvae allows them to live within the boundary layer on the upper surface of stones in rapidly flowing streams. During a study of the taxonomy and distribution of the Australian Psephenidae (subfamily Eubriinae) by one of us (J.A.S.) we have examined some of the flow characteristics produced by larvae of two species, *Sclerocyphon aquaticus* and an undescribed species in the same genus, in an attempt to test this suggestion.

Investigations were made in a flow tank of simple design (Vogel and LaBarbera, 1978) using last instar larvae ranging from 8-10 mm in total length. Larvae can attach only to rough surfaces. In our investigations the larvae were provided with transparent perspex base plates which were roughened locally to permit attachment. Thus photographic quality was sacrificed to experimental technique. Dye visualisation of flow patterns revealed that Australian larval Psephenidae are streamlined (Fig. 2a). Streamlined forms are common in larger swimming organisms but rare among benthic invertebrates (Hynes, 1970).

At low Reynolds number when laminar flow predominates viscous shear stresses exist (Schlichting, 1960; Colinvaux, 1979). The streamlined form
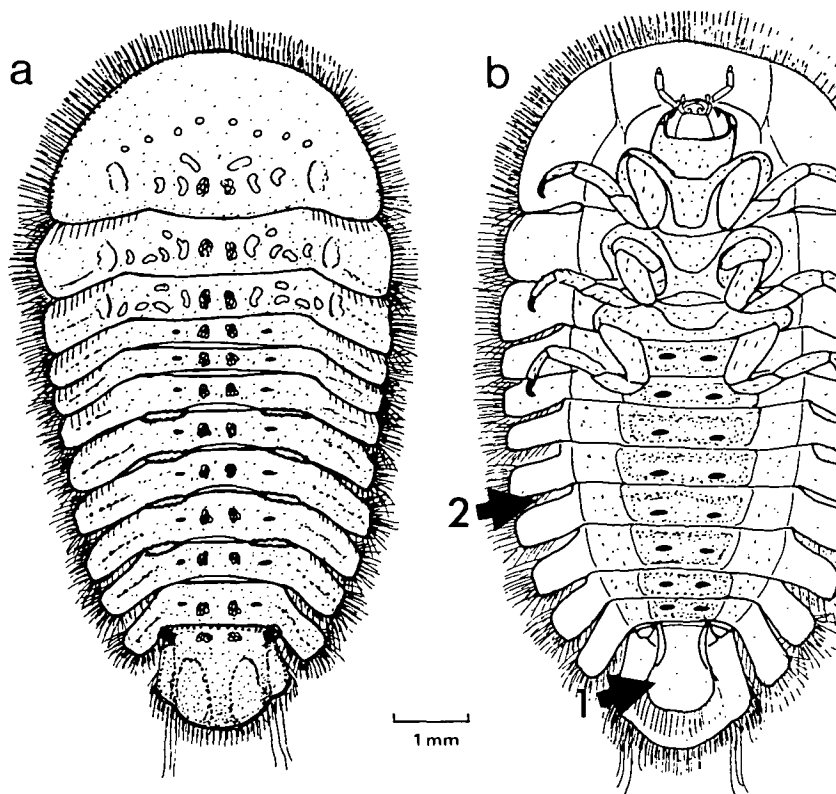
Fig. 1. *Sclerocyphon* sp.n.; a) dorsal; b) ventral; 1. operculum covering retractable gills; 2. slot.

minimises drag forces and allows the larva to maintain position with minimal expenditure of energy.

On further investigation it was found that the streamlined form is not the only mechanism employed by the animals to maintain position in the habitat. Experiments revealed that the larvae exert a powerful grip upon a rough substrate using the thoracic legs. Forces needed to overcome grip and measurements of total drag force were made using calibrated glass-fibre strain gauges. Forces needed to overcome grip (i.e. the force required to dislodge larvae vertically from the substrate) were measured on one *Sclerocyphon* species and ranged from 8.82 x $10^{-3}$N, standard deviation 9.3 x $10^{-3}$N, n=85). Drag forces range from 0.196 x $10^{-3}$ to 1.47 x $10^{-3}$N.

