# THE BIOLOGY OF LEMBOS WEBSTERI AND COROPHIUM BONNELLII (CRUSTACEA : AMPHIPODA) IN RELATION TO TURBULENCE AND TURBIDITY.

(One volume)

Richard Oliver Shillaker B.Sc.

A thesis submitted for the degree of Doctor of Philosophy in the University of Glasgow, following research conducted at the University Marine Biological Station, Millport.

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# DECLARATION.

I hereby certify that the work embodied in this thesis, for the degree of Doctor of Philosophy, is a result of my own work, which has not previously been submitted for any degree.

................................

R.O. SHILLAKER

I certify that this study has been performed under my supervision.

DR. P.G. MOORE

# SUMMARY

The biology of two members of the Laminaria holdfast community, the amphipods Lembos websteri and Corophium bonnellii, was investigated. Information was derived from field sampling and laboratory based observations and experiments. The experiments concentrated on the effects (1) of water movement, and (2) of settling and suspended inorganic particles.

Both species build tubes out of sediment that accumulates in the holdfasts. Tubes constructed from long strands of fine filamentous algae are also occupied. Tube building relies heavily on the activity of the first two pairs of pereopods. Most Corophium occupied tubes which were away from or only loosely attached to the haptera, whilst most Lembos occupied tubes which were more firmly attached to the haptera. Even when attached to the haptera the tubes of both species are easily dislodged. The juxtaposition of Laminaria holdfasts and unstable sand, at Fintray Bay, results in sand accumulating in the holdfasts. Corophium, along with other animals, utilizes this sand to form a dense mat of tubes, which greatly alters the micro-environment of the holdfast.

With the exception of male Lembos, both species rarely leave their tubes. In the absence of females, male Lembos vacate their tubes more frequently at night than during the day. However, the extent to which such a clear cut difference occurs in the field is uncertain. The hypothesis that male Lembos leave their tubes to seek out and enter the tubes of mature females is confirmed with limited data.

Lembos and Corophium ingest a wide variety of food items, with suspended organic detritus being of major importance. Phytoplankton must also be of considerable importance to Corophium, due to its highly efficient fine particle filtering apparatus. In contrast, Lembos is better adapted for filtering larger particles. The more frequent occurrence of Lembos at exposed, rather than sheltered, localities may be due, in part, to larger food particles being more abundant in more turbulent waters. In still water, where suspended particulate detritus is absent, Lembos is more liable than Corophium, to purposely reingest its own faecal pellets and to eat its own tube. Limited diurnal variation in an index of gut fullness is a feature of both species. This variation

may be due, in part, to tidal variation in the suspended solid load around the *Laminaria* holdfasts.

Female *Corophium* can remove embryos from their marsupia and subsequently eat them. Young *Lembos* remain longer in their mother's marsupium and tube, than young *Corophium*. The more lengthy association of recently hatched *Lembos* with their mother may be related to the occupation of wave exposed localities. The behaviour of young in their mother's brood pouch and tube is described. Of particular ethological interest is the avoidance of males by young *Lembos*.

The survival of *Corophium* and possibly also of *Lembos* is independent, over short periods, of natural levels of inorganic turbidity. Contamination of their marsupia is probably one means by which inorganic turbidity can act as a deleterious factor. Inorganic and organic turbidity have only a limited influence on pleopod activity. *Corophium*, due to its stronger pleopod current, is better able than *Lembos* to withstand clay sedimentation. High levels of turbulence are more inhibitory to the normal activity of *Corophium* than *Lembos*.

# GENERAL INTRODUCTION.

"There is a crippling shortage of comprehensive monographs on the biology of individual species .... The benthie biocenose will be better understood only as its constituent taxa become better known."

M.R. Carriker (1967)

"Specialists recognize that much exploration and discovery remain to be accomplished in the Amphipoda."

J.L. Barnard (1969b)

This investigation arose directly from the interest of Dr. P.G. Moore in the structure and functioning of the kelp holdfast community. Moore (1971) conducted a wide scale survey of the fauna of kelp holdfasts (Laminaria hyperborea (Gunn.) Fosl.) in relation to pollution in northeast Britain. On the basis of several multivariate analyses Moore (1974) came to the following conclusion,

> "... any affects of pollution appear to be localized and subordinate in significance to a wider scale response to differences in sea-water turbidity. Matters are complicated, however, by the undoubted contribution of discharges to the suspended solids in the turbid area and whose exact importance is at present difficult to evaluate."

Moore has therefore implicated turbidity as a major factor affecting the structure of the holdfast community and he classified the faunal elements according to their association with this factor.

Further interpretation of his data was however severely hampered (1) because, as with any field survey, statistical correlations can only be interpreted as indications and not proof of causal relationships, and (2) because of the negligible amount of information available on the biology of the component species, the micro-environmental conditions within and immediately surrounding the holdfast and the response of the fauna to changes in these conditions.

In order to provide some of this much needed information Moore is currently examining the distribution of holdfast amphipods around the coast of Britain and their population dynamics at selected localities.

My own laboratory investigation was designed to supplement his field studies by observing and conducting experiments on two potential 'indicator' species. The project had two aims,

(1) To study the biology of two of these poorly known amphipods, *Lembos websteri* Bate 1856 and *Corophium bonnellii* Milne-Edwards 1830.

(2) To test whether the correlations between their presence and/or abundance and the environmental variables, turbulence and turbidity, reflected causal relationships.

Moore (1973b) correlated the absence of both species from certain areas of the northeast coast of Britain with high levels of sea water turbidity. He also has unpublished evidence to suggest that *L. websteri* reach their highest abundance in exposed localities, whilst *C. bonnellii* are more numerous in sheltered localities. Experiments were therefore conducted to examine the response of *Lembos* and *Corophium* to varying conditions of turbulence and turbidity.

Although equal amounts of time were devoted to each of the two aims, problems with experimental design resulted in much less information being gathered on the response of the two species to turbulence and turbidity, than on their general biology. The latter was nevertheless an essential prerequisite to accurate and incisive experimentation.

Both *Lembos* and *Corophium* live in tubes. As life in a tube has a dominant influence on their biology and since a large number of tubicolous amphipod species inhabit kelp holdfasts (Colman, 1940; Jones, 1948; Scarratt, 1961; Barnard, 1969a; Ghelardi, 1971; Jones, 1973; Moore, 1973c), the biology of these two species is particularly compared with the biology of other tubicolous amphipods.

Finally, it is important to appreciate that in the past, *Lembos* websteri and especially Corophium bonnellii, have sometimes been misidentified. Crawford (1937a) discusses the confusion between the identity of C. bonnellii, C. insidiosum n.sp., C. acherusicum Costa and C. crassicorne Bruzelius. Individuals identified as C. pseudacherusicum Schellenberg are considered to be either C. bonnellii or C. insidiosum. Crawford also attempted to judge the validity of references to C. bonnellii in the literature. For instance, he considered that specimens referred to as C. bonnellii, by Ussing and Stephensen (1924), are in fact C. insidiosum.

The validity of some old references to C. bonnellii, not mentioned by Crawford (1937a), have been discussed by other authors. Bassindale (1940) considers that the species from Portishead Dock, referred to by Mathews (1923) as C. bonnellii, may actually be C. acherusicum. The Marine Biological Association (1957) states that the Corophium species collected by Kitching et al. (1934), in south Devon, was C. sextoni Crawford and not C. bonnellii.

Even after Crawford's 1937 paper problems with identification still crop up. Just (1970) concludes that the species from Greenland, referred to as Corophium (bonelli G.O. Sars?) by Stephensen (1944) was in fact C. clarencense Shoemaker. Moore (pers. comm.) has examined the remaining material from kelp holdfasts collected by Scarratt (1961) and proposes that all individuals, from Scotland, identified as C. sextoni are in fact C. bonnellii. Similarly, Moore (pers. comm.) considers that Alexander (1969) might have mistaken C. sextoni for C. bonnellii, on the Northumberland coast.

In contrast to C. bonnellii, very little misidentification of L. websteri has so far come to light. Moore (pers. comm.) has re-examined specimens collected by Scarratt (1961) which he had labelled as Microdeutopus damnoniensis (Bate) and finds them to include individuals of L. websteri.

Ingle (1972) pointed out that in the past most authors have spelt the trivial name of Corophium as bonelli, which he shows is incorrect.

## CHAPTER I. GENERAL MATERIALS AND METHODS

*Lembos* and *Corophium* were collected from (1) *Laminaria* spp. holdfasts from Fintray Bay and Farland Point, Great Cumbrae and (2) the algal turf from Linne Mhuirich Rapids, Loch Sween. All observations and experiments were based on animals collected from Great Cumbrae, with the algal turf only providing some preserved material.

All holdfasts were collected from the sublittoral zone. At Fintray Bay, the holdfasts were attached to isolated boulders which emerged above an expanse of fine sand (plate 1). In contrast, the holdfasts at Farland Point were attached to a virtually continuous rock outcrop. As a result of the abundance of sand at Fintray Bay many of the holdfasts contained a good deal of sand. Only *Laminaria hyperborea* (Gunn.) Fosl. holdfasts were collected from Farland Point, whilst both *L.hyperborea* and *L.saccharina* (L.) Lamour holdfasts were collected from Fintray Bay (plates 2 and 3). Fintray Bay soon replaced Farland Point as the main collecting site, for two reasons. Firstly, Fintray Bay holdfasts contained a larger number of amphipods. Secondly, Fintray Bay was more sheltered and thus presented fewer problems for collections based on S.C.U.B.A. diving from the shore.

The algal turf consisted predominantly of filamentous red algae, *Asparagopsis armata* Harv. (Tetrasporangial phase) and *Bonnemaisonia hamifera* Hariot (Tetrasporangial phase), with a little *Corallina officinalis* Linn. (identification by J.J.P. Clokie).

Regular holdfast collections were made to provide fresh animals for laboratory work. Observations and experiments were never conducted on animals which had been in the laboratory for more than two weeks. Collected holdfasts were placed in a shallow dish and broken up with a strong knife. As a result, many of the

## PLATE 1.

FINTRAY BAY AT A LOW SPRING TIDE IN MARCH 1976. NOTE THE LAMINARIA COVERED BOULDERS. THE SUBLITTORAL KELP ZONE HAS A SIMILAR APPEARANCE. ANJA IS ABOUT 1.5m TALL.

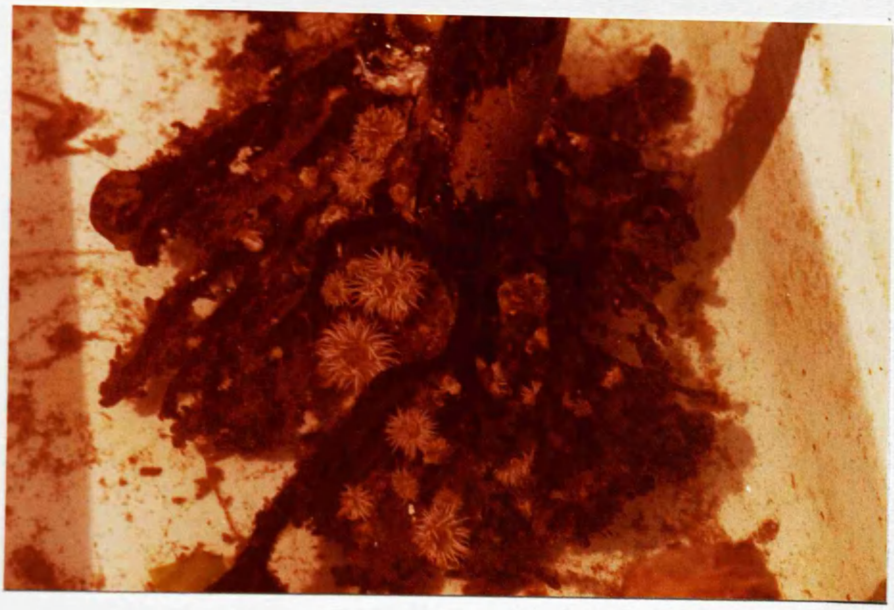
## PLATE 2.

COMPARISON OF THE HOLDFASTS OF *LAMINARIA SACCHARINA* (LEFT)AND *LAMINARIA HYPERBOREA* (RIGHT). DIAMETER OF COIN IS 28mm.

## PLATE 3.

A *LAMINARIA HYPERBOREA* HOLDFAST COVERED BY WATER. NOTE THE SEDIMENT BETWEEN THE HAPTERA.

THE *LAMINARIA* HOLDFASTS, IN BOTH PLATES, ARE FROM FINTRAY BAY.



amphipods moved into the surrounding water. *Lembos* and *Corophium* were identified with the naked eye and were easily caught with a pipette. The appendages and body regions of both species, mentioned later in the text, are illustrated in figures 1 and 2. The pleon and urosome constitute the abdomen. Normally the members of each species were partitioned into different categories according to the following criteria.

*Corophium*

Mature Female - fully developed brood plates forming a functional marsupium.

Immatures - the remainder (there are no morphological male *Corophium*).

*Lembos*

Mature Females - fully developed brood plates forming a functional marsupium.

Males - long, dense setae on the anterior margins of the carpus and propus, of their enlarged gnathopods.

Juveniles - the remainder (not called immatures because sexually mature males can not be identified).

Sometimes no distinction was made between the mature and immature females of each species, all of which bear brood plates. The identification of *L.websteri* is based upon male characteristics. As male *L.longipes* (Lilljeborg) were never found in the collected holdfasts the females were arbitrarily identified as *L.websteri*. Members of the genera *Aora* and *Microdeutopus* were extremely rare in the holdfasts and could be distinguished from *L.websteri* by their lack of a longitudinal, mid-dorsal dark head band (Moore, pers. comm.).

FIG. 1.

A MATURE FEMALE LEMBOS WEBSTERI.
DRAWN FROM A LIVE ANIMAL INHABITING A GLASS TUBE, BY JILL CLOKIE.

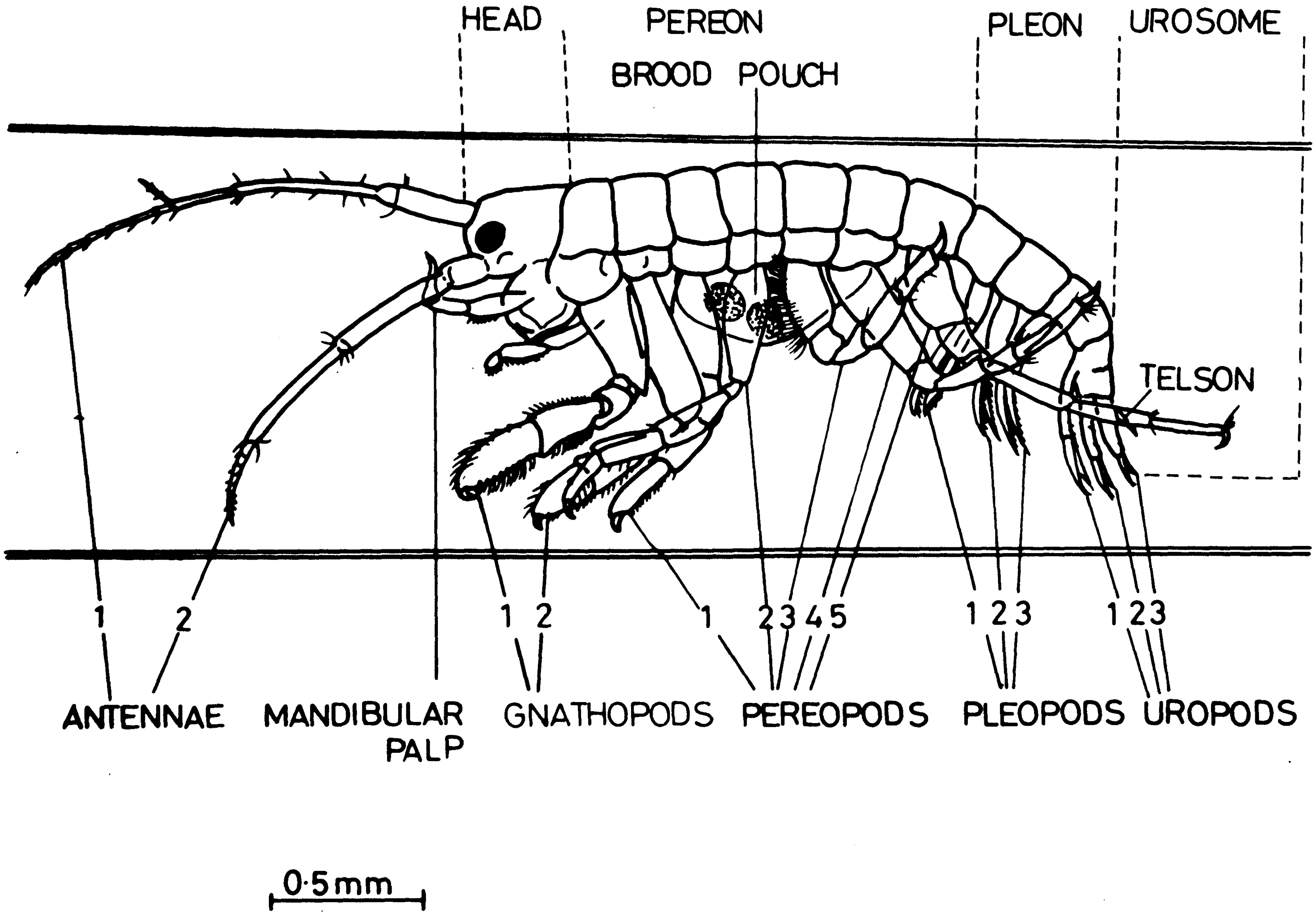
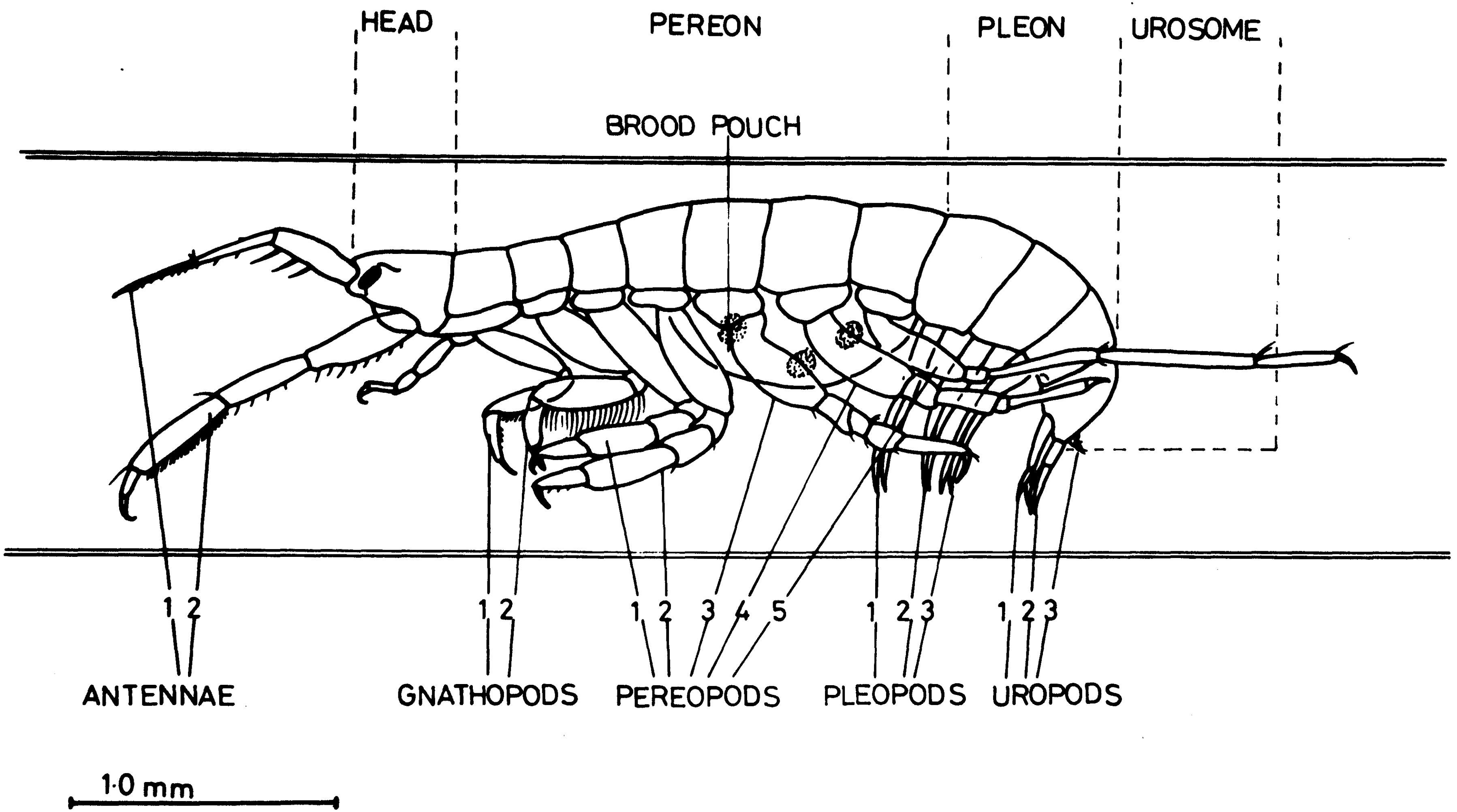

HEAD
PEREON
PLEON
UROSOME
BROOD POUCH
TELSON
1
2
1 2
1
2 3 4 5
1 2 3
1 2 3
ANTENNAE
MANDIBULAR PALP
GNATHOPODS
PEREOPODS
PLEOPODS
UROPODS
0·5mm

FIG. 2.

A MATURE FEMALE *COROPHIUM BONNELLII*.
DRAWN FROM A LIVE ANIMAL INHABITING A GLASS TUBE, BY JILL CLOKIE.


HEAD
PEREON
PLEON
UROSOME
BROOD POUCH
1 2
ANTENNAE
1 2
GNATHOPODS
1 2 3 4 5
PEREOPODS
1 2 3
PLEOPODS
1 2 3
UROPODS
1·0 mm

The amphipods were kept in shallow dishes 50 x 30 cm, filled to a depth of c.5 cm with clear sea water. Organic detritus (from laboratory aquaria) was scattered over the bottom of the dish, to provide a supply of food and tube-building material. The water was regularly agitated to facilitate oxygenation and to redistribute the detritus. The animals were maintained and all observations and experiments were conducted in a room whose air was chilled by the presence of large volumes of running sea water.

Body length, the distance from rostrum to telson along the straightened dorsal surface, was measured to the nearest 0.06 mm. All times are expressed as GMT. Much of the behavioural work was based on observations made, with the aid of a binocular microscope, on animals occupying detritus lined glass tubes.

Three staining techniques were employed. (1) The Mercury-Bromphenol Blue method for proteins. The procedure of Pearse (1968, p.607) was followed, using 1% $HgCl_2$ and 0.05% bromphenol blue in 2% aqueous acetic acid. (2) The Alcian Blue method for acid mucopolysaccharides, according to the procedure of Pearse (1968, p.672). (3) The Alcian Blue 1.0 procedure for sulphated muco-substances, according to the procedure of Pearse (1968, p.673).

BDH acid washed, fine sand was used in many experiments. Before use, this was always washed with boiling water and left overnight in running fresh water.

Unless stated otherwise statistical tests were always two-tailed. Chi-square tests, based on 2 x 2 contingency tables, always included Yates's correction and if any expected value was less than five an exact test was conducted (Bailey, 1964, p.59 and 61).

# CHAPTER II. TUBE BUILDING

## A. INTRODUCTION

The occupation of a home of some permanence, commonly called a tube, nest or burrow, is characteristic of many peracarid crustaceans. The majority of tanaids (Sars, 1899; Greve, 1967; Schiecke, 1973), a large number of amphipod genera (Barnard & Reish, 1959; Barnard, 1969a; Feeley & Wass, 1971; Bousfield, 1973; Fenwick, 1976) and some isopods(Issel, 1912; Schultz, 1969) can be described as being domiciliary. No mysids have been reported to live in burrows or tubes (J. Mauchline pers. comm.) and whilst cumaceans commonly burrow into the sediment, they only build temporary burrows (N.S. Jones, pers. comm.).

Amphipods obtain their homes in a variety of ways. Some species are commensal in the tubes of others, eg.*Listriella clymenellae* in the tube of the maldanaid polychaete *Clymenella torquata* (Mills, 1963), some take over the vacated homes of others, eg *Siphonoecetes sabateri* inhabits the empty shells of small gastropods (Gauthier, 1941), whilst others construct their own homes. This can be achieved by either gathering material together, eg.*Leptocheirus pilosus* (Goodhart, 1939), by burrowing into loose sediment, eg.*Corophium volutator* (Meadows & Reid, 1966) or by boring into a firm structure, eg.*Polycheira osborni* into the Ascidian *Amaroucium* (Skogsberg and Vansell, 1928). Finally, some species, which can not be considered as typically domiciliary, will occasionally occupy a tube, which has been constructed by another species eg. the empty tubes of *Ampithoe rubricata* are often the haunt of *Gammarus locusta* (Skutch, 1926).

A tubicolous existence appears to be characteristic of all species of the genera *Lembos* and *Corophium*. The morphology of field-collected tubes of *L.websteri* and *C.bonnellii* is described below and the relationship of these tubes to various aspects of their environment examined. The process of tube building is described. Finally, experiments were designed to help to explain some aspects of their field distribution.

As it was difficult to obtain undamaged tubes from *Laminaria* holdfasts additional observations were made on tubes located amongst short, turf-forming algae. These algae, being easier to tease apart, allowed more intact tubes to be extracted.

## B. FIELD STUDY: TUBE MORPHOLOGY AND THE RELATIONSHIP OF TUBES TO VARIOUS ASPECTS OF THEIR ENVIRONMENT.

### Materials and Methods.

Holdfasts of *Laminaria hyperborea* and *L.saccharina* were collected from Fintray Bay and algal turf was collected from the Linne Mhuirich Rapids.

The main difficulty was to ensure that the animals did not leave their tubes before the algae were examined. This problem was reduced by immersing the algae in boiling water, the moment they were removed from the sea, and then preserving the algae in formalin. Laboratory trials had shown that most individuals of both species were killed, in their tubes, within second of being immersed in boiling water. The problem of individuals leaving their tubes, as a result of disturbance, during collection, still remained. However, the number of individuals found to have been killed in their tubes was large enough to make this investigation worthwhile.

All observations and measurements refer to tubes occupied by one individual; unoccupied tubes, resembling those of *Lembos* and *Corophium*, were ignored. No distinction, however, was made between intact tubes and tubes which had suffered damage during processing. The tube lengths recorded are therefore only indicies of the true lengths. Measurements of *Corophium* tubes from *Laminaria* holdfasts and the algal turf and *Lembos* tubes from *Laminaria* holdfasts were based on material collected in June, September and October 1975, respectively.

The tubes of *Lembos* and *Corophium*, removed from *Laminaria* holdfasts, were divided into those that were firmly* attached to the haptera and those that were unattached or only loosely attached. A few unattached tubes, which were split open along their length, were ignored. They were probably firmly attached tubes which had been torn off during dissection.

The location of both tube entrances in *Laminaria* holdfasts was sought. It was of particular interest to establish whether the tubes did or did not open into crevices, which provided considerable shelter from the surrounding sea. Only limited success was achieved, as it was difficult to find both entrances of *Corophium* tubes and to judge how much shelter a particular crevice provided.

An analysis of variance was used to compare the slope and position of the regression lines of tube length versus the body length of the tube owner (Mather, 1951 p. 119).

## Results

### The morphology of *Lembos* and *Corophium* tubes from *Laminaria* holdfasts.

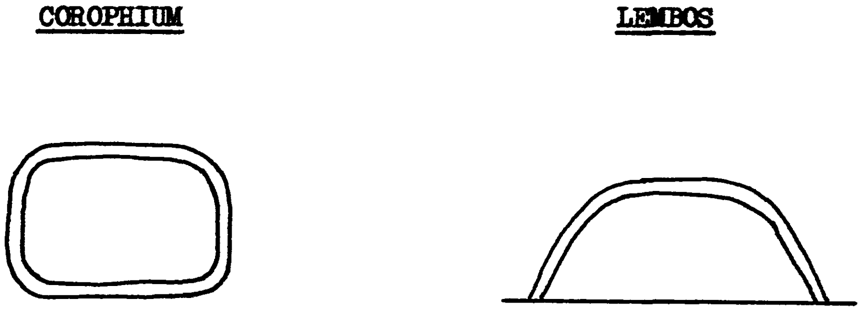
*Lembos* and *Corophium* occupied either straight or bent tubes. Whilst *Lembos* tubes were never more than slightly curved *Corophium* tubes could contain one or more distinct bends to produce a variety of shapes. Only one *Corophium* tube was found to be bent in the form of a symmetrical U. The tubes of both species had an entrance at each end which was of slightly smaller internal diameter than the rest of the tube (which was of constant diameter). In transverse section,

* This is a very much weaker attachment than is shown by some other sedentary animals, eg. adult barnacles.

away from the entrances, a *Corophium* tube resembles a square with rounded corners, while a *Lembos* tube resembles a hemisphere.

Fig. 3.

COROPHIUM AND LEMBOS TUBES IN TRANSVERSE SECTION


COROPHIUM

LEMBOS

The shape and size of the tubes of both species in transverse section was such that the tube formed a very close fit around the occupant. One small *Corophium* was found to be living in the tube of a larger individual and to have reduced the internal diameter by laying down new walls inside the old tube.

The tubes of both species consisted of a combination of sand and organic detritus. In some tubes sand predominated, whilst in others detritus predominated. Of lesser significance were small pieces of shell and small fragments of algae. The outside of each tube was rough, whilst the inside was smooth and glazed. There was often a thin layer of organic detritus on the inside of the central part of the tube. In both species the walls were thin, flexible and easily torn open. The walls of *Corophium* tubes were slightly less flexible and less easily torn open than those of *Lembos*.

In both species there was a positive logarithmic relationship between tube length and the body length of the occupant (Figs. 4 and 5). Whilst the slopes of the two regression lines are very similar their positions are different. Thus, on average, a 4 mm long *Corophium* occupied a tube just under 6 mm long, whilst the same sized *Lembos*

## FIG. 4.

THE RELATIONSHIP BETWEEN TUBE LENGTH AND BODY LENGTH OF THE TUBE OWNER, FOR COROPHIUM FROM LAMINARIA HOLDFASTS.

$$\log y = 0.6803 + 0.7163 (\log x - \log \bar{x})$$

Rearranged this becomes

$$\log y = 0.7163 \log x + (0.6803 - 0.7163 \log \bar{x})$$

which is equivalent to the equation of a straight line,

$$y = mx + c$$

in which

$$c = (0.6803 - 0.7163 \log \bar{x})$$

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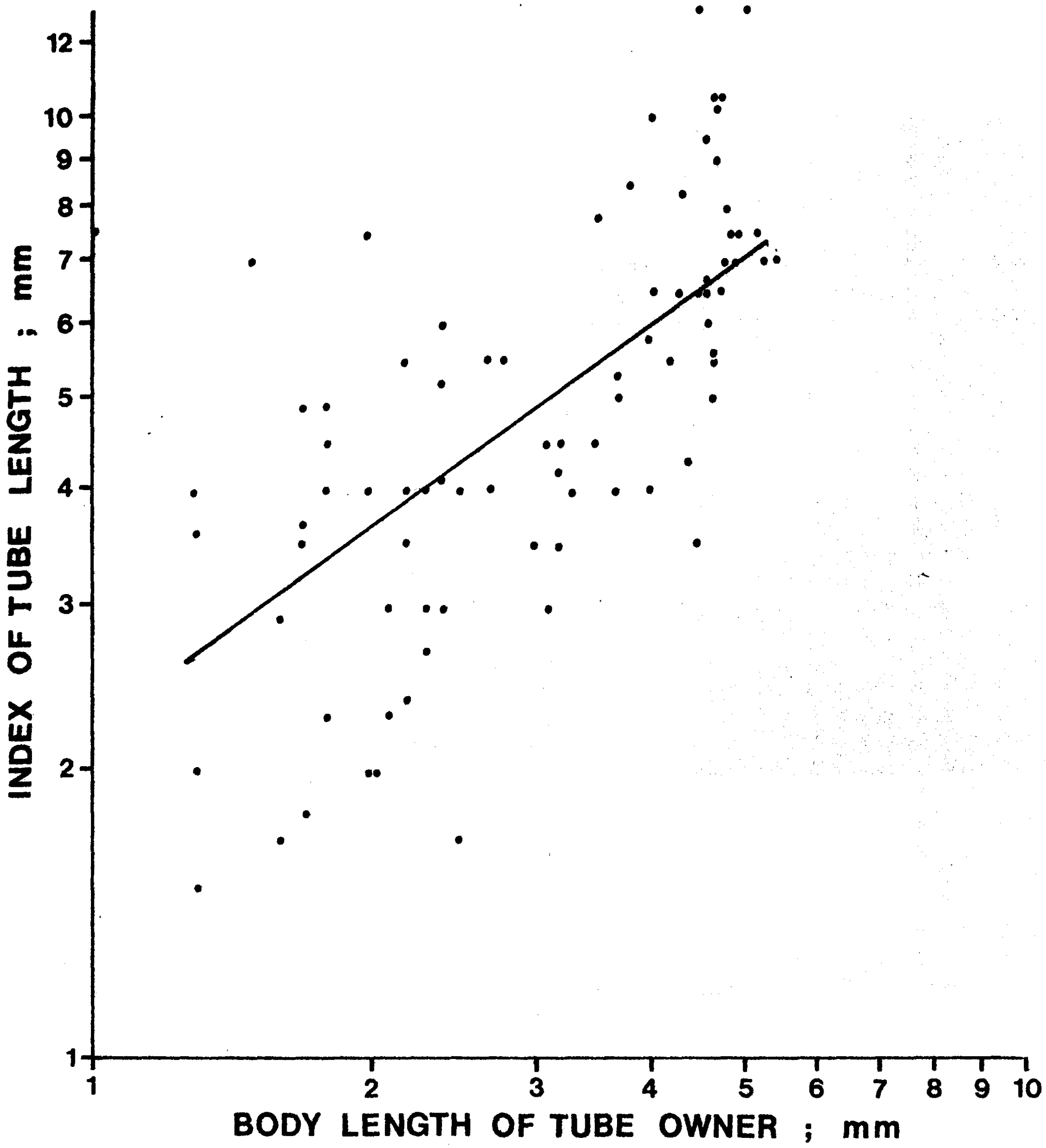

INDEX OF TUBE LENGTH ; mm
12
10
9
8
7
6
5
4
3
2
1
1
2
3
4
5
6
7
8
9
10
BODY LENGTH OF TUBE OWNER ; mm

## FIG. 5.

THE RELATIONSHIP BETWEEN TUBE LENGTH AND BODY LENGTH OF THE TUBE OWNER, FOR LEMBOS FROM LAMINARIA HOLDFASTS.

$$\log y = 0.4062 + 0.7470\,(\log x - \log \bar{x})$$

Rearranged this becomes

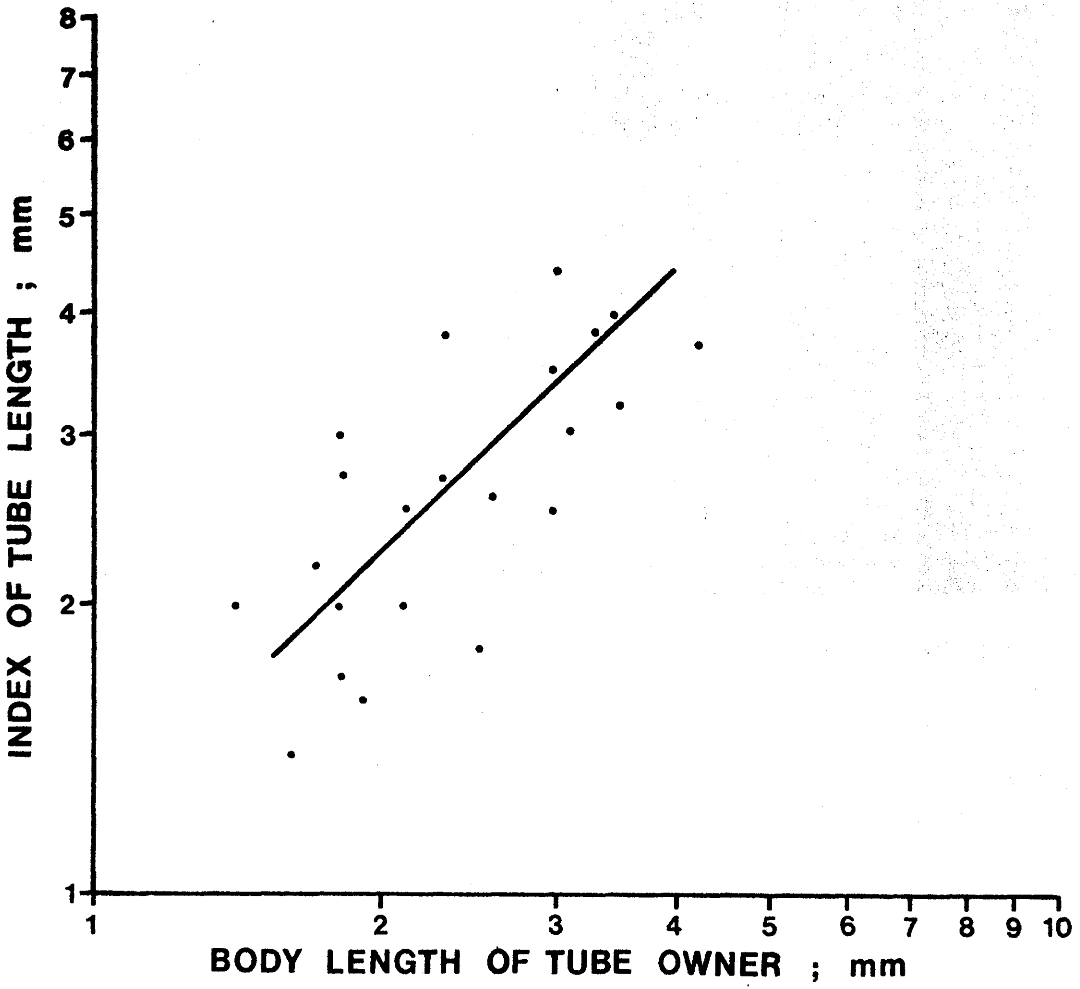
$$\log y = 0.7470 \log x + (0.4062 - 0.7470 \log \bar{x})$$

which is equivalent to the equation of a straight line,

$$y = mx + c$$

in which

$$c = (0.4062 - 0.7470 \log \bar{x})$$


INDEX OF TUBE LENGTH ; mm
8
7
6
5
4
3
2
1
1
2
3
4
5
6
7
8
9
10
BODY LENGTH OF TUBE OWNER ; mm

## FIG. 6.

**THE RELATIONSHIP BETWEEN TUBE LENGTH AND BODY LENGTH OF THE TUBE OWNER, FOR *COROPHIUM* FROM THE ALGAL TURF.**

$$\log y = 0.6911 + 0.8680\,(\log x - \log \bar{x})$$

Rearranged this becomes

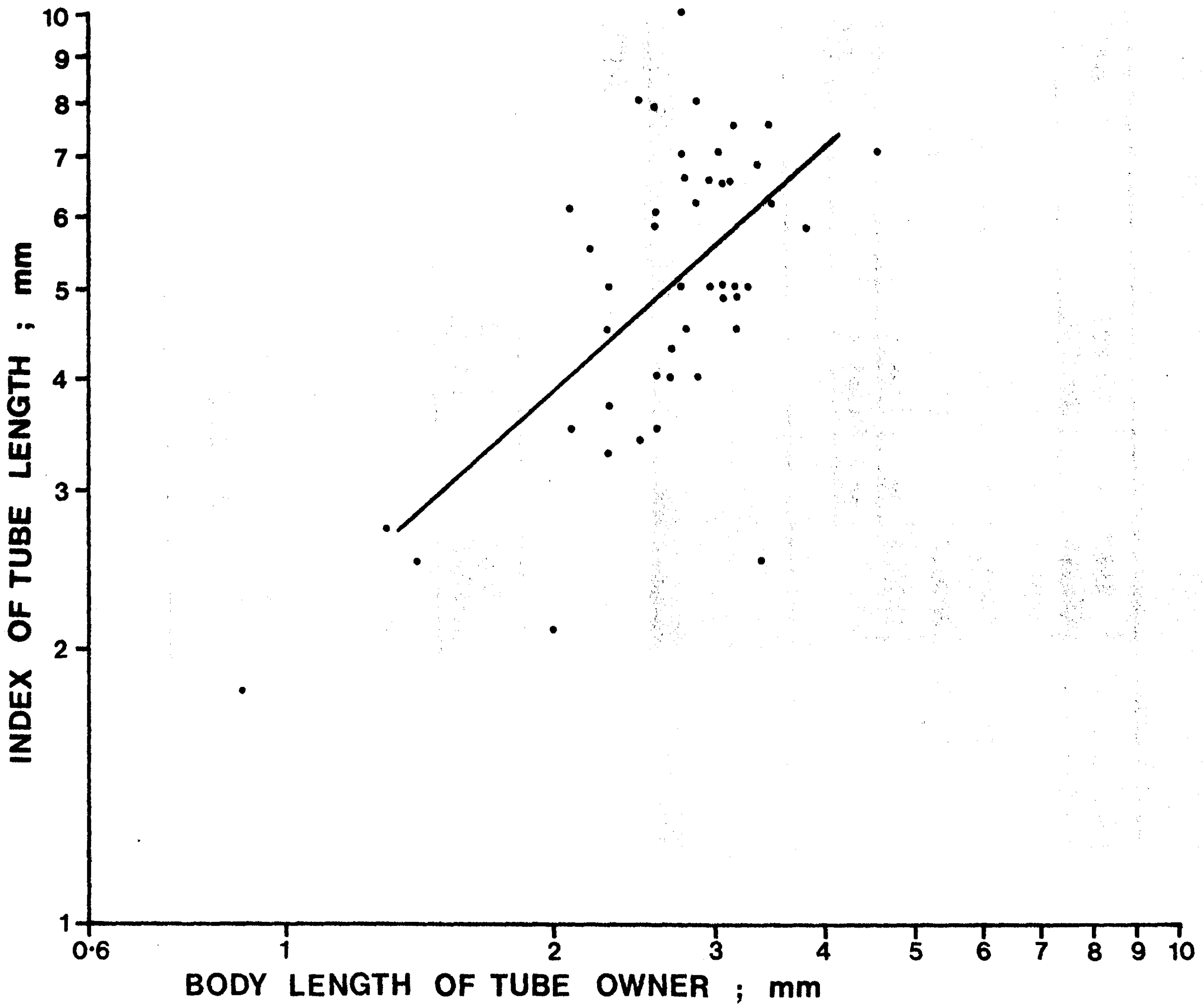
$$\log y = 0.8680 \log x + (0.6911 - 0.8680 \log \bar{x})$$

which is equivalent to the equation of a straight line,

$$y = mx + c$$

in which

$$c = (0.6911 - 0.8680 \log \bar{x})$$


INDEX OF TUBE LENGTH ; mm
10
9
8
7
6
5
4
3
2
1
0·6
1
2
3
4
5
6
7
8
9
10
BODY LENGTH OF TUBE OWNER ; mm

# TABLE 1.

## THE DIFFERENCE BETWEEN THE SLOPE AND POSITION OF REGRESSION LINES.

(a) COROPHIUM FROM LAMINARIA HOLDFASTS VERSUS LEMBOS FROM LAMINARIA HOLDFASTS.

| ITEM | SUM OF SQUARES | N | MEAN SQUARE | t | P |
|---|---|---|---|---|---|
| JOINT REGRESSION | 1.7070 | 1 | 1.7070 | | |
| DIFF. BT. REGRESSIONS | 0.0003 | 1 | 0.0003 | 0.1113 | $> 0.05$ |
| DIFF. BT. MEANS | 0.0036 | 1 | 0.0036 | 0.3865 | $> 0.05$ |
| ERROR | 2.3859 | 99 | 0.0241 | | |
| TOTAL | 4.0968 | 102 | | | |

(b) COROPHIUM FROM LAMINARIA HOLDFASTS VERSUS COROPHIUM FROM THE ALGAL TURF.

| ITEM | SUM OF SQUARES | N | MEAN SQUARE | t | P |
|---|---|---|---|---|---|
| JOINT REGRESSION | 1.9865 | 1 | 1.9865 | | |
| DIFF. BT. REGRESSIONS | 0.0120 | 1 | 0.0120 | 0.7161 | $> 0.05$ |
| DIFF. BT. MEANS | 4.4969 | 1 | 4.4969 | 13.8627 | $< 0.001$ |
| ERROR | 2.8969 | 124 | 0.0234 | | |
| TOTAL | 9.4043 | 127 | | | |

occupied a tube which was only just over 4 mm long. However, an analysis of variance (table 1a) showed that the difference in position of the two regression lines was not significant ($p > 0.05$).

*Corophium* tubes, occupied by an individual of body length 4.00-4.99 mm, were 3.15 ± 1.10 x (mean ± standard deviation) longer than wide ($n = 26$). The width of *Lembos* tubes could not be measured accurately, but tubes occupied by one individual were normally only slightly longer than they were wide.

### The morphology of *Lembos* and *Corophium* tubes from the algal turf (Plates 4, 5 and 6).

Within each species there was a great similarity between the tubes from the algal turf and those from *Laminaria* holdfasts. Some of the similarities and all of the differences will be mentioned.