Larvae are able to use their legs to grip the substrate. Thus, at low Reynolds number, gripping force far exceeds the drag force on the body, that is, the shear stresses which tend to push the larvae downstream. This gripping ability would

also aid in preventing dislodgement by predators such as platypus (Faragher et al., 1979), trout (Jackson, 1978) and freshwater flathead (Hortle and White, in prep.).

As Reynolds number increases transition from laminar to turbulent flow occurs and the boundary layer associated with the rocky substrate also becomes turbulent (Schlichting, 1960). Such turbulent flow normally exists in streams and rivers (Hynes, 1970). However, within the turbulent boundary layer a thin laminar or viscous sublayer always exists in the immediate vicinity of the substrate (Schlichting, 1960). Fig. 2b shows that the particular shape of the psephenid larva modifies the laminar sublayer, increasing the thickness of this sublayer to include the body within it. As the sublayer is a region of reduced, laminar flow the drag forces on larvae are still minimal.

Respiratory exchange across the sublayer must be limited to the slow rate of molecular diffusion. Larvae of Eubriinae (the only psephenid larvae studied alive) overcome the constraints of this situation by creating their own respiratory current with a pair of anal, tracheal gills. The retractable gill tufts are located beneath the last abdominal tergite. Ventilation is intermittent. During ventilation the tergite is lifted and the actively pumping gills are extruded. Pumping creates a turbulent area at the rear of the larval body (Fig. 2c) which does not increase drag forces on the body and greatly enhances respiratory processes and waste removal.

At high Reynolds number, when turbulence is fully developed, the thickness of the laminar sublayer is reduced further. Under such conditions the possibility of boundary layer separation at the surface of the larva arises and the larva is in danger of being swept off the substrate. We suggest that under such conditions boundary layer control by suction is applied by the larva. The spaces between the lateral laminae (see Fig. 1.) are slots through which a small amount of boundary layer fluid passes (Fig. 3). Fluid mechanic theory (Schlichting, 1960; Walz, 1969) and actual suction aerofoils (Tokaty, 1971) demonstrate that suction delays separation of the boundary layer. Such a mechanism makes the larva's own boundary layer thinner but more stable. Thus the laminar profile of that sublayer is maintained keeping the effective drag force on the larval body to a minimum.

Initially, dye visualisation was used to test the suggestion that the spaces between the flexible lateral laminae of psephenid larvae are active suction slots. Dye visualisation of flows around larvae whose lateral slots were blocked with petrolatum showed that separation of the boundary layer occurred soon after the point of minimum pressure. Separation occurred later on untreated larvae, (Fig. 4). When larvae were placed upon a transparent substrate it was observed that dye from the boundary layer passed through the slots and underneath the animal (Fig. 5a). Animals lying askew the stream flow adjusted the slots and dye passed through the downstream slots only (Fig. 5b). It appears that boundary layer control by water pennies is an active compensating process.