There was a positive logarithmic relationship between the length of *Corophium* tubes and the body length of the occupant (Fig. 6). An analysis of variance (table 1b) comparing this regression line with that for *Corophium* tubes from *Laminaria* holdfasts showed that there was no significant difference ($p > 0.05$) between their slopes, whilst there was a significant difference ($p < 0.001$) between their positions, ie. *Corophium* tubes from the holdfasts were longer, in relation to the body length of their occupants, than *Corophium* tubes from the algal turf. This may have been due to the greater sediment accumulation in the former habitat. Too few *Lembos* tubes were found to enable a regression analysis to be carried out.

As occurred in the *Laminaria* holdfasts the tubes of both species had entrances which were slightly narrower than the rest of the tube (table 2). *Corophium* tubes were again slightly more rigid and less easily torn open than *Lembos* tubes.

As compared with *Laminaria*, bent tubes were much less frequent and very few tubes consisted predominantly of sand and organic detritus.

## PLATE 4.

A *COROPHIUM* TUBE, FROM THE ALGAL TURF, BUILT MAINLY OUT OF FILAMENTOUS ALGAE. NOTE THE PRESENCE OF THE TUBE OWNER.

## PLATE 5.

A *COROPHIUM* TUBE, FROM THE ALGAL TURF, BUILT MAINLY OUT OF ORGANIC DETRITUS.

## PLATE 6.

A LEMBOS TUBE, FROM THE ALGAL TURF, ATTACHED TO A SOLID SURFACE. THE TUBE OWNER HAS PARTIALLY EMERGED FROM ONE ENTRANCE. THE TUBE IS BUILT OUT OF DETRITUS AND FILAMENTOUS ALGAE.

# TABLE 2

## DIMENSIONS OF SOME *COROPHIUM* TUBES FROM THE ALGAL TURF.

| BODY LENGTH OF TUBE OWNER * | MAIN PART OF TUBE | | TUBE ENTRANCE | |
|---|---|---|---|---|
| | EXT.DIAM. | INT.DIAM. | EXT.DIAM. | INT.DIAM. |
| 3.3 | 1.7 | 1.2 | 1.4 | 1.0 |
| 3.6 | 1.8 | 1.5 | NOT MEASURED | |
| 2.4 | 1.8 | 1.1 | NOT MEASURED | |
| 3.3 | 1.2 | 0.9 | 0.9 | 0.6 |
| 2.0 | 1.4 | 0.8 | 0.9 | 0.7 |
| 2.5 | 1.7 | 1.1 | NOT MEASURED | |

* ALL MEASUREMENTS IN mm

EXT. DIAM = EXTERNAL DIAMETER

INT. DIAM = INTERNAL DIAMETER

Both species normally occupied straight tubes consisting of filamentous algae (from the algal turf) and organic detritus. In some tubes the algal filaments predominated, whilst in others organic detritus predominated. The algal filaments were orientated so that they ran diagonally or at right angles to the long axis of the tube. Frequently, distinct transverse bands were present, formed by several adjacent filaments running at right angles to the long axis of the tube. A few small pieces of shell, non-filamentous algae and sand grains were also present in most tubes. Shell fragments (ranging from 0.2 to 0.7 mm along their longest axis) were removed from the tube of one small *Corophium* (body length 2 mm).

### The relationship of tubes from *Laminaria* holdfasts, to various aspects of their environment.

The tubes of both species were normally found in the gaps between the haptera. Very few *Lembos* and *Corophium* tubes were attached solely to the outer surface of an outer hapteron. Some *Corophium* tubes, located between the haptera, had both entrances opening into exposed surface crevices. Although some *Lembos* tubes had one entrance opening into an exposed surface crevice, none were found to have both entrances opening into such a crevice. Many *Lembos* tubes were located entirely within one of the narrow, partially occluded crevices, which were away from the surface of the holdfast. No *Corophium* tubes were found to be confined to one of these crevices, although their tubes could pass through them.

Most *Lembos* tubes were found to be 'firmly' attached to the haptera or to epiphytic barnacles and mussels. Most *Corophium* tubes, however, were found to be unattached or only loosely attached to solid surfaces (plate 8). The difference between the two species was highly significant (table 3). The preference of *Lembos* for a solid surface is also shown by individuals found outside their tubes. 79% of these individuals were touching a hapteron ($n = 34$). Normally when a *Lembos* tube was attached to a solid surface, wall material

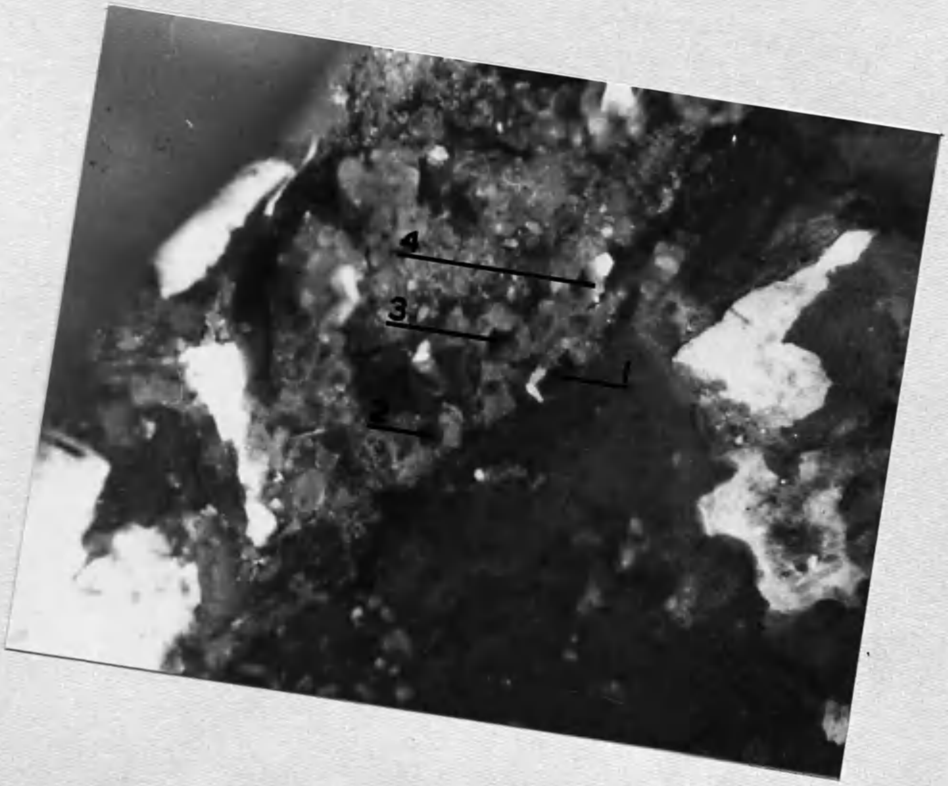
## PLATE 7.

A SMALL MAT OF *COROPHIUM* TUBES IN A *LAMINARIA* HOLDFAST. ONLY THE TUBE ENTRANCES ARE VISIBLE.

## PLATE 8.

DISPERSION OF AMPHIPOD TUBES WITH RESPECT TO SOLID SURFACES IN A *LAMINARIA* HOLDFAST. THE FOLLOWING TUBE ENTRANCES ARE VISIBLE.

1 - A *LEMBOS* TUBE FIRMLY ATTACHED TO A HAPTERON.
2 - A *COROPHIUM* TUBE ATTACHED TO A HAPTERON.
3 & 4 - *COROPHIUM* TUBES AWAY FROM THE HAPTERON.


4
3
1
2

## TABLE 3

## PERCENTAGE OF OCCUPIED TUBES WHICH ARE FIRMLY ATTACHED TO SOLID SURFACES IN LAMINARIA HOLDFASTS.

| SPECIES | HOLDFAST | % TUBES FIRMLY ATTACHED* | N | $\chi^2$ | P |
|---|---|---|---|---|---|
| COROPHIUM | 1 | 24.29 | 70 | ~~†~~<br>0·67 | $>0.05$ |
| COROPHIUM | 2 | 17.65 | 85 | | |
| LEMBOS | 1 | 87.50 | 16 | † | $>0.05$ |
| LEMBOS | 2 | 90.00 | 10 | | |
| COROPHIUM | 1 + 2 | 20.65 | 155 | 45.26 | $<0.001$ |
| LEMBOS | 1 + 2 | 88.46 | 26 | | |

* TO HAPTERA, BARNACLES OR MUSSELS.

† NO $\chi^2$ VALUE FOR EXACT TEST (SEE BAILEY 1964, P.61)

was not laid down against that surface. This was a less frequent occurrence in Corophium.

In addition to being attached to the holdfast, including a few Corophium tubes inside hollow haptera, the tubes of both species could be attached to other tubes. One or more Corophium tubes were frequently found to be closely attached to each other. Corophium tubes could be attached to Lembos tubes. However two Lembos tubes were never found to be attached, even though they could be less than 1 mm apart. In a wide gap between haptera, where sediment (particularly sand) had accumulated, there was often a large number of closely packed tubes, forming a fairly firm mat of tubes and consolidated sediment (plate 7). The mat consisted mainly of occupied and unoccupied Corophium tubes and tubes of spionid polychaetes. Lembos was not an important component of these mats, only occurring in small numbers where the mat joined the haptera. Although the formation of a mat made Corophium tubes harder to detach, than if they had been on their own in loose sediment, they were still relatively easy to dislodge.

Many Corophium tubes had at least one entrance raised 1-3 mm above the level of the surrounding sediment. All Lembos tubes, however, had their entrances flush with the sediment surface.

### The relationship of tubes, from the algal turf, to various aspects of their environment.

Only three Lembos tubes were found and all of them were attached to firm objects, eg. Corallina or shell fragments. Some Corophium tubes were also attached to firm objects but most were closely fastened to the filamentous algae of the turf. The three Lembos tubes were separate from each other. Some Corophium tubes were attached to other Corophium tubes but no mats were found. Two Lembos tubes were attached to Corophium tubes.

## C. THE FUNCTION AND ACTIVITY OF THE FIRST TWO PAIRS OF PEREOPODS.

### Function.

*Lembos* and *Corophium* contain very prominent glandular tissue in the proximal articles of their first and second pereopods. Alcian Blue was used to detect the presence of acid mucopolysaccharides, using intact specimens of both species. Fine filaments, containing acid mucopolysaccharides, were seen trailing from some of the dactyli of the first and second pereopods of *Lembos*. Each filament emerged from an orifice just behind the tip of the dactylus, and then ran along a narrow groove to its tip. These filaments were probably secreted by the glandular tissue.

### Activity.

In both *Lembos* and *Corophium* the term knitting best describes the jabbing action of their first and second pereopods against the tube wall. It always occurred when particles were being attached, but could also occur at other times.

Normally during knitting, all four limbs were active. An individual limb was never seen to knit independently. Occasionally, *Lembos* was seen to knit with the first and second pereopods of one side of the animal only, the two limbs of the opposite side remaining still.

The following description applies to both species. Each limb was extended towards the wall. On contact with the wall the dactylus was slowly and partially flexed, before the limb retracted away from the wall. The limb was then again extended, to jab against another part of the wall. Sometimes a limb jabbed the same point repeatedly (up to 4x). The first pereopods worked inside the second pereopods with the first and second pereopods of each side rarely jabbing the wall far beyond the mid-line of the animal. Sometimes the four limbs jabbed against the wall at different times (ie. they were out of phase).

On other occasions the first and second pereopods of each side were in phase but were out of phase with the first and second pereopods of the other side.

## D. TUBE BUILDING BEHAVIOUR.

On being placed in a dish with a thin layer of sediment many individuals, of both species, would eventually crawl to the edge of the dish. After a period of time they would start to build a tube against the wall of the dish.

### Lembos building tubes on the sediment surface : sand (250-500 $\mu$m).

*Lembos* commenced tube building by knitting the sand surface with its first and second pereopods. The animal then scooped up this sand with its first and second gnathopods to form a slight depression and a small pile of sand. The animal, which was sitting in the depression, then turned over onto its back, and using its anterior appendages scooped up sand from the pile. This sand was loosely stuck together, allowing the animal to cover itself with a flimsy shelter of sand. One edge of this shelter was attached to the wall of the dish, by the knitting activity of the first and second pereopods. The first and second pereopods then worked over the inside of the shelter, presumably to strengthen it.

The shelter was converted into a tube by having more material added to it. Each animal either scooped up sand grains inside its shelter, using its gnathopods, or, much more commonly, partially emerged from its shelter and scooped up sand grains with its second antennae and first gnathopods (see Chapter III for a more complete description of this behaviour). A sand grain was often held by the first gnathopods, close to the animals head and worked over by its mouthparts, before being attached to the tube. When a grain was attached the first gnathopods held it in place, whilst the knitting activity of the first and second pereopods secured it. Each animal could easily somersault round in its tube, to face the opposite direction and therefore was able to extend both ends of its shelter.

Corophium building tubes on the sediment surface : sand (grain size not recorded).

Much of the behaviour was the same as that described for *Lembos*. The animal lay on its back and covered itself with a flimsy shelter of loosely attached sand grains, which were then strengthened and extended into a tube. Only differences in the behaviour of the two species will be mentioned here.

When *Corophium* reached the edge of the dish it lay on its side and scooped sand towards it with its second antennae. This sand was then knitted by its first and second pereopods, sticking the sand grains together.

When *Corophium* partially emerged from its tube it only used its second antennae to scoop up sand grains (see Chapter III for a more complete description of this behaviour). Only very occasionally sand grains were worked over by the mouthparts before being attached to the tube.

Lembos and Corophium building tubes on the sediment surface : organic detritus (from aquaria).

Again both species started by accumulating a small pile of sediment, turning over onto their backs and then lifting the gathered material over themselves, to form a flimsy shelter. *Lembos* was not seen to form a depression in the sediment with its first and second gnathopods, instead it gathered detritus around itself with its second antennae. When *Lembos* lay on its back its flexed abdomen helped to support the gathered detritus.

The initial behaviour of *Corophium* also differed from that on fine sand, in that a little detritus was sometimes attached to the wall of the dish, before the animal turned over onto its back.

Some additional observations on the behaviour of Corophium were made. Frequently, the second antennae curled round onto the outside of the tube and appeared to increase the rigidity of the tube wall, making it easier for the first and second pereopods to attach material. Somersaulting was infrequent, the animal continuing to extend the tube in one direction for some time. Occasionally the animal would arch its body and push against the walls, in order to widen the tube.

### Lembos building tubes in the sediment : sand (250-500 μm).

Lembos burrowed vertically, head first, into the sand. When it had burrowed to a depth equal to its own body length it somersaulted round. It then started to knit with its first and second pereopods, presumably to stop the walls from collapsing. Later on the animal extended the vertical shaft into a U-shaped tube.

### Corophium building tubes in the sediment : sand (250-500 μm).

The second antennae first scooped out a small hollow into which the head penetrated. The first and second gnathopods and the first and second pereopods scooped out more sand and enlarged the hole. Corophium then either burrowed in vertically or at an angle. When it burrowed in vertically the exposed abdomen was held perpendicular to the sediment surface and the pleopods were beaten quickly, presumably to aid penetration. When the animal was virtually under the sediment the abdomen was flexed and extended several times, to provide extra thrust, by pushing against the sand. Once the animal had burrowed to a depth equal to its own body length it somersaulted round and started to knit with its first and second pereopods. Sometimes an effort was made to widen the tube by arching its body. Later, the other end of the tube was extended to create a U-shaped tube. Tubes could be built which extended to a depth equal to twice the body length of the animal, but normally they were shallower than this.

When the animal burrowed in at an angle the exposed abdomen always remained in contact with the sediment surface. A shallow tube was built, which was completed sooner than those built by burrowing vertically.

## E. MORPHOLOGY OF TUBES BUILT IN THE LABORATORY.

The morphology of *Lembos* and *Corophium* tubes, built in the laboratory, closely resembled the field-collected tubes. Only two features will be mentioned here. Firstly, the shape of the tubes could be adapted to meet variations in the topography of their surroundings. This was particularly noticeable in *Corophium* tubes, which sometimes were bent so as to run over a neighbouring tube.

Secondly, both species, after building tubes on or in a layer of fine sand or mud, could raise both entrances above the sediment surface. These extensions were uncommon in *Lembos* and were never more than 1 mm above the substratum. In *Corophium* they were much more common and, under certain circumstances, one entrance was lengthened enormously to produce a J-shaped tube. J-shaped tubes were built by some of the individuals, which were kept singly in small dishes, with a layer of mud but without aeration, for 17 days. 5 individuals, all less than 3.5 mm long, had raised one end of their tubes between 9.5 and 14 mm, above the sediment surface. These extensions were attached to the wall of the dish.

## F. THE TUBE BINDING MATERIAL.

### Materials and Methods.

Acid washed sand (150-400$\mu$m) was placed in two acid washed dishes and covered with filtered sea water (no particles $> 0.3\mu$m). Each dish contained several individuals of the same species. After 16 h the sand tubes were removed and stained to test for the presence of mucopolysaccharides and proteins (see Chapter I for full details).

### Results.

The presence of acid and sulphated mucopolysaccharides was confirmed using Alcian Blue. The presence of proteins was not confirmed using Mercury - Bromphenol Blue.

Staining in Alcian Blue showed that the sand grains were bound together to form a tube, by a closely woven mesh of fine filaments. The web was only present on the faces of the grains, which formed the inside wall of the tube. These filaments were easily torn.

## G. THE PROPORTION OF TUBES WHICH ARE BUILT ON AS OPPOSED TO IN THE SEDIMENT.

### Materials and Methods.

A number of individuals of both species were placed in a dish containing acid washed sand (150-400 $\mu$m) and left for 16 h.

### Results.

All 19 *Lembos* tubes were built on the sediment surface, whilst 9 of the 13 *Corophium* tubes were built in the sediment. This difference in behaviour between the two species, on sand, is supported by other casual observations.

## H. THE PROPORTION OF TUBES WHICH ARE BUILT AGAINST THE WALL OF A DISH.

### Materials and Methods.

Dishes of 9 cm diameter and with vertical sides were used. The dishes were filled with filtered sea water (no particles $> 0.3 \mu$m) and covered to a depth of 1 cm with either acid washed sand (150-400 $\mu$m) or mud (63-125 $\mu$m). On sand, 15-20 individuals of one species were placed in each dish, whilst on mud, 10-15 individuals of one species were placed in each dish. The dishes were left in the dark for 24 h (sand) or 72 h (mud).

As the maximum width of the amphipod tubes was about 2 mm, each circular dish was considered to contain an outer ring, 2 mm from the edge and an inner circle. The area of the inner circle was 10.3x that of the outer ring.

## Results.

The results of several replicates are combined in table 4. Both species built more tubes against the wall of the dish than away from the wall. As the area of the inner circle was 10.3x that of the outer ring, both species showed a clear preference to build their tubes against the wall of the dish.

On both sand and mud the percentage of animals that built their tubes against the wall was higher for *Lembos* than for *Corophium*. The difference between the species was significant ($P<0.01$) on sand.

The percentage of individuals, of both species, which built their tubes against the wall of the dish was lower in the presence of mud than in the presence of sand. However, none of these differences was significant ($P>0.05$).

## I. THE TIME THAT ELAPSES BEFORE ANIMALS BUILD TUBES.

### Materials and Methods.

All experiments were conducted in 9 cm glass dishes containing filtered sea water (no particles > 0.3 $\mu$m) and a 1 cm layer of acid washed sand (150-400 $\mu$m). Each dish contained 14-16 individuals of one species. The water temperature ranged from 14-17°C. After a certain period of time the percentage of individuals in tubes was recorded.

| | | |
|---|---|---|
| Experiment 1 | lasted 35 min | and was conducted in the light. |
| Experiment 2 | lasted 24 h | and was under a natural light/ dark régime. |
| Experiment 3 | lasted 24 h | and was conducted in the dark. |

# TABLE 4

## PERCENTAGE OF INDIVIDUALS BUILDING THEIR TUBES AGAINST THE WALL OF A DISH.

| SPECIES | SUBSTRATUM | °/o | N | $\chi^2$ | P |
|---|---|---|---|---|---|
| LEMBOS | SAND | 92.73 | 55 | 6.95 | $< 0.01$ |
| COROPHIUM | SAND | 74.62 | 130 | | |
| LEMBOS | MUD | 80.95 | 21 | 2.69 | $> 0.05$ |
| COROPHIUM | MUD | 53.85 | 26 | | |
| LEMBOS | SAND | 92.73 | 55 | † | $> 0.05$ |
| LEMBOS | MUD | 80.95 | 21 | | |
| COROPHIUM | SAND | 74.62 | 130 | 3.60 | $> 0.05$ |
| COROPHIUM | MUD | 53.85 | 26 | | |

† No $\chi^2$ VALUE FOR EXACT TEST (SEE BAILEY, 1964, P.61).

### Results.

The results of several replicates are combined in Table 5. Experiment one showed that Corophium built their tubes much sooner ($p < 0.001$) after being put onto sand than female Lembos. Experiment two and three showed that female Lembos built their tubes much sooner ($p < 0.001$), after being put onto sand, than male Lembos.

## J. THE SPEED OF TUBE BUILDING.

### Materials and Methods.

Individual Corophium were timed from the moment they started to build a tube to the time a tube was built which was equal to the body length of the animal. The animals were provided with organic detritus and built their tubes in the edge of a small dish. A supply of detritus, within reach of the animal, was maintained. The water temperature was 16°C.

### Results.

The tubes were built very quickly (table 6). Once the animals started they continued to build without a break. Tube building did not stop when the tube length was equal to the occupant's length.

## K. TUBE BUILDING IN THE ABSENCE OF EXTRANEOUS MATERIAL.

### Materials and Methods.

Experiment 1. Pieces of clean glass tubing 10 mm long and of 1.5 mm internal diameter were placed into two bowls, with filtered seawater (no particles $> 0.3 \mu m$). Each bowl contained 20 individuals of one species. The animals were left for 5 days before the occupied tubes were removed and stained with Alcian Blue.

Experiment 2. Acid clean dishes with vertical sides were filled with filtered sea water (no particles $> 0.3 \mu m$). Each dish contained 20

## TABLE 5

## PERCENTAGE OF INDIVIDUALS IN TUBES AFTER A CERTAIN TIME.

| EXPERIMENT | SPECIES | SEX | °/o IN TUBES | N | P |
|---|---|---|---|---|---|
| 1. | COROPHIUM | FEMALE | 100 | 14 | $< 0.001$ |
| | LEMBOS | FEMALE | 0 | 31 | |
| 2. | LEMBOS | FEMALE | 100 | 14 | $< 0.001$ |
| | LEMBOS | MALE | 0 | 29 | |
| 3. | LEMBOS | FEMALE | 87.10 | 31 | $< 0.001$ |
| | LEMBOS | MALE | 0 | 28 | |

AN EXACT $\chi^2$ TEST PERFORMED (SEE BAILEY, 1964, P.61).

## TABLE 6

## TIME *COROPHIUM* TOOK TO BUILD A TUBE OF LENGTH EQUAL TO ITS OWN BODY LENGTH.

| AN. LENGTH (mm) | TIME (min) |
|---|---|
| 2.7 | 8 |
| 2.4 | 11 |
| 3.2 | 12.5 |
| 2.7 | 8 |
| 2.5 | 10 |

individuals of one species. After 3 days the animals were removed and the dishes stained with Alcian Blue.

## Results.

Experiment 1. 15 *Corophium* and 17 *Lembos* were found to be occupying glass tubes at the end of the experiment. All these tubes were lined with a meshwork of hardened mucus filaments. All *Corophium* had built a tube of filaments of exactly the same size and shape as those built out of detritus particles. Only 6 *Lembos* had built an entire tube, of normal shape and size, out of mucus filaments. The remaining *Lembos* were in partially constructed tubes.

Experiment 2. Both species laid down mucus filaments in the angle of the dish, but no tubes were built. Under the same conditions but on a different occasion a few *Corophium* built mucus tubes in the angle of the dish.

## L. DISCUSSION.

*L. websteri* and *C. bonnellii* are known to be able to build their own tubes (Enequist, 1949; Gomoiu and Müller, 1962; Schiecke, 1973). This was confirmed by my own observations. The morphology of the tubes occupied in the field was the same as those built in the laboratory. This suggests that *Lembos* and *Corophium* built their own tubes in the field. Hamond (1967) also reports that, "hundreds (*C. bonnellii*) were found apparently sharing the tubes of *Ampelisca tenuicornis* with the owners themselves."

The glandular tissue of the first and second pereopods, of both *Lembos* and *Corophium*, probably produced the mucus-containing filaments, which acted as a binding material for tube construction. Tube binding material may also have been derived from other sources. Ingle (1969) considered that the gland in the antennal conical process of *C. volutator* secreted this material. He also demonstrated the presence of mucus in the setule lumens of *C. volutator*. Goodhart (1939) considered that the dermal glands, scattered all over the body of *Leptocheirus pilosus*, probably secreted a mucus cement. *Lembos* may also have applied mucus to the sand grains when they were worked over by its mouthparts. However, staining with Alcian Blue, did not show copious mucus to be present on the mouthparts.

Lakshmana Rao and Shyamasundari (1963) concluded that the glandular tissue in the first and second pereopods of *C. triaenonyx* contained all the precursors of scleroproteins. For instance, they reported a positive protein reaction to Bromphenol Blue. In the present study a negative result was obtained when the tube binding material was subjected to this test. Lakshmana Rao and Shyamasundari do not report the results of any tests for mucopolysaccharides. In the present study the tube binding material was shown to contain acid and sulphated mucopolysaccharides. Further work is obviously needed to reconcile these seemingly conflicting results.

Tube building in both species certainly relies heavily on the knitting activity of the first and second pereopods. Similar behaviour also occurs in the family Ampithoidae (Holmes, 1901; Skutch, 1926; Barrett, 1966; Heller, 1968; Schiecke, 1973). Mills (1967) describes how the first and second pereopods of *Ampelisca abdita* secreted threads, which were stretched out around the body, by the movement of the urosome posteriorly. The location of the mucus containing threads, secreted by *Lembos* and *Corophium*, could not be discerned during tube building. However, in neither species was the urosome seen to move in such a way that suggested it was being used to stretch out threads around the animal.

Gomoiu and Müller (1962) found that field collected *C. bonnellii* occupied tubes 5-12 mm long. This agrees with my own findings. However, the methods I used to investigate the relationship of tube length to animal length and tube length to tube width, had certain limitations. Firstly, each regression analysis of the relationship between animal length and tube length, was based on material collected at different times of the year. Secondly, the tube lengths recorded were only indices of the true lengths, being a function of each tube's susceptibility to damage during dissection. Field collections showed that Corophium built longer tubes, in relation to its body length, than Lembos. Although the difference between the two species was not statistically significant there is reason to believe that a real difference between the two species does exist. Firstly, as Corophium tubes were more susceptible to shortening during dissection, the ratio of tube length to animal length was probably underestimated by a larger amount for Corophium, than for Lembos. Secondly, in the laboratory, Corophium again normally built longer tubes in relation to its body length than single Lembos.

In both species, the length of the tube was positively correlated with the body length of the occupant. This has also been reported in C. lacustre (Faletans, 1958) and C. volutator (Schodduyn, 1926; Noble, 1962). Other factors, including sedimentation, affect tube length. Laboratory observations have shown that both Lembos and Corophium can respond to being smothered by sand by lengthening their tubes. Many Laminaria holdfasts, whose interhaptera spaces were deeply filled with sand, contained particularly long tubes, resembling those of C. bonnellii.

Corophium was able to build a detritus tube equal to its own body length in less than 15 min. Lembos also built tubes very quickly, but individuals were not timed. Many other amphipods, under favourable conditions, build tubes within the same sort of time period as C. bonnellii (Holmes, 1901; Goodhart, 1939; Lakshmana and Shyamasundari, 1963; Barrett, 1966; Heller, 1968). Several of these authors state that amphipods continue to show building behaviour for several days after the tube is built. This also occurs in Lembos and Corophium.

Openings raised above the level of the surrounding sediment were more pronounced and more common in Corophium than Lembos. Raised openings are also features of the tubes of the sediment-burrowing species C. volutator (Meadows and Reid, 1966) and Ampelisca spp.

(Mills, 1967). One function of these raised openings is probably to reduce the chance of burial by mobile sediment. C. bonnellii, therefore, seems to be better prepared to cope with mobile sediment than L. websteri.

In the laboratory, in the absence of extraneous material, both species could build tubes out of tube-binding material. Entire tubes were more frequently occupied by Corophium. This may have been due to Lembos having either a lower tendency to build these tubes or a higher tendency to destroy them (see feeding chapter). Other amphipod species will construct tubes mostly of binding material (Smith, 1882; Heller, 1968; Schiecke, 1973). Such tubes are, however, only temporary, as extraneous material is soon attached to them.

Both Lembos and Corophium preferred to build tubes with, rather than without, extraneous material. In dishes with scattered detritus, both species avoided the bare spaces, only building their tubes in the detritus patches. A better-fitting crevice also appeared to be required before tubes were built in the absence of sediment. When sediment was present, tubes were readily built both in the angle of a dish, and inside the better-fitting crevices (provided by glass tubes). In the absence of sediment, tubes were less readily built in the angle of a dish than inside glass tubes. Tubes built only from binding material were easier to tear open than tubes containing extraneous material. The former were therefore less suited to turbulent conditions.

In the field, both species occupied tubes built out of a variety of materials. The tubes of C. bonnellii but not L. websteri have been described previously from field collections. C. bonnellii has been found in tubes of mud (Crawford, 1937a; König, 1966; Dommasnes, 1968; Forsman, 1970), detritus (Movaghar, 1964) and round and angular sand grains (Gomoiu and Müller, 1962). The materials used to build the tubes of both species probably depend on what is available. For instance, C. bonnellii from the algal turf normally occupied tubes consisting of filamentous algae and detritus, whilst in areas of sand accumulation, sand tubes were occupied. Size selection of particles for tube construction is reported to occur in C. volutator (Meadows, 1967) and is suggested to occur in C. triaenonyx (Lakshmana Rao and Shyamasundari, 1963). There was no obvious size selection of sand grains for tube construction by either species, in Laminaria holdfasts. As it was difficult to separate the tubes from the sediment that had accumulated between them, no attempt was made to confirm this impression by particle size analysis.

Both species can build their tubes out of the sediment that accumulates in the algae. Conditions of turbulence and turbidity which allow at least some sediment to accumulate in the algae must provide favourable conditions for Lembos and Corophium. Scarratt (1961) reports that the Corophiidae (including C. bonnellii) were the dominant family of amphipods in Laminaria holdfasts in conditions of heavy silting. L. websteri and C. bonnellii can be common in other habitats where sediment accumulates. Dahl (1948) reports L. websteri to be the dominant amphipod in a sample of sublittoral red algae, which contained a moderate amount of detritus. Truchot (1963) found L. websteri to be one of the characteristic amphipods in Cystoseira spp., which contained some or a large amount of silt. Leung Tack Kit (1972) found L. websteri to be common in areas of the old Port of Marseille experiencing heavy sedimentation. The following extremely high densities of C. bonnellii have been reported, $42{,}000/m^2$ on sand covered rocks (Gomoiu and Müller, 1962), $39{,}000/m^2$ on silt covered stones (Bacescu et al., 1963) and $25{,}000/m^2$ on Zostera growing on sand (Parker, 1975).

A major difference between Lembos and Corophium in Laminaria holdfasts was that most Corophium occupied tubes which were away from or only loosely attached to the haptera, whilst most Lembos occupied tubes which were firmly attached to the haptera. Also, in the algal turf, whilst many Corophium tubes were found attached to filamentous algae, Lembos tubes were only found attached to firm objects, eg. pieces of shell. Laboratory experiments support these field observations by showing that Lembos had a greater tendency (than Corophium) to build tubes against the walls of a dish.

Both species built tubes by gathering settled particles together or by burrowing into the sediment. On fine sand Corophium was more likely to build a tube by burrowing than Lembos. Corophium has a stronger pleopod current (Foster-Smith and Shillaker, in press), more highly developed setation on the basal articles of its fourth and fifth pereopods, a more depressed body and shorter pereopods, than Lembos. The setation on the basal articles of the fourth and fifth pereopods probably prevent particles from falling into the sediment-free channel in which the pleopods beat. All these features probably make Corophium a more efficient burrower than Lembos. This helps to explain why, in sand filled Laminaria holdfasts, most Corophium tubes were away from or only loosely attached to the haptera, whilst most Lembos tubes were firmly attached to the haptera.

Differences in burrowing abilities may also help to explain why Truchot (1963) found L. websteri to be one of the characteristic amphipods of Cystoseira spp. containing some or much silt, whilst C. acutum was one of the characteristic amphipods in Cystoseira containing sand. The effect of different types of sediment on the amphipod fauna of Laminaria holdfasts is not known, and would seem to be a profitable line of enquiry.

It is interesting to note that Lembos and Corophium did not burrow continuously. Both species somersaulted round, once they had excavated a vertical shaft. C. arenarium shows the same behaviour when burrowing (Ingle, 1966).

In Laminaria holdfasts several Corophium tubes could be attached to each other, forming a mat of tubes. Two Lembos tubes were never found to be attached. Mat formation by C. bonnellii has also been reported to occur on sediment covered rocks and stones (Gomoiu and Müller, 1962; Bacescu, 1972). The ability to form mats probably contributed to Corophium's ability to colonize the sand away from the haptera in Laminaria holdfasts. Isolated tubes surrounded by unconsolidated sediment would be more liable to be washed away than mats of tubes, which consolidate the sediment. The dense tubes of

*C. volutator* and *Ampelisca* spp. have been reported to consolidate the surface layers of sediments and thereby make them more stable (Mills, 1967; Rhoads, 1974; Trewin and Welsh, 1976).

Although in the laboratory, the tubes of both species can be found to be attached to those of conspecifics, the tendency to do so was much greater in *Corophium* than *Lembos*. If *Lembos* were placed in a dish without corners, at a high density and with an even scattering of detritus, tubes were built whose distribution was approximately uniform. These observations suggest that the pattern of distribution of tubes in the field may be influenced by the intensity of intraspecific aggression. Connell (1963) considered that this was an important factor in determining the distribution of the tubicolous amphipod, *Ericthonius brasiliensis*.

Nagle (1968) also considered that interspecific aggression prevented distribution overlap of *Microdeutopus* spp. and *Corophium* spp. (including *C. bonnellii*) on *Zostera*, covered with short epiphytes. As the outcome of these interactions was dependent on the amount of water movement Nagle's conclusions will be stated in full.

> "In quiet water (= still water), the larger *Microdeutopus* is able to pinch *Corophium* with its antennae, driving the smaller form away, but in moving water, *Corophium* is able to turn the tables on *Microdeutopus*. *Microdeutopus* is larger, strongly laterally compressed, and has relatively short fifth pereiopods; in currents, it struggles to hang onto the plant and can be easily dislodged by the smaller *Corophium* which is dorsoventrally compressed and which has longer fifth pereiopods. It presents a lower outline to the current, and its long fifth pereiopods render it more stable; hence it is able to manoeuver freely over the grass during current flow. Under these conditions it can evict *Microdeutopus*."

These experiments were conducted on animals which were completely outside their tubes. It is unknown how the occupation of a tube, by one of the contestants, would have influenced the outcome of the interactions. It would be interesting to conduct similar experiments on *L. websteri* and *C. bonnellii*.

*Corophium* normally started to build a tube within minutes of being put into a dish with fine sand. Gomoiu and Müller (1962) have observed the same behaviour in *C. bonnellii* in the presence of sand. *Lembos*, however, took much longer before it started to build a tube. The greater burrowing abilities of *Corophium* probably contributed to this difference. This however does not appear to be the complete explanation, because the same species difference was observed under a wide variety of conditions, eg. in the presence of particles which were not deep enough to burrow in and in conditions of light and darkness. It therefore seems that *Corophium* is less tolerant, than *Lembos*, of being out of its tube. Other species of *Corophium* have also been reported to start to build their tubes very quickly after being placed on a suitable substratum (Lakshmana Rao and Shyamasundari, 1963; Ingle, 1966; Meadows and Reid, 1966).

It is interesting to note that Meadows and Reid (1966) report that very small *C. volutator* took much longer to build tubes when the water was turbid. It is not known whether this was a direct response to the presence of suspended particles, or an indirect response to either reduced light intensity or increased light polarisation. Meadows and Reid (1966) and Andres (1970) report that increased light intensity stimulates burrowing behaviour in *C. volutator*. Gidney (1969) considered that polarised light might affect the behaviour of *C. volutator*, but he did not investigate this possibility.

Female *Lembos* will begin to build their tubes before males. Campbell and Meadows (1974) report the same difference in behaviour between male and female *C. volutator*.

*Lembos* and *Corophium* built tubes which could easily be ripped open or torn free from their attachments. In *Laminaria* holdfasts, *Corophium* tubes which were built on a smooth, convex hapteron were easier to dislodge than those which passed between the haptera. *Lembos* and *Corophium* tubes were present in both exposed and sheltered spaces in *Laminaria* holdfasts. However all the tubes which remained completely within a well sheltered space, were occupied by *Lembos*.

This suggests that they live in more sheltered spaces than *Corophium* and may be part of the reason why *Lembos* occurs in greater numbers, than *Corophium*, in exposed localities. Although this explanation is only tentative, due to the problem of finding both entrances of *Corophium* tubes, further support for its validity is found in other work. Scarratt (1961) recorded that the nests of Corophiidae (which included *C. bonnellii* but not *L. websteri*) tended to be located on the lower, outer regions of *Laminaria* holdfasts. Nagle (1968) reports that when *Zostera* was covered with long epiphytes the genus *Microdeutopus* lived close to the stalk of the macroplant, whilst the genus *Corophium* (including *C. bonnellii*) lived near the periphery.

It would be interesting to examine this problem experimentally. For instance, does *Lembos* prefer to build its tubes in crevices which provide better contact with its body than *Corophium*? The greater proportion of *Lembos* which built their tubes firmly attached to solid surfaces certainly suggests that this might be the case.

# CHAPTER III. FEEDING

## A. INTRODUCTION.

There is no comprehensive account of the nutritional biology of any species of domiciliary amphipod. Although the feeding behaviour of many species has been described, only a few quantitative studies exist (Greze, 1968, 1970, 1971, 1973; Peacock, 1972; Fenchel et al., 1975). An introductory investigation into the adaptive radiation of feeding behaviour in the Ampeliscidae is reported by Mills (1967). Studies of digestive physiology are restricted to the work of Agrawal (1963) and Kristensen (1972) on *Corophium volutator*.

The feeding biology of *Lembos websteri* has not been studied before and only Enequist (1949) briefly describes the feeding behaviour of *Corophium bonnellii*.

## B. GUT CONTENTS.

### Materials and Methods.

The gut contents of animals from three collections were examined. The first and second collections were made in April 1975 and consisted of *Laminaria* holdfasts from Fintray Bay, Great Cumbrae. The third collection was made in September 1975 and consisted of the short algal turf from Linne Mhuirich Rapids, Loch Sween.

Individuals of both species were killed immediately after removal from the sea, by immersing the algae in 5% formalin. A standard length of gut (0.63-1.25 mm), from a defined region (posterior to the stomach), was excised from each individual, before being squashed under a coverslip to disperse its contents.

In the third collection the length and width of the 3-5 largest particles in the guts of animals, 3.0-3.5 mm in length, were measured.

### Results.

### First collection.

The guts of both *Corophium* and *Lembos* were filled with fine particles which resembled organic detritus. Strands of filamentous algae were also present in Lembos, sometimes in large quantities. The algal filaments were Audouinella sp. (=Kylinia) and Giffordia sp. (identification by J.P. Clokie). No filamentous algae were found in Corophium.

## Second Collection.

The guts of 30 Corophium and 34 Lembos were examined. The gut contents of both species were dominated by fine particles which resembled organic detritus and when clumped together gave the gut contents a yellow-green or yellow-brown colour. Most guts also contained small translucent particles, of variable shape, which could not be identified.

Most guts, of both species, contained three types of larger particles. (1) Naviculoid diatoms, resembling those attached to sand grains in the holdfast, were more common in Lembos than Corophium (table 7). However, even in Lembos there were usually only a few present. The diatoms were mostly colourless, whilst similar forms in the holdfast sediment were green. (2) Laminar shaped particles of a red-brown or dark brown colour, which were probably algal fragments. (3) Particles of the shape and refractive quality of sand grains.

If individuals of approximately the same size were compared, particles in the gut contents of Lembos could reach a larger size than those of Corophium.

The only evidence of gut parasites was of trematode cercariae in Lembos. They were found in 21% of the females (n = 24) and 67% of the males ( n = 12) examined. They were normally found in the anterior part of the mid gut, often clumped together. The maximum number found in a single clump was 12.

## Third Collection.

The guts of 10 Corophium and 26 Lembos were examined. As in the second collection the gut contents of both species were dominated by fine particles, which resembled organic detritus. Most guts also contained small translucent particles which could not be

## TABLE 7

## PERCENTAGE OF LEMBOS AND COROPHIUM WITH NAVICULOID DIATOMS IN THEIR GUTS.

| SPECIES | CATEGORY | BODY * LENGTH(mm) | N | °/o WITH DIATOMS |
|---|---|---|---|---|
| COROPHIUM | MAT. FEMALE | 3.90±0.07 | 20 | 20.00 |
| | IMMAT. | 3.18±0.06 | 10 | 0 |
| LEMBOS | FEMALE | 4.24±0.15 | 13 | 69.23 |
| | MALE | 4.07±0.13 | 11 | 72.73 |
| | JUV. | 2.97±0.12 | 10 | 40.00 |

* MEAN ± STANDARD ERROR

identified and small particles which resembled sand grains.

In male and female *Lembos*, the larger particles included naviculoid diatoms, fragments of filamentous and non-filamentous algae, arthropod appendages and unidentifiable particles (table 9). Some of the filamentous algae was *Bonnemaisonia hamifera* (=Tetrasporangial phase); a component of the algal turf. No fragments of filamentous algae, naviculoid diatoms or arthropod appendages were found in *Corophium*.

The length and width of the longest gut particles of *Lembos* were respectively, $2.6^{x}$ and $1.5^{x}$ the size of those of *Corophium*. Both these differences were statistically significant (table 8).

## C. CAN LEMBOS AND COROPHIUM REMOVE ATTACHED DETRITUS FROM OUTSIDE THEIR TUBES?

### Materials and Methods.

Organic detritus, collected from laboratory aquaria, was allowed to attach to a dish by being left undisturbed for several weeks. The loose detritus was then tipped away and the dish refilled with clear sea water. 4 *Lembos* and 10 *Corophium*, occupying detritus-lined glass tubes, were placed in the dish.

### Results.

After 19 h all four *Lembos* had removed attached detritus from around both tube entrances, resulting in prominent detritus free areas. After the same period of time only one *Corophium* had removed enough detritus to produce a prominent detritus free area, around one tube entrance. It took a further 3 days for all the *Corophium* to produce these detritus free areas. It seems very likely that both species ingested this material.

## D. DEPOSIT FEEDING : QUALITATIVE OBSERVATIONS.

Both *Lembos* and *Corophium* could scoop up unattached organic and inorganic detritus from inside and outside their tubes and transfer it to their mouthparts. Inside their tubes they used their gnathopods to scoop up detritus. When partially emerged from their tubes, they would scoop up detritus with their antennae, with or without the help

## TABLE 8

### THE SIZE OF THE LARGEST PARTICLES IN THE GUT OF ANIMALS 3.0-3.55mm LONG.

| SPECIES | MAX. LENGTH OF PARTICLES (μm) * | D.F. | STATISTICAL VALUE | P. |
|---|---|---|---|---|
| LEMBOS | 62 ± 9 | 26 | $d = 4.03$ | $< 0.001$ |
| COROPHIUM | 24 ± 3 | | | |
| | WIDTH OF LONGEST PARTICLES (μm) | | | |
| LEMBOS | 24 ± 2 | 41 | $t = 3.17$ | $< 0.01$ |
| COROPHIUM | 16 ± 2 | | | |

* MEAN ± STANDARD ERROR.

## TABLE 9

### PERCENTAGE OCCURRENCE OF VARIOUS OBJECTS IN THE GUTS OF MALE AND FEMALE LEMBOS.

| OBJECT | FEMALE | | MALE | |
|---|---|---|---|---|
| | % | N | % | N |
| NAVICULOID DIATOM | 12.50 | 16 | 10.00 | 10 |
| FILAMENTOUS ALGAE | 43.75 | 16 | 60.00 | 10 |
| ARTHROPOD APPENDAGE | 12.50 | 16 | 20.00 | 10 |

of their gnathopods. This behaviour normally only lasted a few seconds, before the animal retreated quickly into its tube, with the gathered detritus. Some of the pereopods always remained in contact with the inside of the tube when an animal emerged, though occasionally an animal emerged so far that only the long, last pair of pereopods remained in contact. Once back in the tube the gathered detritus could either be transferred to the mouthparts by the first gnathopods, attached to the tube wall or removed from the tube.

When Corophium was partially out of its tube the second antennae were normally used to scoop up detritus. From time to time the first antennae and the first gnathopods were also used. Corophium picked up loose material in its tube by crawling forwards and scooping it up with the long filtering setae of its second gnathopods or with the dactyli of its first gnathopods. Corophium could also suck settled detritus, which had accumulated just outside one tube entrance, into its tube, by rapidly beating its pleopods.

When Lembos was partially out of its tube both pairs of antennae, both pairs of gnathopods and the first two pairs of pereopods have all been observed to scoop up detritus. However, the use of the first two pairs of pereopods was very unusual and normally only the second antennae, with or without the first gnathopods, were used. Lembos often continued to beat its pleopods when partially out of its tube and the resultant current sometimes sucked settled detritus into its tube.

## E. DEPOSIT FEEDING : QUANTITATIVE OBSERVATIONS.

### Materials and Methods.

Mature and immature Corophium were kept singly (n = 17) in 9 cm dishes which contained mud to a depth of 1 cm. The water was clear, unagitated, and ranged in temperature from 14.5 to 17.0° C.

Each tube was observed for 5 min, during the hours of daylight, on the first, third and fifth days following the start of the experiment.

The number of times each individual partially emerged from its tube and the total amount of time each individual spent partially out of its tube were recorded.

Results (table 10).

The mean number of times an individual partially emerged per 5 min observation period varied from 0.18 to 0.88. On all three occasions the animals spent less than 5% of their time partially out of their tubes.

Additional observations were made on other individuals en passant. These combined results may be summarized thus: (1) Individuals could partially emerge from either of the two tube entrances. (2) Out of the 38 instances of partial emergence recorded 34 involved the animal emerging by less than half its body length. (3) The mean duration spent partially out of their tubes was 8.8 s (n = 38).

## F. FILTER FEEDING : OBSERVATIONS.

### Corophium.

Filter feeding occurred when Corophium was positioned well inside its tube, with no appendages protruding. Water laden with suspended particles was sucked into the tube by the metachronal beating of its pleopods. The speed and amplitude of pleopod beating varied according to the position in which the abdomen was held. When the abdomen was held parallel to the rest of the body, the speed and amplitude of pleopod beating reached their maximum values. This rarely occurred. Normally, the abdomen was slightly flexed during filtering periods. The pleopod current flowed, with very few eddies, in an anterior to posterior direction past the animal.

Particles suspended in the pleopod current were filtered off by the highly modified second gnathopods. Each second gnathopod has two rows of long setae, bearing short setules, arising from the posterior margin of its merus. When held in the filtering position both second gnathopods are orientated so that their long setae are directed forwards. In this position each gnathopod has the tips of one row of setae touching the tube and the tips of the other row touching the ventral surface of the animal's head. Each gnathopod therefore carries a V-shaped filter basket, whose mouth is directed forwards. The filter basket of each second gnathopod overlaps slightly to form one large filter basket, which practically fills the whole cross-sectional area of the tube ventral to the animal. Thus virtually all of the pleopod current flows through

## TABLE 10

## QUANTITATIVE DATA ON COROPHIUM'S PARTIAL EMERGENCE BEHAVIOUR.

| DAYS IN DISH | % TIME SPENT PARTIALLY OUT OF THE TUBE * | MEAN NO. OF TIMES AN. EMERGES PER OBS. PERIOD OF 5 min. |
|---|---|---|
| 1 | 3.19±1.64 | 0.76 |
| 3 | 0.39±0.37 | 0.18 |
| 5 | 1.91±0.73 | 0.88 |

* MEAN ± STANDARD ERROR.

the gnathopod filter basket.

Adult Corophium could trap both large particles, eg. flocs of organic detritus, and very fine particles, eg. clay, in their gnathopod filter basket. The distance between the origins of two adjacent setules was measured in five adults of body lengths 3.8-4.7 mm. The intersetule distances were approximately the same within any one filter basket and between different individuals, always falling within the range 1.4-3.5 $\mu$m. The intersetule distances of five young (body length 1.1 mm), which had been removed from their mothers brood pouch, fell within the range 1.4-2.8 $\mu$m. However, they did not possess a true gnathopod filter basket, only a few long setae being present.

Particles trapped by the gnathopod filter basket are combed out by the short, stout setae which arise from the posterior margin of the first gnathopods. After a short period of filtering the first gnathopods move back together to meet the second gnathopods, which move slightly forwards. By this time the first gnathopods have twisted a little, so that their combing setae are parallel to the filtering setae of the second gnathopods. Both first gnathopods then move together to comb through the gnathopod filter basket, once only. Immediately afterwards the first gnathopods move towards the maxillipeds, where the two first gnathopods are rubbed quickly against each other. These movements probably transfer particles to the maxillipeds. Both organic detritus and inorganic clay particles have been seen to be transferred in this manner from the gnathopod filter basket to the mouthparts.

Corophium could pump water through its tube without filtering off particles. This was achieved by lifting the second gnathopods up under the animal's head. In this position the long setae run parallel to the long axis of the animal and only the slightly down-curved tips of the bottom row of setae trapped a few particles.

The gnathopod filter basket acted as the main filtering mechanism. Suspended particles were also trapped, to a very much lesser extent, by three other filters. Large particles, eg. flocs of organic detritus, could be trapped if they were carried into the space between the bases of the antennae. The closely placed antennae and their sparse short setae provide the trapping mechanism. The accumulated particles were infrequently combed out by the dactylus of one first gnathopod and transferred either to the maxillipeds or directly to the tube wall for attachment. The first gnathopods also infrequently trapped suspended particles.

An eddy current, which flowed around the base of the fourth and fifth pereopods, also carried particles into setae on the posterior margin of the basis of the fifth pereopods. Observing the animal from its left side the eddy was seen to flow in an anticlockwise direction. The setae were dense, long and in two rows to form a V-shaped filter. The setae bore setules which could trap very fine particles, eg. clay and dinoflagellates (c. 16 $\mu$m diameter). Large particles were not trapped. Removal of the accumulated material was not observed but was probably carried out by the scooping movements of the first gnathopods, when the abdomen was flexed under the body.

Once Corophium left its tube it appeared to be unable to filter feed because the pleopod current no longer flowed through the gnathopod filter basket. The pleopods mostly drew water from the sides of the animal. Some water did flow past the anterior end of the animal but it appeared to flow around and not through the filter basket.

### Lembos.

Filter feeding occurred when Lembos was positioned well inside its tube and when it was positioned such that its first and second antennae could protrude from one entrance. In both cases, water laden with suspended particles, was sucked into the tube by the metachronal beating of its pleopods. In the latter position, natural water turbulence also provided Lembos with suspended particles.

Again, the speed and amplitude of pleopod beating varied according to the position in which the abdomen was held. When the abdomen was held parallel to the rest of the body the speed and amplitude of pleopod beating reached their maximum values. As with Corophium, this only rarely occurred. Normally, the abdomen was flexed, but to a greater degree than Corophium, being held mostly at c. 90° to the rest of the body during filtering periods. The pleopod current flowed past the animal in an anterior to posterior direction, with a slightly more pronounced eddy current around the base of the fourth and fifth pereopods, than occurred in Corophium. Howevever, unlike Corophium there are no well developed pereopod setae to remove particles from this current.

Lembos had two main methods of trapping suspended particles, either of which could be used when an individual was positioned well inside its tube or when it had its antennae protruding outside. Firstly, each gnathopod was held still, with the larger first pair in front of the second pair. Particles suspended in the pleopod current were trapped by the expanded propal and carpal articles and by the inwardly-directed setae, which arise from the posterior margin of these two articles. Only a few of these setae bear fine setules and these are restricted to their distal margins. The intersetule distances were approximately the same on any one gnathopod and did not vary between individuals of different size and sex, so allowing each individual to filter very fine particles (table 11). Lembos, however, was better adapted at trapping large particles. This was due to the presence of gnathopods and setae, which did not completely fill the whole of the cross sectional area of the tube ventral to the animal and to the infrequent occurrence of setules on these setae. Particles trapped by the gnathopods were either transferred to the maxillipeds by the gnathopods moving forwards and upwards or rejected posteriorly (see later for a complete description of this behaviour). By lifting the gnathopods up under its head Lembos, like Corophium, could pump water through its tube without filtering off particles.

Secondly, the first antennae, second antennae and mandibular palps by flexing ventrally, could carry particles towards the animal's head, where they were either snatched by the gnathopods or transferred directly to the mouthparts. The antennae did not always flex ventrally after making contact with a suspended particle. The gnathopods would also snatch particles from suspension and this was sometimes associated with the animal jerking slightly forwards. All of these methods are better adapted for trapping larger particles.

Suspended particles are also trapped by other means. Sometimes large flocs of organic detritus, which had been carried by the pleopod current into the tube of a brooding female, became lodged between the swollen brood pouch and the tube wall. The second gnathopods can remove this material and transfer it to the mouthparts. The ventrally directed setae on the maxillipeds were also seen to trap a few particles.

## TABLE 11

## THE DISTANCE BETWEEN THE SETULES ON THE GNATHOPOD SETAE OF *LEMBOS*.

| GNATHOPOD | CATEGORY | BODY LENGTH(mm) | N | INTERSETULE DISTANCE (µm) | |
|---|---|---|---|---|---|
| | | | | MIN | MAX |
| 1 | FEMALE | 4.7-5.7 | 4 | 1.1 | 2.8 |
| 2 | | | | 0.7 | 2.1 |
| 1 | MALE | 4.9-5.3 | 4 | NOT MEASURED | * |
| 2 | | | | 0.7 | 2.1 |
| 1 | YOUNG FROM MOTHER'S MARSUPIUM | 1.1 | 3 | 0.5 | 0.5 |
| 2 | | | | NOT MEASURED * | |

N = No. OF ANIMALS EXAMINED.

* - NOT MEASURED BECAUSE THE ORIGIN OF ADJACENT SETULES WERE NOT DISTINCT.

## G. CAN LEMBOS AND COROPHIUM FILTER AND INGEST THE DINOFLAGELLATE CRICOSPHAERA SP.?

### Materials and Methods.

Two dishes, each containing 12 Lembos (4.40-5.25 mm in length) and 12 Corophium (3.85-5.63 mm in length), were used. The animals occupied tubes, which they had built themselves out of fine acid-washed sand. The amphipods had been starved for 3 days prior to the experiment to reduce the amount of material in their guts and make the green Cricosphaera cells easier to detect. The experimental dish contained a suspension of Cricosphaera cells whose diameter (mean ± S.D.) was $15.99 \pm 1.94\,\mu$m ($n = 31$). The control dish contained filtered sea water (no particles $> 0.3\,\mu$m). Both dishes were agitated by a magnetic stirrer for a 7 h exposure period.

### Results.

No control individuals had green material in their guts. All Corophium and most male and female Lembos, from the experimental dish, had bright green material in the main part of their guts and in their anterior gut caecae. The anterior gut caeca~~e~~ of both species from the experimental dish were frequently distended, due to the large amount of green material they contained.

Although individual dinoflagellate cells were never found in the guts of the experimental animals the super-abundance of green material suggests that they were ingested. Unfortunately, the ability of Lembos and Corophium to filter and ingest Cricosphaera was not proven, as one species may have filtered the Cricosphaera and produced faecal pellets, which were then ingested by the other species. To avoid this possibility further experiments were conducted, with only one species in each experimental dish. Again both species had green material in their guts indicating that Cricosphaera had been ingested. However, it did not prove that they could filter individual cells because, in every experiment, a considerable number of cells aggregated into large flakes.

## H. PREFERENCE TESTS FOR ALGAL FRAGMENTS.

### Materials and Methods.

1 mm lengths of *Polysiphonia* sp. (randomly selected) and 1 mm cubes of *Laminaria hyperborea* (from the meristematic region of the base of the lamina) were removed, on the day of the experiment, from algae which had been kept for a few days in an aquarium with running sea water.

Individual animals, occupying glass tubes, were offered single algal fragments, which were placed against the animal's antennae. The following measures of preference were used. Did the animal pick up and work over the fragment within 60 s of presentation? If it did, how many seconds out of the next 200 s did it continue to do so? The last measure is referred to as the index of mouthpart activity.

Each animal was tested once with one algal fragment. Most animals were provided with organic detritus prior to the experiments, some however were starved for 5-7 h before-hand.

### Results (tables 12 and 13).

#### Comparison 1. *Lembos* (not starved) offered *Laminaria* versus *Lembos* (not starved) offered *Laminaria*.

The percentage of individuals that picked up and worked over the algae and the index of mouthpart activity was very similar in the two replicates. As the results did not differ significantly ($p > 0.05$) the two sets of data are combined for use in comparisons 2 and 3.

#### Comparison 2. *Lembos* (not starved) offered *Laminaria* versus *Lembos* (starved) offered *Laminaria*.

The percentage of individuals that picked up and worked over algae and the index of mouthpart activity were, respectively, $1.50^{x}$ and $1.87^{x}$ greater in starved animals. Both differences were statistically significant.

#### Comparison 3. *Lembos* (not starved) offered *Laminaria* versus *Corophium* (not starved) offered *Laminaria*.

The percentage of individuals that picked up and worked over algae

# TABLE 12

## PERCENTAGE OF LEMBOS AND COROPHIUM WHICH PICKED UP AND WORKED OVER OFFERED ALGAL FRAGMENTS.

| COMPARISON | SPECIES | STARVED | TEST ALGA | DAYS ALGA IN LAB. | N | °/oPICK UP AND WORK OVER | $\chi^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | LEMBOS | NO | LAMINARIA | 6 | 38 | 57.89 | 0.45 | $>0.05$ |
| | LEMBOS | NO | LAMINARIA | 7 | 28 | 46.43 | | |
| 2 | LEMBOS | NO | LAMINARIA | 6+7 | 66 | 53.03 | 6.26 | $< 0.05$ |
| | LEMBOS | YES | LAMINARIA | 5 | 39 | 79.49 | | |
| 3 | LEMBOS | NO | LAMINARIA | 6+7 | 66 | 53.03 | 22.96 | $< 0.001$ |
| | COROPHIUM | NO | LAMINARIA | 3 | 35 | 2.86 | | |
| 4 | COROPHIUM | NO | LAMINARIA | 3 | 35 | 2.86 | 16.51 | $< 0.001$ |
| | COROPHIUM | NO | POLYSIPHONIA | 3 | 38 | 47.37 | | |

N = NO. OF ANIMALS TESTED.

## TABLE 13

## THE INDEX OF MOUTHPART ACTIVITY FOR INDIVIDUALS WHICH PICKED UP AND WORKED OVER OFFERED ALGAL FRAGMENTS.

| COMPARISON | SPECIES | STARVED | TEST ALGA | DAYS ALGA IN LAB. | N | INDEX OF MOUTH-PART ACTIVITY (s) * | STAT. VALUE | P |
|---|---|---|---|---|---|---|---|---|
| 1 | LEMBOS | NO | LAMINARIA | 6 | 22 | 61.95±17.72 | t=-0.05 | > 0.05 |
| | LEMBOS | NO | LAMINARIA | 7 | 13 | 60.62±23.62 | | |
| 2 | LEMBOS | NO | LAMINARIA | 6&7 | 35 | 61.46±13.97 | t=-2.66 | =0.01 |
| | LEMBOS | YES | LAMINARIA | 5 | 31 | 115.03±14.46 | | |
| 4 | COROPHIUM | NO | POLYSIPHONIA | 3 | 18 | 15.78±6.45 | - | - |
| | COROPHIUM | NO | LAMINARIA | 3 | 1 | 5.00 | | |

* MEAN ± STANDARD ERROR.

N = NO. OF ANIMALS TESTED

was 18.5$^{x}$ greater in *Lembos* than *Corophium*. The only *Corophium* to pick up and work over an algal fragment did so for 5.0 s whilst *Lembos* did so for, on average, 61.5 s.

### Comparison 4. *Corophium* (not starved) offered *Laminaria* versus *Corophium* (not starved) offered *Polysiphonia*.

The percentage of *Corophium* which picked up and worked over algae was 16.6$^{x}$ greater when *Polysiphonia* was presented than when *Laminaria* was presented. However, both species were worked over for less than 20 s out of the potential 200 s.

## I. ANIMAL FOOD.

*Lembos* used its gnathopods to catch harpacticoid copepods which entered its tube. *Lembos* then bit into either the anterior or posterior ends of the copepod. *Corophium* could catch and ingest barnacle nauplii which entered its tube. Both species have been observed to catch ostracods in their gnathopods. The ostracod reacted by closing its valves and therefore remained undamaged when the amphipod manipulated the potential prey item in its mouthparts. When starved both species will eat dead conspecifics.

*Lembos* will readily ingest the cold, cooked yolk of chicken eggs! Mature female *Corophium* can remove and ingest eggs from their own brood pouches. The females of each species will also consume the eggs of the other species.

## J. EATING TUBE MATERIAL.

Both *Lembos* and *Corophium* could remove and ingest material from the walls of their tubes, particularly from the tube entrances. This was particularly common when individuals were kept without food. Under these conditions *Lembos* always removed more material than *Corophium*. *Lembos* either (a) pulled material off with the dactyli of its first gnathopods, (b) scooped it off using the inwardly directed setae of its second gnathopods or (c) bit it off directly with its mouthparts.

## K. REFECTION.

The defaecation behaviour of *Corophium* and *Lembos* was observed under the same conditions (in the presence of suspended detritus, suspended clay and filtered sea water). 98 *Lembos* defaecations were recorded with a maximum of 2 from the same individual. In 97 cases the faecal pellet was caught by the gnathopods, as soon as it emerged, and was transferred to the mouthparts. The mouthparts then worked over the pellet and, frequently, at least part of it was ingested. Of the 12 *Corophium* defaecations observed, all of which were from different individuals, only 1 faecal pellet was transferred by the gnathopods to the mouthparts, where it was briefly worked over.

Refection was therefore very common in *Lembos* but rather rare in *Corophium.* Casual observations of hundreds of other individuals, during the course of this study, support this conclusion.

Refection was equally common in male and female *Lembos* and was also shown by young individuals, which were in their mother's tube. Refection always consisted of a particular sequence of behaviour. The sequence started with the abdomen being flexed ventrally under the thorax and the gnathopods being extended back to meet it. The gnathopods were sometimes rubbed against the urosome before the faecal pellet emerged. Usually, only the second gnathopods were involved, with the two limbs working in phase and appearing to rub each side of the urosome, a few times, with their inwardly directed setae. Once the abdomen was flexed it contracted 1-$3^{x}$, causing a faecal pellet to be separated from the rest of the gut contents, at a point about half way along the first urosome segment. The pellet then moved quickly out of the anus and was caught by the second gnathopods. The second gnathopods transferred it to the first gnathopods, which in turn transferred it to the mouthparts. Only on two occasions did the second gnathopods appear to attempt to pull the faecal pellet out of the anus.

At 14.5° C two individuals 3mm and 4mm long took, respectively, 270 s and 180 s to ingest an entire faecal pellet.

Normally when *Corophium* defaecated, its abdomen was lifted up so as to be parallel with the thorax, the pleopod beat frequency and amplitude increased for a few seconds and the faecal pellet emerged quickly from the anus, to be carried out of the tube by the increased flow of the pleopod current. Occasionally, particularly when feeding conditions were poor, long faecal pellets were produced, which remained trailing from the animal's anus for a long time. Sometimes, when the animal flexed its abdomen under its thorax, the long pellet was transferred by the first gnathopods to the mouthparts.

## L. ARE COROPHIUM'S FAECAL PELLETS A FOOD SOURCE FOR LEMBOS?

### Materials and Methods.

Freshly produced Corophium faecal pellets were offered to Lembos. Each pellet was held in fine forceps outside an occupied Lembos tube. 4 Lembos were tested 3-4$^x$ with different pellets.

### Results.

All 4 Lembos partially emerged from their tubes to grab the offered pellets with their gnathopods, which were then worked over by the mouthparts. Although 3 individuals broke up these pellets it was not possible to ascertain whether material was ingested.

## M. THE MOVEMENT OF THE MOUTHPARTS WHEN WORKING OVER FOOD.

It is difficult to interpret the movement of the mouthparts as they are of small size, closely packed together, only partially visible and move quickly over small distances. In both species working over involved holding, rotating, breaking up, transport of particles towards and into the mouth and rejection of material away from the mouthparts. Every time a food item was worked over some or all of these processes occurred.

### Lembos.

Holding and rotation of material always occurred. The latter was a discontinuous but frequent process. Small narrow objects, eg. algal fragments or faecal pellets, were orientated such that their narrow side was held between the two maxillipeds, with the cylinder shaped faecal pellets being rotated end over end. When viewed from the animal's left side rotation was normally anticlockwise. Clockwise movements occurred infrequently, but they were so slight, that they were only brief interruptions of the normal direction of rotation.

When small objects were rotated the maxillules, maxillae and maxillipeds moved quickly, probably causing the object to rotate. Larger objects, eg. a large bolus of detritus, were held and rotated by the distal ends of the mouthparts, with the aid of the first gnathopods and sometimes the second gnathopods and first pereopods.

When eating soft material, eg. detritus or a faecal pellet, the maxillules, maxillae and maxillipeds moved, on average, much faster than the mandibles. The mandibles moved at a constant rate, in one plane, towards and away from each other. The other mouthparts, however, showed a considerable amount of variation in speed and moved with more of a scooping motion. When working over tougher items, eg. Ulva fragments, the maxillules, maxillae and maxillipeds moved much more slowly, in time with the movements of the mandibles.

Only after a period of starvation did the animals work over food for several minutes non-stop. Interruptions were often associated with the animal defaecating and working over the faecal pellet instead. During such periods the food item was either held by the gnathopods or was dropped, to lie on the floor of the tube.

Uningested material was either added to the tube (particularly near the two entrances) or rejected. Faecal pellets and detritus boluses were broken up and transformed into a laminar shape, before being added to the wall. Rejection normally involved the first and second gnathopods making rapid scooping movements, which carried material backwards under the animal's body. At the same time the pleopod current was briefly increased and carried material out of the tube. Less commonly, material was pushed by the gnathopods, out of the entrance the animal was facing.

## Corophium.

Small items were held by the mouthparts, whilst large masses were held with the help of the first gnathopods. Material which was not ingested was added to the tube or rejected. Like Lembos, Corophium most frequently attached material near the tube entrances, but unlike Lembos the faecal pellets were not normally broken up prior to attachment. Rejection behaviour was the same as occurred in Lembos, differing only in that the backwards scooping movements were restricted to the first gnathopods.

## N. THE INDEX OF GUT FULLNESS.

### Materials and Methods.

Laminaria holdfasts were collected on the 14th-15th December, 1974, 17-18th March, 1975, 14-15th June, 1975 and 10-11th October, 1975 from Fintray Bay, Great Cumbrae. Each sampling occasion commenced five days after the appearance of the new moon, ie. at the same time in the lunar month. During each 24 h sampling session 3 holdfasts were collected every 3 h. As the processing of each collection was very time consuming only the December, 1974 and June, 1975 collections have been worked through.

Immediately after collection the holdfasts were gently shaken in dilute formalin, causing many amphipods to leave the holdfasts before dying. Corophium and Lembos were then segregated into 5 categories; immature and mature Corophium and juvenile, male and female or mature female Lembos. Each category normally contained 30 individuals. Sometimes, due to the scarcity of animals in the holdfasts, some categories contained fewer individuals.

Immersion in formalin often resulted in hatched young leaving their mother's brood pouch. In order to ensure that the two categories, immature Corophium and juvenile Lembos, were composed solely of free living young no individuals smaller than the largest young known to occupy a female's brood pouch (1.5 mm) were included.

Gut contents were defined as any material of a dark colouration. They were easily seen through the body wall of Corophium. In Lembos, however, the gut contents were harder to see. Each animal had to be observed from all directions and occasionally a dissection was performed to verify the visual assessment. A dissection was also required, in both species, to observe the gut contents of females with extremely swollen ovaries.

In both Lembos and Corophium the gut, excluding the anterior and posterior caecae, resembles a tube. This tube, excluding the short oesophagus, runs parallel to the long axis of the animal from about half way along the head to the base of the telson. As gut length approximates quite closely to body length an index of gut fullness was calculated by expressing the length of the gut contents as a fraction of the body length. The width of the gut contents was not measured. Although the gut contents were sometimes very narrow, normally there was very little variation within or between individuals of the same species.

The mean index of gut fullness and its 95% confidence limits were calculated for each 3-hourly sample of each category.

$$\text{Mean Index of Gut Fullness} = R = \frac{\sum_{i=1}^{n} Y_i}{\sum_{i=1}^{n} X_i}$$

where

$Y_i$ = length of gut contents
$X_i$ = body length
n = number of individuals measured.

$$\text{95\% confidence limits of the mean index of gut fullness} = s(R) \times t_{(n-1)}$$

where s(R) = standard error of the mean
t = statistic t.
n = number of individuals measured.

As the mean index of gut fullness was a ratio, its standard error was calculated using the formula suggested by Snedecor and Cochran (1967, p. 537).

$$\text{Standard Error of Mean Index of Gut Fullness} = s(R) = \frac{1}{\bar{x}} \sqrt{\frac{\sum_{i=1}^{n} (Y_i - RX_i)^2}{n(n-1)}}$$

where, (J. Proctor, pers. comm.)

n = number of individuals measured

$$\bar{x} = \frac{\sum_{i=1}^{n} X_i}{n}$$

Mr. Proctor also confirmed the validity of using this formula in this particular context.

To calculate the mean index of gut fullness and its 95% confidence limits for some or all of the 3-hourly samples of each category the following formulae were used.

$$\text{Mean} = \frac{\sum_{i=1}^{n} R_i}{n}$$

$$\text{95\% confidence limits of the mean} = \sqrt{\frac{\sum_{i=1}^{n} (\text{95\% confidence limits of } R_i)^2}{n}}$$

where n = number of 3-hourly samples

Many of the frequency distributions of the index of gut fullness were not normal. However, these distributions were neither transformed nor analysed by non-parametric statistics, because for large samples, even when the underlying distributions are not normal, standard normal tests are approximately valid. The Central Limit Theorems guarantee that the mean and variance have asymptotically the same distribution, as if the underlying population were normal (J. Proctor, pers. comm.).

To test whether any two mean indices of gut fullness were significantly different at the 5% level the following calculations were performed (K. Donnelly, pers. comm.).

Estimated difference between the means = $R_1 - R_2$

95% confidence limits for this difference is

$$\pm \sqrt{(\text{95\% confidence limits of } R_1)^2 + (\text{95\% confidence limits of } R_2)^2}$$

If the estimated difference between the means ± 95% confidence limits does not include 0, then the difference between the means is significantly different at the 5% level.

This test can be applied when the sum of the individuals from both samples is more than 35 and when the variances are or are not equal.

The limits of day and night were defined by the times of sunrise and sunset in Glasgow, which is 11 km north of Fintray Bay. The tidal cycle was divided into low and high tide periods. The limits of each period were defined by the times of mid-ebb and mid-flood. These times were obtained from the tide gauge situated on Keppel Pier, Millport.

Did the vigorous body contortions evoked in an individual on being immersed in formalin result in a loss of gut contents? In order to investigate this possibility animals, whose guts contained material in at least the posterior region of their pleon, were immersed in 5% formalin.

In the first experiment the number of faecal pellets produced by each test animal was recorded. In the second experiment the number of faecal pellets and their lengths in relation to the body lengths of the animals were recorded.

## Results.

### Loss of gut contents when animals were immersed in formalin.

Immersion in formalin resulted in 2% of *Lembos* and 41% of *Corophium* producing faecal pellets (table 14). Experiment 2 showed that these pellets were equivalent to 10% of the body length of *Lembos* (n = 1) and 12% of the body length of *Corophium* (n = 10).

This suggests that *Corophium's* index of gut fullness would be underestimated. It must be realised, however, that during the sampling programme *Laminaria* holdfasts were immersed in formalin, which had a concentration less than 5% and the effects of formalin of this strength, on faecal pellet production, are not known.

### Index of gut fullness : comparison of different categories of each species. (table 15).

The between category comparisons which are significant at the 5% level are indicated below.

# TABLE 14

## PERCENTAGE OF INDIVIDUALS PRODUCING FAECAL PELLETS AS A RESULT OF IMMERSION IN 5°/o FORMALIN.

| EXP. | SPECIES | °/o PROD.F.P. | N |
|---|---|---|---|
| 1 | LEMBOS | 0 | 27 |
| | COROPHIUM | 52.6 | 19 |
| 2 | LEMBOS | 3.3 | 30 |
| | COROPHIUM | 33.33 | 30 |
| 1+2 | LEMBOS | 1.8 | 57 |
| | COROPHIUM | 40.8 | 49 |

N = NO. ANIMALS TESTED

## TABLE 15

### INDEX OF GUT FULLNESS : COMPARISON OF DIFFERENT CATEGORIES OF EACH SPECIES.

| DATE | SPECIES | CATEGORY | INDEX (A MEAN) | 95°/o C.L. | N | SIGNIFICANCE AT 5°/o LEVEL |
|---|---|---|---|---|---|---|
| DEC 1974 | COROPHIUM | MAT.FEMALE | 0.6642 | 0.0338 | 136 | SIG.DIFF |
| DEC 1974 | COROPHIUM | IMMATURE | 0.6180 | 0.0192 | 252 | |
| DEC 1974 | LEMBOS | FEMALE | 0.6433 | 0.0301 | 240 | NOT SIG.DIFF |
| DEC 1974 | LEMBOS | MALE | 0.6013 | 0.0316 | 250 | |
| DEC 1974 | LEMBOS | MALE | 0.6013 | 0.0316 | 250 | NOT SIG.DIFF |
| DEC 1974 | LEMBOS | JUVENILE | 0.5614 | 0.0327 | 218 | |
| DEC 1974 | LEMBOS | FEMALE | 0.6433 | 0.0301 | 240 | SIG.DIFF |
| DEC 1974 | LEMBOS | JUVENILE | 0.5614 | 0.0327 | 218 | |
| JUNE 1975 | COROPHIUM | MAT.FEMALE | 0.4852 | 0.0290 | 239 | SIG.DIFF |
| JUNE 1975 | COROPHIUM | IMMATURE | 0.3661 | 0.0281 | 231 | |
| JUNE 1975 | LEMBOS | MAT.FEMALE | 0.4665 | 0.0311 | 238 | SIG.DIFF |
| JUNE 1975 | LEMBOS | MALE | 0.3949 | 0.330 | 240 | |
| JUNE 1975 | LEMBOS | MALE | 0.3949 | 0.0330 | 240 | NOT.SIG.DIFF |
| JUNE 1975 | LEMBOS | JUVENILE | 0.3620 | 0.0442 | 166 | |
| JUNE 1975 | LEMBOS | MAT.FEMALE | 0.4665 | 0.0311 | 238 | SIG.DIFF. |
| JUNE 1975 | LEMBOS | JUVENILE | 0.3620 | 0.0442 | 166 | |

N = NO. OF INDIVIDUALS
95°/o C.L. = 95°/o CONFIDENCE LIMITS
INDEX = LENGTH OF GUT CONTENTS AS A FRACTION OF BODY LENGTH

## TABLE 16

## INDEX OF GUT FULLNESS : LEMBOS VERSUS COROPHIUM

| DATE | SPECIES | CATEGORY | INDEX (A MEAN) | 95°/o C.L. | N | SIGNIFICANCE AT 5°/o LEVEL |
|---|---|---|---|---|---|---|
| DEC 1974 | COROPHIUM | MAT. FEMALE | 0.6642 | 0.0338 | 136 | NOT SIG. DIFF |
| DEC 1974 | LEMBOS | FEMALE | 0.6433 | 0.0301 | 240 | |
| JUNE 1975 | COROPHIUM | MAT. FEMALE | 0.4852 | 0.0290 | 239 | NOT SIG. DIFF. |
| JUNE 1975 | LEMBOS | MAT. FEMALE | 0.4665 | 0.0311 | 238 | |

N = NO. OF INDIVIDUALS

## TABLE 17

## INDEX OF GUT FULLNESS : DECEMBER 1974 VERSUS JUNE 1975.

| DATE | SPECIES | CATEGORY | INDEX (A MEAN) | 95°/o C.L. | N | SIGNIFICANCE AT 5°/o LEVEL |
|---|---|---|---|---|---|---|
| DEC 1974 | COROPHIUM | MAT. FEMALE | 0.6642 | 0.0338 | 136 | SIG. DIFF |
| JUNE 1975 | COROPHIUM | MAT. FEMALE | 0.4852 | 0.0290 | 239 | |
| DEC 1974 | COROPHIUM | IMMATURE | 0.6180 | 0.0192 | 252 | SIG. DIFF |
| JUNE 1975 | COROPHIUM | IMMATURE | 0.3661 | 0.0281 | 231 | |
| DEC 1974 | LEMBOS | FEMALE | 0.6433 | 0.0301 | 240 | SIGN. DIFF |
| JUNE 1975 | LEMBOS | MAT. FEMALE | 0.4665 | 0.0311 | 238 | |
| DEC 1974 | LEMBOS | MALE | 0.6013 | 0.0316 | 250 | SIG. DIFF |
| JUNE 1975 | LEMBOS | MALE | 0.3949 | 0.0330 | 240 | |
| DEC 1974 | LEMBOS | JUVENILE | 0.5614 | 0.0327 | 218 | SIG. DIFF |
| JUNE 1975 | LEMBOS | JUVENILE | 0.3620 | 0.0442 | 166 | |

N = NO. OF INDIVIDUALS.

## TABLE 18

INDEX OF GUT FULLNESS : NIGHT VERSUS DAY.

| DATE | SPECIES | CATEGORY | NIGHT/ DAY | INDEX (A MEAN) | 95°/o C.L. | N | SIGNIFICANCE AT THE 5°/o LEVEL |
|---|---|---|---|---|---|---|---|
| DEC 74 | COROPHIUM | IMMATURE | NIGHT | 0.6178 | 0.0222 | 194 | NOT SIG.DIFF. |
| | | | DAY | 0.6187 | 0.0387 | 58 | |
| DEC 74 | COROPHIUM | MAT.FEMALE | NIGHT | 0.6790 | 0.0406 | 85 | NOT SIG.DIFF. |
| | | | DAY | 0.6199 | 0.0585 | 51 | |
| DEC 74 | LEMBOS | JUVENILE | NIGHT | 0.5610 | 0.0367 | 163 | NOT SIG.DIFF. |
| | | | DAY | 0.5626 | 0.0702 | 55 | |
| DEC 74 | LEMBOS | FEMALE | NIGHT | 0.6486 | 0.0354 | 180 | NOT SIG.DIFF. |
| | | | DAY | 0.6274 | 0.0566 | 60 | |
| DEC 74 | LEMBOS | MALE | NIGHT | 0.5959 | 0.0362 | 192 | NOT SIG.DIFF. |
| | | | DAY | 0.6173 | 0.0648 | 58 | |
| JUNE 75 | COROPHIUM | IMMATURE | NIGHT | 0.3358 | 0.0574 | 60 | NOT SIG.DIFF. |
| | | | DAY | 0.3763 | 0.0321 | 171 | |
| JUNE 75 | COROPHIUM | MAT.FEMALE | NIGHT | 0.4151 | 0.0656 | 60 | SIG.DIFF. |
| | | | DAY | 0.5085 | 0.0318 | 179 | |
| JUNE 75 | LEMBOS | JUVENILE | NIGHT | 0.3769 | 0.1180 | 38 | NOT SIG.DIFF. |
| | | | DAY | 0.3571 | 0.0439 | 128 | |
| JUNE 75 | LEMBOS | MAT.FEMALE | NIGHT | 0.4426 | 0.0663 | 60 | NOT SIG.DIFF. |
| | | | DAY | 0.4745 | 0.0351 | 178 | |
| JUNE 75 | LEMBOS | MALE | NIGHT | 0.3649 | 0.0642 | 60 | NOT SIG.DIFF. |
| | | | DAY | 0.4049 | 0.0384 | 180 | |

# TABLE 19

## INDEX OF GUT FULLNESS : LOW TIDE PERIOD VERSUS HIGH TIDE PERIOD.

| DATE | SPECIES | CATEGORY | TIDE PERIOD | INDEX (A MEAN) | 95°/oC.L. | N | SIGNIFICANCE AT 5°/o LEVEL |
|---|---|---|---|---|---|---|---|
| DEC 74 | COROPHIUM | IMMAT | LOW | 0.6419 | 0.0270 | 134 | SIG. DIFF. |
| | | | HIGH | 0.5942 | 0.0274 | 118 | |
| DEC 74 | COROPHIUM | MAT.FEMALE | LOW | 0.6731 | 0.0326 | 77 | NOT SIG.DIFF. |
| | | | HIGH | 0.6553 | 0.0592 | 59 | |
| DEC 74 | LEMBOS | JUV. | LOW | 0.5580 | 0.0474 | 114 | NOT SIG. DIFF. |
| | | | HIGH | 0.5648 | 0.0450 | 104 | |
| DEC 74 | LEMBOS | FEMALE | LOW | 0.6702 | 0.0379 | 120 | NOT SIG. DIFF. |
| | | | HIGH | 0.6163 | 0.0468 | 120 | |
| DEC 74 | LEMBOS | MALE | LOW | 0.6009 | 0.0447 | 132 | NOT SIG. DIFF. |
| | | | HIGH | 0.6017 | 0.0448 | 118 | |
| JUNE 75 | COROPHIUM | IMMAT | LOW | 0.4178 | 0.0357 | 111 | SIG. DIFF. |
| | | | HIGH | 0.3145 | 0.0433 | 120 | |
| JUNE 75 | COROPHIUM | MAT.FEMALE | LOW | 0.5151 | 0.0385 | 120 | SIG. DIFF. |
| | | | HIGH | 0.4552 | 0.0434 | 119 | |
| JUNE 75 | LEMBOS | JUV | LOW | 0.4211 | 0.0533 | 96 | SIG. DIFF. |
| | | | HIGH | 0.3030 | 0.0705 | 70 | |
| JUNE 75 | LEMBOS | MAT.FEMALE | LOW | 0.5273 | 0.0435 | 118 | SIG. DIFF. |
| | | | HIGH | 0.4058 | 0.0444 | 120 | |
| JUNE 75 | LEMBOS | MALE | LOW | 0.4404 | 0.0486 | 120 | SIG.DIFF. |
| | | | HIGH | 0.3494 | 0.0446 | 120 | |

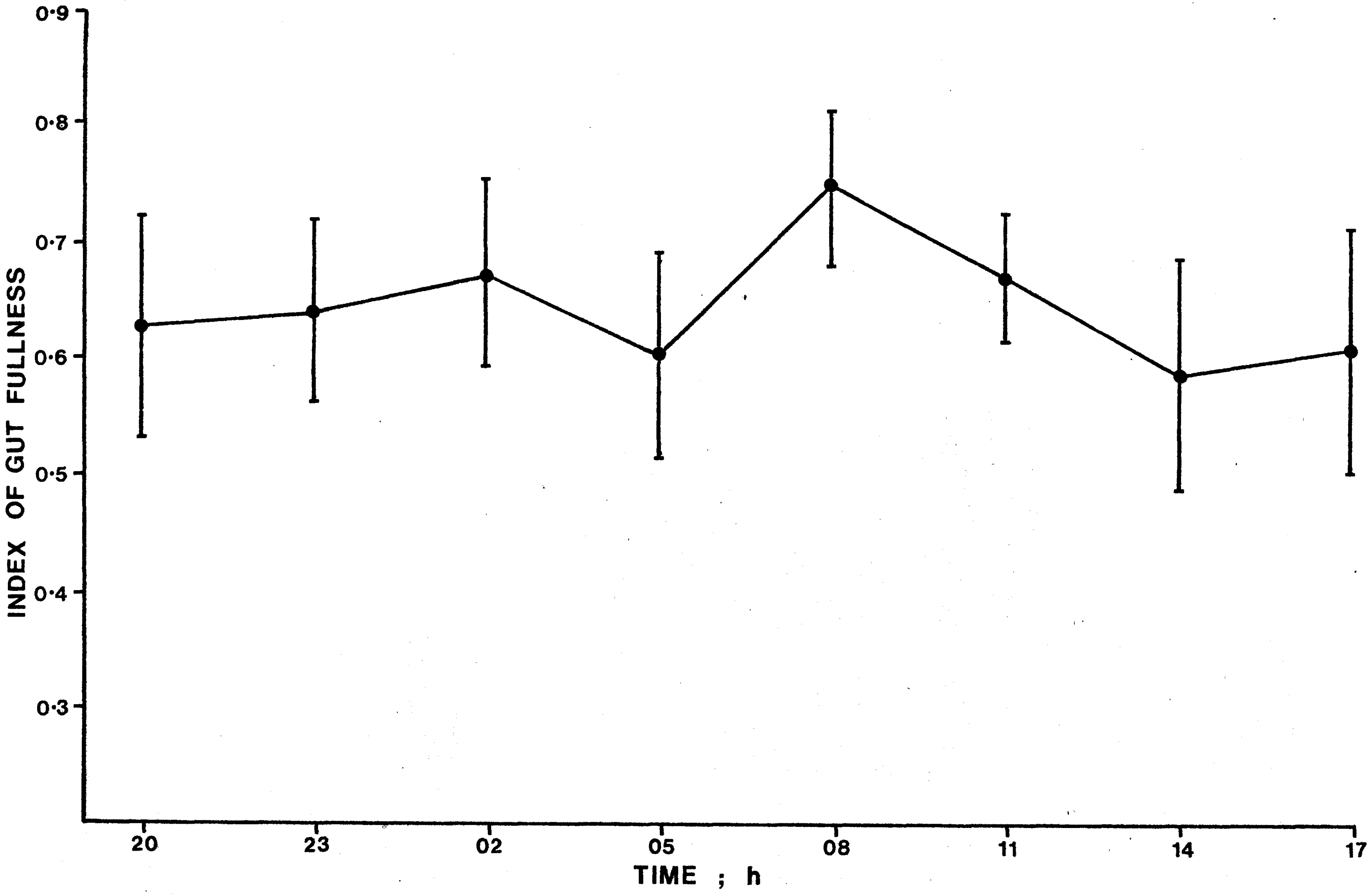
## FIG. 7a.

INDEX OF GUT FULLNESS: VARIATION WITHIN A 24 HOUR PERIOD.
FEMALE LEMBOS IN DECEMBER 1974.