Only a small volume of fluid needs to be removed by suction to maintain boundary layer control (Schlichting, 1960). Investigation by simple manometer and pressure transducer indicated that momentary pressure decreases occurred beneath larvae when stream shear stresses were increased. This negative pressure,
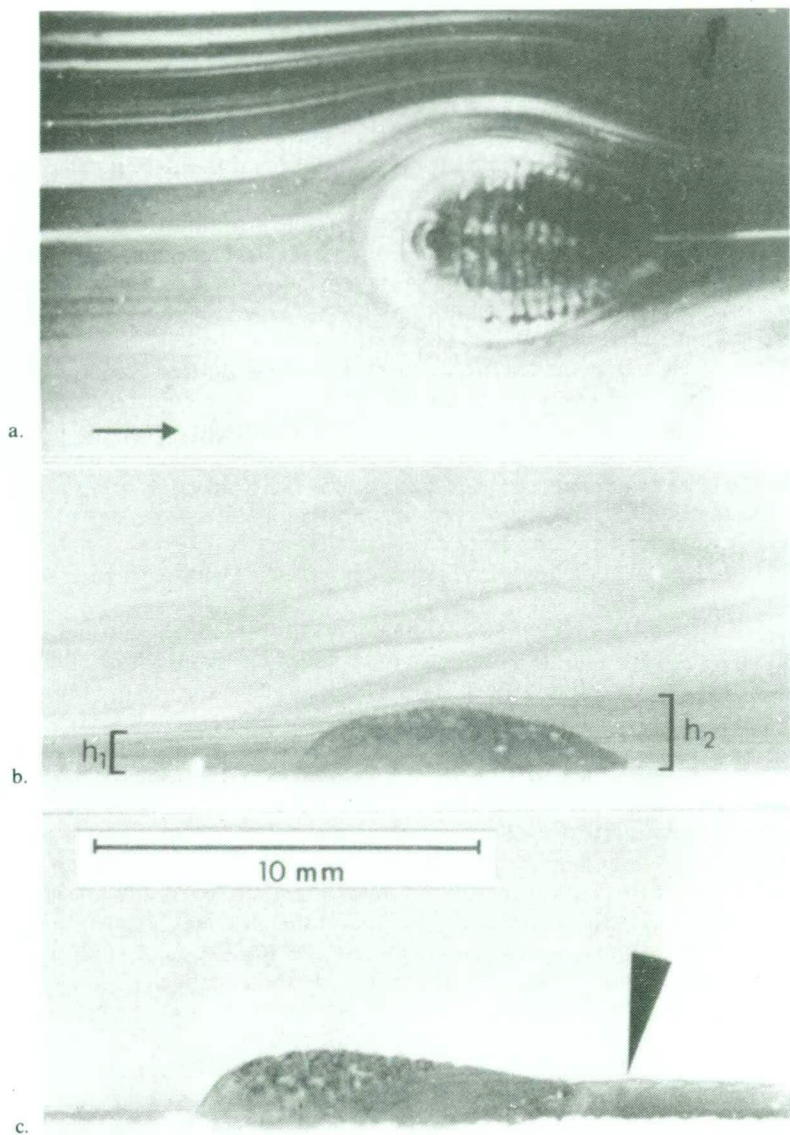
Fig. 2. *Sclerocyphon* sp.n.; a) streamlines around larva at low Reynolds number; b) larva within molecular sublayer at low Reynolds number, free stream turbulence present above sublayer; $h_1$ = height of stream sublayer, $h_2$ = height of modified sublayer; c) larva with anal gills actively ventilating. Note turbulence (arrowed) created by rapidly pumping gills. All visualisation with Indian ink. Flow direction (indicated by stream arrow) and scale similar for all figures.
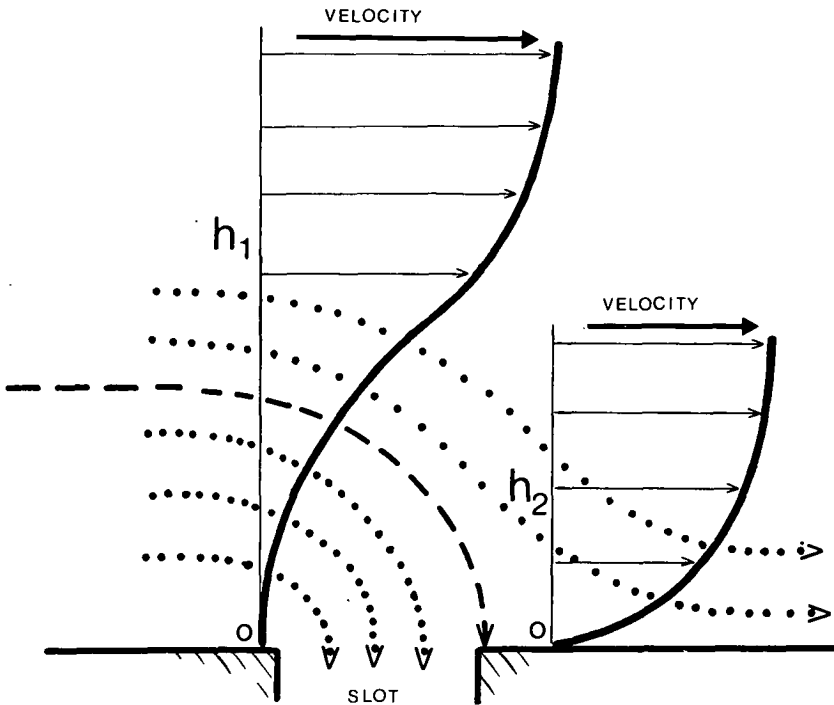
Fig. 3. Theoretical velocity profiles and lines of flow in the vicinity of a suction slot. Stagnation point streamline dashed; other streamlines dotted. $h_1$ = initial height of velocity profile; $h_2$ = height of velocity profile after suction. After Walz (1969).