INDEX = LENGTH OF GUT CONTENTS AS A FRACTION OF BODY LENGTH.
EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNRISE 08.44 SUNSET 15.43.

| | |
|---|---|
| LOW TIDE | 20.55 |
| HIGH TIDE | 03.30 |
| LOW TIDE | 08.40 |
| HIGH TIDE | 15.35 |


0·9
0·8
0·7
0·6
0·5
0·4
0·3
INDEX OF GUT FULLNESS
20
23
02
05
08
11
14
17
TIME ; h

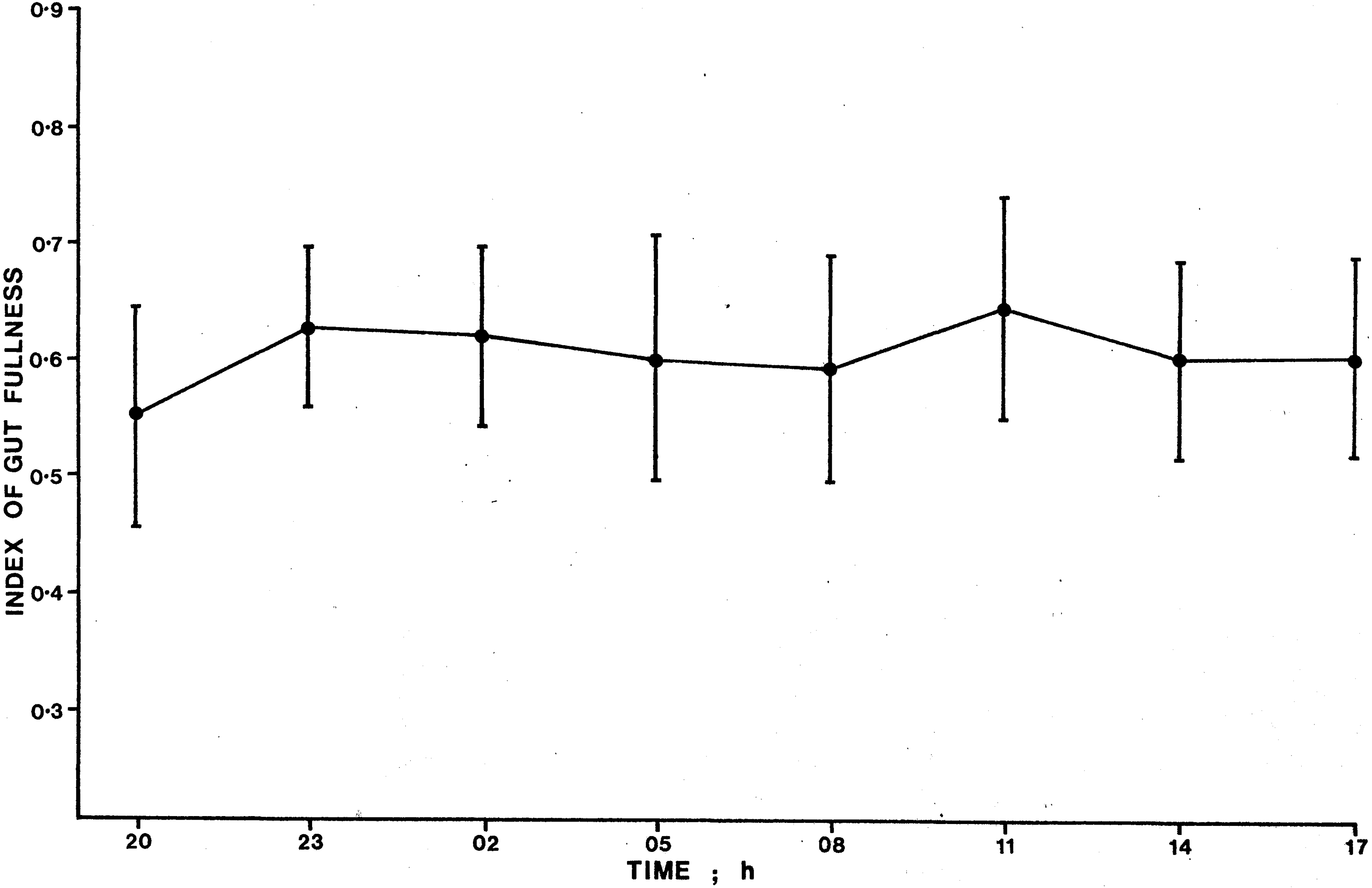
# FIG. 7b.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
MALE *LEMBOS* IN DECEMBER 1974.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNRISE 08.44 SUNSET 15.43

LOW TIDE 20.55
HIGH TIDE 03.30
LOW TIDE 08.40
HIGH TIDE 15.35


INDEX OF GUT FULLNESS
0·9
0·8
0·7
0·6
0·5
0·4
0·3
20
23
02
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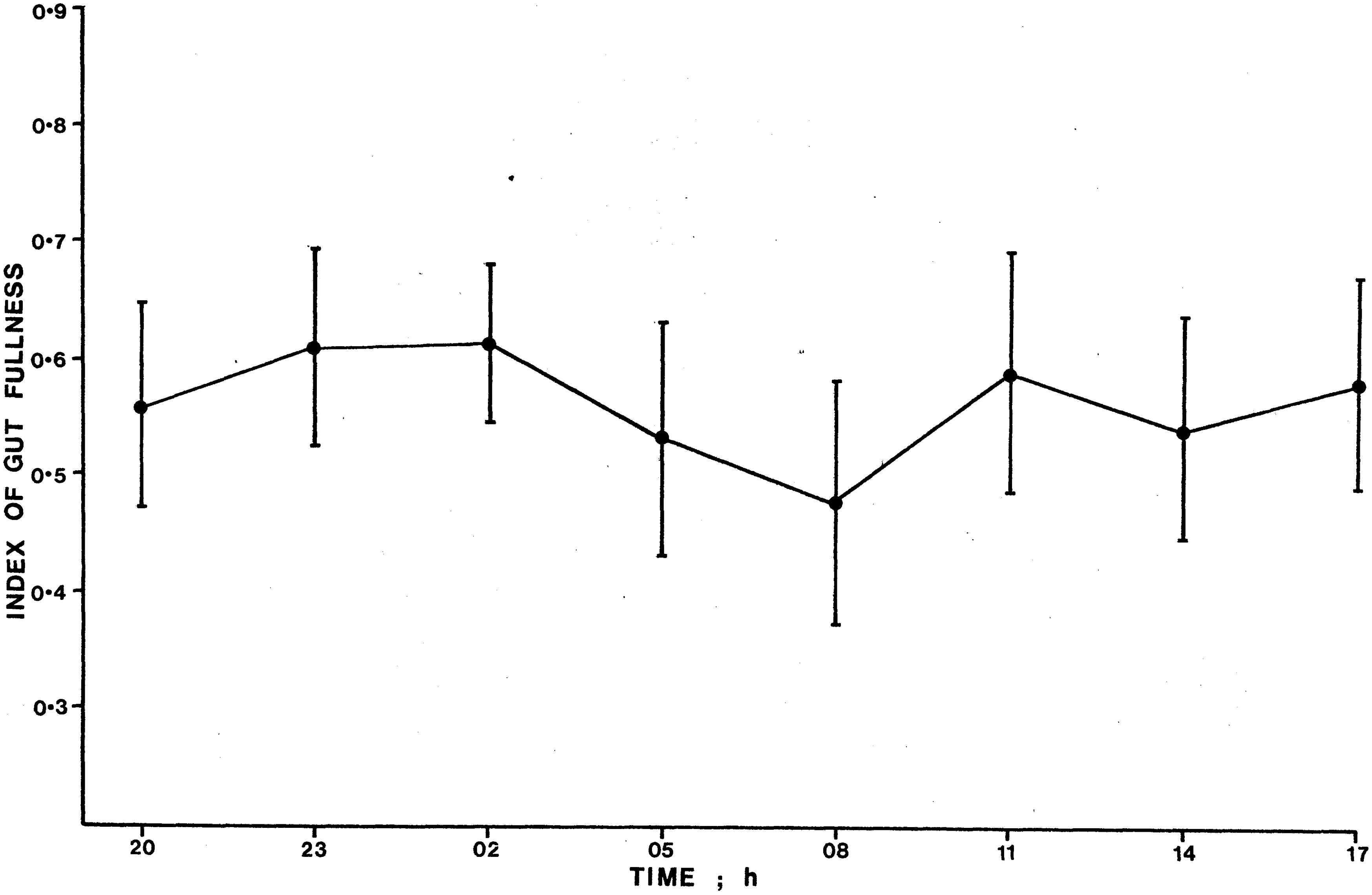
08
11
14
17
TIME ; h

## FIG. 7c.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
JUVENILE *LEMBOS* IN DECEMBER 1974.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNRISE 08.44 SUNSET 15.43
LOW TIDE 20.55
HIGH TIDE 03.30
LOW TIDE 08.40
HIGH TIDE 15.35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INDEX OF GUT FULLNESS
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14
17
TIME ; h

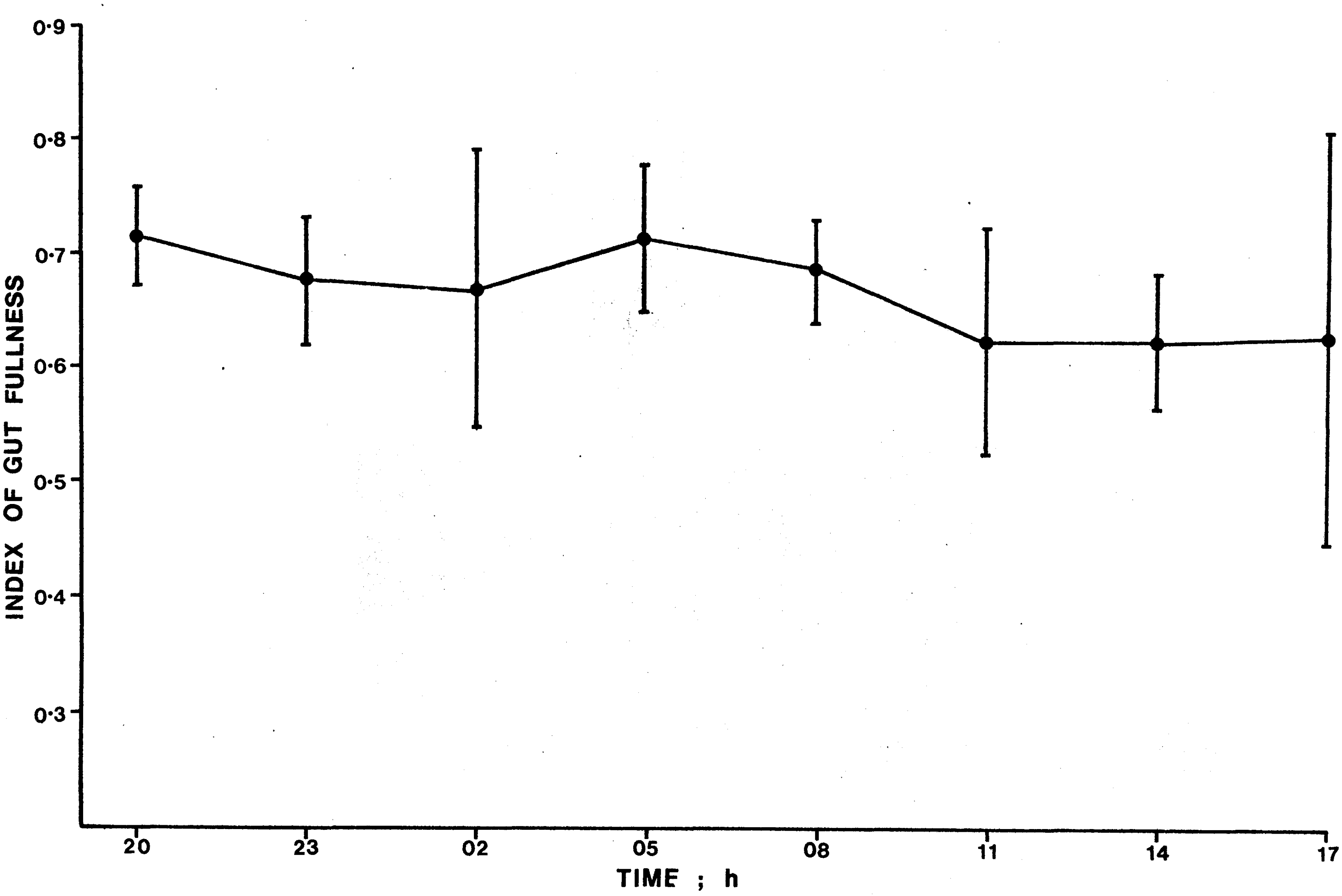
## FIG. 7d.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
MATURE FEMALE COROPHIUM IN DECEMBER 1974.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNRISE 08.44 SUNSET 15.43

LOW TIDE 20.55
HIGH TIDE 03.30
LOW TIDE 08.40
HIGH TIDE 15.35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INDEX OF GUT FULLNESS
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TIME ; h

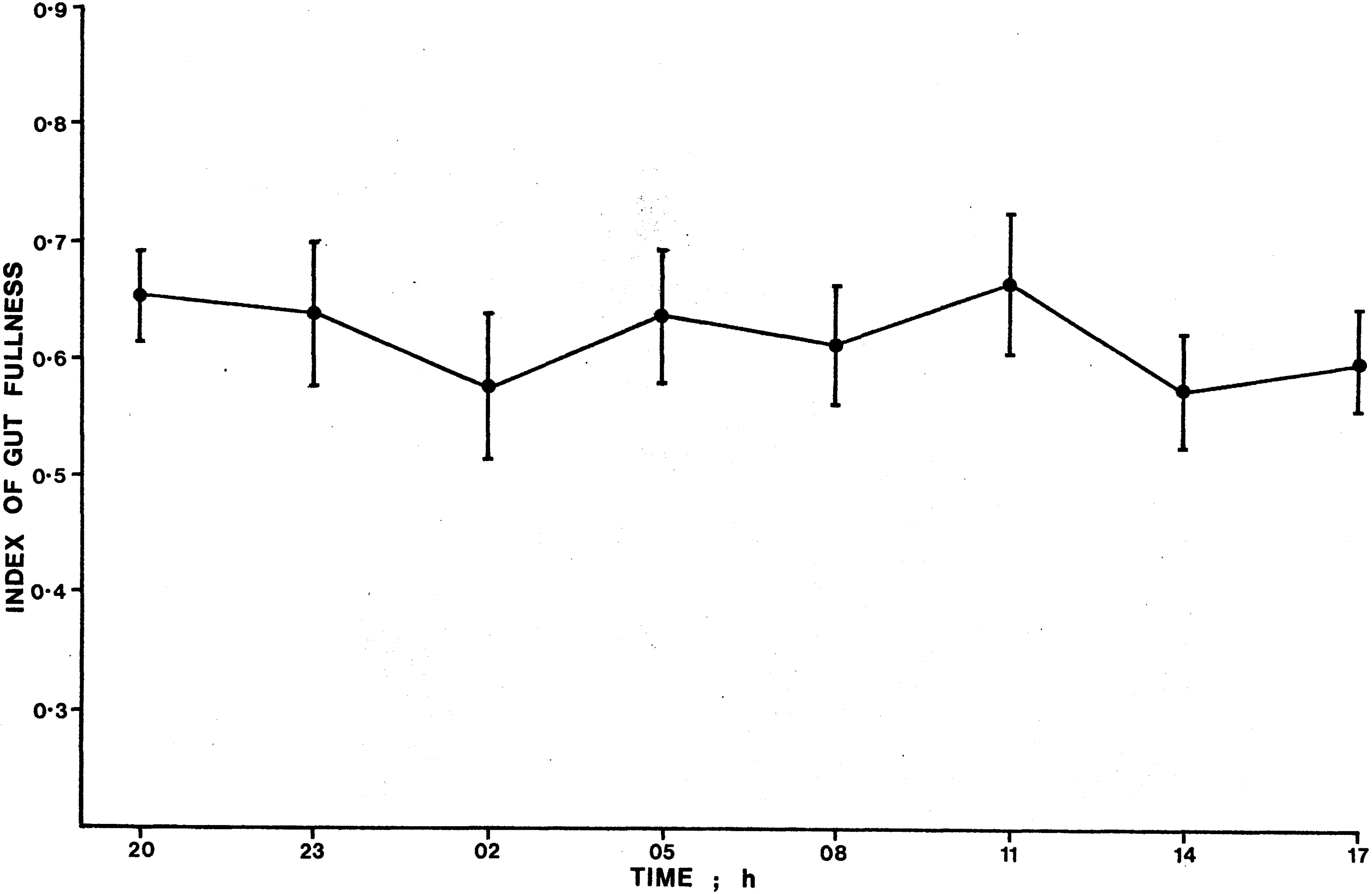
## FIG. 7e.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
IMMATURE CO<u>ROPHIUM</u> IN DECEMBER 1974.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNRISE 08.44 SUNSET 15.43

LOW TIDE 20.55
HIGH TIDE 03.30
LOW TIDE 08.40
HIGH TIDE 15.35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INDEX OF GUT FULLNESS
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17
TIME ; h

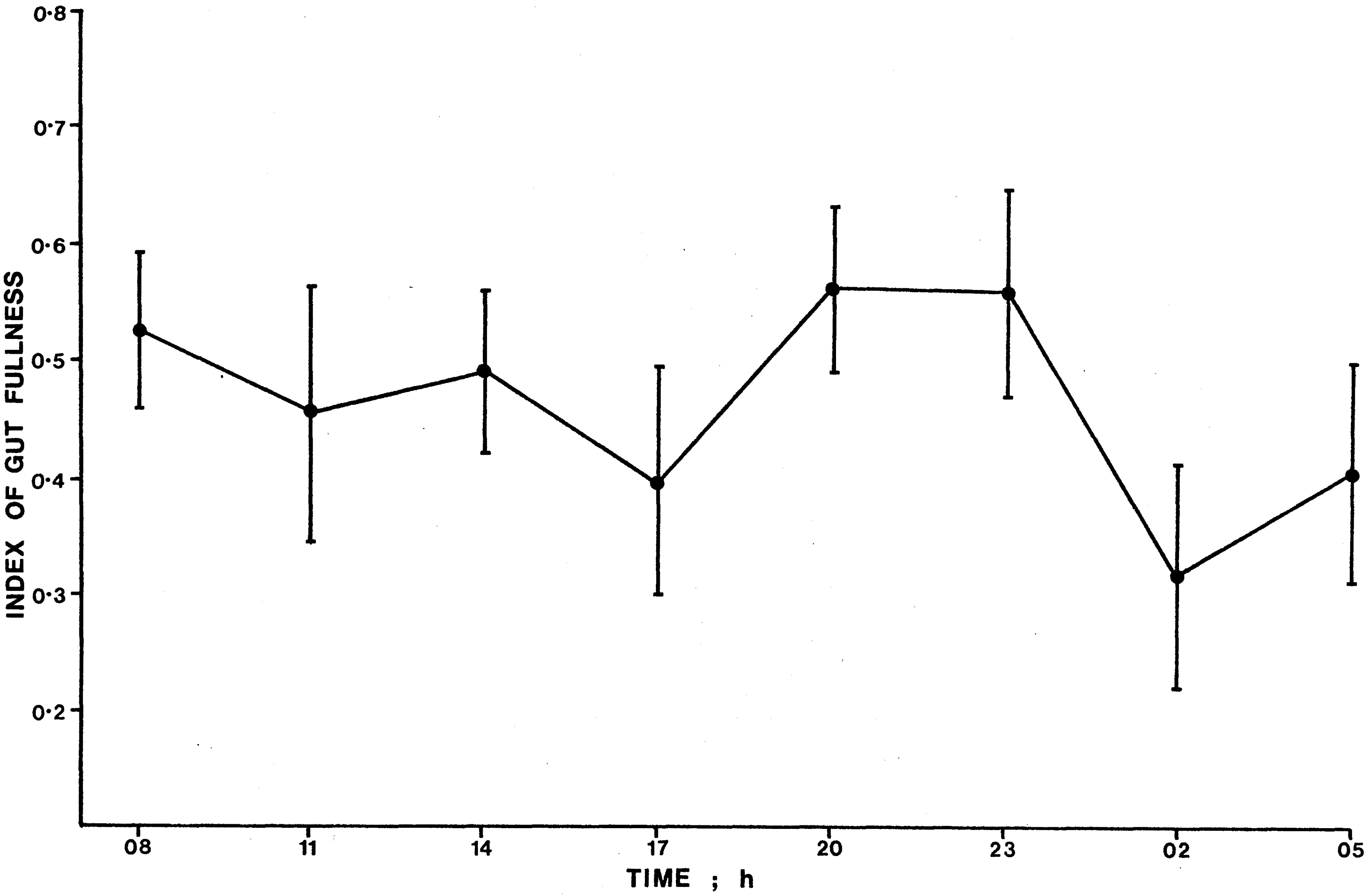
## FIG. 7f.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
MATURE FEMALE *LEMBOS* IN JUNE 1975.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNSET 21.04 SUNRISE 03.30

LOW TIDE 08.40
HIGH TIDE 15.55
LOW TIDE 21.25
HIGH TIDE 03.50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INDEX OF GUT FULLNESS
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TIME ; h

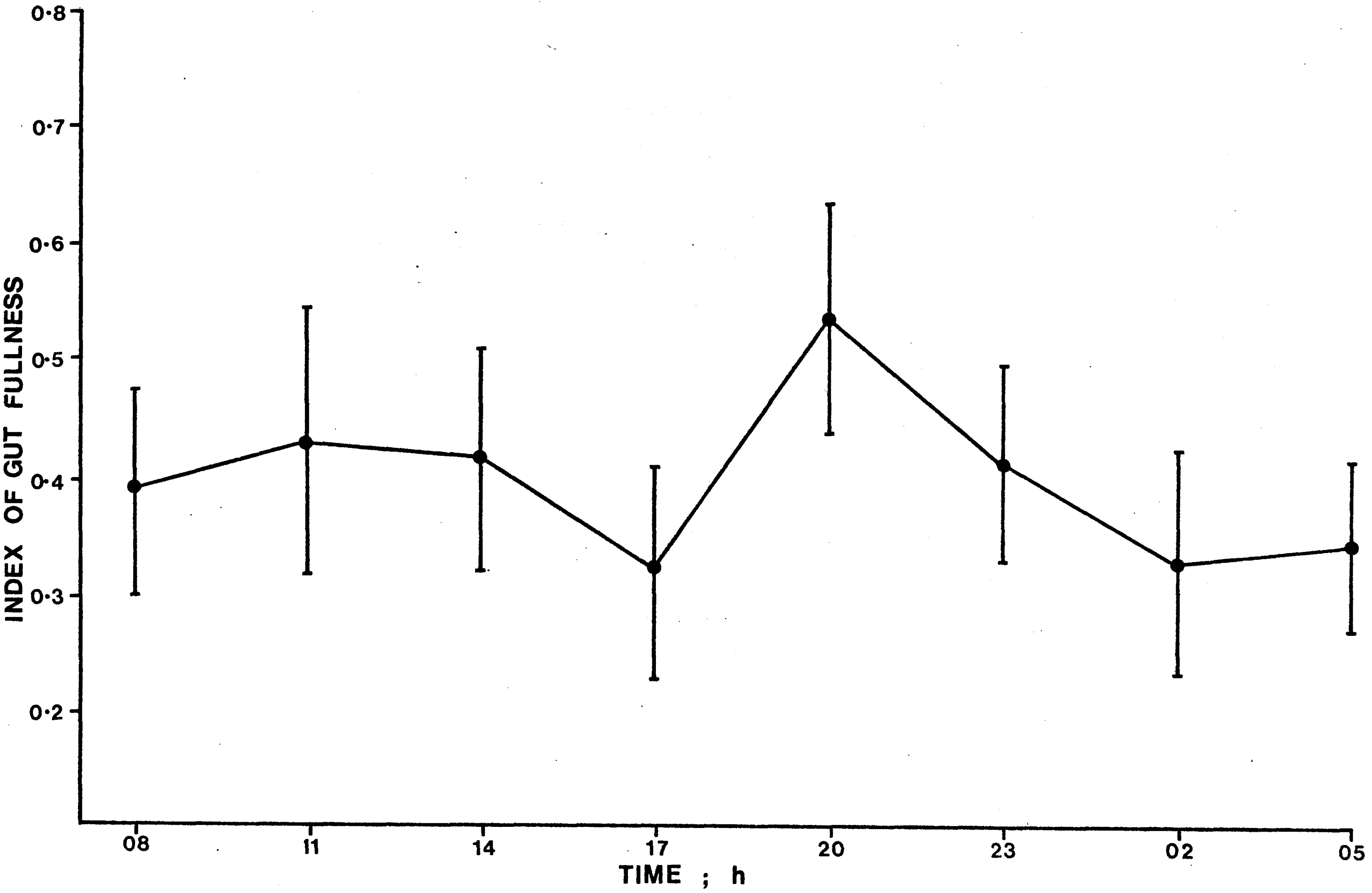
## FIG. 7g.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
MALE LEMBOS IN JUNE 1975.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNSET 21.04 SUNRISE 03.30

LOW TIDE 08.40
HIGH TIDE 15.55
LOW TIDE 21.25
HIGH TIDE 03.50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INDEX OF GUT FULLNESS
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TIME ; h

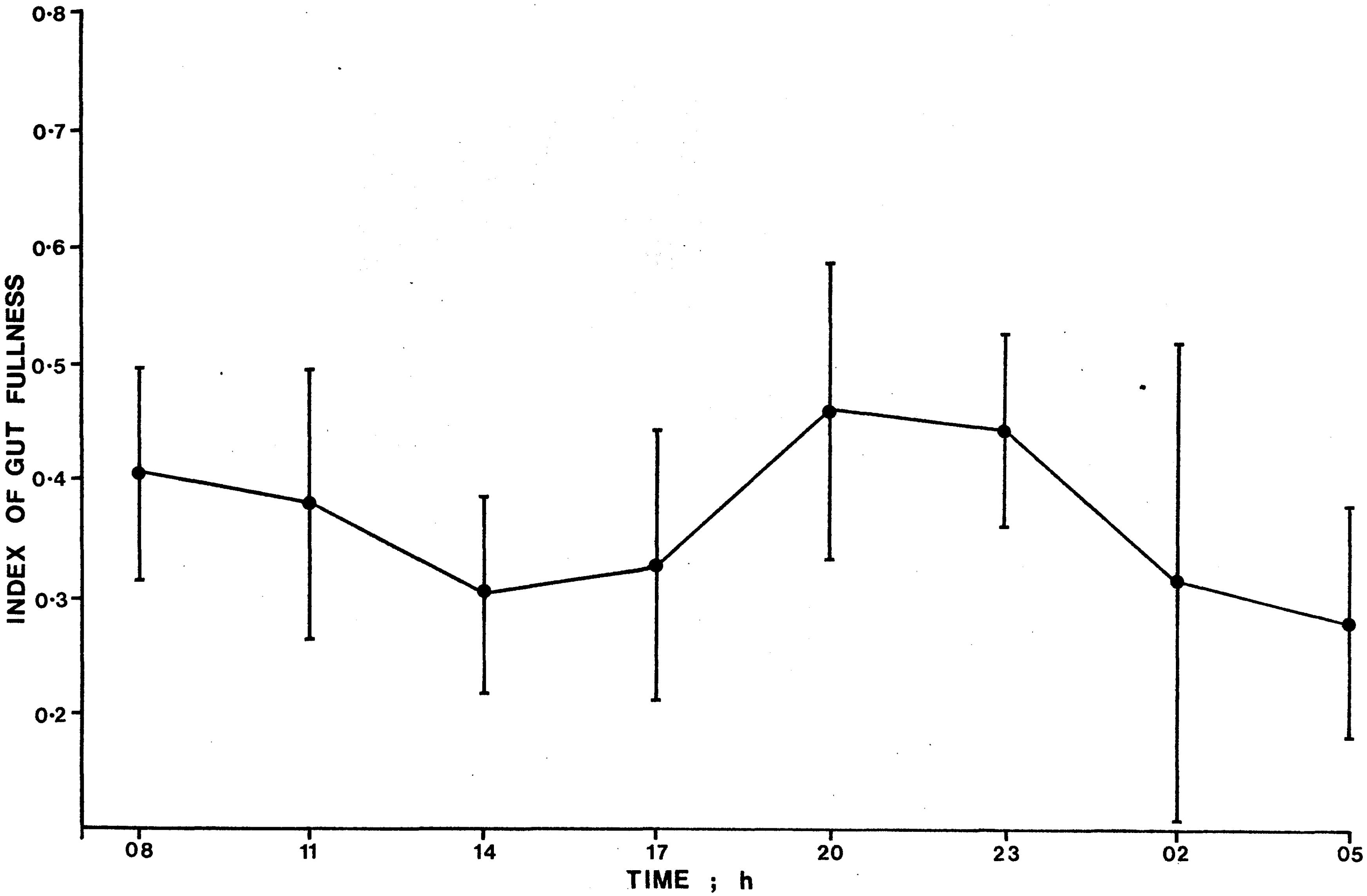
## FIG. 7h.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
JUVENILE LEMBOS IN JUNE 1975.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNSET 21.04 SUNRISE 03.20

LOW TIDE 08.40
HIGH TIDE 15.55
LOW TIDE 21.25
HIGH TIDE 03.50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INDEX OF GUT FULLNESS
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02
05
TIME ; h

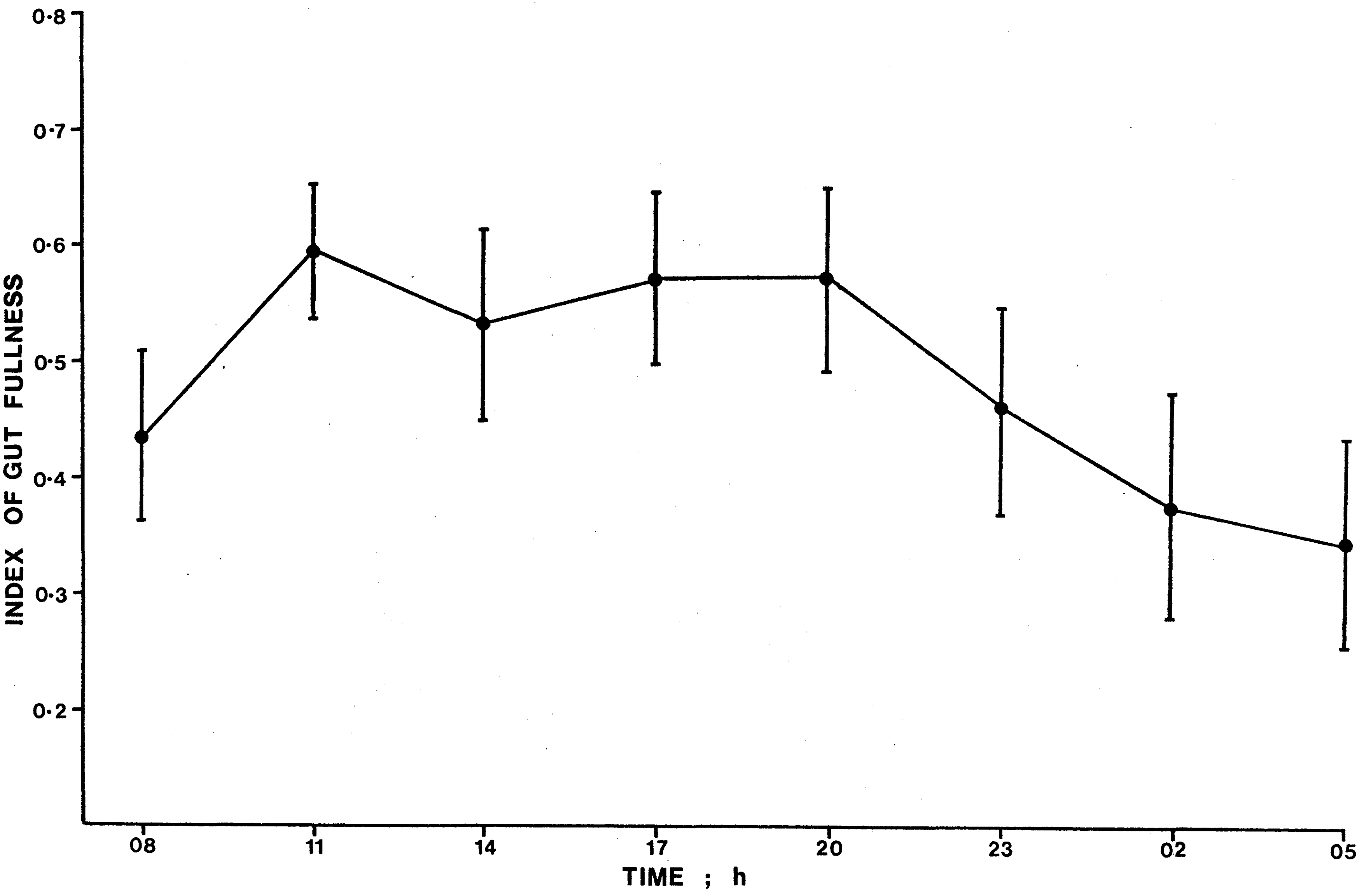
## FIG. 7i.

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
MATURE FEMALE *COROPHIUM* IN JUNE 1975.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNSET 21.04 SUNRISE 03.20

LOW TIDE 08.40
HIGH TIDE 15.55
LOW TIDE 21.25
HIGH TIDE 03.50


INDEX OF GUT FULLNESS
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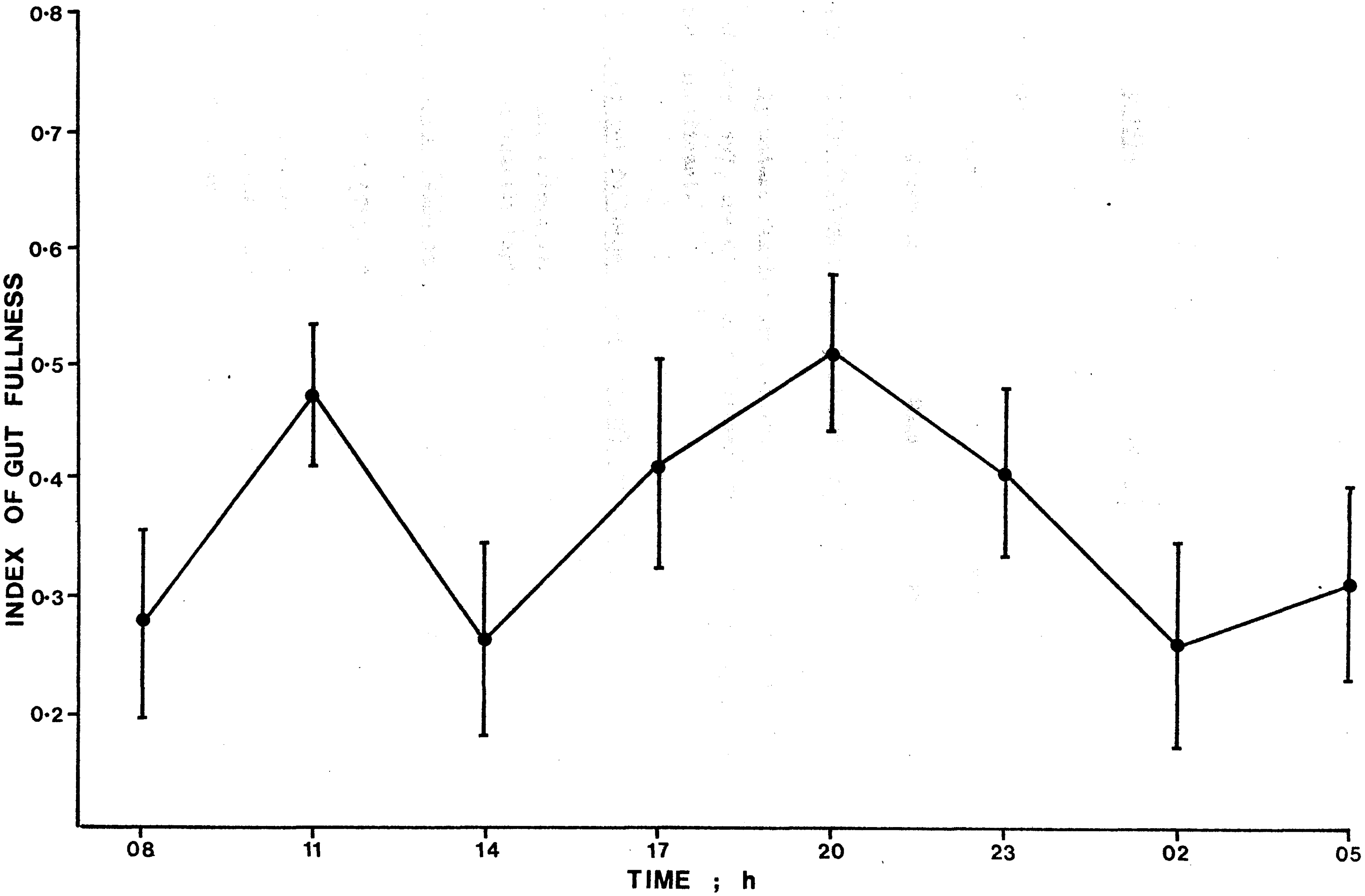
TIME ; h

**FIG. 7j.**

INDEX OF GUT FULLNESS : VARIATION WITHIN A 24 HOUR PERIOD.
IMMATURE *COROPHIUM* IN JUNE 1975.

EACH POINT REPRESENTS THE MEAN ± ITS 95°/o CONFIDENCE LIMITS.

SUNSET 21.04 SUNRISE 03.20
LOW TIDE 08.40
HIGH TIDE 15.55
LOW TIDE 21.25
HIGH TIDE 03.50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INDEX OF GUT FULLNESS
08
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TIME ; h

### *Corophium*.

December 1974 and June 1975.

Mature Female > Immature
*

### *Lembos*.

December 1974

Female
// *
Male = Juvenile

June 1975

Mature Female
*/ *
Male = Juvenile

### Index of gut fullness : *Lembos* versus *Corophium* (table 16)

Only ~~mature~~ females are compared. In both December, 1974 and June, 1975 the difference between *Lembos* and *Corophium* was not significant.

### Index of gut fullness : December 1974 versus June 1975 (table 17).

In all categories of both species the index of gut fullness was significantly higher in December, 1974 than in June, 1975.

### Index of gut fullness : variation within a 24 hour period.

#### December 1974 (figs. 7a - 7e)

In all categories of *Lembos* and *Corophium* there was very little variation in the index of gut fullness over the 24 hour period. The ratio of the largest to the smallest value, in each category over the 24 hour period, varied from 1.16 to 1.28.

#### June 1975 (figs. 7f - 7j)

In all categories of *Lembos* and *Corophium* there was more variation in the index of gut fullness over the 24 hour period than in December, 1974. The ratio of the largest to the smallest value, in each category over the 24 hour period, varied from 1.66 to 1.96.

### Index of gut fullness : night versus day. (table 18)

#### December 1975

In all categories of *Lembos* and *Corophium* there was no significant difference between night and day in the index of gut fullness.

#### June 1975

In all categories of *Lembos* and *Corophium*, except mature female *Corophium*, there was no significant difference between night and day in the index of gut fullness. Mature female *Corophium* had significantly fuller guts during the day than during the night.

### Index of gut fullness : low water period versus high water period (table 19).

#### December 1974.

In all categories of *Lembos* and *Corophium*, except immature *Corophium*, there was no significant difference between low and high water periods in the index of gut fullness. Immature *Corophium* had significantly fuller guts during the low water period than during the high water period.

#### June 1975.

All categories of *Lembos* and *Corophium* had significantly fuller guts during the low water period than during the high water period.

## O. DO COROPHIUM AND LEMBOS DEFAECATE THROUGHOUT THE 24 HOUR DAY?

### Materials and Methods.

These experiments were conducted on the 14th-15th June, 1975 and 10th-11th October, 1975, during the sampling sessions for the index of gut fullness. *Laminaria* holdfasts were collected every 6 h for 24 h. Each collection provided animals for one experiment.

In order to facilitate the selection of animals, with material completely filling the posterior third of their guts, both species were encouraged to occupy glass tubes. The first 15 individuals (sometimes less) of each species which fulfilled this criterion were then placed singly in the upper cells of the faecal pellet collecting apparatus (fig. 8). This always occurred within 1.5 h of the animals being removed from the sea. The upper cells were partially filled with filtered sea water (no particles $> 0.3 \mu$ m).

Each compartment in the faecal pellet collecting apparatus had upper and lower cells separated by plankton netting of pore diameter 0.4 mm. Pores of this size allowed the faecal pellets, but not the animals, to pass through. The plate containing the upper cells was separated from the plate containing the lower cells by four spacers. This arrangement reduced the amount of suction created by removal of the upper plate at the end of the experiment. Excessive suction would have washed faecal pellets out of the lower cells. Precautions were also taken to prevent the formation of air bubbles under the plankton netting.

At the end of each 3 h experiment the water in the tank was siphoned off until its level was below the top of the lower cells. This reduced still further the chance of faecal pellets being sucked out of the lower cells when the upper plate was removed. Before the upper plate was removed the faecal pellets, which had remained on the netting, were pushed through into the lower cells. The accumulated faecal pellets were then counted and measured. Many of the Lembos pellets were broken up, as a result of being worked over by the mouthparts. Only those pellets which retained their cross sectional shape were measured.

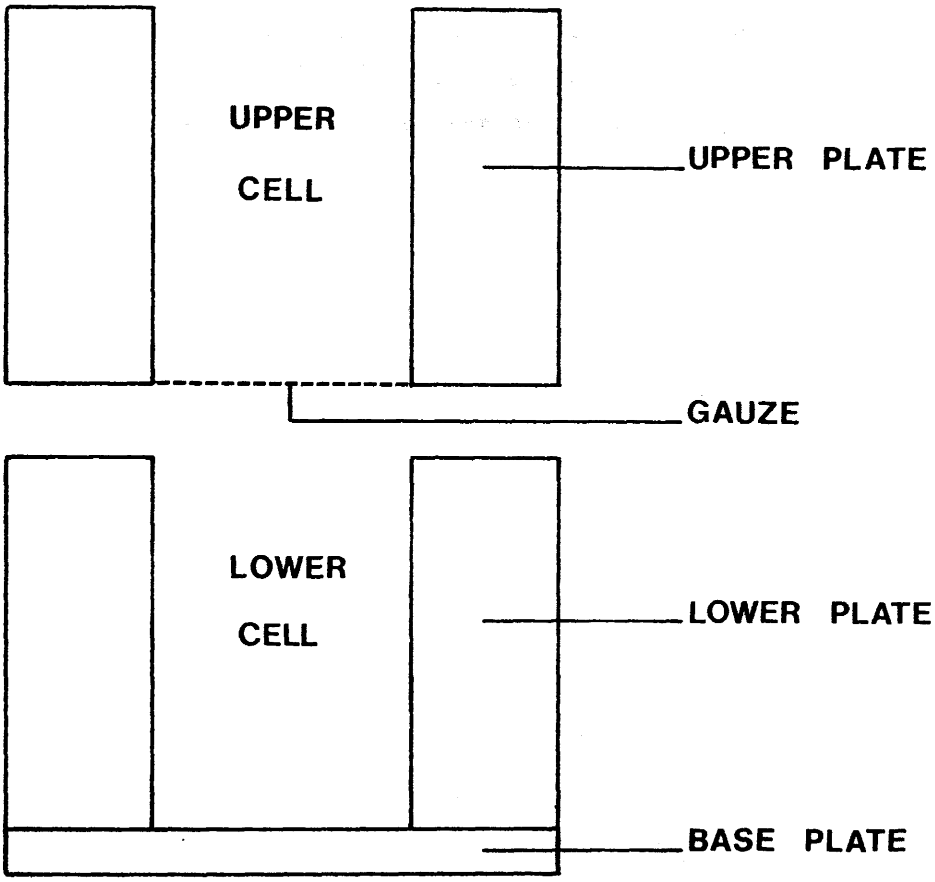
Before the apparatus was used again the base plate was removed and the apparatus was thoroughly cleaned with a soft scrubbing-brush.

The range in water temperature was 16.25-18.25°C and 18.25-19°C in June and October, respectively.

The length of faecal pellets produced per 3 h was expressed as a fraction of the length of gut contents at the start of the experiment. In June as faecal pellets were sucked out of the cells,

**FIG. 8.**

L/S OF ONE COMPARTMENT IN THE FAECAL PELLET COLLECTING APPARATUS.
EACH CELL = 9x5x20mm.


UPPER
CELL
UPPER PLATE
GAUZE
LOWER
CELL
LOWER PLATE
BASE PLATE

by mistake, at the end of the experiment, only the mean defaecation rate could be calculated.

$$\text{Mean Defaecation Rate} = \frac{\sum \text{lengths of faecal pellets of all individuals}}{\sum \text{lengths of gut contents of all individuals} + \sum \text{lengths of faecal pellets of all individuals}}$$

$\sum$ lengths of gut contents includes the faecal pellets lost when the animals were killed in formalin.

In October the defaecation rates of individuals were calculated separately. The mean and 95% confidence limits were then calculated according to the methods described for the index of gut fullness.

### Results (tables 20a and 20b)

#### June

In both species defaecation occurred throughout the 24 h. The highest defaecation rate of Lembos was $1.3^x$ the lowest, whilst the highest defaecation rate of Corophium was $2.4^x$ the lowest.

#### October

In both species defaecation occurred throughout the 24 h. The highest defaecation rate of Lembos was $3.3^x$ the lowest whilst the highest defaecation rate of Corophium was $2.7^x$ the lowest. Within each species none of the differences between experiments was statistically significant ($p<0.05$).

## P. TIME TAKEN FOR FOOD TO PASS THROUGH THE GUT.

### Materials and Methods.

The rate at which food passed through an individual's gut was measured using a coloured marker. Powdered blue chalk was used in one experiment (Corophium in the absence of food), whilst in all others ferric oxide (red) was used.

# TABLE 20

## DEFAECATION RATE OF LEMBOS AND COROPHIUM.

### a. JUNE.

| TIME(h) / SPECIES | 09.45-12.45 | | 15.45-1845 | | 21.25-00.25 | | 03.40-0640 | |
|---|---|---|---|---|---|---|---|---|
| | RATE | N | RATE | N | RATE | N | RATE | N |
| LEMBOS | 0.37 | 9 | 0.36 | 15 | 0.45 | 14 | 0.37 | 12 |
| COROPHIUM | 0.58 | 14 | 0.69 | 15 | 0.70 | 15 | 0.29 | 8 |

### b. OCTOBER.

| TIME(h) / SPECIES | 10.00-13.00 | | 15.15-18.15 | | 21.30-00.30 | | 03.10-06.10 | |
|---|---|---|---|---|---|---|---|---|
| | RATE* | N | RATE* | N | RATE* | N | RATE* | N |
| LEMBOS | 0.08±0.06 | 15 | 0.10±0.07 | 15 | 0.20±0.08 | 15 | 0.25±0.15 | 15 |
| COROPHIUM | 0.24±0.11 | 15 | 0.36±0.19 | 15 | 0.35±0.13 | 15 | 0.13±0.11 | 15 |

RATE = LENGTH OF FAECAL PELLETS PRODUCED PER 3h., EXPRESSED AS A FRACTION OF THE LENGTH OF GUT CONTENTS AT THE START OF THE EXPERIMENT.

* MEAN ± 95°/o CONFIDENCE LIMITS

N = NO. OF ANIMALS.

Prior to each experiment individuals inhabiting glass tubes were kept in the presence of settled organic detritus. These tubes were then placed into a dish containing suspended and settled particles of the marker for 8 min. Individuals with the marker in their stomachs were then placed either into filtered sea water (without food) or into dishes containing settled organic detritus and unfiltered sea water (with food). In one experiment (Corophium in the absence of food) the animals were provided with glass tubes.

The time taken for the marker to pass through the gut was estimated using the formula;

$$\text{Passage Time} = \frac{D + C}{2} - \frac{A + B}{2}$$

where A = Time individual put into dish with marker.
B = Time marker found in stomach.
C = Time of observation immediately prior to D.
D = Time when marker first found in the region of the gut in which the next faecal pellet would be formed or in a faecal pellet itself.

Observations were made at least once an hour, enabling the passage times to be expressed to the nearest hour. As Lembos often reingested its faecal pellets observations were made every half hour.

Statistical analysis was based on the comparison of animals from particular size categories.

## Results. (table 21)

### The passage times of animals with versus those without food.

In Corophium the passage time was significantly shorter when food was present than when food was absent (comparison 1), even though the animals with food were larger.

In Lembos also, the passage time was shorter when food was present (comparisons 2 and 3). However, only in comparison 3 was the difference statistically significant.

# TABLE 21

## TIME TAKEN FOR FOOD TO PASS THROUGH THE GUT OF *LEMBOS* AND *COROPHIUM*

| COMPARISON | SPECIES | BODY LENGTH(mm) | FOOD | T$^{\circ}$C. | MEAN TIME (h) | STATISTIC | D.F. | P |
|---|---|---|---|---|---|---|---|---|
| 1 | COROPHIUM | 2.00-2.99 | NO | 12.5-14 | 7.2 | t=7.32 | 15 | $< 0.001$ |
| | COROPHIUM | 3.00-3.99 | YES | 13.5-14.5 | 2.5 | | | |
| 2 | LEMBOS | 2.00-2.99 | NO | 12.5-14 | 2.3 | t=1.75 | 8 | $> 0.05$ |
| | LEMBOS | 2.00-2.99 | YES | 13.5-14 | 1.7 | | | |
| 3 | LEMBOS | 3.00-3.99 | NO | 12.5-14 | 7.0 | d=2.63 | 4 | $< 0.01$ |
| | LEMBOS | 3.00-3.99 | YES | 13.5-14 | 1.9 | | | |
| 4 | COROPHIUM | 2.00-2.99 | NO | 12.5-14 | 7.2 | t=6.98 | 6 | $< 0.001$ |
| | LEMBOS | 2.00-2.99 | NO | 12.5-14 | 2.3 | | | |
| 5 | COROPHIUM | 3.00-3.99 | YES | 13.5-14.5 | 2.5 | t=1.26 | 25 | $> 0.05$ |
| | LEMBOS | 3.00-3.99 | YES | 13.5-14 | 1.9 | | | |

### The passage times of Corophium versus Lembos.

In the absence of food the passage time of Lembos was 3.1$^x$ faster than that of Corophium (comparison 4). This difference was statistically significant. In the presence of food the passage time of Lembos was 1.3$^x$ faster than that of Corophium (comparison 5). This difference was not statistically significant.

## Q. DISCUSSION.

Both species obtained their food by filter feeding, deposit feeding, catching motile meiofauna, eating their own eggs, eating their own tubes and, in the case of Lembos, by refection. Neither species could be described as feeding primarily by the last four techniques. Eating their own eggs and tubes normally only occurred, to any degree, when other food sources were scarce. Although Lembos virtually always worked over its faecal pellets immediately they were produced, ingestion of these pellets was much more prevalent under poor feeding conditions. Arthropod appendages were only a component of the gut contents of Lembos and then only infrequently.

No quantitative date are available on the relative importance of filter and deposit feeding to the two species. However, apparatus designed for observing the behaviour of animals under conditions of turbulence and turbidity (see chapter VI) allowed animals to choose between settled and suspended detritus, of originally the same physical, chemical and biological characteristics. Both species appeared to ingest more of the suspended than the settled detritus. This suggests that both species are primarily filter feeders. The problem needs to be examined experimentally, eg. by comparing the speed with which a coloured marker passes along their guts, when animals are exposed to settled versus suspended particles. As a result of a thorough study of the genus Corophium, Crawford (1937a) proposed that, as the form of the limbs chiefly used in feeding is so constant throughout the genus, it is probable that the species differ only in the proportion of their food supply derived from deposit and filter feeding. The relative importance of these two techniques, in C. volutator, has been discussed by Hart (1930), Enequist (1949) and Meadows and Reid (1966). However, as with C. bonnellii, no firm statement can be made, as the necessary experiments have still to be conducted.

The gut contents of Lembos and Corophium were very similar in that they were dominated by finely - divided material. The gut contents of other Corophium spp. are also dominated by fine particles (Lakshmana Rao and Shyamasundari, 1963; Nagle, 1968; Odum and Heald, 1972; Fenchel et. al., 1975). The gut contents of L. websteri and C. bonnellii had a texture which resembled that of organic detritus. In C. bonnellii particularly, with its very efficient setae, this material probably also consisted of the indiscernible remains of digested phytoplankton. The gut contents of the two species differed in that particles reached a larger size in Lembos. This indicates, assuming that no size reduction of particles occurred after ingestion, that Lembos could ingest larger particles than Corophium. Agrawal (1963) suggests that C. volutator masticates food in its stomach. The contrary opinion is held by Kanneworf and Nicolaisen (1969), who, after a more thorough investigation, speculated that mastication is not a feature of the amphipod stomach.

The importance of the size of the mouth in limiting the size range of particles that can be ingested was seen very clearly in Lembos. One animal attempted to force a sand grain into its mouth with its maxillules and mandibles. The animal failed because the grain was too large and after a while it was rejected by being pushed away by the distal ends of the maxillules. By recording the ability of Lembos and Corophium to ingest particles of known dimensions, it should be possible to define the largest particle that each species can ingest.

The larger particles, eg. arthropod appendages, were more resistant to fragmentation than organic detritus. The more frequent occurrence of larger particles in Lembos, as opposed to Corophium, would have been aided by the former's stronger mouthparts. Practical proof of this is shown, (1) by the greater ease with which Lembos tore open Lembos embryos, and (2) by that fact that only Lembos has been recorded fragmenting macroalgae (Ulva).

Lembos picked up and worked over algal fragments and sand grains more readily than Corophium. This behaviour probably resulted in the removal and ingestion of attached detritus and micro-organisms from the sand grains. Nagle (1968) describes how some species of Microdeutopus and Corophium work over algal fragments to remove the attached detritus. It is not known if Lembos and Corophium ingested any algal tissue when they worked over the algal fragments.

Benthic diatoms were found infrequently in the gut contents of both species. Fenchel *et. al*. (1975) report that *C. volutator* ingests benthic diatoms and Johannes (1964) kept *L. intermedius* alive for months on a diet of benthic diatoms and their attendant bacteria.

The importance of detritus in the diet of *L. websteri* and *C. bonnellii* is supported by laboratory observations. Both species are voracious eaters of organic detritus and can be kept alive for several weeks with organic detritus as the sole source of food. The relative importance of refractory organic detritus and its associated micro-organisms in the nutrition of these two species is unknown. *C. volutator* can remove the associated micro-organisms from ingested detritus very efficiently (Fenchel, 1972). In addition, Kristensen (1972) has shown that *C. volutator* has weak to strong powers of digesting the structural carbohydrates chitin and alginic acid. Is the well developed refection behaviour in *Lembos* associated with the digestion of the refractory material?

Both species can deposit-feed by partially emerging from their tubes and gathering up settled detritus. As the amount of detritus available is restricted to a small area around each entrance a certain amount of turbulence is required to replenish these areas. For the same reasons Enequist (1949) considers that water movement is a factor of importance in the ecology of *C. volutator*, a species which deposit-feeds in the same way as *C. bonnellii* (Meadows and Reid, 1966). Enequist (loc. cit.) interprets Hart's (1930) observation that *C. volutator* deposit-feeds by crawling about on the substratum as a response to poor feeding conditions, induced by keeping animals in aquaria with completely still water. Enequist observed that *C. bonnellii* can use its gnathopod filter basket to sift mud, which had been collected by the second antennae during deposit feeding. I have never seen the gnathopods being used in this manner when *C. bonnellii* collected settled organic detritus.

Both species can filter feed by removing particles from their pleopod current with their setate gnathopods. The same behaviour has been described in *C. bonnellii* (Enequist, 1949), *C. acutum* (Nagle, 1968; Krapp- Schiekel, 1969), *C. insidiosum* (Nagle, 1968), *C. sextoni* (Hughes, 1975), *C. triaenonyx* (Lakshmana Rao and Shyamasundari, 1963), *C. volutator* (Hart, 1930; Meadows and Reid, 1966; Ingle, 1969) and *Lembos longipes* (Enequist, 1949). When *C. bonnellii* holds its gnathopod filter basket in the filtering position virtually all the pleopod current flows through it. Ingle (1969), however, reports that the greater part of the pleopod current of *C. volutator* circumvents the gnathopod filter basket. This might have been an artifact induced by keeping the animals in tubes of too wide a bore. The intersetule distances of the gnathopod filter basket of *C. volutator* are 4 $\mu$m (Fenchel *et. al.*, 1975) and are therefore virtually the same as those of *C. bonnellii*.

Being suspension feeders both species relied upon water movement to keep particulate material in suspension. The more frequent occurrence of *Lembos* at exposed as opposed to sheltered localities may be associated with the more turbulent waters suspending the larger particles on which *Lembos* feeds. Although both species can filter off extremely small particles, *Corophium* does so more efficiently; proof of this came from observing animals in the presence of suspended clay. As both species occupied tubes of a similar bore the maximum size of particle that could enter their tubes was similar. When positioned at the mouth of its tube, *Lembos* could easily trap large particles, even under very turbulent conditions. If a particle was too large to enter the tube it was broken up before being pulled inside. *Corophium*, however, even though it has a stronger pleopod current (Foster-Smith and Shillaker, in press), was not always able to suck in some of the larger detritus particles, which passed close to the tube entrance. This was particularly noticeable under more turbulent conditions.

The difference in the particle size distribution filtered by *Lembos* and *Corophium* needs to be studied quantitatively. A technique, which would seem to be suitable for these two species, is described by Peacock (1972). He provided *Tritaeta gibbosa* with a suspension of nutritionally inert particles and compared the particle size distribution in the suspension with that in the animal's faecal pellets.

A major difference between the two species was the much greater tendency of *Lembos* to work over its own faecal pellets immediately they were produced. Behaviour similar to that of *Lembos* has been recorded in the domiciliary genera *Ampithoe* (Holmes, 1901; Barrett, 1966; Heller, 1968; Greze, pers. comm.), *Chelura* (Kühne and Becker, 1964), *Ericthonius* (Greze, 1970), *Grubia* (Greze, pers. comm.), *Microdeutopus* (Myers, pers. comm.), and *Pleonexes* (Greze, pers. comm.) but never in *Corophium* nor in *Leptocheirus*. *Leptocheirus pilosus*, like the genus *Corophium*, has a large gnathopod filter basket (Goodhart, 1938), whose setae are densely covered with setules (Kaestner, 1970). There therefore appears to be a correlation between tubicolous amphipods, which are efficient fine particle filter feeders and the absence of well developed refection behaviour. This may be because a faecal pellet is a large particle.

The more developed refection behaviour in *Lembos* may also be due to *Lembos* having a lower assimilation efficiency than *Corophium*. There is some evidence to support this hypothesis, (1) Fenchel (1972) reports that *C. volutator* can remove 98% of the bacteria, 100% of the protozoa and 80% of the diatoms from ingested detritus, (2) Johannes (1964) reports that the phosphorus assimilation efficiency of *L. intermedius* is only about 16%. However, *L. intermedius* was provided with a superabundant food supply (benthic diatoms) and therefore the animals may have been eating and voiding their food at a rate too high for them to digest it fully.

Refection was more pronounced in *Lembos* when food was scarce. In accordance with this observation Kühne and Becker (1964) report that *Chelura terebrans* eats more of its faecal pellets when feeding on hard wood, which it finds difficult to chew, than when feeding on soft wood. Similarly, Schiecke (1973) believes that coprophagy in *Ericthonius brasiliensis* is a response to still water conditions, when suspended food particles are not available. *Lembos* also ate its tube, in response to poor feeding conditions, more readily than *Corophium*. *Lembos* therefore seems better adapted than *Corophium* to withstand periods of low food availability. The suspended particles on which *Lembos* feeds, being on average larger than those which *Corophium* ingests, are likely to be rarer, as they require a greater degree of turbulence to keep them in suspension. Even at exposed localities, where *Lembos* is more common, periods of calm occur.

*Corophium* species will ingest the faeces and pseudofaeces of oysters (McCloskey, 1970; Tenore *et. al.*, 1974) and barnacles (McCloskey, 1970). Preliminary experiments suggest that the faecal pellets of *C. bonnellii* are not readily ingested by *L. websteri*. Apart from this, the importance of the faecal pellets of other species to *C. bonnellii* and *L. websteri* is unknown. It is also possible that aged faecal pellets of conspecifics are ingested by *C. bonnellii*, as

Fenchel (1970) has shown for the detritus-eating amphipod Parhyalella whelpleyi.

Mills (1967) believed that the accumulation of faecal pellets (and silt) between the tubes of the burrowing species Ampelisca abdita increased the instability of the substratum, making the tubes more susceptible to being washed away by strong currents. Rhoads and Young (1970) also comment on the instability of substrata rich in faecal pellets. However, Trewin and Welsh (1976) stated that the faecal pellets of C. volutator assisted in the binding of the sediment on mud flats. It seems likely that, except in the most sheltered localities, the faecal pellets of Lembos and Corophium would not affect the stability of the sediment trapped in Laminaria holdfasts, as water movement would not allow the pellets to accumulate.

In both Lembos and Corophium ~~mature~~ females always had more food in their guts than any other category. This possibly reflects a greater feeding intensity by mature females, to support the extra energy expenditure of producing numerous eggs. These differences were slightly more pronounced in June, when reproductive activity was greater. Time was not available to test for variation in the index of gut fullness of mature females, at different stages of their moult cycle, (shown by the stage of development of their brooded young). Bregazzi (1972) discovered such variation in mature female Cheirimedon femoratus.

The index of gut fullness was slightly higher in Corophium than Lembos. Even if account had been taken of the greater loss of faecal pellets by Corophium, when animals were killed in formalin, it seems likely that the species difference would not have been large. Both species had more material in their guts in December, 1974 than in June, 1975. Although caution must be exercised when extrapolating from such limited data, seasonal variation in feeding intensity is suggested, perhaps due to more storm-induced turbulence in winter, increasing the availability of suspended detritus.

Limited diurnal variation in the index of gut fullness occurred in both species. The index was frequently higher during low water than during high water periods. For a given sea state, turbulence around *Laminaria* holdfasts would have been greater during low water periods. The greater turbulence would resuspend more particles and therefore increase the amount of food available to *Lembos* and *Corophium*. A tidal rhythm of feeding activity has been discovered in some littoral amphipods, but not in response to variations in the degree of turbulence (Martin, 1966; Mohan Joseph, 1972).

Experiments showed that *Lembos* and *Corophium* continued to defaecate throughout the 24 hour day. Although the defaecation rate varied, both species must have eaten continuously throughout the 24 hour day to have maintained a fairly constant index of gut fullness. The same continuity of feeding is reported to occur in the detritus-eating amphipod *Ampelisca diadema* (Greze, 1973). Direct measurements of the feeding rate need to be conducted to test the validity of these conclusions.

The passage time of gut contents was similar in *Lembos* and *Corophium*, being c. 2 h at $13.5^{\circ}$C, when eating organic detritus. As both species probably fed continuously they would refill their guts $12^{x}$ per day. In contrast, the passage time for a related species, *Ericthonius brasiliensis*, was 12 h when feeding on the alga *Cystoseira* at $20-22^{\circ}$C (Greze, 1971). In the absence of food the reingestion of faecal pellets by *Lembos* probably accounted for the passage time of *Lembos* being much faster than that of *Corophium*.

# CHAPTER IV. COMPLETE EMERGENCE.

## A. INTRODUCTION.

Within the genus Corophium diurnal, tidal and lunar cycles of emergence activity have been reported. Morgan (1965) showed that intertidally collected C. volutator, placed in non-tidal aquaria, lay still on the bottom over the period of low water. During the period of high water more animals were active after the time of high tide than before it, with the peak of activity occurring just after the time of high tide. These experiments also gave Morgan the impression that C. volutator was more active during the spring tide periods than during the neap tide periods. Gidney (1969) conducted field experiments and found more C. volutator swimming during the night-time ebb tide than during the day-time ebb tide.

Austin and Williams (1972) collected amphipods, from the water column, during the night-time flood tide period of bimonthly spring tides. They found C. lacustre to be significantly more abundant on nights when the moon was new than on nights when the moon was full.

Both Robertson (1888) and Fincham (1968) found C. crassicorne in the plankton at night. Although Fincham (loc. cit.) found this species to be more abundant during the day the significance of this result is uncertain as the sample size was small and some of the daytime hauls occurred when the sea was rough.

Nocturnal emergence has also been recorded in C. acherusicum (Nagata, 1966), C. curvispinum (Kaestner, 1970), C. nobile (Zaitsev, 1970) and C. uenoi (Nagata, 1966).

Goss-Custard (1966) studying the availability of C. volutator as a prey item for the Redshank Tringa totanus L. listed the following factors as affecting the emergence of C. volutator; mud temperature, water content of the mud, rainfall and pressure on the mud surface. No animals emerged when the mud temperature was less than 3°C. Above 6°C the number appearing increased with increasing temperature. Hart (1930) and Gidney (1969) also report more *C. volutator* are to be seen crawling about on estuarine mud-flats on sunny days.

Less is known about emergence activity in the genus *Lembos*. Austin and Williams (1972) report *L. smithii* to be more common in the water column on nights of a full moon than on nights of a new moon. Macquart-Moulin (1968) also found one *L. longipes* swimming in the sea at night.

## B. DIURNAL VARIATION IN THE PERCENTAGE OF ANIMALS PRESENT WHICH COMPLETELY EMERGED FROM THEIR TUBES.

### Materials and Methods.

These experiments were conducted in the laboratory in shallow dishes 50 x 30 cm, filled to a depth of 5 cm with clear sea water. In order to enhance the conspicuousness of the amphipods, the water was not agitated and the white bottomed dishes were only sparingly covered with organic detritus.

One category of each species was placed in each dish and left overnight to build tubes. The next day the animals that had not built tubes were removed. Then, every 3 h for the next 48 h, each dish was examined for 5 min, during which time the number of animals out of their tubes and their behaviour were recorded. The latter was randomised by recording what each animal was doing the instant it was sighted and repeating this procedure at one minute intervals. The number of individuals out of their tubes was expressed as a percentage of the total number present. As a few died during each experiment the number present was expressed as the mean of the number present at the beginning and end of the experiment. The number of individuals per dish varied between 15 and 112.

The dishes were positioned under a skylight and exposed to a natural light - dark cycle. To allow observation of the animals at night a white light was used. All dishes, except the one being observed, were covered so as to exclude most of this light. All replicates, except C, started at approximately the same time in the lunar month. Each replicate started within 2 days of the animals being collected. Further details of each replicate are included in table 22.

The limits of day and night were defined by the times of sunrise and sunset in Glasgow.

Where the percentage emergence during the day and during the night were compared one - tailed significance tests were conducted. They were permissible since preliminary experiments had shown that very few individuals leave their tubes during the day and therefore the percentage which emerged at night could hardly be expected to be less than during the day.

## Results.

### Complete emergence (%) : day versus night (table 23)

The percentage of amphipods, which completely emerged during the day, was very small in all categories of both species. The percentage which emerged completely at night, was significantly larger than during the day, in all categories of both species. Nocturnal emergence was most marked in male Lembos ($4.5^{x}$ day emergence).

### Complete emergence (%) at night : comparison of different categories (table 24)

The results may be summarised in the following manner,

**Lembos**

Male
***          ***
$4.7^{x}$ ∨          ∨ $7.0^{x}$
Mature > Juvenile
Female $1.8^{x}$
 ***

**Corophium**

Mature > Immature
Female $1.8^{x}$

# TABLE 22

## DETAILS OF THE REPLICATES OF EMERGENCE EXPERIMENT 1.

| REPLICATE | DATE STARTED | STATE OF MOON* | WATER TEMP. (°C) |
|---|---|---|---|
| A | 31.5.74 | 5 | 14.5-16.5 |
| B | 30.9.74 | 7 | 16.5-18 |
| C | 20.1.75 | 0 | ? |
| D | 24.4.75 | 5 | 15.5-16.5 |
| E | 22.6.75 | 6 | 16.5-17.5 |

* = NUMBER OF DAYS PAST FIRST QUARTER

## TABLE 23

## COMPLETE EMERGENCE (°/o) : DAY VERSUS NIGHT.

| REPLICATES | SPECIES | CATEGORY | DAY/ NIGHT | °/o EMERGENCE | N | $\chi^2$ | P |
|---|---|---|---|---|---|---|---|
| A,B,C,D,E. | LEMBOS | MALE | NIGHT | 17.9 | 1524.5 | 215 | $<0.001$ |
| | | | DAY | 3.4 | 2097.5 | | |
| A,B,C,D,E | LEMBOS | MATURE FEMALE | NIGHT | 3.8 | 1699 | 43.1 | $<0.001$ |
| | | | DAY | 0.8 | 2596.5 | | |
| B,C,D | LEMBOS | JUVENILE | NIGHT | 2.0 | 1966.5 | 5.8 | $<0.01$ |
| | | | DAY | 0.9 | 1175 | | |
| A,B,D,E | COROPHIUM | MATURE FEMALE | NIGHT | 1.8 | 1170 | 32.2 | $<0.001$ |
| | | | DAY | 0.1 | 2128.5 | | |
| B,C | COROPHIUM | IMMATURE | NIGHT | 0.5 | 1515 | † | $=0.03$ |
| | | | DAY | 0 | 806 | | |

N = SUM OF THE NO. OF AMPHIPODS RECORDED INSIDE AND OUTSIDE THEIR TUBES DURING EACH OBSERVATION PERIOD OF EACH REPLICATE.

† - No $\chi^2$ VALUE FOR EXACT TEST (SEE BAILEY, 1964, P.61)

## TABLE 24

## COMPLETE EMERGENCE (°/o) AT NIGHT : COMPARISON OF DIFFERENT CATEGORIES.

| REPLICATES | SPECIES | CATEGORY | °/o EMERGENCE | N | $\chi^2$ | P |
|---|---|---|---|---|---|---|
| A,B,C,D,E | LEMBOS | MALE | 17.9 | 1524.5 | 170.1 | $< 0.001$ |
| | LEMBOS | MAT. FEMALE | 3.8 | 1699 | | |
| B.C.D. | LEMBOS | MALE | 13.9 | 1177.5 | 169.8 | $< 0.001$ |
| | LEMBOS | JUVENILE | 2.0 | 1966.5 | | |
| B.C.D | LEMBOS | MAT. FEMALE | 3.5 | 1211 | 5.6 | $< 0.01$ |
| | LEMBOS | JUVENILE | 2.0 | 1966.5 | | |
| B | COROPHIUM | MAT. FEMALE | 2.1 | 513 | 0.8 | $> 0.05$ |
| | COROPHIUM | IMMATURE | 1.2 | 423 | | |
| A,B,D,E | LEMBOS | MALE | 22.7 | 1098.5 | 233.4 | $< 0.001$ |
| | COROPHIUM | MAT. FEMALE | 1.8 | 1170 | | |
| A,B,D,E | LEMBOS | MAT. FEMALE | 2.5 | 1283 | 1.1 | $> 0.05$ |
| | COROPHIUM | MAT. FEMALE | 1.8 | 1170 | | |

N = SUM OF NO. OF AMPHIPODS RECORDED INSIDE AND OUTSIDE THEIR TUBES DURING EACH OBSERVATION PERIOD OF EACH REPLICATE

## TABLE 25

## COMPLETE EMERGENCE (°/o) OF MALE *LEMBOS* : DAY VERSUS NIGHT.

| DATE STARTED | DAY/ NIGHT | °/o EMERGENCE | N | $\chi^2$ | P |
|---|---|---|---|---|---|
| 31.5.74 | NIGHT | 35.1 | 225 | 71.0 | $< 0.001$ |
| | DAY | 9.6 | 540 | | |
| 30.9.74 | NIGHT | 24.6 | 418.5 | 114.5 | $< 0.001$ |
| | DAY | 0.9 | 465 | | |
| 20.1.75 | NIGHT | 5.6 | 426 | 0.2 | $> 0.05$ |
| | DAY | 4.2 | 144 | | |
| 24.4.75 | NIGHT | 11.1 | 333 | 45.9 | $< 0.001$ |
| | DAY | 0.9 | 555 | | |
| 22.6.75 | NIGHT | 24.6 | 122 | 80.2 | $< 0.001$ |
| | DAY | 1.0 | 393.5 | | |

N = SUM OF NO. OF AMPHIPODS RECORDED INSIDE AND OUTSIDE THEIR TUBES DURING EACH OBSERVATION PERIOD.

## TABLE 26

### PERCENTAGE OF INDIVIDUALS OUT OF THEIR TUBES WHICH MOVED ABOUT.

| SPECIES | CATEGORY | DAY/ NIGHT | °/o MOVE | N | $\chi^2$ | P |
|---|---|---|---|---|---|---|
| LEMBOS | MALE | NIGHT | 44.2 | 919 | 32.6 | < 0.001 |
| LEMBOS | MALE | DAY | 24.9 | 281 | | |
| LEMBOS | MATURE FEMALE | NIGHT | 29.2 | 233 | 8.7 | < 0.01 |
| LEMBOS | MATURE FEMALE | DAY | 11.1 | 72 | | |
| LEMBOS | JUVENILE | NIGHT | 27.3 | 150 | 0.01 | > 0.05 |
| LEMBOS | JUVENILE | DAY | 25.0 | 36 | | |
| LEMBOS | MALE | NIGHT | 44.2 | 919 | 16.6 | < 0.001 |
| LEMBOS | MATURE FEMALE | NIGHT | 29.2 | 233 | | |
| LEMBOS | MATURE FEMALE | NIGHT | 29.2 | 233 | 0.1 | > 0.05 |
| LEMBOS | JUVENILE | NIGHT | 27.3 | 150 | | |
| COROPHIUM | MATURE FEMALE | NIGHT | 80.8 | 57 | 2.5 | > 0.05 |
| COROPHIUM | IMMATURE | NIGHT | 86.5 | 52 | | |
| LEMBOS | MALE | NIGHT | 44.2 | 919 | 27.3 | < 0.001 |
| COROPHIUM | MATURE FEMALE | NIGHT | 80.7 | 57 | | |
| LEMBOS | MALE | NIGHT | 44.2 | 919 | 33.8 | < 0.001 |
| COROPHIUM | IMMATURE | NIGHT | 86.5 | 52 | | |

# TABLE 27

## PERCENTAGE OF INDIVIDUALS MOVING ABOUT OUTSIDE THEIR TUBES WHICH SWAM.

| SPECIES | CATEGORY | DAY/ NIGHT | °/o SWIM | N |
|---|---|---|---|---|
| LEMBOS | MALE | DAY | 0 | 70 |
| LEMBOS | MALE | NIGHT | 1.7 | 406 |
| LEMBOS | MATURE FEMALE | DAY | 0 | 8 |
| LEMBOS | MATURE FEMALE | NIGHT | 2.9 | 68 |
| LEMBOS | JUVENILE | DAY | 0 | 9 |
| LEMBOS | JUVENILE | NIGHT | 2.4 | 41 |
| COROPHIUM | MATURE FEMALE | DAY | 0 | 2 |
| COROPHIUM | MATURE FEMALE | NIGHT | 0 | 46 |
| COROPHIUM | IMMATURE | NIGHT | 0 | 45 |

FIG. 9a.

COMPLETE EMERGENCE (°/o) OF MALE <u>LEMBOS</u> : DIURNAL VARIATION IN MAY/JUNE 1974.

ARROWS REPRESENT THE TIMES OF SUNRISE AND SUNSET.

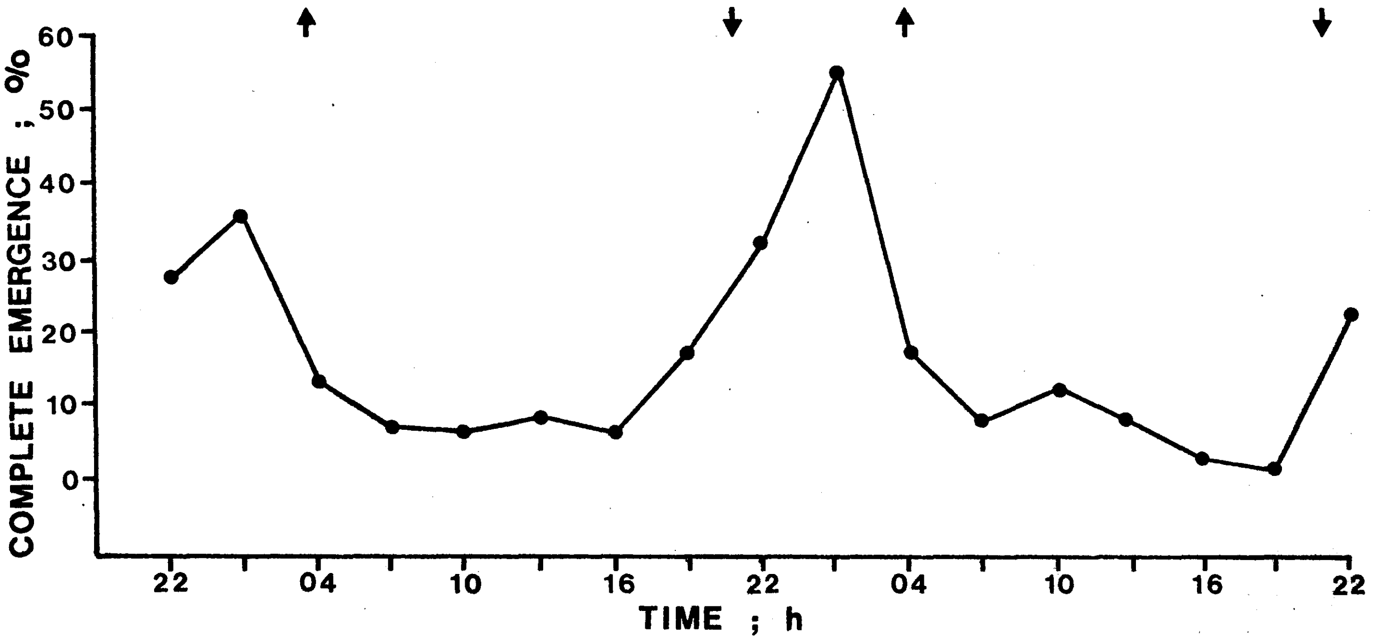

60
50
40
30
20
10
0
COMPLETE EMERGENCE ; %
22
04
10
16
22
04
10
16
22
TIME ; h

FIG. 9b.

COMPLETE EMERGENCE (°/o) OF MALE *LEMBOS* : DIURNAL VARIATION IN SEPTEMBER/OCTOBER 1974.

ARROWS REPRESENT THE TIMES OF SUNRISE AND SUNSET.

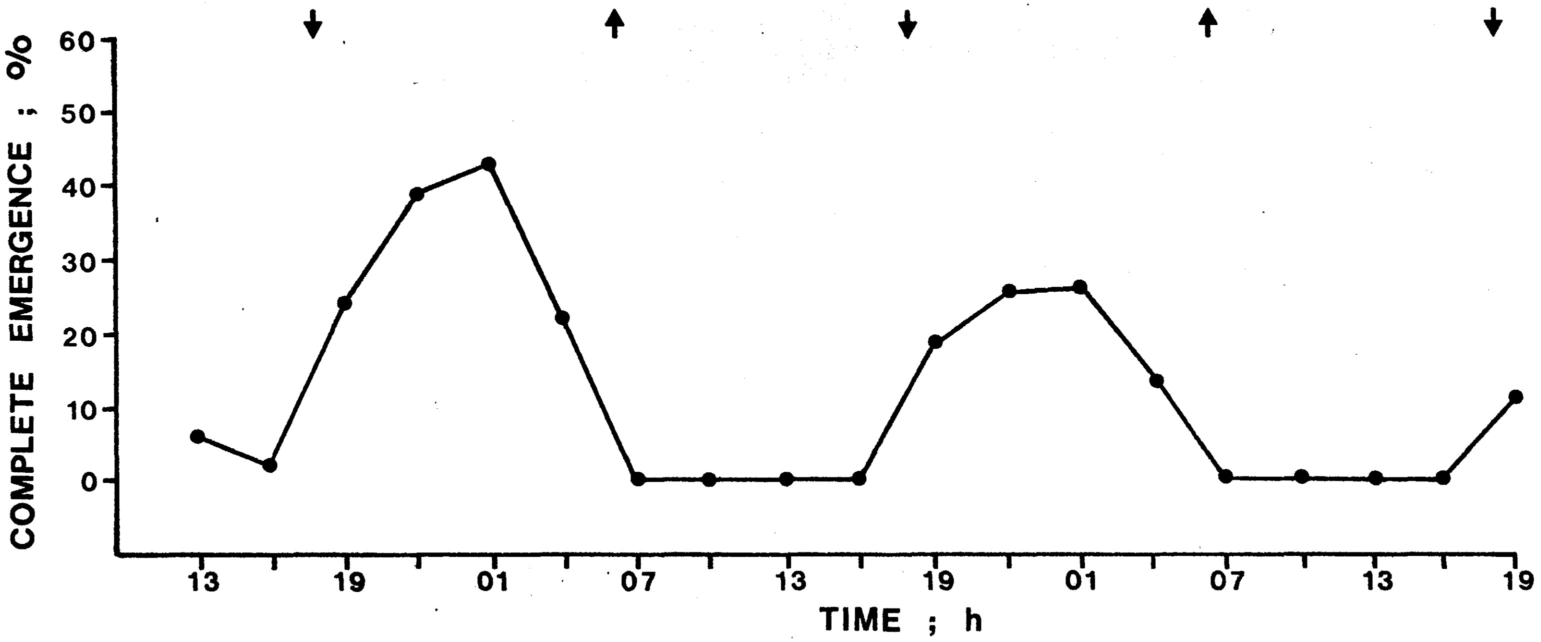
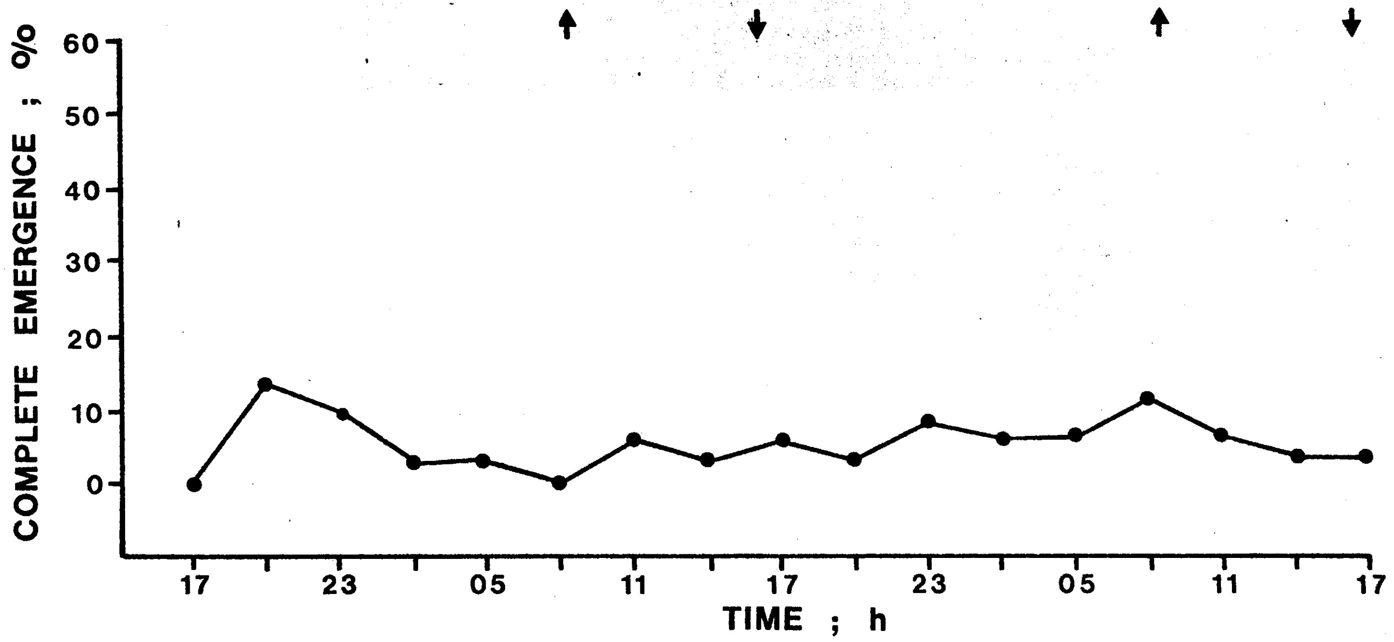

COMPLETE EMERGENCE ; %
60
50
40
30
20
10
0
13
19
01
07
13
19
01
07
13
19
TIME ; h

FIG. 9c.

COMPLETE EMERGENCE (°/o) OF MALE <u>LEMBOS</u> : DIURNAL VARIATION IN JANUARY 1975.

ARROWS REPRESENT THE TIMES OF SUNRISE AND SUNSET.


COMPLETE EMERGENCE ; %
60
50
40
30
20
10
0
17
23
05
11
17
23
05
11
17
TIME ; h

## FIG. 9d.

COMPLETE EMERGENCE (°/o) OF MALE LEMBOS : DIURNAL VARIATION IN APRIL 1975.

ARROWS REPRESENT THE TIMES OF SUNRISE AND SUNSET.

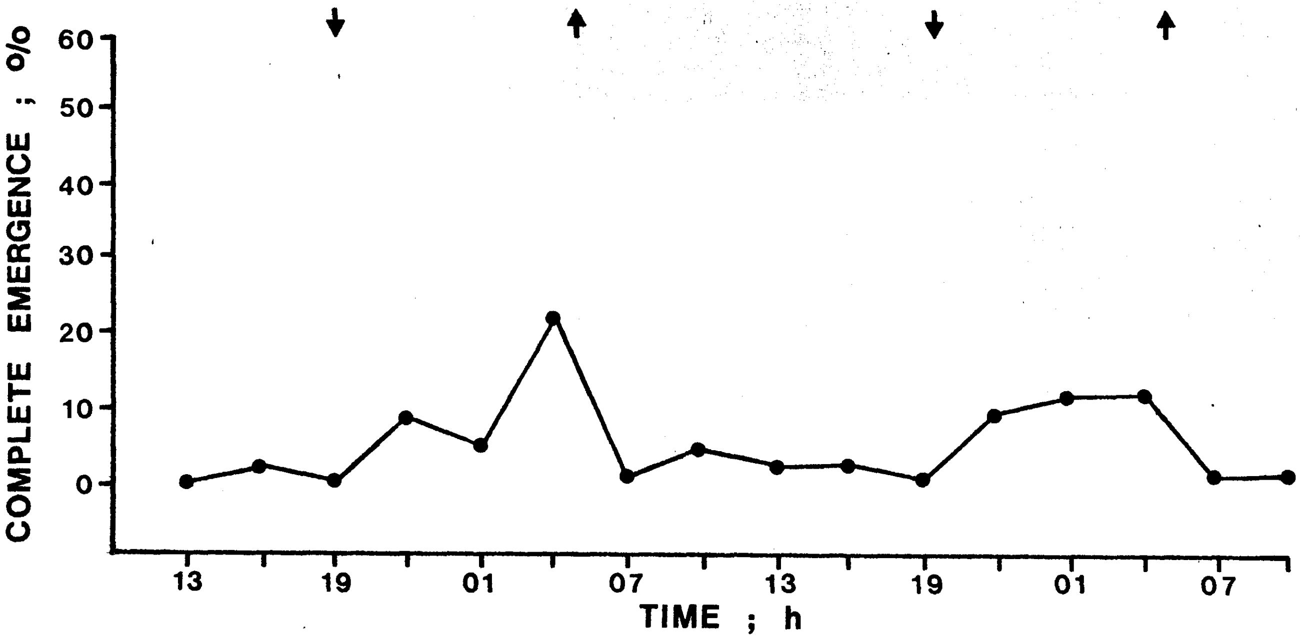
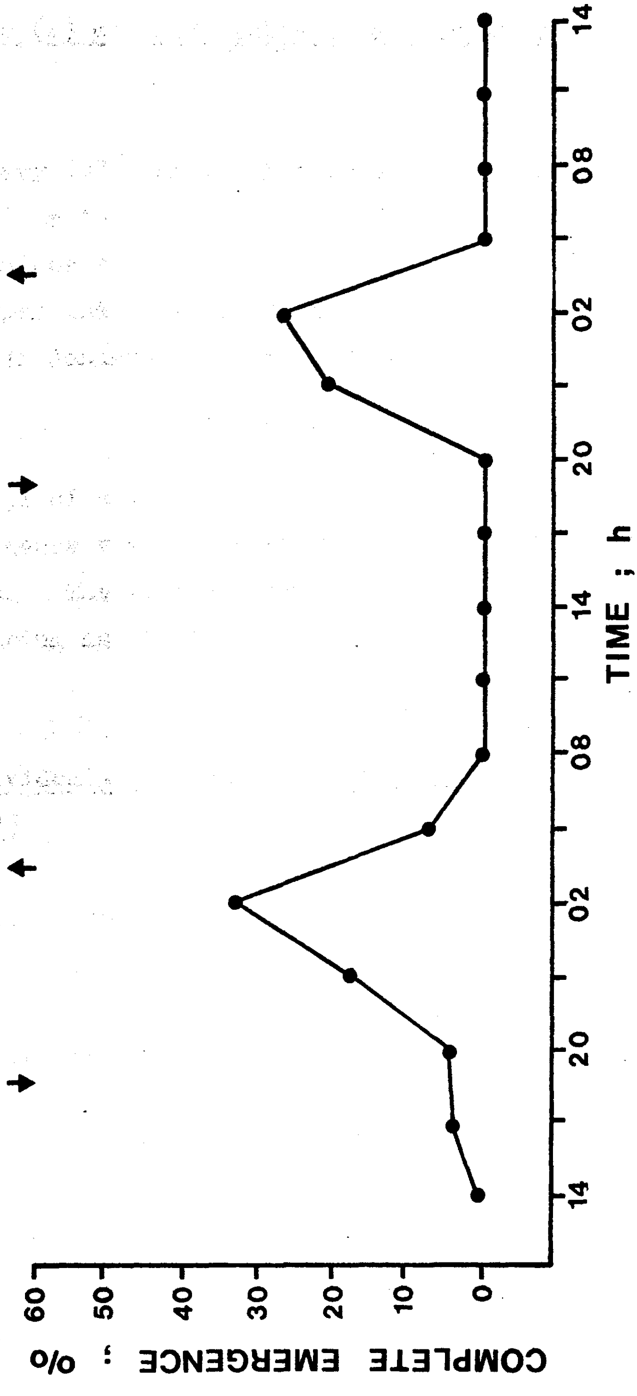

COMPLETE EMERGENCE ; %
60
50
40
30
20
10
0
13
19
01
07
13
19
01
07
TIME ; h

FIG. 9e.

COMPLETE EMERGENCE (°/o) OF MALE *LEMBOS* : DIURNAL VARIATION IN JUNE 1975.

ARROWS REPRESENT THE TIMES OF SUNRISE AND SUNSET.


COMPLETE EMERGENCE ; %
60
50
40
30
20
10
0
14
20
02
08
14
20
02
08
14
TIME ; h

### *Lembos* versus *Corophium*.

| | | |
|---|---|---|
| Male *Lembos* | $\overset{***}{12.6^{x}}$ | |
| | $>$ | Mature Female *Corophium* |
| Mature Female *Lembos* | $<$ | |
| | $1.4^{x}$ | |

### Complete emergence (%) of male *Lembos* : day versus night. (table 25 and fig. 9)

Only in January 1975 was the percentage which emerged at night virtually as small as the percentage which emerged during the day. On all other occasions the percentage which emerged at night was significantly larger than during the day. The lowest percentage emergence was 6% in January 1975, whilst the highest was 35% in May/ June 1974.

The percentage of males emerging varied during each night, with the greatest emergence always occurring after the first nocturnal recording session. The highest percentage of males recorded out of their tubes during any 5 min recording session was 56% in May/ June 1974.

### Behaviour of individuals when they are completely out of their tubes (tables 26 and 27)

An individual *Lembos* or *Corophium* would frequently stand on the substratum with its abdomen flexed under its body, supporting itself on its pereopods. The ventral surface of its thorax would be directed towards the substratum.

Both species can swim, crawl or climb up a smooth (glass) vertical surface. Both species normally swam on their backs, relying on their rapidly beating pleopods for thrust. *Lembos* frequently derived additional thrust by quickly flexing and straightening its abdomen. Neither species are fast swimmers and neither species swam for more than a few minutes at a time. Even when swimming, both species often stopped beating their pleopods for a few seconds and sank a little before starting to swim again. *Corophium* stopped swimming less frequently than *Lembos*.

The speed at which each species will crawl varies, with Corophium normally moving faster than Lembos. When moving slowly the abdomen was markedly flexed and only the pereopods provided thrust. To move rather faster the abdomen was uncurled and both the pereopods and pleopods provided thrust. Finally, both species will lift the abdomen parallel with the thorax and beat the pleopods rapidly in order to dart rapidly across the substratum.

The percentage of male and mature female Lembos which moved about, when completely out of their tubes, was significantly higher at night than during the day. The proportion of juvenile Lembos which were active was similar during the day and night ($p > 0.05$). So few Corophium were recorded out of their tubes during the day that such a comparison is not possible.

At night male Lembos were more active than mature female Lembos ($p < 0.001$). Male Lembos were however less active than either mature female or immature Corophium ($p < 0.001$). The amount of nocturnal activity was similar between mature female and juvenile Lembos and between mature female and immature Corophium ($p > 0.05$).

Swimming was unusual in both species throughout the 24 hour day. Other behaviours observed were aggressive encounters over tube ownership and, very infrequently, the construction of a new tube.

## C. PERCENTAGE OF ANIMALS PRESENT IN THE HOLDFAST WHICH MOVED ABOUT OVER ITS SURFACE.

### Materials and Methods.

### Laboratory Experiments.

Freshly collected Laminaria hyperborea holdfasts were placed singly in 5 l aquaria. Every 3 h for 48 h the holdfasts were examined for 2 min and the number of individuals of each species, which were visible on the holdfast, counted. At the end of the experiment the number of individuals in each holdfast were counted.

5 holdfasts were observed in May 1974 (water temperature 12.5-13.5°C) and 2 in June 1975 (temp. 16.5-17.5°C). Both experiments started within 24 h of collection. The tanks were aerated and exposed to a natural light - dark régime. A white

light was used to observe the holdfasts at night. The holdfasts not being observed were kept in the dark. When the holdfasts were examined in May 1974, they were gently moved about, to allow all the upper holdfast surfaces to be clearly seen. In June 1975 this was not done, as it appeared to stimulate a few individuals to leave the holdfast.

### Field Experiment.

*In situ* observations were made at Farland Point, Great Cumbrae, on the 13th June 1974. Every 3 h for 24 h, two marked *Laminaria hyperborea* holdfasts were each watched for 7 min. The plants were located by swimming along a well marked clearing in the kelp forest from an anchor to which a surface buoy was attached. At night, observations were made with the aid of an underwater torch. At the end of the experiment the holdfasts were collected and the number of individuals of *Lembos* and *Corophium* in each holdfast counted.

### Results.

### Laboratory Experiments (table 28)

Only a very small percentage of the individuals present emerged from their tubes and moved about on the surface of the holdfasts. With the exception of *Corophium* in May 1974 there was no difference, between day and night, in the percentage which moved about on the surface of the holdfast. In May 1974 there were slightly more *Corophium* visible on the holdfast during the night than during the day.

### Field Experiment.

No individuals of either species were seen moving about on the surface of either holdfast. However, there was only one individual of each species in one holdfast and 13 *Lembos* and 8 *Corophium* in the second holdfast.