momentarily set up beneath the larval shield, may be sufficient to operate suction. We suggest that this mechanism is controlled by adjustment of the volume under the body. This mechanism allows maintenance of body streamlines at times of rapid increase in stream flow. Such shear stress increases occur during stream spates and when the animal changes position in the habitat. We have examined larvae of species of Eubriinae, one of the two subfamilies with anal tracheal gills. The larvae of the other subfamilies (Psepheninae and Eubrianaciinae) possess ventral tracheal gills. Examination of preserved specimens and iullustrations (Hynes, 1970; Blackwelder, 1930; West, 1929) of larvae with ventral gills lead us to suggest that suction through slots between the lateral laminae may be the only means of maintaining adequate water flow over the gills in those animals. Exhalent anal flow would also maintain anal streamlines and isolate the animal
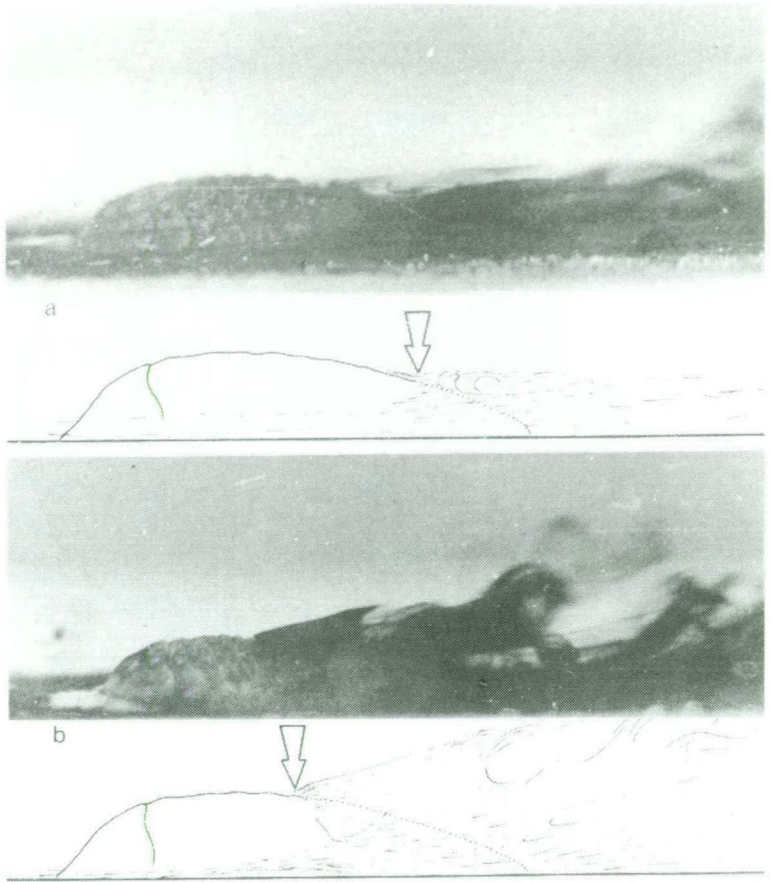
Fig. 4. *Sclerocyphon aquaticus;* boundary layer separation at high Reynolds number (animal
approx. 10 mm long). a) normal live larva; b) live larva with slots between lateral lamina
blocked with petrolatum. Large arrows indicate the transition point in both cases.