## D. THE FUNCTION OF THE NOCTURNAL EMERGENCE OF MALE *LEMBOS*.

### Aim.

This experiment was designed to test the hypothesis that male *Lembos* emerged from their tubes at night to locate and enter the tubes of mature female *Lembos*. To test this, the emergence of males, with and without mature females in their tubes, were compared. Females

## TABLE 28

## PERCENTAGE OF INDIVIDUALS INHABITING *LAMINARIA* HOLDFASTS WHICH MOVED ABOUT ON ITS EXTERNAL SURFACE.

| DATE STARTED | SPECIES | CATEGORY | DAY/ NIGHT | °/o ON HOLDFAST | N |
|---|---|---|---|---|---|
| 6.5.74 | LEMBOS | ALL | DAY | 0.5 | 96 |
| | | ALL | NIGHT | 0.3 | |
| 6.5.74 | COROPHIUM | ALL | DAY | 0.5 | 35 |
| | | ALL | NIGHT | 4.3 | |
| 22.6.75 | LEMBOS | MALE | DAY | 0.1 | 64 |
| | | MALE | NIGHT | 0.4 | |
| 22.6.75 | COROPHIUM | MAT.FEMALE | DAY | 0 | 80 |
| | | MAT.FEMALE | NIGHT | 0 | |

N = NO. OF INDIVIDUALS PRESENT IN THE HOLDFASTS.

which were probably at an attractive phase in their moult cycle, ie. quite near to moulting, were used.

## Materials and Methods.

Mature females carrying well developed embryos, ie. embryos with limbs, were placed singly in 9 cm dishes, within one day of collection. They were left overnight to build tubes out of organic detritus. Those dishes in which a female had built a tube were then divided into two groups. In the first group, one male was encouraged to join each female in her tube. In the second group, all the females were removed before one male was encouraged to enter each vacated tube. A little detritus was placed around both entrances of each tube, to reduce the chance of males leaving due to lack of food. Finally, 3 pieces of glass tubing, 1 cm long, were placed equidistant from each other round the angle of the dish. These alternative shelters were provided to reduce the chance of males re-entering their vacated detritus tubes.

The experiment started on the 29th July 1976 and every hour for 24 h each male was recorded as being inside or outside its detritus tube. The dishes were exposed to a natural light - dark régime. To allow observation of the animals at night a white light was used. The water temperature ranged from 18.5-19.5°C.

## Results (tables 29 and 30)

15 paired and 19 single males were used. 7 of the females sharing a tube with a male moulted during the experimental period. These dishes were excluded as a male was more likely to leave its tube once it had copulated and copulation occurred soon after the female's moult. Therefore the frequency of tube vacation in 19 single males was compared with that in 8 paired males, whose partners had not moulted during the experimental period.

The percentage of males recorded outside their detritus tubes was higher in single than in paired males ($p=0.01$). The single males that vacated their tubes were larger than those that did not. However, the difference was not statistically significant ($p>0.05$).

## TABLE 29

## COMPLETE EMERGENCE (°/o) OF MALE LEMBOS : PAIRED VERSUS SINGLE MALES.

| | COMPLETE EMERGENCE(°/o) | N | P |
|---|---|---|---|
| PAIRED | 0 | 8 | =0.01 |
| SINGLE | 52.6 | 19 | |

AN EXACT $\chi^2$ TEST PERFORMED (SEE BAILEY, 1964, P.61)

## TABLE 30

## MEAN BODY LENGTH OF SINGLE MALE LEMBOS : INDIVIDUALS WHICH EMERGED VERSUS THOSE THAT DID NOT.

| EMERGENCE | MEAN(mm) | D.F. | STATISTIC | P |
|---|---|---|---|---|
| YES | 4.43 | 17 | t=2.09 | $>0.05$ |
| NO | 3.97 | | | |

## E. DISCUSSION.

All categories of Lembos and Corophium were found more frequently out of their tubes at night than during the day. As both species, when out of their tubes, show a pronounced negative phototactic reaction, total emergence during the day is probably inhibited, at least in part, by the associated high light intensity. A rapid increase in light intensity has been shown to inhibit swimming in Corophium volutator (Gidney, 1969) and Tritaeta gibbosa (Jones et. al., 1973).

Whilst several workers have found domiciliary species out of their homes at night, eg. the ten year field study analysed by Austin and Williams (1972), only Ledoyer (1962, 1964b), Mills (1967), Gidney (1969) and Jones et. al. (1973) provide evidence, from field studies, of nocturnal emergence being greater than daytime emergence. The reverse situation was reported by Fincham (1968), who found that several tubicolous species were more abundant during daytime plankton hauls. However, since his sample size was small and some of the daytime hauls occurred when the sea was rough, these comparisons are of doubtful significance.

Complete emergence was common only in male Lembos. It is interesting to note that not only were mature female Lembos less likely than males to leave their tubes they also had a greater tendency, once displaced, to build or enter a vacated tube. Although it is not known how long individual male Lembos remain outside their tubes at night, males can be found out of their tubes throughout the night. There is no indication that they emerged suddenly at certain hours of the night, as occurs in male Dexamine spinosa(Macquart-Moulin, 1968). The suggestion that emergence in male Lembos is size dependent requires further examination.

There are indications from other studies on domiciliary species, that males have a greater tendency, than other categories, to vacate their homes, viz. Ampithoe lacertosa (Heller, 1968), A. podoceroides (Robertson, 1888), Corophium volutator (Watkin, 1941a; Muus, 1967), Grandidierella japonica (Chapman and Dorman, 1975) and Jassa falcata (Sexton and Reid, 1951; Heller, 1968). Mills (1967) reports that the last male moult of Ampelisca abdita almost amounts to a metamorphosis. This, he proposed, made the males stronger swimmers, allowing them to spend their short adult lives free-swimming in the water column.

However, he provides no evidence of males being more abundant, than any other category, in night plankton hauls. The situation with male Tritaeta gibbosa is also unclear. Whilst nocturnal plankton hauls contained more males than females, there was no difference in the percentage of males and females swimming, under conditions of darkness, in the laboratory (Jones et. al., 1973).

Although the present experiments show a marked emergence of male Lembos at night, there is evidence to suggest that more observations are required to determine the true extent of this behaviour in nature. (1) Some Lembos tubes are found in partially occluded crannies inside Laminaria holdfasts. During the day these crannies must be quite dark and therefore intra-holdfast activity may not be precluded at this time. (2) These experiments were conducted on unpaired males. Casual observations suggest that paired males often leave their female partner during the day. (3) Moulting is most frequent during the day (pers. obs.). As copulation occurs within 1 h of moulting (Schiecke, 1973), the males are 'free' to leave during the day.

Swimming was rare, in both species, when individuals emerged from their tubes. Both species moved mostly by crawling along the bottom of the dish. Within the genus Corophium the locomotory behaviour of C. volutator is particularly well documented. Whilst many authors have described this species crawling and swimming in its estuarine habitat (Clay, 1965), no mention is made as to which behaviour is more frequent. The experiments of Morgan (1965), which were conducted in unnatural conditions (no sediment), suggest that swimming is more frequent in C. volutator than in C. bonnellii. In fact, the frequent field reports (excluding studies where a net has been dragged across the substratum and thereby could have disturbed the animals and/or their tubes) of the planktonic occurrence of species, other than C. volutator, suggest that C. bonnellii is a rather atypical member of the genus in this respect (Robertson, 1888; Nagata, 1966; Zaitsev, 1970; Austin and Williams, 1972; Achuthankutty et. al, 1973). Although the locomotory behaviour of the genus Lembos is poorly known, L. smithii appears to have a greater tendency to swim than L. websteri (Austin and Williams, 1972).

Although, in laboratory dishes, male Lembos would frequently emerge from their tubes at night, they were rarely seen on the surface of

Laminaria holdfasts, held in aquaria. This suggests that they were moving about in the interior crannies, in places where some of their tubes have been found.

The absence of male Lembos on the surface of the holdfasts and their infrequent excursions into the water column are probably adaptations to living in exposed localities. Although Lembos can maintain their position on the bottom of a dish when the water is strongly agitated they would not be able to hang onto the holdfast surface in a rough sea. Also, being a weak swimmer, Lembos would not be able to maintain its position in such a sea. Morgan (1965) reports that Corophium volutator normally swims upwards at 2 to 3.5 cm $sec^{-1}$, with occasional bursts of up to 6 cm $sec^{-1}$. These speeds would not allow C. volutator to swim against the ebb and flood current in the Ythan estuary (Gidney, 1969). Peacock (1972) has shown that Tritaeta gibbosa is unable to swim against a current of 0.44 knots (=22.7 cm $sec^{-1}$).

It would be interesting to compare the differing degrees of turbulence required to dislodge Lembos websteri and the isopod Janiropsis breviremis Sars, 1899 from a Laminaria hapteron. J.breviremis was very active on the surface of Laminaria holdfasts at night (in the laboratory).

The function of emergence in tubicolous amphipods has not previously been sought by experiment. The hypothesis that male Lembos emerge from their tubes at night to seek out and enter the tubes of mature females is confirmed by the limited data available, but further replication would be desirable.

Further evidence for the reproductive function of male emergence comes from the fact that emergence appears to show seasonal variation, being more frequent in summer (the reproductive period) than winter (the non-reproductive period). However, it must be remembered that the January experiment was conducted at a different stage of the lunar cycle from the other experiments.

Do male Lembos select the tubes occupied by mature female Lembos, from all the other tubes in a Laminaria holdfast, with reference to chemical clues? Dahl, et al., (1970) have shown that pheromones produced by female Gammarus duebeni can attract males.

As female *Corophium bonnellii* probably reproduce by parthenogenesis there is no need for them to emerge from their tubes for reproductive purposes. This probably explains why emergence is much less frequent in *Corophium* than *Lembos*.

Watkin (1941a) and Mills (1967) suggest that tube emergence occurs in *Corophium volutator* and *Ampelisca abdita* to allow the two sexes to meet and mate in the water column. This may or may not be true, as mating in these species has never been observed.

Another function of complete emergence is dispersal. Very little is known about this in *Lembos websteri* and *Corophium bonnellii*. The important questions are, (1) What is the relative importance of active and passive dispersal? (2) Is there any particular time or category associated with active dispersal? Passive dispersal probably includes, (A) the detachment and transport of *Laminaria* holdfasts, in strong seas, (B) the transport of *Laminaria* plants, attached to pebbles, by strong currents, (C) the colonization of floating objects, eg. *C. bonnellii* has been found in cork washed ashore on the Dutch coast (Stock and Bloklander, 1952), (D) the transport of individuals by water currents. With respect to active dispersal, Scarratt (1961) suggests that in Loch Fyne *C. sextoni* (=*C. bonnellii*, P.G. Moore, pers. comm.) is a very mobile species with the population in some *Laminaria* holdfasts increasing dramatically at night. Unfortunately his sampling technique was poorly designed and no such conclusion can in fact be made (see Moore, 1971). Young *C. bonnellii* and *L. websteri* are not very active in the short period between leaving their mother's tube and building tubes of their own. Wide dispersal does not therefore appear to be a feature of this stage in their life cycle. McLusky (1971) suggests that it is the adults of *C. volutator* which colonize the upper reaches of the Ythan estuary in summer, as the salinity of these waters becomes more favourable.

Of particular interest is the hypothesis of Mills (1967) connecting substratum instability, tube emergence and dispersal in *Ampelisca abdita*. With the passage of time established patches of *Ampelisca* tubes become more susceptible to being washed away, as silt and faecal pellets accumulate between the tubes. Mills proposed that brood carrying females emerged from their tubes in order to be scattered into previously unoccupied areas, where the substratum is more stable.

# CHAPTER V. BROODING BIOLOGY AND THE BEHAVIOUR OF YOUNG IN THEIR MOTHER'S TUBE.

## A. INTRODUCTION.

Very little has been published concerning the reproductive biology of *Lembos websteri* and *Corophium bonnellii*. Stephensen (1929, 1940a) collected ovigerous *Corophium* in the Faroes, from May to October and in Iceland, from May to September. At Plymouth, ovigerous *Corophium* have been found in collections made in April, July, August and September (Crawford, 1937a). Duhig (1960), working in Ireland, found ovigerous *Corophium* and *Lembos* from June to August and from July to September, respectively. Finally, Bousfield (1973), in his guide book to the amphipods of the New England region of North America, reports that these two species are ovigerous from May to July and May to September, respectively. Dr. P.G. Moore's unpublished researches will eventually supply further data on breeding biology.

Of major interest in the fact that only one morphological male *Corophium bonnellii* has ever been found (Toulmond and Truchot, 1964) in the many thousands of individuals examined, from a wide geographical area (Sars, 1890; Stebbing, 1906; Chevreux and Fage, 1925; Crawford 1937a; Stephensen, 1940b; Schellenberg, 1942; Gomoiu and Müller, 1962; Movaghar, 1964; Turquier, 1965; Hamond, 1967; Bousfield, 1973; Moore, 1973c). The only other published information on the reproductive biology of these two species is that female *Lembos* lay eggs 50 min after moulting (Schiecke, 1973) and that *Corophium*, from the Black Sea, carry 6-19 eggs per individual (Gomoiu and Müller, 1962).

Detailed studies on the reproductive behaviour of domiciliary amphipods are restricted to *Chelura terebrans* (Kühne and Becker, 1964), *Ampithoe valida* (Barrett, 1966) and *A. lacertosa* (Heller, 1968). Although I have observed many aspects of the reproductive behaviour of *L. websteri* and *C. bonnellii*, only data, pertaining to their brooding biology and the behaviour of young in their mother's tube, are presented here.

No attempt has been made to test the well-founded hypothesis that *C. bonnellii* reproduces parthenogenetically. The definitive test would be to see if individuals, that have been reared in isolation from the time they hatched, can produce viable offspring. I hope to conduct this test at some later date.

The only other amphipods which are thought to be parthenogenetic are *Talitrus alluadi* (Crawford, 1937a; Stephensen, 1940b), *Rhabdosoma minor* and *R. brevicaudatum* (Fage, 1954). Dennel (1934) could only identify female *Haustorius arenarius* and therefore proposed that the species might be parthenogenetic. This seems unlikely following Watkin's (1941,b) discovery of male *H. arenarius*. Forsman (1956) presents evidence against parthenogenesis occurring in *Leptocheirus pilosus*. Kaestner (1970) provides some information on parthenogenesis in isopods. *Trichoniscus pusillus* has a triploid parthenogenetic race, whilst *Armadillium vulgare* and *Cylisticus convexus* have parthenogenetic females in their diploid bisexual races.

## B. EFFECT OF TURBULENCE AND TURBIDITY UPON BROOD SURVIVAL.

### Materials and Methods.

Female *Lembos* and *Corophium*, which would soon lay eggs, were examined twice a day. When a female was found with eggs in her brood pouch it was transferred, along with its glass tube, to a dish with either still or moving water. The "still" dish contained 200 ml of water and had a scattering of settled organic detritus. The "moving" dish contained 100 ml of water and 3 ml of organic detritus, which was maintained in suspension by a propeller, of 4 cm diameter, rotating at 104-112 r.p.m. Each dish contained one female of each species.

Once a day each dish was checked for the presenceof recently released young. A brood was defined as having survived if at least one young was released successfully. The more informative measure of brood survival, namely the number of young released successfully as a fraction of the number of eggs laid, was not calculated. This was due to the impossibility of accurately counting the number of eggs laid.

The mean of each daily maximum and minimum water temperature was calculated. Any settled detritus, in the moving water dishes, was resuspended daily and, every two days, the water and detritus, in all dishes, were changed. Further details of the experiment are presented in table 31.

## Results (table 32)

The brood survival of Lembos and Corophium was significantly greater in moving than in still water. In both still and moving water the brood survival of Corophium was better than that of Lembos but only in moving water was the difference statistically significant.

## C. BROODING TIME.

### Materials and Methods.

Brooding time is the length of time a brood remains in a female's brood pouch, ie. between egg laying and the end of brood release. The times were derived from the previous experiment, where females were exposed to suspended detritus. As each female was observed only about once a day, egg laying and the end of brood release were not normally recorded. Thus egg laying occurred between the known times A and B and the end of brood release occurred between the known times C and D. Therefore the interval between egg laying and the end of brood release must have been at least Xh (C-B) and at the most Yh (D-A), assuming that young did not re-enter the brood pouch after time D. Brooding time was defined as the mean of X and Y and was expressed to the nearest day.

The mean daily temperature of the brooding period was calculated separately for each brood.

### Results (table 33)

The brooding times of Lembos and Corophium were alike, at similar water temperatures. In both species brooding time was inversely related to water temperature.

## D. HATCHING TIME.

### Experiment 1.

### Materials and Methods.

Hatching time is the time that elapses between egg laying and

## TABLE 31

## DETAILS OF THE BROOD SURVIVAL EXPERIMENT.

| SPECIES | WATER CONDITIONS | DATE | MEAN WATER T°c. |
|---|---|---|---|
| LEMBOS | STILL | JULY+AUG'74 | 16.8 |
| | MOVING | AUG+SEPT'75 | 18.2 |
| COROPHIUM | STILL | JULY+AUG'74 | 16.1 |
| | MOVING | AUG+SEPT'75 | 18.4 |

## TABLE 32

## BROOD SURVIVAL UNDER DIFFERENT CONDITIONS OF TURBULENCE AND TURBIDITY

| SPECIES | WATER CONDITIONS | BROOD SURVIVAL (°/o) | N | $\chi^2$ | P |
|---|---|---|---|---|---|
| LEMBOS | STILL | 18.8 | 16 | 8.56 | $< 0.01$ |
| LEMBOS | MOVING | 72.7 | 22 | | |
| COROPHIUM | STILL | 45.5 | 11 | † | =0.0002 |
| COROPHIUM | MOVING | 100 | 18 | | |
| LEMBOS | STILL | 18.8 | 16 | † | $>0.05$ |
| COROPHIUM | STILL | 45.5 | 11 | | |
| LEMBOS | MOVING | 72.7 | 22 | † | =0.02 |
| COROPHIUM | MOVING | 100 | 18 | | |

† NO $\chi^2$ VALUE FOR AN EXACT TEST (SEE BAILEY, 1964, P.61).

# TABLE 33

## BROODING TIMES

| LEMBOS | |
|---|---|
| BROODING TIME (DAYS) | MEAN DAILY TEMP. (°c) |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 11 | 18.75 |
| 10 | 18 |
| 10 | 18 |
| 11 | 18 |
| 11 | 17.5 |
| 11 | 17.5 |
| 11 | 17.5 |
| 11 | 17.25 |
| 12 | 17.25 |
| 12 | 17.25 |

| COROPHIUM | |
|---|---|
| BROODING TIME (DAYS) | MEAN DAILY TEMP. (°c) |
| 9 | 19.25 |
| 9 | 19.25 |
| 9 | 19.25 |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 9 | 19 |
| 10 | 19 |
| 10 | 19 |
| 10 | 19 |
| 10 | 16.5 |
| 11 | 16.5 |
| 10 | 16.5 |
| 10 | 16.5 |
| 10 | 16.5 |
| 11 | 16.5 |
| 11 | 16.5 |

hatching out of the egg membrane(s). Females which would soon lay a new brood of eggs were examined about twice a day. Once a new brood had been laid the eggs were left to separate from each other before 5 of them were transferred to a dish containing 50 ml of filtered sea water (no particles $> 1\,\mu m$). 5 broods from each species were treated in this manner. Each brood was kept in a separate dish, which was gently aerated. Every day the eggs were examined, the water changed and the maximum and minimum water temperature of the previous day recorded.

As neither egg laying nor hatching were normally observed, hatching times were calculated in the previous manner. Both times were expressed to the nearest day.

### Results.

Out of the 50 eggs cultured none hatched. Only 2 Corophium eggs developed to the eyed-embryo stage.

### Experiment 2.

### Materials and Methods.

The techniques employed in experiment 1 were modified for this experiment. Firstly, eggs were only removed from their mother's brood pouch once they had reached the eyed-embryo stage. Secondly, all glassware was autoclaved and siliconized. These precautions were taken to reduce the chance of eggs becoming diseased and/or sticking to the glass surfaces (the latter was common in experiment 1).

### Results.

Hatching success was 21 our of 22 for Lembos and 21 out of 23 for Corophium. The hatching times for Lembos and Corophium were 10.1±0.1 days and 10.3±0.1 days ($\bar{x}$±S.E.) respectively, at a mean daily water temperature of 17.4°C (range, 16-19°C).

## E. LENGTH OF TIME HATCHED YOUNG STAY IN THEIR MOTHER'S BROOD POUCH.

### Materials and Methods.

Running concurrently with the previous experiment, on hatching times, was an experiment to determine brooding times. This permitted the length of time hatched young spend in their mother's brood pouch to be calculated (brooding time minus hatching time) for a particular mean daily water temperature.

Brooding times were determined by keeping females, which had recently laid eggs, singly, in dishes with 100 ml of water and 3 ml of organic detritus. The detritus was maintained in suspension by a propeller, of 4 cm diameter, rotating at 104-112 r.p.m. Once a day each dish was checked for the presence of recently hatched young. Both the hatching and brooding times were expressed to the nearest day.

### Results (table 34)

The mean daily water temperature was 17.3°C (range, 16-19°C). The length of time hatched young spent in their mother's brood pouch was about one day (*Lembos*) and, at the most, a few hours (*Corophium*). Therefore, *Lembos* has a slightly longer brooding time than *Corophium*.

## F. INTERACTION OF THE MOTHER WITH HER BROOD DURING THE PRE-HATCHING PERIOD.

For a while after laying, the eggs of *Lembos* and *Corophium* appear as two separate masses. One female *Corophium*, with eggs as two separate masses, frequently pushed against the sides of her brood pouch with the ischial region of her gnathopods. This behaviour, "elbowing", also occurs in both species after the eggs have been dispersed throughout the brood pouch. The long setae which originate from the ischial region of *Corophium's* first pair of gnathopods were probably forced inside the brood pouch during this behaviour. One female *Corophium*, observed for five one minute periods about one hour after egg laying, showed this behaviour 19 times per minute, 18.9±0.4min$^{-1}$ ($\bar{x}$±S.E.) . "Elbowing" causes the eggs to move very slightly in the marsupium, as does flexing the abdomen, a frequent behaviour in both species.

One female *Corophium* was seen to put her gnathopods into her brood pouch, remove several eggs and then ingest them. Although female *Lembos* have not been seen to remove eggs from the brood pouch, one female was observed to ingest one egg, whilst holding two more

# TABLE 34

## HATCHING AND BROODING TIMES FOR *LEMBOS* AND *COROPHIUM* AT ABOUT 17°c.

| SPECIES | HATCHING TIME (DAYS) * | N | BROODING TIME (DAYS) * | N |
|---|---|---|---|---|
| L.WEBSTERI | 10.1±0.1 | 21 | 11.3±0.2 | 6 |
| C.BONNELLII | 10.3±0.1 | 21 | 10.4±0.2 | 7 |

* MEAN ± STANDARD ERROR.

in her second pair of gnathopods. These eggs could only have come from her own brood pouch.

If an egg-carrying female Corophium becomes involved in a dispute over tube ownership eggs are occasionally forced out of her marsupium. These eggs can be replaced once the dispute has ended. One female achieved this by flexing her thorax ventrally, forcing two displaced eggs into her brood pouch. Egg loss, during tube ownership disputes, has never been observed in Lembos.

## G. REACTION OF EMBRYO-BEARING FEMALES TO OTHER EMBRYOS BEING INTRODUCED INTO THEIR TUBES.

### Materials and Methods.

Each test female occupied a glass tube. The reaction of test females to test embryos being pipetted into their tubes was recorded. The test embryos were not derived from the test females but from other females of the same or different species. All test embryos were used within 1 h of being removed from their mother's brood pouch.

### Results. (tables 35 and 36)

Although a female C. bonnellii frequently placed an embryo derived from another C. bonnellii into its brood pouch, this never occurred when embryos of a different species were offered. A female L. websteri never placed an embryo derived from another L. websteri into its brood pouch.

C. bonnellii pushed embryos into its brood pouch through the anterior opening, by the combined "elbowing" action of the second pair of gnathopods. At the same time the thorax was flexed ventrally, enlarging the gaps between the brood plates and therefore making it easier for the embryo to enter. Infrequently, embryos which had been carried by the pleopod current past the gnathopods, without being caught, entered the brood pouch solely as a result of ventral flexing of the thorax. Less accentuated thorax flexing occurred infrequently, immediately after C. bonnellii had rejected embryos of L. websteri and C. volutator. L. websteri was never observed to flex its thorax during this experiment.

One female C. bonnellii attached one introduced embryo, of its own

## TABLE 35

## REACTION OF EMBRYO-BEARING FEMALES TO OTHER EMBRYOS BEING INTRODUCED INTO THEIR TUBES.

| TEST FEMALE | TEST EMBRYO | PUT INTO MARSUPIUM | INGEST | OTHER REACTIONS | TOT. |
|---|---|---|---|---|---|
| C.BONNELLII | C.BONNELLII | 16 | 1 | 7 | 24 |
| | C.VOLUTATOR | 0 | 0 | 13 | 13 |
| | L.WEBSTERI | 0 | 6 | 3 | 9 |
| L.WEBSTERI | C.BONNELLII | 0 | 1 | 0 | 1 |
| | L.WEBSTERI | 0 | 9 | 0 | 9 |

## TABLE 36

## PERCENTAGE OF EMBRYOS INTRODUCED INTO THE TUBE OF AN EMBRYO-BEARING FEMALE WHICH THE FEMALE THEN PUT INTO HER MARSUPIUM.

| FEMALE | NO. OF FEMALES | EMBRYO | NO. OF EMBRYOS | % PUT IN | P |
|---|---|---|---|---|---|
| C.BONNELLII | 10 | C.BONNELLII | 24 | 66.67 | $<0.001$ |
| C. BONNELLII | 5 | L.WEBSTERI | 9 | 0 | |
| C. BONNELLII | 10 | C.BONNELLII | 24 | 66.67 | $<0.001$ |
| C. BONNELLII | 6 | C.VOLUTATOR | 13 | 0 | |
| C. BONNELLII | 10 | C. BONNELLII | 24 | 66.67 | $<0.001$ |
| L. WEBSTERI | 5 | L. WEBSTERI | 9 | 0 | |

species, to the inside of its tube, by the knitting activity of its first two pairs of pereopods. The next female C. bonnellii tested removed the attached embryo and worked it over with its maxillipeds, for about one minute, before pushing it into its brood pouch.

All embryos offered to L. websteri were ingested, even by individuals with completely full guts. Some embryos, particularly L. websteri embryos, offered to C. bonnellii were ingested. Corophium appeared to have greater difficulty than Lembos in breaking up Lembos embryos.

## H. HATCHING.

### Lembos

One embryo was observed continuously for c. 1 h prior to hatching. The embryo kept its abdomen flexed under its body and remained still for long periods. From time to time the embryo moved very slightly by either arching up its thorax, lifting up its head or flexing or straightening its abdomen. The pereopods would occasionally move but the pleopods remained still. For the whole time the embryo was watched there were regular cardiac contractions.

Just before hatching the egg's surface was distended by the abdomen being straightened out. As the tip of the urosome was the first part of the embryo to emerge this distension probably produced the initial rupture. The animal then freed itself by flexing its abdomen in a pronounced, but not a very vigorous manner. About 3 min after the initial rupture the antennae were free to straighten up and assume their normal position. The mouthparts were seen to move at this time. The animal was completely free within another minute.

3.5 min after emerging its behaviour resembled that of young which had hatched several hours previously, ie. it crawled about, beat its pleopods, and occasionally swam.

Recently hatched young frequently flexed their abdomens. When several were in the same dish they did not cluster together, except for short periods when they appeared to get their pereopods entangled. They also did not cling to hair-like objects. Their pleopods appeared to beat virtually continuously. All other aspects of their behaviour resembled that of adults.

### Corophium.

One embryo was observed from time to time several hours before it hatched. Its behaviour prior to hatching was exactly the same as that described for Lembos, except that observations on cardiac activity were not made and the mouthparts were seen to move slightly.

The immediate pre-hatching behaviour was not observed. When the embryo was next observed the tip of the urosome and the tips of some pereopods were already projecting through the ruptured egg. The animal freed itself in the same manner as Lembos. After c. 1 min the antennae were free to straighten up and assume their normal position. After another minute the animal was completely free, except for a small piece of egg membrane which remained attached to the urosome.

After emerging, observations continued for another 12 min. During this time the animal continued to flex its abdomen whilst lying still on the bottom of the dish and beating its pleopods irregularly. Normally, recently hatched young crawl about the dish. They do not cluster together.

## I. BEHAVIOUR OF HATCHED YOUNG IN THE BROOD POUCH.

### Activity.

In spite of the cramped conditions which occurred when a large number of hatched young were present the young of both species were quite active. They could crawl about, somersault, protrude their antennae and partially emerge. Often a high proportion of the brood would be active at any one time. The periods of activity appeared to be more frequent as time progressed and were often associated with young leaving the brood pouch. When not moving the young flexed their abdomens and were normally orientated such that their long axes were parallel to the long axis of the female.

Locomotion within the brood pouch seemed to rely mainly on the thrust from the pereopods and on the frequent flexing and extension of the abdomen. The pleopods were never seen to assist.

### Young Corophium feeding.

Females, preserved immediately after removal from the sea, have been found to carry hatched young with food in their guts. Several means by which young can obtain food have been observed in the laboratory.

Young can feed on the organic detritus trapped by their mother's gnathopods. The young would partially emerge (sometimes two together) from the anterior end of the brood pouch. The second antennae were then hooked around the detritus, which had accumulated on the gnathopod filter basket. This was then pulled back into the brood pouch. The mother appeared neither to help nor to hinder this behaviour. A young animal could reach so far forwards that its head appeared to be directly over its mother's mouth. No young, however, were seen to remove detritus from the mass which was held by the mother's maxillipeds.

Young will partially emerge from the ventral surface of the brood pouch and scrape the tube with their antennae. However, no material was ever seen to be removed.

Quite often a large number of antennae protruded from the brood pouch. Although they were never seen to trap suspended particles, they sometimes tore small pieces off the large boluses of organic detritus which became lodged between the brood pouch and the wall of the tube. This material was pulled inside the brood pouch before being ingested. The large boluses originated either from material rejected by the female or from material displaced from female's mouthparts when she somersaulted round in the tube.

Occasionally fine, water-borne particles of detritus were either carried into the brood pouch or became trapped between the setae of the brood plates. The young were never seen to feed on these particles.

There is no conclusive evidence of hatched young eating unhatched embryos. However, in one brood pouch several young were seen moving their mouthparts very close to an unhatched embryo.

Defaecation was never observed.

Young *Lembos* feeding.

As with *Corophium* there is field evidence for hatched young feeding whilst in their mother's brood pouch.

Young Lembos can feed on organic detritus trapped by the female's gnathopods. As some of the details differ from those described for Corophium a full description will be given. Young would partially emerge from the anterior end of the brood pouch, either through the anterior opening or from between the brood plates. The antennae were then used to hook around detritus on the setae of their mother's gnathopods. This material was pulled back into the brood pouch, with the aid of its gnathopods, and subsequently eaten. The female appeared to neither help nor hinder this behaviour. The sudden appearance of organic detritus in their mother's pleopod current sometimes caused the young to turn round and face the anterior end of the brood pouch.

Young will partially emerge from the ventral surface of the brood pouch and scrape the tube with their gnathopods (c.f. Corophium used their antennae). No material was ever seen to be removed.

Occasionally antennae were seen waving gently outside the brood pouch. They were never seen to trap suspended particles nor to pull small pieces off large boluses of detritus, which became trapped between the brood pouch and the wall of the tube.

Occasionally fine, water-borne particles of detritus were carried into the brood pouch, but the young were never seen to ingest them.

Defaecation was never observed and so it is not known if refection occurs.

## J. DO HATCHED YOUNG MOULT WHILST IN THEIR MOTHER'S BROOD POUCH?

### Materials and Methods.

20 young Corophium and 15 young Lembos, which had recently hatched outside their mothers' marsupia, were kept individually in small dishes with a few ml of water and a little organic detritus. Once a day the dishes were checked for exuviae and the water changed.

### Results.

The young quickly died. 6 Corophium and 6 Lembos lived for at least 2 days after hatching, which is longer than the young appeared to spend in the brood pouch but no exuviae were found. 3 Corophium and 2 Lembos were still alive 4 days after hatching but again no exuviae were found.

## K. IRRIGATION OF THE BROOD POUCH.

A mature female of either species can create an anterior to posterior current, through an empty brood pouch, by beating her pleopods. This was proven by watching individuals, with one egg in their brood pouch, somersault round in their tubes. As a result of the somersault the egg rolled from the posterior to the anterior end of the brood pouch. When an individual started to beat its pleopods again the egg was sucked to the posterior end.

In a brood pouch full with embryos or young the effectiveness of this current will be considerably reduced. Additional water movements will be created by the mother slightly moving her brood plates, towards and away from her mid-line and by the young beating their pleopods.

When a female Lembos or Corophium, with a full brood pouch, beat its pleopods and drew a suspension of detritus into its tube, very few particles entered the brood pouch via its ventral surface. This suggests that the ventral surface was not an important site for water entry. In order to establish the most important sites for water entry, egg bearing females occupying glass tubes, were kept in a suspension of ferric oxide. It seemed likely that the sticky particles of ferric oxide would build up around the main sites for water entry. After 1.5 h there were no areas of ferric oxide accumulation in the brood pouches of either Lembos or Corophium. This suggests that there were no particular sites for water entry.

## L. DURATION OF RELEASE OF HATCHED YOUNG FROM THE BROOD POUCH.

### Materials and Methods.

24 brooding female Lembos were observed from time to time. Brood release must have started between the known times A and B and ended between the known times C and D. Thus in each female brood release must have been at least Xh (C-B) and at the most Yh (D-A), assuming young did not re-enter the brood pouch after time D.

As young Corophium left their mother's tube soon after emerging from the brood pouch, it was impossible to ascertain exactly when emergence started and thus no data are available for the duration of brood release in Corophium.

### Results (table 37)

Brood release normally lasted less than one day at both c. $16.5^{\circ}$C and c. $19.5^{\circ}$C. One exceptionally long period of release lasted for more than 31 h.

### M. INTERVAL BETWEEN THE END OF BROOD RELEASE AND THE FEMALE'S MOULT.

### Materials and Methods.

33 brooding Lembos and 6 brooding ~~Lembos~~ Corophium were observed discontinuously. Again the duration of this interval is only known to occur between upper and lower limits.

### Results (table 38)

At c. $16.5^{\circ}$C the interval for Lembos was normally less than one day, whilst that for Corophium was normally greater than two days. The interval for Lembos, at c. $19.5^{\circ}$C, was also normally less than one day.

### N. BEHAVIOUR OF MOTHER AND YOUNG DURING BROOD RELEASE.

The young of both species mostly emerged from the brood pouch without any assistance from their mother. They emerged easily from the anterior or posterior openings of the brood pouch or through the gaps between adjacent brood plates, by flexing their abdomens. Young Corophium emerged from the posterior opening less frequently than from other parts of the brood pouch. Sometimes, when a young Corophium did try to emerge from the posterior opening the mother flexed her own abdomen and so blocked its escape.

Young emerged singly or in pairs, with several young frequently emerging within minute of each other. At such times there would often be a great deal of activity in the brood pouch. Partial emergence and antennae protrusion, at such times, probably represented exploratory behaviour. One young Corophium was seen to partially emerge several

# TABLE 37

## DURATION (IN HOURS) OF BROOD RELEASE; AT TWO DIFFERENT WATER TEMPERATURES : LEMBOS

| 16.4±0.2°C * | 19.5±0.1°C* |
|---|---|
| 0-3.5 | 0-3 |
| 0-5.25 | 0-3.75 |
| 0-5.75 | 0-3.75 |
| 0-7 | 0-4 |
| 0-17 | 0-4 |
| 3.25-19 | 0-13.5 |
| 7-20.25 | 0-15.25 |
| 10-38.5 | 0-15.25 |
| >31 | 0-15.75 |
| | 3-10 |
| | 3-16.25 |
| | 3-16.25 |
| | 3.75-24.25 |
| | 4-23 |
| | 6-22.5 |

* **MEAN ± STANDARD ERROR.**

## TABLE 38

## INTERVAL (IN HOURS) BETWEEN THE END OF BROOD RELEASE AND THE FEMALE'S MOULT, AT TWO DIFFERENT WATER TEMPERATURES.

| 16.4±0.2°C * | | 19.5±0.1°C * |
|---|---|---|
| COROPHIUM | LEMBOS | LEMBOS |
| 35.5-49.75 | 0 | 0-3 |
| 56-93.25 | 0-1.25 | 0-3.75 |
| 57-79.25 | 0-1.75 | 0-4 |
| 70.5-112 | 0-3.25 | 0-4 |
| 71.75-101.75 | 0-3.5 | 0-4.75 |
| 88-119.75 | 0-3.75 | 0-11.75 |
| | 0-5.25 | 0-13.5 |
| | 0-9 | 0-14.75 |
| | 0-12 | 0-15.25 |
| | 0-12.5 | 0-15.25 |
| | 0-21.5 | 0-16.25 |
| | 0-23.75 | 0-16.25 |
| | 0.5-2.75 | 0-20.75 |
| | 6.25-15.25 | 3.75-21.75 |
| | 10.25-24 | 4.75-24 |
| | 26.75-42 | 20.75-34.25 |
| | | 29-48.5 |

* **MEAN ± STANDARD ERROR.**

times in quick succession before completely emerging.

There was only one instance (in *Lembos*) where emergence of young occurred only seconds before the female moulted. In that particular case the brood plates separated slightly prior to the young emerging.

One female *Lembos* and four female *Corophium* were seen to flex their abdomens, placing the urosome inside the brood pouch. Further forward movement of the urosome then forced several young out of the brood pouch. The maximum number forced out was four (by *Corophium*).

One female *Lembos* was observed to put one of her second gnathopods into her brood pouch. Although the gnathopod was not seen to push any of the hatched young out of the brood pouch one did appear in the tube immediately after the gnathopod was removed. *Corophium* will also put their first gnathopods into the brood pouch but they were never observed to force young out.

Young of both species have been seen to emerge immediately after a female's somersault. This did not occur after every somersault, being recorded only on two occasions in *Lembos* and four in *Corophium*. Immediately after *Corophium* somersaulted one or two young were partially out of the brood pouch. These young only left after the female had flexed her thorax ventrally several times, causing the brood plates to separate slightly. Flexing of the thorax immediately following a somersault was not observed in *Lembos*. Ventral flexing of the thorax, resulting in young emerging, can also occur in *Corophium* without first being preceeded by somersaulting. This was observed on two occasions and resulted in one and three young emerging. Also during disputes over tube ownership, vigorous body contortions, including ventral flexing of the thorax, can result in young *Corophium* being forced out of the brood pouch. On one occasion a female was seen to use her first gnathopods to replace a displaced youngster. This was aided by ventral flexing of her thorax.

The young of both species after remaining in their mother's tube for a while, would frequently re-enter her brood pouch. Only rarely did young re-enter their mother's brood pouch after having wandered outside her tube. Re-entry was achieved as easily as emergence. Although the mother did not help this process, the beating of her pleopods appeared to hinder re-entry through the posterior opening of her brood pouch. Some Lembos but no Corophium re-entered through this opening. The young of both species re-entered through the anterior opening and through the gaps between the brood plates. Occasionally, after emerging from the brood pouch, a young Lembos would lie quite still on the female's ventral surface, just behind the brood pouch. After a few seconds it re-entered the brood pouch, sometimes urosome first.

## O. COMPARISON OF THE LENGTH OF TIME THAT YOUNG LEMBOS AND YOUNG COROPHIUM CAN BE FOUND IN THEIR MOTHER'S TUBE.

### Materials and Methods.

16 female Lembos and 18 female Corophium were kept singly in glass tubes, c. 10 mm long, and provided with suspended organic detritus. The tubes were examined once a day. The mean daily water temperature was $17 \pm 0.2^{\circ}C$ ($\bar{x} \pm S.E.$).

### Results.

Ten Lembos but no Corophium were found to have young in their tubes. Thus young Lembos must have stayed longer, than young Corophium, in their mother's tube. This result is supported by numerous other observations. Sometimes young Corophium only stayed in their mother's tube for a few minutes.

## P. THE RESIDENCE TIME OF BROODS OF HATCHED YOUNG IN THE TUBES OF FEMALE LEMBOS.

### Materials and Methods.

18 glass tubes, c. 10 mm long, were kept separately in dishes with settled organic detritus. Each tube contained one female, carrying well-developed embryos and one male (the male did not always remain there). As the tubes were observed discontinuously the residence time of each brood is only known to occur between lower and upper limits.

### Results (table 39)

At a mean daily water temperature of $16.4 \pm 0.2^{\circ}C$ ($\bar{x} \pm S.E.$) the

## TABLE 39

### THE RESIDENCE TIME (IN HOURS) OF BROODS OF HATCHED YOUNG IN THE TUBES OF FEMALE LEMBOS.

| |
|---|
| 10-37.5 |
| 18.75-72.75 |
| 19.5-28.5 |
| 20- ? |
| 23- ? |
| 23.75-31 |
| 27.25-45 |
| 29.5-87.75 |
| 30.75-45.5 |
| 34.25-49.5 |
| 36-62.5 |
| 39.25- ? |
| 39.75-52.5 |
| 45.25-58.25 |
| 66-78.25 |
| 76.5-? |
| 79- ? |
| 115-172 |

residence time was frequently at least one day but rarely longer than four days.

## Q. POSITION OF YOUNG LEMBOS IN THEIR MOTHER'S TUBE.

### Materials and Methods.

Less than seven separate observations were made on each of 19 glass tubes containing a male, female and recently hatched young. The position of each young animal was recorded as being either, nearer to the female, nearer to the male or of equal distance from both.

### Results (table 40).

As only 2 of the 238 observations were assigned to the last category they were excluded from the analysis. If the young had been distributed equally relative to both parents,

$$p \text{ (nearer to female)} = q \text{ (nearer to male)} = 0.5$$

In this case,

$$\hat{p} = 0.84 \quad \left(\frac{199}{236}\right) \qquad \hat{q} = 0.16 \quad \left(\frac{37}{236}\right)$$

To test the significance of this imbalance the following formula was applied (Clarke, 1967, p. 48).

$$d = \frac{\hat{p} - p}{\sqrt{pq/N}}.$$

Where N is the total number of observations.

In this case $d = 10.45$ which is highly significant ($p < 0.001$). Therefore there were significantly more young sitting near the female than near the male.

Often when a young animal crawled towards the male it would stop, turn around and crawl back to the female. There was also a slight indication that young, on first emerging from the brood pouch, remained close together but as time progressed moved further apart.

# TABLE 40

## POSITION OF YOUNG LEMBOS IN THEIR MOTHER'S TUBE.

| NEARER TO FEMALE | NEARER TO MALE | OF EQUAL DISTANCE FROM BOTH | TOTAL |
|---|---|---|---|
| 199 | 37 | 2 | 238 |

## R. BEHAVIOUR OF YOUNG LEMBOS IN THEIR MOTHER'S TUBE.

Except for beating the pleopods fairly continuously, the young were inactive for much of the time. When standing still their bodies were either at right angles to, or adpressed against, the tube wall. The young crawled forwards, backwards and upside-down. They also crawled over the female's body without eliciting any discouraging behaviour from her. Somersaulting was frequent.

The young had food in their guts and were observed to employ seven different feeding techniques.

1. Pick up loose organic detritus in the tube.
2. Pick up loose sand grains in the tube.
3. Remove detritus from the tube wall.
4. Trap suspended detritus from their mother's pleopod current.
5. Remove detritus from their mother's gnathopods.
6. Partially emerge from the tube and scoop up settled detritus.
7. Refection.

The actions involved in each of these feeding techniques were very similar to those already described for the adults. One difference was that young animals did not pick up sand grains of 250-500 μm, before working them over with their mouthparts. Another was that the young sometimes let rejected faecal pellets accumulate inside the tube.

Females will tolerate young feeding upon the detritus held by their gnathopods, even when they are also feeding upon this material. On two occasions more than half the young in the tube converged on their mother's gnathopods when she caught and started to eat a large bolus of detritus. The young were never seen to remove detritus from the male's gnathopods.

The young cleaned their abdomens, pleopods, heads and antennae, with their gnathopods, in exactly the same manner as adults.

## S. EMERGENCE OF YOUNG FROM THEIR MOTHER'S TUBE.

The young of both species mostly crawled out of their mother's tube without any help from their mother. Young Corophium would often leave the tube immediately after emerging from their mother's brood pouch. Female Corophium often hindered the activity of young in their tube. This never occurred in Lembos. Young Corophium which tried to pass by the female's head were often grabbed by her first pair of gnathopods or elbowed backwards by her second pair. Young Corophium also found difficulty in passing by their mother's gnathopod filter basket, when it was held in the filtering position. Sometimes the females of both species would actively encourage their young to leave. A female Corophium either used her gnathopods or the basal region of her antennae to push the young forwards or made flicking movements with her abdomen to push them backwards. A female Lembos normally pushed the young forwards with her first pair of gnathopods. In addition, one young left after being tapped by the female's antennae, and one was forced out as a result of the female somersaulting in the tube.

The young of both species only rarely re-entered their mother's tube. One female Lembos used her gnathopods to prevent a young animal re-entering.

## T. DISCUSSION.

Female Corophium and probably female Lembos can remove embryos from their marsupia and subsequently eat them. The only other proof of peracarid crustaceans removing embryos from the brood pouch, before they have hatched, is provided by Rossi et.al. (1975). They report that female Asellus aquaticus can eject dead embryos from their marsupia.

In still and moving water the brood size of Lembos and Corophium fell as development proceeded. The same phenomenon has been reported in field-collected C. volutator (Noble, 1962). This could have been due to females removing embryos from their marsupia or to the decomposition of moribund eggs. The fact that brood survival, in Lembos and Corophium, was significantly greater in moving than in still water could have been due (1) to there being more food available in the former situation and therefore less of a need to gain nourishment by ingesting their own embryos, (2) to a higher oxygen tension in moving water; this is important to the members of a crowded marsupium. It was also observed that in still water the females of both species often had poorly developed ovaries and did not produce another brood of eggs at their next moult. Therefore, it seems possible that low food availability has a fairly rapid effect on the reproductive output of Lembos and Corophium.