from mainstream turbulence. Whether increases in stream stresses result ir
additional boundary layer control remains unknown for non-eubriinin(
Psephenidae.

Streamlining and associated boundary layer control allows water pennies t(
move across substrates in fast, turbulent stream flows. Thus Psephenidae are abl(
to exploit food sources on the surfaces of rocks exposed to high energy flows
Such resources are unavailable to other benthic invertebrates which do no
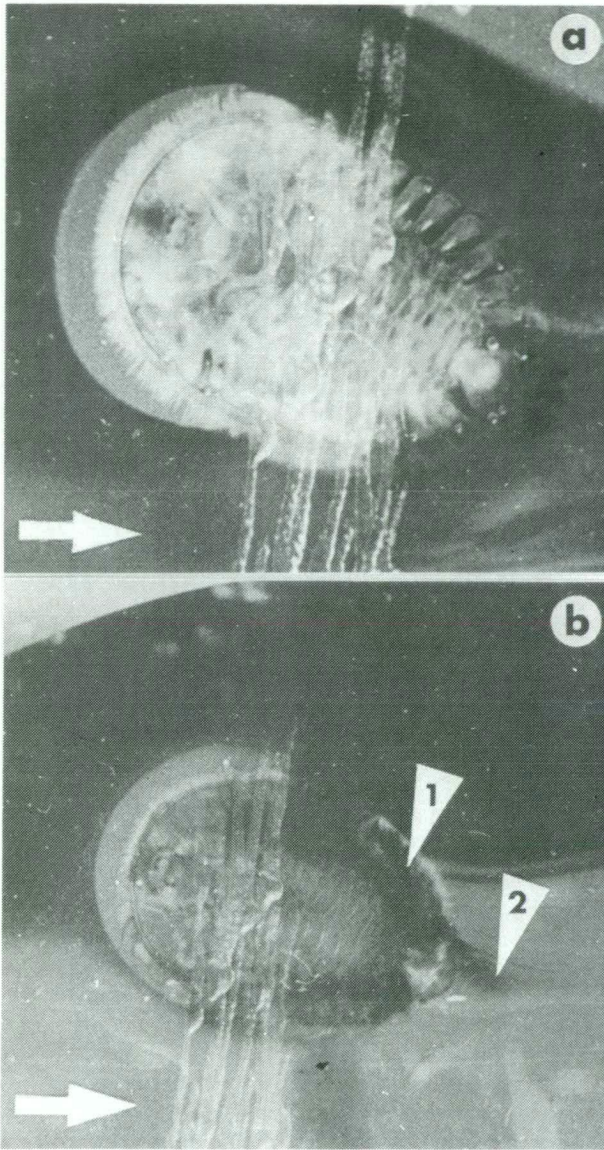possess these hydrodynamic advantages.

Fig. 5. *Sclerocyphon aquaticus;* a) ventral view of live larvae showing dye from boundary layer in slots; b) ventral view of live larva showing flow in dye from lateral slots moving beneath body shield (1) and being discharged below laster tergite during ventilation (2). Dye visualisation with Indian ink. Scratches on the acrylic substrate provide attachment points for the larvae.

## RÉSUMÉ

On montre que les larves de Psephenidae contrôlent la couche limite par aspiration et que le processus de compensation est actif.

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