In both moving and still water, brood survival was poorer in Lembos than Corophium. Did Lembos eat more of its embryos than Corophium? Lembos is more prone to eat its own faecal pellets and tube material. These reactions require further study. (1) When do feeding conditions become so unsatisfactory that the animals are forced to use these alternatives? (2) Is Lembos better able to withstand poor feeding conditions, because of its more pronounced use of these alternatives? (3) How long are these alternatives utilized before the tube is vacated?

The brooding time was similar in Corophium and Lembos being 10-12 days at c. 17°C. The brooding time of C. volutator has been reported variously as, just over 14 days (Hart, 1930), 17 days (Watkin 1941a) and a maximum of 28 days (Segerstrale, 1959). The brooding time of C. arenarium is reported to be 18 days (Vaughan, 1958). However, the absence of data on water temperature prevents close comparison with the C. bonnellii results.

The brooding time was inversely related to water temperature, in both species. This is a well known phenomenon in amphipods (Heller, 1968). Additional evidence is provided by Lim and Williams (1971) and Mathais (1971).

All eggs which were removed from the marsupia, soon after ovulation, died before hatching occurred. In contrast, a very high hatching success was achieved, if removal was delayed until the eggs had developed to the eyed-embryo stage. Emmart (1936) solved the problem of rearing embryos of Carcinogammarus mucronatus, outside the marsupia, in a similar manner. Eggs which were removed after ovulation usually died at the gastrulation stage. Embryo survival was much higher if the embryos were removed only after the onset of gastrulation. Once in the culture dishes, the embryos were turned over and had their water changed, every 6 h. Other techniques, for ensuring the successful development of isolated amphipod embryos, include adding an antibiotic (Vlasbolm, 1969), and rocking the culture vessel, in order to keep the eggs in continuous motion (Sheader, 1973).

The hatching time was the same in both species (10 days) at the same water temperature (c. 17°C) and similar to that (11+days) of another temperature water species C. arenarium (Vaughan, 1938). The maximum sea temperatures at Millport in the years 1974, 1975 and 1976 were 15.C, 17.5 and 16.4°C, respectively. An intruiging situation is revealed if these results are compared with those of Shyamasundari, working with the tropical species C. triaenonyx. The hatching time of C. triaenonyx was 10 days, at a temperature of 28-29°C and a salinity of c. 30‰ (Shyamasundari and Hanumantha Rao, 1974). The maximum sea temperature, in the locality where the animals were collected, was 30°C in the years 1961, 1962 and 1963 (Shyamasundari, 1973). Thus the hatching times of C. bonnellii and C. triaenonyx were the same, at temperatures close to the maximum experienced by the two species in nature. Similarly, some flatfish from Scottish and Indian beaches have respiration rates which are almost the same, at the average temperature of each location (Steele, 1976).

The residence time of hatched young in their mother's marsupium was c. one day for Lembos and, at the most, a few hours for Corophium, at c. 17°C and in the presence of suspended organic detritus. If their residence times are inversely related to water temperature these times will normally be longer, as the sea at Millport rarely reaches 17°C. This possibility is supported by Barrett (1966), who found the residence times of Ampithoe valida to be longer at 8-10°C than at 11.5-15°C. The residence time, for other Corophium species, are at least 5 days (Hart, 1930) and from 5 to 7 days (Vaughan, 1938). Unfortunately temperature data were not presented by these authors. Much longer residence times (19-42 days) are reported by Vlasblom (1969) in Marinogammarus marinus from Holland, at a temperature (15°C) similar to that experienced by Lembos and Corophium.

It is probable that (1) food availability (concentration and type of suspended particles) and (2) brood biomass in relation to brood pouch volume and the efficiency of brood pouch irrigation, also influence the residence time of hatched young. It would be interesting to see if the latter relationship has any bearing on Sheader and Chia's (1970) discovery that the residence time of Marinogammarus obtusatus is positively related to the body length of the mother. Brood pouch irrigation did not appear to be particularly efficient when Lembos and Corophium carried a large number of hatched young. This might have contributed to their short residence times, ie. the young soon vacated the marsupium in response to low oxygen tensions.

Corophium has narrower brood plates than Lembos and relies upon long setae to bridge the gaps between these plates. Corophium therefore has a less rigid brood pouch than Lembos. This probably predisposes Corophium to the occasional loss of brood members, as a result of vigorous body movements associated with tube defence. Lembos was never observed to loose brood members under similar circumstances. As a consequence of this, only Corophium appears to have evolved a behavioural mechanism for replacing displaced embryos. In addition, Corophium can distinguish between embryos of its own species and similar sized embryos of C. volutator and L. websteri, only placing embryos of C. bonnellii into its marsupium.

The replacement of displaced embryos also forms part of the behavioural repertoire of Melita zeylanica (Krishnan and John, 1974). These authors show that all pre-hatching stages of M. zeylanica are equally acceptable to mature females, irrespective of (1) whether the female has a brood and (2) the development stage of the female's brood. Melita, like Corophium, picks up embryos with its gnathopods and forces them through the anterior opening of its brood pouch. Melita, however, exhibits the additional refinement of using one pair of gnathopods to place embryos inside the marsupium and the other pair to push embryos to the back of the marsupium.

Hatching appears to be similar in Lembos and Corophium with rupture of the egg relying upon extension of the urosome. It is likely that the urosome bears hatching spines that tear through the egg membrane(s). The presence of hatching spines on the urosome of embryos of gammaridean amphipods is well documented (Le Roux, 1933; Weygoldt, 1958; Davis, 1968; Sheader and Chia, 1970; Fish, 1975). The movements of the abdomen of Lembos and Corophium suggest that the hatching spines make the initial tear, with further rupture being dependent upon strong body movements. This resembles hatching in Bathyporeia spp. (Fish, 1975) but is different from that in Gammarus duebeni (Davis, 1968). In the latter species, complete rupture of the egg membranes depends upon the hatching spines acting as a 'manual tin-opener'.

The hatched young of some amphipod species moult during occupation of their mother's brood pouch, eg. *Marinogammarus obtusatus* (Sexton and Spooner, 1940), whilst the young of other species do not, eg. *Ampithoe valida* (Barrett, 1966). Experiments to determine the situation in *Lembos* and *Corophium* gave inconclusive results, because the absence of moulting may have been due to the factor(s) which quickly killed the young.

Additional information suggests that moulting does not occur in the brood pouch. (1) The time that young remained in the marsupium was very short. (2) Exuviae were never found in marsupia containing hatched young. However, it is possible that they were eaten by the young, as occurs in *Parathermisto* spp. (Sheader, 1973). (3) Although moulting has been reported to occur at the time of hatching in some species (Le Roux, 1933; Fish, 1975), exuviae were not released when *Lembos* and *Corophium* hatched. (4) Three species, *Ampithoe lacertosa*, *Parathermisto gracilipes* and *P. gaudichaudii*, which are known to moult in their mother's marsupium, show a pronounced change in behaviour associated with their first or second marsupial moult (Heller, 1968; Sheader, 1973). The young change from being inactive and, in the case of *A. lacertosa*, clustered together, into quite active individuals. In contrast, the recently hatched young of *Lembos* and *Corophium* were neither inactive nor clustered together.

Evidence against the young of other species moulting in the marsupium includes, the limited size range of the young (Bregazzi, 1972) and their constant number of flagellar articles (Barrett, 1966). These features should be checked in *Lembos* and *Corophium*.

Young *Corophium* and *Lembos* could partially emerge from the brood pouch and remove material from that which was held by their mother. Similar behaviour has been described in the genus *Ampithoe*. In this manner young *A. valida* feed on their mother's own faecal pellets and young *A. lacertosa* feed on algal material (Barrett, 1966; Heller, 1968). Whilst some of the material, on which young *Lembos* feed, probably consists of the broken up faecal pellets of their own mother, it is not their major food source, as Barrett reports for young *A. valida*.

Young *A. lacertosa* can also trap particles suspended in their mother's pleopod current (Heller, *loc. cit.*). Young *Lembos* and *Corophium* were not seen to do this. The rather enclosed nature of the brood pouch probably prevents *Lembos* from using its antennae and gnathopods to snatch passing particles. Neither species succeeded in removing detritus from that lining the glass tubes. However, the lining was rather scanty and in a natural tube they might have more success. Young *Lembos* and *Corophium* may have eaten the ruptured egg membranes and, in the case of *Lembos*, their own faecal pellets.

Whilst the young of some amphipod species emerge from their mother's marsupia without any assistance, eg. *Ischyrocerus inexpectatus* (Schiecke, 1973), others have been observed to emerge as a consequence of the behaviour of their mother or an associated male. Embody (1911) reports that the females of some gammarids usually mate again before the young have vacated their marsupia. At such times the activities of the male usually causes the young to leave! Similar behaviour was not observed in *Lembos*. Embody (*loc. cit.*) also notes that females sometimes moult prematurely and that young are lost in the exuvia. Again, similar behaviour was not observed in *Lembos* and *Corophium*. The females of some species use their gnathopods to force young out of their marsupia (Skutch, 1926; Skogsberg and Vansell, 1928; Harrison, 1940). This possibly occurs in *Corophium* and probably also in *Lembos*. Sheader (1973) reports that the initial release of young *Parathemisto* spp. is due to the scraping activity of the female's flexed urosome. This behaviour differs from that observed in *Lembos* and *Corophium* in that the urosome is not placed inside the brood pouch but remains outside and dislodges young which have already partially emerged. Another form of assistance is the creation or widening of the gaps between the brood plates. In *Lembos* this was probably a direct consequence of the female starting to moult. Similar behaviour, in other species, eg. *Cheirimedon femoratus* and *Parathemisto* spp., occurs sometimes before the female moults (Bregazzi, 1972; Sheader, 1973).

Some female amphipods also actively prevent young from leaving their marsupia. Female *Grandidierella* and *Melita* can block both the anterior and posterior openings of the marsupium (Nayar, 1956; Krishnan and John, 1974). A similar phenomenon sometimes occurs in *Corophium*, when young attempt to leave via the posterior opening.

Young *Lembos* and *Corophium* frequently re-entered their mother's marsupium. It is interesting to note that Ingle (1969) reports that young *C. volutator* are unable to do this, as are young *Melita palmata* (Krishnan and John, 1974). In the latter species the young make earnest attempts at re-entering but are prevented from succeeding by various aspects of their mother's behaviour. In other amphipod species re-entry is a feature of their brooding biology and, to date, is known to occur in *Gammarus locusta* (Bate and Westwood, 1863), *Eucrangonyx gracilis* (Embody, 1911), *Gammarus chevreuxi* (Sexton and Mathews, 1913), *Grandidierella bonnieri* (Nayar, 1958), *Neohaustorius schmitzi* (Croker, 1968), *Marinogammarus obtusatus*, *M. finmarchius* (Sheader and Chia, 1960) and, probably, in *Orchestia pallustris* (Smallwood, 1905). Only Sheader and Chia (*loc. cit.*) have taken their investigations beyond the preliminary descriptive phase.

Young *Lembos* and *Corophium* can remain for a while in their mother's tube, as do *C. volutator* (Thamdrup, 1935; Watkin, 1941a) and *C. arenarium* (Crawford, 1937a; Vaughan, 1938). In the presence of suspended detritus young *C. bonnellii* spent less than a day in their mother's tube, whilst young *L. websteri* normally spent longer than a day. In still water, young *Lembos* normally stayed for less than four days. These figures are only indications of the situation in nature, as factors such as turbulence, turbidity, tube length and the presence of a male (in the case of *Lembos*) were not investigated. Young *Lembos* also remained longer in their mother's brood pouch than young *Corophium*. *Corophium's* short residence times may be associated with the species greater abundance in sheltered waters. On leaving their mother's tube, recently hatched *Corophium* will experience less turbulent waters and therefore require less strength to avoid dislodgment, than recently hatched *Lembos*. One proximate reason for the species difference in tube residence times is probably that female *Lembos* are more tolerant, than female *Corophium*, of the presence of young in their tubes.

Longer tube residence times are possibly a feature of the domiciliary species *Podocerus variegatus*, *Leptocheirus pilosus* and *Phronima* sp. . Bate and Westwood (1863) found one tube occupied by young *P. variegatus*, of two different sizes. Goodhart (1939) reports that young *L. pilosus* remain in their mother's brood pouch until after the first moult, while they remain in the tube of the mother until the second, and possibly later. Finally, Hardy (1956) states that

*Phronima* sp. 'rear' their young in hollowed out salps. In contrast, young *Chelura terebrans* leave their mother's tunnel immediately after emerging from her brood pouch (H. Kühne, pers. comm.).

As the behaviour of young animals in their mother's tube is not well documented it is interesting to note the preference of young *Lembos* for proximity to their mother, rather than her associated male. Clumping of recently-released young around the mother has also been recorded in the free-living species *Gammarus locusta* and *Ischyrocerus inexpectatus* (Bate and Westwood, 1863; Schiecke, 1973).

At least some young *C. volutator* and *C. arenarium* leave their mother's tube by burrowing through the walls of her tube and into the surrounding sediment. They then build a tube of their own, in contact with their mother's tube (Thamdrup, 1935; Crawford, 1937a; Vaughan, 1938). Thamdrup (*loc. cit.*) describes how young *C. volutator* convert these extensions, of their mother's tube, into completely independent tubes. Young *C. bonnellii* and *L. websteri* do not build tubes by burrowing through the wall of their mother's tube.

# CHAPTER VI. EXPERIMENTS ON THE EFFECTS OF WATER MOVEMENT, TURBIDITY AND SEDIMENTATION

## A. INTRODUCTION.

Many factors, in both space and time, determine the distribution and abundance of a species. Moore (1971, 1973b, c) proposed that turbulence and turbidity are significant factors affecting Lembos websteri and Corophium bonnellii in northern Britain. However, it must not be forgotten that he has only examined one of their habitats (Laminaria hyperborea holdfasts), from one part of their geographical range (plus unpublished work on other British coasts), over a limited time scale (May and July, 1969, plus unpublished later work). In order to provide a wider perspective, vis-à-vis total species ecology, attention will first be paid to other ecological factors which, from the literature, appear to impinge on these two species.

The importance of biotic factors, i.e. predators, parasites and competitors, is virtually unknown. The only documented predators of C. bonnellii and L. websteri are fish. Corophium is known to be eaten by the Saithe, Pollachius virens (Stephensen, 1942; Lie, 1961) and Blennius tentacularis (Gomoiu and Müller, 1962). The latter species must have a marked effect on the abundance of Corophium in the Black Sea, as it feeds exclusively on Corophium, by swallowing the animal together with its sandy tube. Scott (1922) found "C. bonnellii" in the stomachs of young Plaice, Pleuronectes platessa. However, the validity of this record is uncertain as the paper is not discussed by Crawford (1937a). L. websteri is known to be eaten by two species of Hake, Urophycis regius and U. floridanus in North America (Sikora et al., 1972). Laverack and Blackler (1974) also refer to an old record of Lembos being found in the stomach of the Haddock, Melanogrammus aeglefinus.

It would be interesting to know if interspecific competition between Corophium bonnellii and Corophium sextoni, influences the distribution of these two species. Crawford (1937a) reports that hundreds of C. bonnellii were found in each of several collections made in Plymouth Sound between 1889 and 1911. However, in 1934 only five individuals were found. The place of *C. bonnellii* was taken by *C. sextoni*, a species not present in earlier dredgings. Although Crawford considers that *C. sextoni* is not indigenous to Plymouth, he could not suggest its original locality. Turquier (1964, 1965) also considers that *C. sextoni* is a recent introduction to the Channel coast of France.

Although *L. websteri* and *C. bonnellii* can occur together in the same region, eg. northern Britain, there are four main differences in their known geographical distribution (table 41).

(1) Only *Corophium* has been found in both hemispheres; *Lembos* is restricted to the northern hemisphere.

(2) In the northern hemisphere the distribution of both species centres around the Atlantic Ocean and its adjoining seas. *Corophium*, however, also extends into the Pacific Ocean, being found in the Bering Sea.

(3) Following Tait's (1968) classification of the world's marine biogeographical regions, *Corophium*, in the northern hemisphere, has an arctic, boreal and warm temperate distribution, whilst *Lembos* has a boreal, warm temperate and tropical distribution.

This indicates that water temperature is a factor of ultimate importance in the ecology of these two species, with the distribution of *Lembos* being centred in warmer waters than that of *Corophium*. There is very little overlap in the distribution of *Lembos* and *Corophium* on the American coast, in contrast to the much broader overlap on the European coast (table 42). This coincides with the rapid change in the annual isotherms, between Cape Cod and Cape Hatteras, on the American coast. In contrast, the same isotherms, on the European coast, span five times the latitudinal distance (Ekman, 1953).

(4) Although *Lembos* has frequently been recorded from the Mediterranean, it has never been found in the Black Sea. In contrast, *Corophium* has frequently been recorded from the Black Sea, but is only presumed to occur in Mediterranean (Crawford, 1937a) on the basis of

## TABLE 41

## THE GEOGRAPHICAL DISTRIBUTION OF *LEMBOS WEBSTERI* AND *COROPHIUM BONNELLII*

<table>
<tr><th>LEMBOS WEBSTERI</th><th>COROPHIUM BONNELLII *</th></tr>
<tr><td><u>SCOTLAND</u></td><td></td></tr>
<tr><td>BATE AND WESTWOOD (1863)</td><td></td></tr>
<tr><td>MILLPORT RECORDS (1901, 1950)</td><td></td></tr>
<tr><td></td><td>CRAWFORD (1937a)</td></tr>
<tr><td colspan="2">REID (1941)</td></tr>
<tr><td colspan="2">DAHL (1948)</td></tr>
<tr><td>GAULD ET AL. (1953)</td><td></td></tr>
<tr><td></td><td>SCARRATT (1961)**</td></tr>
<tr><td></td><td>GAGE (1972a)</td></tr>
<tr><td colspan="2">GAGE (1972b)</td></tr>
<tr><td colspan="2">MOORE (1973a)</td></tr>
<tr><td colspan="2">LAVERACK AND BLACKLER (1974)</td></tr>
<tr><td><u>IRELAND</u></td><td></td></tr>
<tr><td>MACDONALD (1945, 1951)</td><td>CRAWFORD (1937a)</td></tr>
<tr><td>WILLIAMS (1954)</td><td></td></tr>
<tr><td colspan="2">DUHIG (1960)</td></tr>
<tr><td></td><td>SLOANE ET AL. (1961)</td></tr>
<tr><td colspan="2">ROUND ET AL. (1961)</td></tr>
<tr><td></td><td>KITCHING ET AL. (1976)</td></tr>
<tr><td><u>ENGLAND AND WALES</u></td><td></td></tr>
<tr><td>BATE AND WESTWOOD (1863)</td><td></td></tr>
<tr><td>STEBBING (1906)</td><td></td></tr>
<tr><td>KITCHING ET AL. (1934)</td><td></td></tr>
<tr><td></td><td>CRAWFORD (1937a, b)</td></tr>
<tr><td>COLMAN (1940)</td><td></td></tr>
<tr><td colspan="2">JONES (1948)</td></tr>
<tr><td colspan="2">MARINE BIOLOGICAL ASSOCIATION (1957)</td></tr>
<tr><td colspan="2">SCARRATT (1961)</td></tr>
<tr><td colspan="2">BRUCE ET AL. (1963)</td></tr>
<tr><td colspan="2">CROTHERS (1966)</td></tr>
</table>

TABLE 41 (CONT'D)

<table>
<tr><th>LEMBOS WEBSTERI</th><th>COROPHIUM BONNELLII</th></tr>
<tr><td>ENGLAND AND WALES (CONTIN.)</td><td></td></tr>
<tr><td></td><td>HAMOND (1967)</td></tr>
<tr><td colspan="2">MOORE (1973b)</td></tr>
<tr><td></td><td>JONES (1973)</td></tr>
<tr><td colspan="2">HISCOCK AND HOARE (1975)</td></tr>
<tr><td colspan="2">FRANCE (EXCLUDING MEDITTERANEAN COAST), HOLLAND AND GERMANY</td></tr>
<tr><td>CHEVREUX AND FAGE (1925)</td><td></td></tr>
<tr><td></td><td>CRAWFORD (1937a)</td></tr>
<tr><td colspan="2">SCHELLENBERG (1942)</td></tr>
<tr><td></td><td>STOCK AND BLOKLANDER (1952)</td></tr>
<tr><td>L'HARDY (1962)</td><td></td></tr>
<tr><td>TRUCHOT (1963)</td><td></td></tr>
<tr><td colspan="2">TOULMOND AND TRUCHOT (1964)</td></tr>
<tr><td></td><td>MOVAGHAR (1964)</td></tr>
<tr><td>LEDOYER (1964a)</td><td></td></tr>
<tr><td></td><td>TURQUIER (1964, 1965)</td></tr>
<tr><td></td><td>KÖNIG (1966)</td></tr>
<tr><td>SCANDINAVIA</td><td></td></tr>
<tr><td>SARS (1890)</td><td></td></tr>
<tr><td></td><td>CRAWFORD (1937a)</td></tr>
<tr><td>SCHELLENBERG (1942)</td><td></td></tr>
<tr><td colspan="2">STEPHENSEN (1942)</td></tr>
<tr><td colspan="2">DAHL (1946)</td></tr>
<tr><td></td><td>DAHL (1948)</td></tr>
<tr><td></td><td>ENEQUIST (1949)</td></tr>
<tr><td></td><td>LIE (1961)</td></tr>
<tr><td></td><td>MUUS (1967)</td></tr>
<tr><td></td><td>DOMMASNES (1968)</td></tr>
<tr><td></td><td>NAGLE (1968)</td></tr>
<tr><td></td><td>FORSMAN (1970)</td></tr>
<tr><td></td><td>RASMUSSEN (1973)</td></tr>
</table>

TABLE 41 (CONT'D)

| LEMBOS WEBSTERI | COROPHIUM BONNELLII |
|---|---|
| ICELAND AND FAROES. | CRAWFORD (1937a) |
| | STEPHENSEN (1940a) |
| EUROPEAN POLAR SEAS | |
| | STEPHENSEN (1942) |
| | ZENKEVITCH (1963) |
| MEDITERRANEAN SEA | |
| CHEVREUX AND FAGE (1925) | |
| | CRAWFORD (1937a) |
| COSTA (1960) | |
| LEDOYER (1968b) | |
| LEDOYER (1969 ) | |
| KRAPP-SCHICKEL (1969) | |
| BELLAN-SANTINI (1971) | |
| LEUNG TACK KIT (1972) | |
| COUSTALAIN (1972) | |
| CHARDY (1973) | |
| BELLAN-SANTINI AND LEDOYER (1973) | |
| SCHIECKE (1973) | |
| KRAPP-SCHICKEL AND KRAPP (1975) | |
| BLACK SEA | |
| | MILOSLAVASKAYA (1939) |
| | STEPHENSEN (1942) |
| | GOMOIU AND MÜLLER (1962) |
| | BACESCU ET AL. (1963) |
| | REMANE (1971) |
| | BACESCU (1972) |
| TROPICAL WEST AFRICA | |
| REID (1951) | |

## TABLE 41 (CONT'D)

| LEMBOS WEBSTERI | COROPHIUM BONNELLII |
|---|---|
| **ATLANTIC COAST OF NORTH AMERICA** | |
| | CRAWFORD (1937a) |
| | SHOEMAKER (1947) |
| | BOUSFIELD AND LEIM (1958) |
| | NAGLE (1968) |
| MCCLOSKEY (1970) | |
| SIKORA ET AL. (1972) | |
| BOUSFIELD (1973) | |
| | PARKER (1975) |
| **BRAZIL** | |
| | CRAWFORD (1937a) |
| **SOUTHERN TIP OF SOUTH AMERICA AND FALKLAND ISLANDS** | |
| | CRAWFORD (1937a) |
| | SHOEMAKER (1947) |
| **BERING SEA** | |
| | GURJANOVA (1951) |

* Due to problems of misidentification only records from the time of Crawford's (1937) review of the genus *Corophium* are included.

** Re-examination of Scarratt's Scottish samples has shown that at least some specimens identified as *C. sextoni* are in fact *C. bonnellii* (Moore, pers. comm.)

## TABLE 42

### THE KNOWN NORTHERN AND SOUTHERN LIMITS OF LEMBOS WEBSTERI AND COROPHIUM BONNELLII IN THE NORTHERN HEMISPHERE.

| NORTH AMERICA | C. BONNELLII | L. WEBSTERI |
|---|---|---|
| NORTHERN LIMIT | EASTERN CANADA (1) | SOUTH SIDE OF CAPE COD (1) |
| SOUTHERN LIMIT | MASSACHUSETTS (CAPE COD) AND CONNECTICUT (1) | GEORGIA AND NORTHERN FLORIDA (1) |
| **EUROPE AND AFRICA (EXCLUDING MEDITERRANEAN AND BLACK SEAS)** | | |
| NORTHERN LIMIT | NOVAYA ZEMLYA (2) | WEST NORWAY (62-65°N) (2) |
| SOUTHERN LIMIT | NORTHERN FRANCE (3) | WEST AFRICA (9°N) (4) |

**SOURCES**

| | | |
|---|---|---|
| (1) | BOUSFIELD | (1973) |
| (2) | STEPHENSEN | (1942) |
| (3) | CRAWFORD | (1937a) |
| (4) | REID | (1951) |

one earlier record (Della Valle, 1893). In the Black Sea, Miloslavskaya (1939) records that Corophium is absent from the Karadag region and the southern Crimea coast. In this context it is extremely interesting to quote Miloslavskaya's comments, on this phenomenon, in full.

> "In 1930 I already presented evidence confirming the idea that the southern Crimean coast constitutes an area best preserving the population of the preceding epoch, when the Black Sea bore, in the modern sense, a more "Mediterranean" character, than at present. It may be supposed that the absence of these four forms (including C. bonnellii) * along all the southern coast of Crimea, also, to a certain extent, confirms the idea mentioned above."

The difference in the faunal composition of the Black and Mediterranean Seas is well known (Ekman, 1953). Ekman considers that three factors contribute to these differences. Firstly, open communication with the Mediterranean is, geologically speaking, recent. Secondly, the temperatures of the coastal waters of the Black Sea sink, during winter, to 3-6°C, whilst in the Mediterranean the temperature only falls to 12-13.5°C in the northern parts (with patches at 10°C). Here is further evidence of Corophium living in cooler waters than Lembos. Thirdly, the salinity of the Black Sea is much less than that of the Mediterranean. Bacescu et al. (1963) found C. bonnellii to be flourishing in one part of the Black Sea, which was experiencing salinities of 15-18‰. In contrast, L. websteri has been reported from Crête, in the eastern Mediterranean (Ledoyer, 1969), where the surface salinity, in August, is c. 39‰ (Pickard, 1975).

Most records of L. websteri and C. bonnellii are from fully marine situations, with salinities of c. 35‰ . Barnes (1955) recorded the grand mean surface salinity at Keppel Pier, Millport, as 32.1‰, for the five year period 1949-1953. Under exceptional circumstances the salinity, 1 m below chart datum at Keppel Pier, can sink to c. 25‰ (Mr. J.J.P. Clokie, pers. comm.) Dahl's (1948) studies on algal faunas showed that both species were absent, except for an isolated population of Corophium, from the brackish waters (8-30‰) off the Swedish west coast. Jones (1973), in his study of the Laminaria holdfast community, found Corophium to be present on

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* My addition.

the polluted, open coast near Newcastle but to be absent from polluted estuary of the Firth of Forth.

The isolated population of C. bonnellii found by Dahl in brackish waters, again suggests that Corophium is more tolerant of reduced salinities than Lembos. Further evidence is provided by Movaghar (1964), who only recorded C. bonnellii on the hydroid-covered buoys at the mouth of the Elbe estuary and by the work of Gage (1972a, b) and Moore (unpublished) on the west coast of Scotland. Gage found C. bonnellii to be present in the deeper waters ( >3m) of the neighbouring lochs, Crenan and Etive, whilst L. websteri was only present in Loch Crenan. In winter, the deeper waters of Loch Etive have a much lower salinity than the deeper waters of Loch Crenan. At the head of Loch Fyne, an area where, in winter, dramatically lowered surface salinities intrude into the sublittoral at low tide, C. bonnellii is abundant yet L. websteri is scarce, in Laminaria holdfasts, (P.G. Moore, pers. comm.).

Neither species has a solely littoral or sub-littoral distribution, for instance on the Isle of Man Lembos and Corophium occupy both zones (Jones, 1948). The importance of depth, per se, has not been investigated. The maximum depths at which Corophium and Lembos have been found are 220-230 m and 65 m, respectively (Enequist, 1949; Reid, 1951).

The substrata on which Lembos and Corophium flourish are firm surfaces, usually algae, sedentary animals or rocks, on which sediment can accumulate (see discussion of Chapter II). Accumulation is dependent upon the interaction of particle availability and water movement (Moore, 1972). Whilst water movement is necessary to bring particles into the neighbourhood of the firm surfaces, sedimentation is dependent on relatively still conditions. In extremely sheltered conditions, eg. Abereiddy Quarry, Pembrokeshire, Lembos and Corophium can colonize open rock surfaces, which are overlain with sediment (Hiscock and Hoare, 1975). In more wave exposed localities the animals are restricted to sediment containing crevices, eg. Laminaria holdfasts (Moore, 1973c).

Moore (1973a) measured the silting levels of Laminaria holdfasts, on a four point scale, from category 0 (clean) to category +++ (very silty). The mean holdfast density of Lembos and Corophium, at each site, was not related to the mean silting level of that site (table 43). However, there is slight evidence to suggest that very high silt levels are unfavourable to these two species. One holdfast, from St. Abbs, Craster, Marsden, Robin Hood's Bay and Flamborough, was classified as category +++. At. St. Abbs (the only site with a high mean density of Lembos and Corophium), the density, in the very silty holdfast, was 1 and 16, respectively. This was much less than the mean density for each species at St. Abbs (table 43). It must be realised that this form of analysis is rather crude, because no account is taken of the precise relationship between amphipod abundance and the silting level within the sampling unit, the holdfast.

Closely associated with holdfast silting is sea water turbidity. After working the coast between St. Abbs and Flamborough Head, Moore (1973a) considered that his stations north of the River Coquet experienced clear water, whilst his stations south of that river experienced, for two-thirds of the year, turbid water. On the basis of several multivariate analyses, of presence/absence data, Moore (1973b) concluded that both species were characteristic of the clear water stations. Whilst the association with clear water was very pronounced for Corophium, it was less so for Lembos. The same pattern emerges, with the important exception of Corophium at Redcar, from Moore's quantitative data (table 43). Suspended solids measurements in July 1969 (Moore, 1973a) showed that Redcar was the most turbid station (but the consistency of this feature is unknown). Thus, although Corophium appears to be a member of the clear water, Laminaria holdfast community, it can also flourish in turbid waters. The only other environmental factor which, from Moore's data, makes Redcar different from all other turbid water stations, is nutrient concentration. In July 1969 Redcar had the highest concentration of nutrients and in January 1970 it was amongst a group of stations with the highest concentration of nutrients (Moore, 1973a).

The only evidence in support of Moore's hypothesis is provided by Bousfield and Leim (1958), who worked in an offshoot of the Bay of Fundy. They report that C. bonnellii is present in clear waters but is absent from waters made turbid by silt. Unfortunately, the significance of this observation is difficult to assess, as temperature and salinity varied between the clear and turbid waters. The results of several studies appear to contradict Moore's hypothesis. This may

# TABLE 43

## MEAN LEVEL OF HOLDFAST SILTING AND MEAN NUMBER OF INDIVIDUALS PER HOLDFAST, BASED ON MOORE (1971, APPENDIX 2; 1973, APPENDIX 1)

| SITE | HOLDFAST * SILTING | COROPHIUM | LEMBOS |
|---|---|---|---|
| ST. ABBS | 2.4 | 80.4 | 14.2 |
| SPITTAL | 2.2 | 51.6 | 0 |
| INNER FARNE | 0 | 32.6 | 1.4 |
| BEADNELL | 2.4 | 17.0 | 0.2 |
| CRASTER | 2.8 | 4.2 | 2.0 |
| NEWBIGGIN | 2.0 | 0.2 | 0 |
| ST. MARY'S ISLE | 2.0 | 0 | 0 |
| MARSDEN | 2.6 | 0 | 0 |
| SEAHAM | 2.0 | 0 | 0 |
| REDCAR | 2.2 | 34.4 | 0.4 |
| STAITHES | 2.4 | 0 | 0.2 |
| ROBIN HOOD'S BAY | 2.6 | 0 | 0.4 |
| BURNISTON | 2.2 | 0 | 0 |
| FILEY | 2.3 | 0 | 0 |
| FLAMBOROUGH | 2.6 | 0 | 0 |

* TO CALCULATE MEAN LEVEL OF HOLDFAST SILTING

0 = 0
+ = 1
++ = 2
+++ = 3

be due, in part, to the characteristics of the suspensions, eg. particle size distribution, being poorly known (Moore, in press). Of particular interest is Jones' (1973) work on the fauna of *Laminaria hyperborea* holdfasts, from the same stretch of coast as Moore explored. Jones found *C. bonnellii* to be present (abundance?) at four of Moore's turbid water stations, where Moore reported the species to be absent. *L. websteri* is also very common in a coral community in North Carolina, at a location where there is an abundance of silt and organic matter in suspension (McCloskey, 1970) and is common in part of the turbid, old Port of Marseille (Bellan-Santini, 1971; Leung Tack Kit, 1972). Likewise, *C. bonnellii* is unusually numerous in the Koster Channel, where there is an abundance of dark grey, semi-suspended detritus (Enequist, 1949). A seemingly self-contradictory report is presented by Chardy (1973). He found the distribution of *L. websteri* to be positively correlated with water clarity (measured photo-electrically) but to be independent of turbidity (subjectively assessed on a two point scale). However, the biological significance of these results is hard to gauge as there is no evidence of these two physical parameters being regularly measured.

Directly affecting both sea water turbidity and holdfast silting is the degree of water movement. Moore (1973b) concluded that *Lembos* was particularly associated with the clear water stations of St. Abbs and the Inner Farnes. St. Abbs is situated on a wave-exposed headland, whilst the Inner Farnes station experiences strong tidal currents. Thus *Lembos* appears to favour sites which have both clear and strongly moving water. Although *Corophium* was also abundant at these sites, Laminaria holdfasts collected from a fully exposed site, on the west coast of Scotland (Moore, 1971), only contained *Lembos websteri*. Moore also has unpublished evidence to suggest that *Lembos* is more abundant at sites experiencing a high degree of water movement, whilst *Corophium* is more abundant in quieter waters.

Several reports support Moore's water-movement hypothesis, ie. as water movement increases, conditions become more favourable for *Lembos* but less favourable for *Corophium*. (1) Knight-Jones (*pers. comm.*) informs me that *Corophium* is common in an area under the Menai Straits suspension bridge, which is sheltered from water currents, whilst Lembos is commonest outside the Menai Straits (in more wave exposed locations? *). (2) In the extreme shelter of Abereiddy

* my addition.

Quarry *Corophium* flourished whilst *Lembos* did not, (Hiscock and Hoare, 1975). (3) *Corophium* is more abundant on algae in the quiet waters, on either side of the Lough Ine rapids, than in the rapids themselves (Sloane *et al*., 1961). (4) Dommasnes (1968) compared the fauna of sublittoral populations of *Corallina officinalis* at three sites of increasing exposure. At a depth of <1m, *Corophium* was only present at the most sheltered site, where considerable quantities of sediment accumulated. (5) Forsman (1970) considers that *Corophium bonnellii* is characteristic of algae from quiet waters, where sediment accumulates. (6) *Lembos* is known to live on the hydroid, *Sertularia operculata*, in the Lough Ine rapids (Round *et al*., 1961). (7) Bousfield (1973) reports that *Lembos* lives in localities experiencing a moderate current.

There is also evidence against Moore's water-movement hypothesis. (1) *C. bonnellii* was frequent on the sill, at the entrance to Abereiddy Quarry, an area which experiences strong currents during spring tides (Hiscock and Hoare, 1975). (2) Parker (1975) reports that *C. bonnellii* is most abundant in the Channel eelgrass beds of Hadley Harbour. Strong currents flow along these Channels. The work of Truchot (1963) and Krapp-Schickel and Krapp (1975) on the amphipod fauna of littoral algae also appears, at first sight, to conflict with Moore's hypothesis. These workers concluded that *Lembos* was most abundant on sheltered shores, where sediment accumulated. However, it seems likely that (1) *Laminaria* holdfasts provide greater protection from water movement than the algae, eg. *Cystoseira* spp. and *Sargassum* sp., which dominated the littoral studies and (2) on exposed shores, the degree of water movement in the sublittoral, where Moore collected his holdfasts, will be less than in the littoral, where the other work was conducted. This highlights the limited extent to which field data, on the importance of water movement, can be interpreted. Interpretation is hindered by the absence of absolute measures of water movement, particularly that which the animal actually experiences, ie. within a clump of *Cystoseira*. Additionally, it is possible that the water movement requirements of each species vary over their geographical range, as Lewis (1964) reports for *Patella vulgata*.

Experiments were designed to see if the correlations between turbidity and turbulence and species presence/abundance, described by Moore, were due to cause and effect relationships. The effect of of turbidity on survival and the effect of turbidity and turbulence on behaviour were examined, as was the response of the two species to sedimentation.

Moore (1973a) suggested that the abundance of suspended particles, south of the River Coquet, was due to erosion of superficial coastal deposits, ie. the particles were mainly inorganic. Effort was therefore directed towards assessing the significance of suspended inorganic particles to Lembos and Corophium. Three substances were selected: boulder clay, kaolin and silica. Boulder clay was chosen because the cliffs between Robin Hood's Bay and Scarborough consist almost wholly of boulder clay (Moore, 1973a). Kaolin was chosen because of recent concern about pollution of the aquatic environment by the Cornish china clay industry (see Probert, 1973, 1975 and also Nuttal and Bielby, 1973; Bradfield et al., 1976). Silica was chosen because it is one of the four dominant constituents of naturally occurring inorganic particles in the sea (Armstrong and Atkins, 1950). Two other common constituents, namely alumina and ferric oxide, were tested but rejected, as they were difficult to maintain in suspension. Fine sand was used in the sedimentation experiments because rough seas, in Fintray Bay (Cumbrae), have been known to disturb the sand enough to bury some of the Laminaria holdfasts.

The major problem encountered in the turbidity survival experiments was the setting out of suspended particles. Obviously this could be overcome by increasing the degree of water movement. However, it was decided that water movement could only be increased to a level at which the animals, on leaving their tubes, could still crawl about on the bottom of the dish. Therefore only particles, which required the minimum of water movement to maintain them in suspension could be used.

The first technique which was developed had to be rejected because of excess sedimentation. This apparatus was designed to test the effect of turbidity on the survival of known individuals. Particles were maintained in suspension by a vertically oscillating plate. The experimental animals were kept singly in small cages, 14 x 5 x 20mm, which were covered with plankton netting of pore diameter 0.4mm. Unfortunately, silica accumulated both on the outside and inside the cages.

## B. THE EFFECT OF SUSPENDED INORGANIC PARTICLES ON SURVIVAL : EXPERIMENTS WITH VERTICALLY OSCILLATING PLATES.

### Materials and Methods.

These experiments were conducted in glass beakers, of 1l capacity. As it was of the utmost importance not to overlook animals at the end of the experiment, only the largest animals available were selected. In all experiments, except experiment 4, each beaker contained 30 individuals of one species. In experiment 4 each beaker contained 2 species, with 30 individuals per species.

The animals were left overnight, with a scattering of fine acid-washed sand, to build tubes attached to the bottom of the beakers. A fluorescent light was left on to encourage tube building. Each beaker was evenly illuminated in order to prevent the animals crowding together and concentrating their building activities in the most shaded part of the beaker. Large clumps of tubes were undesirable, as they tended to trap suspended particles. The next morning the sand, which had not been incorporated into the tubes, and animals, which were not in tubes, were removed. The excess sand was removed because of the efficiency with which it trapped suspended particles. The water was also changed and replaced with 1l of filtered sea water (no particles $>0.3\mu m$), containing 50mg of antibiotic (crystamycin), 0.3ml of organic detritus and a known weight of inorganic particles.

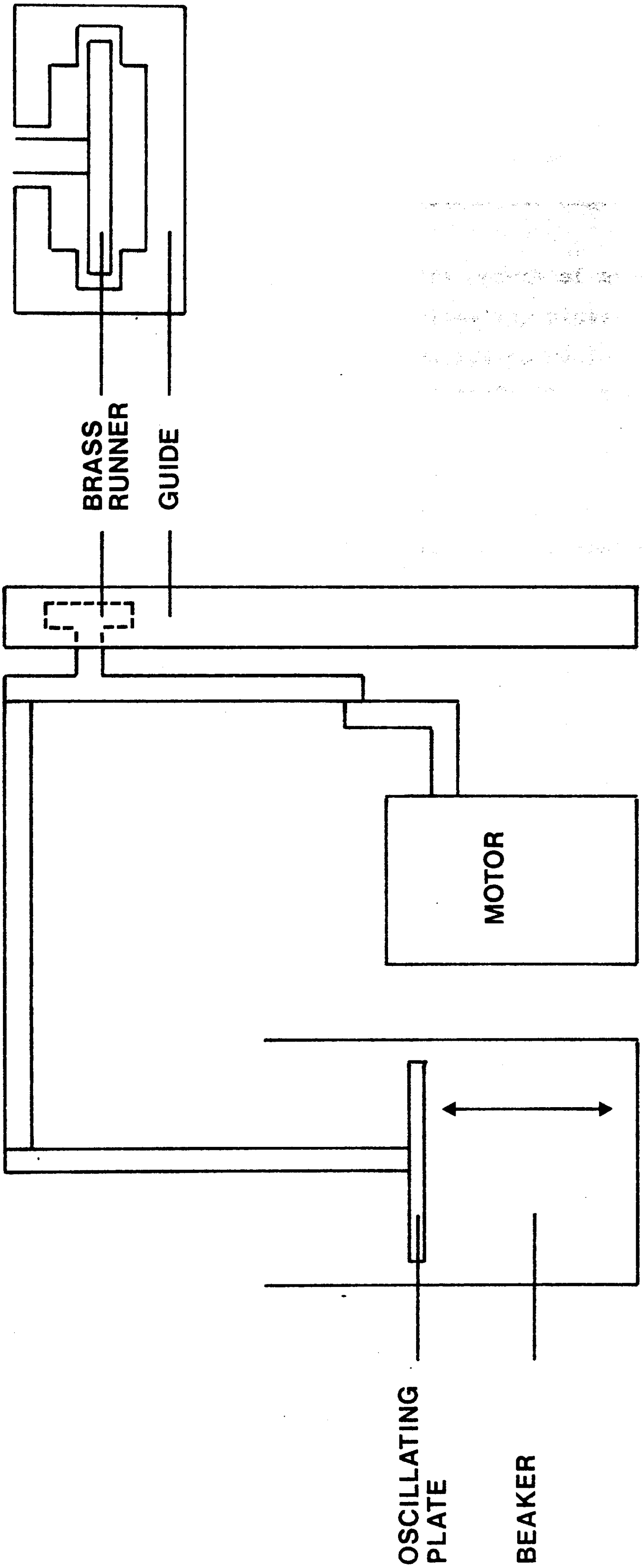
The detritus and inorganic particles were maintained in suspension by a vertically oscillating plate (fig. 10). Each plate was octagonal, of 7.4cm diameter and moved up and down at a rate of 18 cycles per min. The distance between the top of the up-stroke and the bottom of the down-stroke was 11cm. At the bottom of the down-stroke the plate was within 1cm of the bottom of the beaker.

All experiments started within one day of the animals being collected and lasted for 10 days. Every day water lost through evaporation was replaced, by adding distilled water and the minimum and maximum water temperatures of the previous day were recorded. After 5 days another 0.15ml of organic detritus was added to each beaker.

At the end of the experiment the number of live animals in each beaker were counted. An individual was defined as being alive if it

FIG. 10.

THE APPARATUS FOR MAINTAINING PARTICLES IN SUSPENSION WITH A VERTICALLY OSCILLATING PLATE, INCLUDING A CROSS SECTION OF THE GUIDE WITH BRASS RUNNER.


BRASS RUNNER
GUIDE
MOTOR
OSCILLATING PLATE
BEAKER

could beat its pleopods. All individuals were then killed, before being sexed and measured.

An experimental duration of ten days was chosen as it was quite long in relation to the life of the animal, c. 1 year, but short enough to permit sufficient replication within the experimental period.

An antibiotic was used to restrict the growth of micro-organisms on the walls of the beaker and on the oscillating plate. An attached film of micro-organisms might have trapped suspended particles. Crystamycin contains penicillin and streptomycin in a ratio, by weight, of 3:5. Marshall and Orr (1958), working with Calanus finmarchius, report that streptomycin, at a concentration of $50mgl^{-1}$ had no significant effect on respiration rate, and that the same concentration of either stretomycin or penicillin had little or no effect on feeding.

An attempt was made to use detritus of the same quality in all experiments, by keeping a supply (originally collected from the bottom of laboratory aquaria) in a refrigerator at c.-15°C. The volume used in the experiments was measured by letting the defrosted detritus settle for c. 1 min in an inverted syringe.

Various features of the inorganic particles are itemized in tables 45 and 46. The amounts used are expressed as dry weights. Silica and kaolin were available as dry powders but the boulder clay contained a certain percentage of water. The water content was calculated by drying samples to a constant weight, at 80°C.

Chi-square tests were used to examine the statistical significance of differences in the proportion of animals surviving under the various conditions of turbulence and turbidity. This was either a 2x2 analysis (Bailey, 1964, p. 58), when 2 proportions were compared or a 2xC analysis (Snedecor and Cochran, 1967, p.240), when more than 2 proportions were compared. If, in the latter analysis, most of the expected values in the contingency table were substantially greater than 1, a simple formula could be applied (table 46). However, if most of expected values were not substantially greater than 1, Snedecor and Cochran recommend that the more laborious procedure of Haldane (1945) be followed. Even after transformation into a more manageable form (carried out by Mr. J. Proctor, table 46) it is still a very time consuming test.

## TABLE 44

### CHARACTERISTICS OF THE INORGANIC SOLIDS USED FOR THE TURBIDITY SURVIVAL EXPERIMENTS.

| SUBSTANCE | GRADE | SOURCE | PARTICLE SIZE |
|---|---|---|---|
| SILICA | POWDERED | B.D.H. | 63-125 μm |
| KAOLIN | E | ENGLISH CHINA CLAYS SALES CO. LTD. | 25°/o $<2\mu m$<br>0.03°/o $>53\mu m$ |
| BOULDER CLAY | - | CLIFFS AT ROBIN HOOD'S BAY, YORKSHIRE | ? |

## TABLE 45

### APPROXIMATE MINERAL COMPOSITION OF THE BOULDER CLAY.

| MINERAL | °/o DRY WT. OF CLAY |
|---|---|
| QUARTZ | 35-40 |
| ILLITE | 35-40 |
| KAOLIN | 17-23 |
| CALCITE | 3 |

## TABLE 46

## VARIANCE TESTS FOR HOMOGENEITY OF THE BINOMIAL DISTRIBUTION.

$$\begin{array}{ccc|c}
a_1 & a_2 & a_n & A \\
b_1 & b_2 & b_n & B \\
\hline
s_1 & s_2 & s_n & S
\end{array}$$

$$p_1 = {b_1}/{s_1} \qquad p_2 = {b_2}/{s_2} \qquad p_n = {b_n}/{s_n} \qquad \bar{p} = \frac{B}{S}$$

(1) Formula of Snedecor and Cochran.

$$\chi^2 = \frac{\sum s_i \ (p_i - \bar{p})^2}{\bar{p}\ \bar{q}}$$

(2) Procedure of Haldane

Calculate (i) $\chi^2$ as above

(ii) $K = S^2/_{AB}$

$R_1 = \sum(s_i^{-1})$

$R_2 = \sum(s_i^{-2})$

(iii) $K_1 = (n-1)(1+S^{-1})$

$K_2 = 2(n^{-1})+(K-6)R_1 - \left[(K-4)(n^2+2n-2)-2(4n+1)\right] \ S^{-1}$

$K_3 = 8(n-1)+2\left[11(K-5)-1\right] R_1 + \left[(K-15)^2-105\right] R_2 -2(3n-2)\left[(K-4)(3n+8)-12\right] S^{-1}$

(iv) $h = 1 - \dfrac{K_1 K_3}{3K_2^2}$

(v) $\xi = \left[\left(\dfrac{\chi^2}{K_1}\right)^h + \dfrac{h(1-h)}{2K_1} - 1\right] \dfrac{K_1}{h\sqrt{K_2}}$

Compare $\xi$ with N(0, 1) tables.
If it exceeds + 1.645 $\chi^2$ is $5^o/o$ sig.

## TABLE 47

## COMPARISON OF THE PROCEDURE OF SNEDECOR AND COCHRAN WITH THAT OF HALDANE.

| | | | | | |
|---|---|---|---|---|---|
| 25 | 27 | 28 | 30 | 27 | 137 |
| 4 | 1 | 1 | 0 | 1 | 7 |
| 29 | 28 | 29 | 30 | 28 | 144 |

$\chi^2$ OF SNEDECOR AND COCHRAN = 6.86 with 4 d.f.

$\chi^2$ OF HALDANE = 6.65 with 4 d.f.

Most of the 2xC contingency tables had many of the expected values less than 5. In order to test whether the simpler procedure of Snedecor and Cochran gave an acceptable measure of probability, for this data, the two procedures were compared. A contingency table with half the expected values less than 2 was selected. Table 47 shows that the value of chi-square was virtually the same using the two procedures. In consequence all 2xC contingency tables were analysed by the simpler procedure of Snedecor and Cochran.

Four sets of experiments were conducted. Silica was used in experiment 1, kaolin in experiment 2 and boulder clay in experiments 3 and 4. In the first three experiments <u>Lembos</u> and <u>Corophium</u> were tested separately and exposed (A) to still water with no inorganic particles, (B) to moving water with no inorganic particles and (C) to moving water with suspended inorganic particles, whose initial concentration varied between 0.01 and $1.0gl^{-1}$. In experiment 4 both species were tested together and exposed to moving water with suspended clay, at an initial concentration of $6.75gl^{-1}$.

## Results.

In experiments 1, 2 and 3 only experiment 1B showed any significant difference in the proportion of individuals surviving, between the five sets of conditions of turbulence and turbidity (table 48). In that experiment <u>Lembos</u> survived better in the presence of high concentrations of suspended silica.

In the presence of suspended boulder clay the survival of <u>Lembos</u> and <u>Corophium</u> was not significantly different between an initial concentration of $6.75gl^{-1}$ and that in the range, $0.5\text{-}1.0gl^{-1}$ (table 49).

There was also no significant difference between the proportion of individuals surviving suspensions of kaolin, silica and boulder clay with initial concentrations in the range $0.5\text{-}1.0gl^{-1}$ (<u>Corophium</u>, $\chi^2 = 0.47$, 2d.f., $P>0.05$; <u>Lembos</u>, $\chi^2 = 1.56$, 2d.f., $P>0.05$). In addition, the proportion surviving in these three suspensions did not differ significantly between the two species ($\chi^2 = 2.55$, 1d.f., $P>0.05$).

Various features (eg. size and sex) of the animals used for these

## TABLE 48

### PROPORTION OF INDIVIDUALS SURVIVING IN THE TURBIDITY EXPERIMENTS WITH VERTICALLY OSCILLATING PLATES.

| EXP. | SPECIES | SUS-PENSION | | STILL | ← | TURBULENT | | → | $\chi^2$ | D.F. | P |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | **0g | 0g | 0.01g | 0.1g | 1.0g | | | |
| 1A | COROPHIUM | SILICA | PROP.* SURV. | 0.97 | 0.96 | 1.00 | 1.00 | 0.93 | 3.32 | 4 | > 0.05 |
| | | | N | 30 | 28 | 25 | 30 | 30 | | | |
| 1B | LEMBOS | SILICA | PROP. SURV. | 0.37 | 0.40 | 0.43 | 0.80 | 0.87 | 28.18 | 4 | < 0.001 |
| | | | N | 30 | 30 | 30 | 30 | 30 | | | |
| 2A | COROPHIUM | KAOLIN | PROP. SURV. | 1.00 | 1.00 | 1.00 | 0.97 | 0.97 | 3.05 | 4 | > 0.05 |
| | | | N | 30 | 30 | 30 | 30 | 30 | | | |
| 2B | LEMBOS | KAOLIN | PROP. SURV. | 0.87 | 0.87 | 0.83 | 0.70 | 0.93 | 6.65 | 4 | >0.05 |
| | | | N | 30 | 30 | 30 | 30 | 30 | | | |
| | | | | 0g | 0g | 0.01g | 0.04g | 0.48g | | | |
| 3A | COROPHIUM | CLAY | PROP. SURV. | 0.86 | 0.96 | 0.97 | 1.00 | 0.96 | 6.86 | 4 | >0.05 |
| | | | N | 29 | 28 | 29 | 30 | 28 | | | |
| | | | | 0g | 0g | 0.01g | 0.08g | 0.97g | | | |
| 3B | LEMBOS | CLAY | PROP. SURV. | 0.89 | 0.80 | 0.86 | 0.90 | 0.83 | 1.66 | 4 | >0.05 |
| | | | N | 27 | 30 | 29 | 30 | 29 | | | |

* = PROPORTION SURVIVING

** = WEIGHT $l^{-1}$

## TABLE 49

## PROPORTION OF INDIVIDUALS SURVIVING IN THE TURBIDITY EXPERIMENTS WITH VERTICALLY OSCILLATING PLATES.

| EXP. | SPECIES | CLAY ($gl^{-1}$) | PROP.SURV. | N | $\chi^2$ | D.F. | P |
|---|---|---|---|---|---|---|---|
| 3A | COROPHIUM | 0.48 | 0.96 | 28 | 2.18 | 1 | >0.05 |
| 4 | COROPHIUM | 6.75 | 0.79 | 52 | | | |
| 3A | LEMBOS | 0.97 | 0.83 | 29 | 0.95 | 1 | >0.05 |
| 4 | LEMBOS | 6.75 | 0.92 | 53 | | | |

experiments are itemized in tables 53 and 54, and the range of water temperatures for each experiment are presented in table 55.

## C. THE EFFECT OF SUSPENDED INORGANIC PARTICLES ON SURVIVAL : EXPERIMENTS WITH ROTATING PROPELLERS.

### Materials and Methods.

The techniques employed differed in several ways from the previous experiments. Only these differences will be mentioned here. Small dishes, each of which contained 100ml of sea water and 10 animals, were stirred by propellers, of 4 cm diameter, rotating at 104-112 r.p.m. (plate 9). Defrosted detritus was provided as the tube building material instead of fine sand, since sand tubes, built close together, trapped suspended particles. In order to provide a more abundant food supply, the amount of organic detritus added, at the start of the experiment, was increased to 1.5ml $l^{-1}$. No extra detritus was added after 5 days. Although sedimentation was less of a problem in these experiments, settled material was resuspended once a day with a pipette.

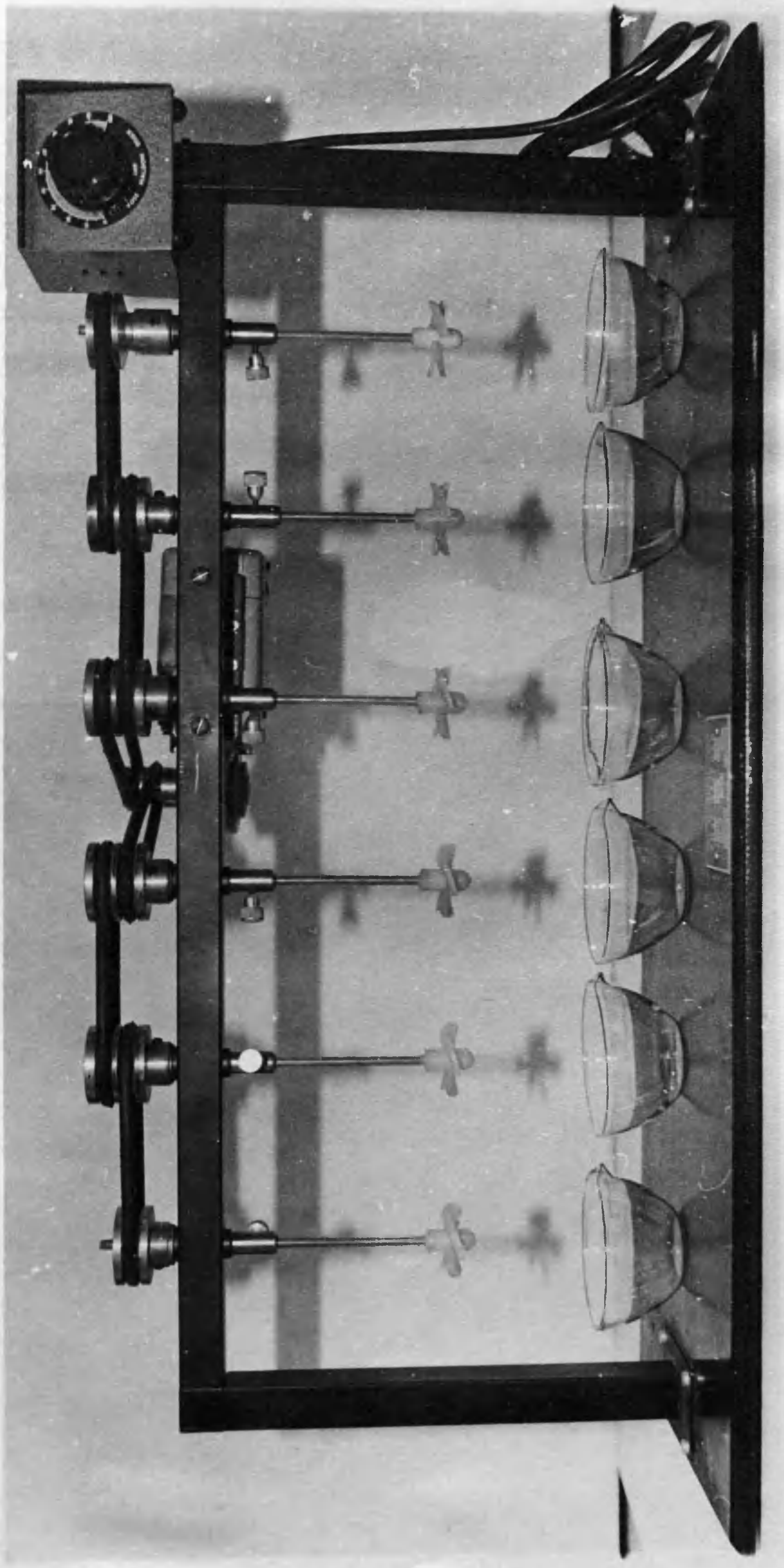
Three replicates were run on the effect of suspended boulder clay on the survival of Corophium. The animals were exposed (1) to still water with no clay, (2) to moving water with no clay and (3) to moving water with suspended clay at initial concentrations of 0.1, 1.3 and 6.4-6.6gl$^{-1}$. Replicates A and C ran for 10 days but a faulty motor only allowed replicate B to run for 6.7 days.

As well as modifying the techniques for these experiments information on two additional topics was collected. Namely, the weight of material in suspension at the end of the experiment and the body condition of the surviving animals.

The weight of material in suspension at the end of the experiment was calculated for replicates A and C, 24 h after the sedimented fraction had been resuspended. A 20 ml aliquot was taken from each dish and filtered under vacuum, using pre-weighed sartorius membrane filters ($> 0.45\mu m$). Each filter was then washed with distilled water and dried (80°C) overnight, then reweighed and the weight of suspended particles determined. Inspection of the filters suggested that most of the particles were clay, with few organic particles being present.

## PLATE 9.

THE APPARATUS FOR MAINTAINING PARTICLES IN SUSPENSION WITH ROTATING PROPELLERS.



## TABLE 50

PROPORTION OF INDIVIDUALS SURVIVING IN THE TURBIDITY EXPERIMENTS WITH ROTATING PROPELLERS.

| EXP. | SPECIES | SUS-PENSION | | STILL | TURBULENT | | | | $\chi^2$ | D.F. | P |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *0g | 0g | 0.1g | 1.3g | 6.4<br>6.6g | | | |
| 5A | COROPHIUM | CLAY | PROP. SURV. | 1.00 | 0.94 | 0.92 | 0.89 | 0.92 | 1.97 | 4 | $>0.05$ |
| | | | N | 15 | 36 | 38 | 38 | 39 | | | |
| 5B | COROPHIUM | CLAY | PROP. SURV. | 0.87 | 0.92 | 1.00 | 0.96 | 0.93 | 4.16 | 4 | $>0.05$ |
| | | | N | 30 | 26 | 23 | 26 | 30 | | | |
| 5C | COROPHIUM | CLAY | PROP. SURV. | 0.97 | 0.97 | 0.97 | 0.97 | 0.97 | 0.01 | 4 | $>0.05$ |
| | | | N | 30 | 30 | 30 | 30 | 29 | | | |

* = WEIGHT $1^{-1}$.

# TABLE 51

## CONCENTRATION OF SUSPENDED CLAY AT THE START AND TOTAL SUSPENDED SOLIDS AT THE END OF THE TURBIDITY SURVIVAL EXPERIMENTS.

| EXP. | START $gl^{-1}$ | END $gl^{-1}$ | $\frac{\text{END}}{\text{START}}$ |
|---|---|---|---|
| 5A | 6.5777 | 1.8950 | 0.2881 |
| | 6.5632 | 1.6600 | 0.2529 |
| | 1.3168 | 0.0660 | 0.0501 |
| | 1.3081 | 0.0680 | 0.0520 |
| | 0.1307 | 0.0440 | 0.3366 |
| | 0.1281 | 0.0380 | 0.2966 |
| 5C | 6.5130 | 3.0050 | 0.4614 |
| | 6.5090 | 2.2600 | 0.3472 |
| | 6.5080 | 2.6400 | 0.4057 |
| | 1.3020 | 0.6450 | 0.4954 |
| | 1.3080 | 0.3000 | 0.2294 |
| | 1.2960 | 0.5150 | 0.3974 |

## TABLE 52

## BEHAVIOURAL ASSAY OF BODY CONDITION : THE PROPORTION OF INDIVIDUALS OCCUPYING TUBES AFTER ONE HOUR.

| SPECIES | | STILL | TURBULENT | | | | $\chi^2$ | D.F. | P |
|---|---|---|---|---|---|---|---|---|---|
| | | 0g * | 0g | 0.1g | 1.3g | 6.5g | | | |
| CORОPHIUM | PROP. IN TUBES | 0.83 | 1.00 | 0.93 | 0.93 | 0.86 | 6.53 | 4 | $>0.05$ |
| | N | 29 | 29 | 29 | 29 | 28 | | | |

* = WEIGHT $l^{-1}$

## TABLE 53

**DATA ON THE SURVIVORS OF THE TURBIDITY SURVIVAL EXPERIMENTS : LEMBOS.**

| EXP. | WATER MOVEMENT | CONC. $(gl^{-1})$ | NOS. | | | LENGTH (mm) | | * |
|---|---|---|---|---|---|---|---|---|
| | | | MAT. FEMALE | MALE | JUV. | MEAN | S.D. | PROP. WITH MAT. IN GUT |
| 1B | STILL | 0 | 5 | 3 | 3 | 3.33 | 0.90 | 1.00 |
| | TURBULENT | 0 | 3 | 4 | 5 | 3.37 | 0.61 | 1.00 |
| | TURBULENT | 0.01 | 3 | 4 | 6 | 3.70 | 0.50 | 1.00 |
| | TURBULENT | 0.1 | 7 | 7 | 10 | 3.56 | 0.53 | 0.92 |
| | TURBULENT | 1.0 | 12 | 7 | 7 | 3.67 | 0.53 | 1.00 |
| 2B | STILL | 0 | 11 | 12 | 3 | 3.81 | 0.55 | 0.88 |
| | TURBULENT | 0 | 9 | 12 | 5 | 3.69 | 0.50 | 1.00 |
| | TURBULENT | 0.01 | 15 | 10 | 0 | 3.82 | 0.62 | 0.96 |
| | TURBULENT | 0.1 | 11 | 9 | 1 | 4.00 | 0.45 | 1.00 |
| | TURBULENT | 1.0 | 13 | 13 | 2 | 3.69 | 0.55 | 1.00 |
| 3B | STILL | 0 | 12 | 12 | 0 | 4.57 | 0.45 | 1.00 |
| | TURBULENT | 0 | 14 | 10 | 0 | 4.54 | 0.43 | 1.00 |
| | TURBULENT | 0.01 | 13 | 12 | 0 | 4.36 | 0.41 | 1.00 |
| | TURBULENT | 0.08 | 15 | 12 | 0 | 4.49 | 0.42 | 1.00 |
| | TURBULENT | 0.97 | 15 | 9 | 0 | 4.61 | 0.29 | 1.00 |
| 4A | TURBULENT | 6.75 | 36 | 13 | 0 | 4.87 | 0.32 | 1.00 |

* = PROPORTION WITH MATERIAL IN THEIR GUTS.

# TABLE 54

## DATA ON THE SURVIVORS OF THE TURBIDITY SURVIVAL EXPERIMENTS COROPHIUM

| EXP. | WATER MOVEMENT | CONC. ($gl^{-1}$) | NOS. | | LENGTH (mm) | | PROP. WITH * MAT. IN GUTS |
|---|---|---|---|---|---|---|---|
| | | | MAT. FEMALE | IMMAT. | MEAN | S.D. | |
| 1A | STILL | 0 | 28 | 1 | 3.33 | 0.47 | 0.69 |
| | TURBULENT | 0 | 25 | 2 | 3.26 | 0.31 | 1.00 |
| | TURBULENT | 0.01 | 28 | 2 | 3.28 | 0.29 | 1.00 |
| | TURBULENT | 0.1 | 22 | 2 | 3.39 | 0.23 | 1.00 |
| | TURBULENT | 1.0 | 24 | 4 | 3.25 | 0.27 | 0.89 |
| 2A | STILL | 0 | 28 | 1 | 3.47 | 0.25 | 1.00 |
| | TURBULENT | 0 | 28 | 2 | 3.55 | 0.26 | 1.00 |
| | TURBULENT | 0.01 | 29 | 1 | 3.55 | 0.27 | 0.97 |
| | TURBULENT | 0.1 | 29 | 0 | 3.59 | 0.40 | 1.00 |
| | TURBULENT | 1.0 | 29 | 0 | 3.50 | 0.27 | 0.86 |
| 3A | STILL | 0 | 23 | 1 | 4.13 | 0.35 | 0.96 |
| | TURBULENT | 0 | 27 | 0 | 4.24 | 0.41 | 1.00 |
| | TURBULENT | 0.01 | 28 | 0 | 4.06 | 0.34 | 0.89 |
| | TURBULENT | 0.04 | 30 | 0 | 4.13 | 0.33 | 0.93 |
| | TURBULENT | 0.48 | 27 | 0 | 4.02 | 0.37 | 0.93 |
| 4A | TURBULENT | 6.75 | 41 | 0 | 3.89 | 0.49 | 1.00 |
| 5A | STILL | 0 | 15 | 0 | 3.26 | 0.27 | 1.00 |
| | TURBULENT | 0 | 30 | 0 | 3.25 | 0.34 | 0.93 |
| | TURBULENT | 0.1 | 35 | 0 | 3.34 | 0.36 | 0.91 |
| | TURBULENT | 1.3 | 34 | 0 | 3.28 | 0.25 | 0.97 |
| | TURBULENT | 6.4-6.6 | 36 | 0 | 3.32 | 0.30 | 0.83 |
| 5B | STILL | 0 | 25 | 1 | 3.36 | 0.34 | 0.88 |
| | TURBULENT | 0 | 23 | 1 | 2.95 | 0.28 | 0.92 |
| | TURBULENT | 0.1 | 23 | 0 | 3.36 | 0.29 | 0.91 |
| | TURBULENT | 1.3 | 24 | 0 | 3.19 | 0.39 | 0.75 |
| | TURBULENT | 6.4-6.6 | 24 | 1 | 3.37 | 0.42 | 0.92 |

* = PROPORTION WITH MATERIAL IN THEIR GUTS.

## TABLE 55

## TURBIDITY SURVIVAL EXPERIMENTS : WATER TEMPERATURES.

| EXP. | TEMP. RANGE($^{o}$C) |
|---|---|
| 1A | 10.0 - 14.5 |
| 1B | 11.0 - 14.5 |
| 2A | 11.5 - 17.0 |
| 2B | 12.3 - 16.0 |
| 3A | 12.8 - 18.8 |
| 3B | 14.0 - 18.3 |
| 4A | 15.3 - 19.3 |
| 5A | 11.5 - 15.0 |
| 5B | 12.3 - 15.8 |
| 5C | 12.0 - 17.0 |

A behavioural assay (tube building ability) was conducted to determine the body condition of the survivors. At the end of replicate C the survivors were placed, at one minute intervals, into separate small dishes. Each dish contained 2 ml of organic detritus and 50 ml of sea water. After one hour, the number of individuals occupying tubes was recorded.

## Results.

In all three replicates there was no significant difference in the proportion of individuals surviving between the five sets of conditions of turbulence and turbidity (table 50). The proportion of individuals surviving exposure to initial concentrations of 6.4-6.6$gl^{-1}$ for 10 days did not differ significantly between replicates A and C ($\chi^2 = 0.05$, d.f. = 1, $P>0.05$).

The weight of the total suspended solids at the end of replicates A and C was on average 30 ± 4% ($\bar{x}$±S.E.) of the weight of clay in suspension at the start of the experiment (table 51).

The behavioural assay of body condition showed that there was no significant difference in the proportion of individuals which were occupying tubes one hour after being removed from replicate C (table 52). Virtually all animals were occupying tubes after one hour.

Various features (e.g. size and sex) of the animals used for these experiments are itemized in tables 53 and 54, and the range of water temperatures for each experiment are presented in table 55.

## D. THE EFFECT OF TURBULENCE AND TURBIDITY ON BEHAVIOUR.

## Materials and Methods.

A number of animals, always those that had been in the laboratory for less than two weeks, were left overnight in dishes with glass tubes and organic detritus (from laboratory aquaria). The glass tubes were c. 10mm long and had an internal diameter of 1.5mm. The next morning occupied glass tubes were selected for the experiments on the basis of the following criteria,

(1) Each tube had to be detritus-lined and occupied by one individual.

(2) At least one wall of the glass tube had to be incompletely

lined with detritus, so that the direction the animal pointed and whether it was beating its pleopods could be determined.

(3) If spaces between the detritus-lining and the glass tube were present, no water flow along them was permitted.

The selected tubes were then placed singly into the experimental apparatus (fig. 11), which had the following features;

(1) A motor driven propeller, of 4.5 cm diameter, which stirred water in a circular dish of 9 cm diameter.

(2) A tachometer, which measured the propeller's speed of rotation. The following speeds were used, c. 150 r.p.m. (low turbulence), c. 425 r.p.m. (medium turbulence) and c. 830 r.p.m. (high turbulence).

(3) An L-shaped arrangement of two interconnecting glass tubes. The animal's glass tube fitted into the toe of the L. The left entrance of the animal's tube was therefore inside the L apparatus but the right entrance, due to a purposefully imposed constriction in the L apparatus, protruded outside. The toe of the L was tilted slightly upwards to prevent the animal's tube being dislodged by the surrounding turbulence.

The L apparatus had two functions. Firstly, to reduce the ability of the propeller to drive water through the animal's tube. A propeller induced current (flowing from right to left) was only recorded in conditions of medium and high turbulence. This current was very much slower than the speed of the circulating water in the dish. Secondly, to allow one entrance (the right one) to be exposed to the full force of the turbulence, whilst virtually eliminating turbulence outside the opposite entrance. Both requirements would have been better met if the left entrance had opened into a sealed container. However, such an arrangement would have been unsatisfactory as the animals would have had to pump against an unyielding volume of water.

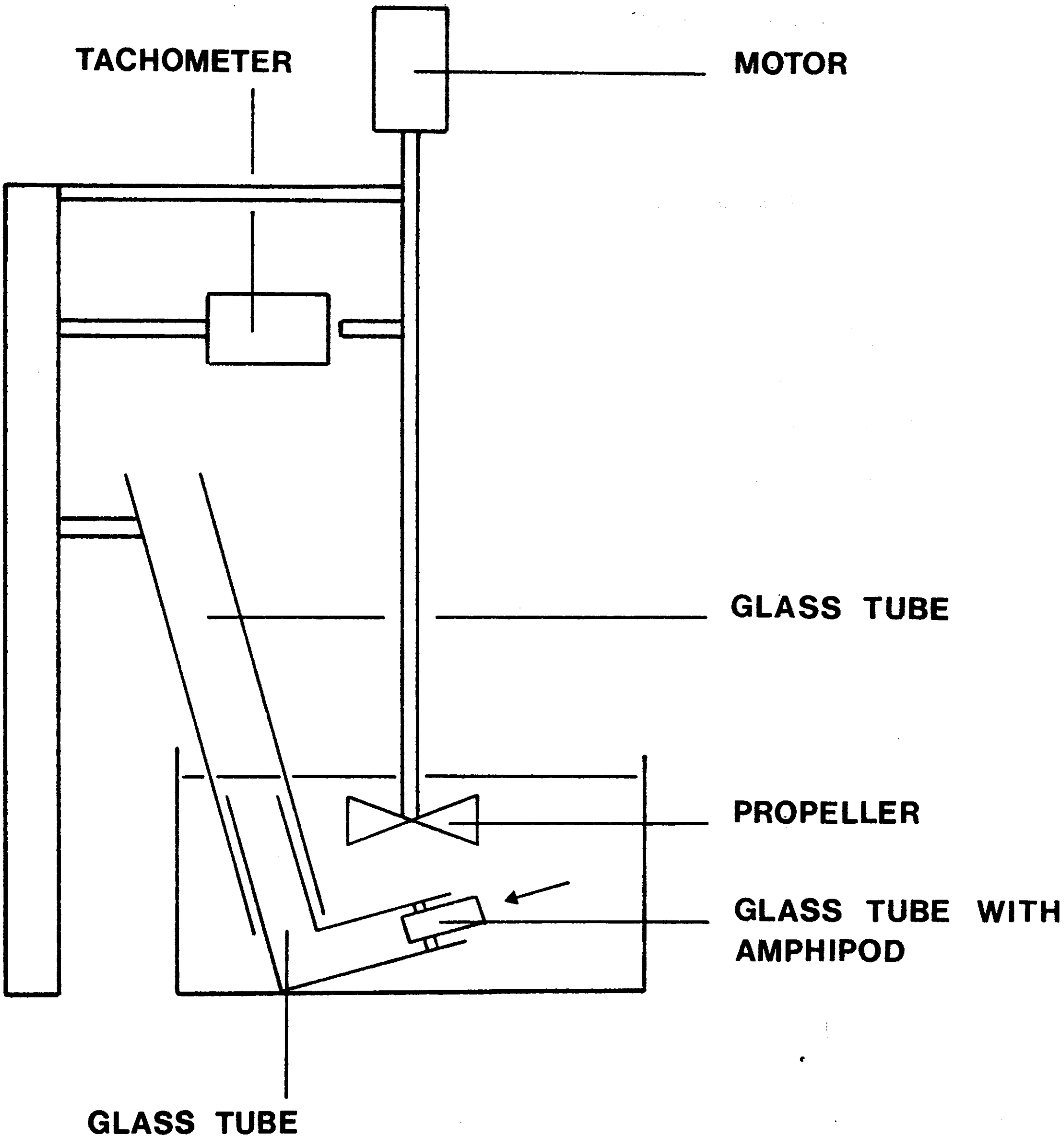
(4) A binocular microscope, for observing the animal in its tube, through the side of the dish. This was facilitated by a lamp (power not recorded) positioned 40 cm above the centre of the animal's tube.

Once in the apparatus observations were made on the animal's

## FIG. 11.

THE APPARATUS USED IN THE EXPERIMENTS ON THE EFFECT OF TURBULENCE AND TURBIDITY ON BEHAVIOUR.

THE ARROW SHOWS THE DIRECTION OF THE CURRENT THROUGH THE OCCUPIED GLASS TUBE, UNDER CONDITIONS OF MEDIUM AND HIGH TURBULENCE.


TACHOMETER
MOTOR
GLASS TUBE
PROPELLER
GLASS TUBE WITH AMPHIPOD
GLASS TUBE

behaviour. This experimental design formed the basis of three separate experiments, the details of which are described below.

## The effect of different degrees of turbulence.

The effect of zero, low, medium and high turbulence were compared. Organic detritus (from laboratory aquaria) was present in the dish at a concentration of 4.0ml $l^{-1}$. A little detritus was also placed outside the left entrance of the animals tube. This provided the animal with a source of settled detritus. All detritus particles were in the size range 0.38-0.70 mm (at the start of each day's trials).

Each animal was exposed once to one level of turbulence.

Each trial lasted 300 s, during which time two aspects of the animal's behaviour were recorded.

(1) The length of time the animal pointed towards the right. Each animal could either point towards the left or towards the right by somersaulting round in its tube, ie. in turbulent conditions the animal could either point towards turbulent or towards still water.

(2) The length of time the animal beat its pleopods, when it pointed towards the right. This was expressed as a percentage.

If an individual left its tube before the 300 s had elapsed the first measure was disregarded.

## The effect of different types of suspended particles.

The effect of suspended organic detritus was compared with that of suspended boulder clay. The effect of filtered sea water was also examined. The latter acted as a standard to allow comparison between experiments. All treatments were conducted at low turbulence. The suspended particles were at a concentration of 8ml $l^{-1}$. The organic detritus had the same features as in the previous experiment. The boulder clay had the same characteristics as that used in the turbidity survival experiments.

Each animal was exposed to each of the three treatments in the order, filtered water, suspended detritus and suspended clay, with a gap of c.5 min between each.

Each trial lasted 300 s, during which time the length of time the animal beat its pleopods, when it pointed towards the right, was recorded.

### The effect of different concentrations of suspended boulder clay.

The effect of suspended boulder clay at concentrations of 0.1 and $1.0 gl^{-1}$ were compared. The effect of filtered sea water was also compared. The latter acted as a standard to allow comparison between experiments. All treatments were conducted at low turbulence. The boulder clay had the same characteristics as that used in the turbidity survival experiments. The experimental media and the dishes containing the experimental animals were kept gently aerated prior to the trials.

Each animal was exposed to each of the three treatments, in the order, filtered water, $0.1 gl^{-1}$ clay and $1.0 gl^{-1}$ clay, with a gap of c.5 min between each.

Each trial lasted 300 s, during which time the length of time the animal beat its pleopods, when it pointed towards the right, was recorded.

Certain features were common to all three experiments. Firstly, the sea water used in all experiments was filtered (no particles $> 0.3 \mu m$) and its temperature was measured after each trial (table 61). Secondly, after all experiments the animals were killed, before being sexed and measured (tables 62 and 63).

The results of many treatments did not have a normal distribution. Therefore, differences between treatments were tested statistically by nonparametric analogues of both the one and two-way analysis of variance. Table 56 itemizes the features of the raw data, which were taken into consideration when selecting the appropriate test. Of the three tests for between treatment heterogeneity only the nonparametric STP method performed multiple comparisons. Therefore, if either the Kruskal-Wallis Test or Friedman's Method gave a significant result a further test had to be performed, to pinpoint the source of this heterogeneity. This entailed comparing the treatments in pairs. It must be stressed that the results of these tests (Mann-Whitney U and Wilcoxon's signed rank tests) are less reliable than those derived from the nonparametric STP method, as they do not take into account the

## TABLE 56

## STATISTICAL TESTS USED IN THE EXPERIMENTS ON THE EFFECT OF TURBULENCE AND TURBIDITY ON BEHAVIOUR

| EXPERIMENT | BEHAVIOUR MEASURED | FEATURES OF DATA | STATISTICAL TESTS | |
|---|---|---|---|---|
| | | | COMPARISON OF ALL TREATMENTS | COMPARISON OF IND. TREATMENTS (IN PAIRS). |
| EFFECT OF DIFF. DEGREES OF TURBULENCE | LENGTH OF TIME AN. POINTS RIGHT | EQUAL SAMPLE SIZE NOT PAIRED | NONPARAMETRIC STP TEST | - |
| | °/o TIME ANS. SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT. | UNEQUAL SAMPLE SIZE NOT PAIRED | KRUSKAL-WALLIS TEST | MANN-WHITNEY U - TEST |
| EFFECT OF DIFF. TYPES OF SUSP. PARTICLES.<br>EFFECT OF DIFF. CONCS. OF SUSP. CLAY | °/o TIME ANS. SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT. | EQUAL SAMPLE SIZE PAIRED | FRIEDMAN'S METHOD. | WILCOXON'S SIGNED-RANKS TEST |

## TABLE 57

## EFFECT OF DIFFERENT DEGREES OF TURBULENCE ON THE TIME ANIMALS POINT TOWARDS THE RIGHT.

### (a) STATISTICAL SIGNIFICANCE OF COMPARISONS BETWEEN TREATMENTS.

| | LEMBOS | | | COROPHIUM | | |
|---|---|---|---|---|---|---|
| TURBULENCE | SAMPLE SIZE | TIME (s) | $P < 0.05$ | SAMPLE SIZE | TIME (s) | $P < 0.05$ |
| ZERO | 20 | 162±64 | | 20 | 143±64 | |
| LOW | 20 | 198±97 | ** | 20 | 139±63 | *    * |
| MEDIUM | 20 | 235±69 | ** | 20 | 205±74 | |
| HIGH | 20 | 158±51 | | 20 | 155±65 | * |

TIME EXPRESSED AS A MEAN ± ONE STANDARD DEVIATION

* = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

### (b) VALUES OF $U_s$ IN THE NONPARAMETRIC STP TEST.

**LEMBOS**

| | LOW | MED. | HIGH |
|---|---|---|---|
| ZERO | 258 | 319 ** | 203 |
| LOW | | 241 | 264 |
| MED. | | | 333 ** |
| HIGH | | | |

**COROPHIUM**

| | LOW | MED. | HIGH |
|---|---|---|---|
| ZERO | 203 | 308 * | 221 |
| LOW | | 307 * | 233 |
| MED. | | | 300 * |
| HIGH | | | |

## TABLE 58

### EFFECT OF DIFFERENT DEGREES OF TURBULENCE ON THE PERCENTAGE OF TIME ANIMALS SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT.

### (a) STATISTICAL SIGNIFICANCE OF COMPARISONS BETWEEN TREATMENTS.

| | LEMBOS | | | COROPHIUM | | |
|---|---|---|---|---|---|---|
| TURBULENCE | SAMPLE SIZE | TIME (%) | $P < 0.05$ | SAMPLE SIZE | TIME (%) | $P < 0.05$ |
| ZERO | 23 | 91±10 | | 19 | 26±20 | |
| LOW | 17 | 96±4 | | 20 | 17±13 | * |
| MEDIUM | 20 | 95±6 | ** *** | 18 | 14±13 | *** *** |
| HIGH | 11 | 71±28 | *** | 19 | 3±5 | *** |

TIME EXPRESSED AS A MEAN ± ONE STANDARD DEVIATION.

### (b) VALUES OF $U_s$ IN THE MANN-WHITNEY U-TEST.

LEMBOS

| | LOW | MED. | HIGH |
|---|---|---|---|
| ZERO | 241 | 266 | 207** |
| LOW | | 181 | 179*** |
| MED. | | | 198*** |
| HIGH | | | |

COROPHIUM

| | LOW | MED. | HIGH |
|---|---|---|---|
| ZERO | 234 | 242* | 334*** |
| LOW | | 212 | 335*** |
| MED. | | | 290*** |
| HIGH | | | |

## TABLE 59

## EFFECT OF DIFFERENT TYPES OF SUSPENDED PARTICLES ON THE PERCENTAGE OF TIME ANIMALS SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT.

### (a) STATISTICAL SIGNIFICANCE OF COMPARISONS BETWEEN TREATMENTS.

| | LEMBOS | | | COROPHIUM | | |
|---|---|---|---|---|---|---|
| TREATMENT | SAMPLE SIZE | TIME(°/o) | $P < 0.05$ | SAMPLE SIZE | TIME (°/o) | $P < 0.05$ |
| FILT. WATER | 11 | 90±11 | | 13 | 28±27 | * |
| SUSP. DETRITUS | 11 | 95±5 | | 13 | 38±32 | |
| SUSP. CLAY | 11 | 85±27 | | 13 | 39±28 | |

TIME EXPRESSED AS A MEAN ± ONE STANDARD DEVIATION.

### (b) VALUES OF $T_s$ IN WILCOXON'S SIGNED-RANKS TEST.

COROPHIUM

| TREATMENTS | $T_s$ |
|---|---|
| FILT. WATER<br>SUSP. DET. | +17 * |
| FILT. WATER<br>SUSP. CLAY | +19 |
| SUSP. DET.<br>SUSP. CLAY | -43 |

# TABLE 60

## EFFECT OF DIFFERENT CONCENTRATIONS OF SUSPENDED CLAY ON THE PERCENTAGE OF TIME ANIMALS SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT.

### (a) STATISTICAL SIGNIFICANCE OF COMPARISONS BETWEEN TREATMENTS.

| | LEMBOS | | | COROPHIUM | | |
|---|---|---|---|---|---|---|
| TREATMENT | SAMPLE SIZE | TIME(°/o) | $P<0.05$ | SAMPLE SIZE | TIME(°/o) | $P<0.05$ |
| FILT. WATER | 19 | 89±15 | | 17 | 37±28 | |
| $0.1gl^{-1}$ CLAY | 19 | 97±3 | | 17 | 42±34 | |
| $1.0gl^{-1}$ CLAY | 19 | 95±11 | | 17 | 40±31 | |

TIME EXPRESSED AS A MEAN ± ONE STANDARD DEVIATION.

### (b) VALUES OF $T_s$ IN WILCOXON'S SIGNED-RANKS TEST.

LEMBOS

| TREATMENTS | $T_s$ |
|---|---|
| FILT. WATER<br>$0.1gl^{-1}$ CLAY | +47 |
| FILT. WATER<br>$1.0gl^{-1}$ CLAY | +49 |
| $0.1gl^{-1}$ CLAY<br>$1.0gl^{-1}$ CLAY | -79 |

## TABLE 61

## WATER TEMPERATURES IN THE EXPERIMENTS ON THE EFFECT OF TURBULENCE AND TURBIDITY ON BEHAVIOUR.

| EXPERIMENT | LEMBOS | COROPHIUM |
|---|---|---|
| | * TEMP (°C) | * TEMP (°C) |
| EFFECT OF DIFF.DEGREES OF TURBULENCE | | |
| ZERO | 12.52 ± 0.32 | 11.84 ± 0.47 |
| LOW | 11.63 ± 0.13 | 11.18 ± 0.44 |
| MEDIUM | 12.00 ± 0.44 | 11.85 ± 0.32 |
| HIGH | 11.77 ± 0.24 | 12.16 ± 0.13 |
| EFFECT OF DIFF.TYPES OF SUSP. PARTICLES | 10.95 ± 0.27 | 11.19 ± 0.40 |
| EFFECT OF DIFF.CONCS. OF SUSP. CLAY | 9.50 ± 0.55 | 9.78 ± 0.49 |

* MEAN ± ONE STANDARD DEVIATION

# TABLE 62

## NUMBER OF INDIVIDUALS IN EACH CATEGORY OF EACH SPECIES USED IN THE EXPERIMENTS ON THE EFFECT OF TURBULENCE AND TURBIDITY ON BEHAVIOUR.

| EXPERIMENT | BEHAVIOUR MEASURED | LEMBOS | | | | COROPHIUM | | |
|---|---|---|---|---|---|---|---|---|
| | | MALE | MAT. FEMALE | JUV. | ? | MAT. FEMALE | IMMAT. | ? |
| EFFECT OF DIFFERENT DEGREES OF TURBULENCE | | | | | | | | |
| ZERO | LENGTH OF TIME AN.POINTS RIGHT | 10 | 1 | 8 | 1 | 3 | 16 | 1 |
| LOW | | 9 | 5 | 6 | 0 | 2 | 18 | 0 |
| MEDIUM | | 11 | 2 | 7 | 0 | 3 | 17 | 0 |
| HIGH | | 8 | 4 | 8 | 0 | 3 | 17 | 0 |
| ZERO | °/o OF TIME ANS.SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT. | 10 | 3 | 9 | 1 | 3 | 15 | 1 |
| LOW | | 9 | 4 | 4 | 0 | 2 | 18 | 0 |
| MEDIUM | | 11 | 2 | 7 | 0 | 3 | 15 | 0 |
| HIGH | | 5 | 2 | 4 | 0 | 3 | 18 | 0 |
| EFFECT OF DIFF.TYPES OF SUSP. PARTICLES | °/o OF TIME ANS. SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT. | 5 | 3 | 3 | 0 | 3 | 10 | 0 |
| EFFECT OF DIFF.CONCS. OF SUSP.CLAY | | 7 | 1 | 10 | 1 | 1 | 16 | 0 |

## TABLE 63

## BODY LENGTHS OF ANIMALS USED IN THE EXPERIMENTS ON THE EFFECT OF TURBULENCE AND TURBIDITY ON BEHAVIOUR.

| EXPERIMENT | BEHAVIOUR MEASURED | LEMBOS | COROPHIUM |
|---|---|---|---|
| | | *BODY LENGTH(mm) | *BODY LENGTH (mm) |
| EFFECT OF DIFF. DEGREES OF TURBULENCE | | | |
| ZERO | LENGTH OF TIME AN. POINTS RIGHT. | 3.42 ± 0.22 | 2.84 ± 0.35 |
| LOW | | 3.52 ± 0.29 | 3.12 ± 0.31 |
| MEDIUM | | 3.32 ± 0.37 | 3.26 ± 0.25 |
| HIGH | | 3.53 ± 0.32 | 3.20 ± 0.27 |
| ZERO | °/o OF TIME ANS. SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT. | 3.46 ± 0.22 | 2.84 ± 0.36 |
| LOW | | 3.48 ± 0.33 | 3.12 ± 0.31 |
| MEDIUM | | 3.38 ± 0.40 | 3.24 ± 0.26 |
| HIGH | | 3.55 ± 0.29 | 3.19 ± 0.26 |
| EFFECT OF DIFF. TYPES OF SUSP. PARTS. | °/o OF TIME ANS. SPENT BEATING THEIR PLEOPODS, WHEN POINTING TOWARDS THE RIGHT. | 3.39 ± 0.38 | 3.15 ± 0.39 |
| EFFECTS OF DIFF. CONCS. OF SUSP. CLAY. | | 3.31 ± 0.35 | 3.16 ± 0.30 |

* MEAN ± ONE STANDARD DEVIATION

complete within-experiment variation. A full discussion of all these tests is available in Sokal and Rohlf (1969, pp. 387-402).

Results.

Effect of different degrees of turbulence on the length of time animals spent pointing towards the right (table 57a and b).

*Lembos* spent longer pointing towards water of low and medium turbulence than towards still or highly turbulent water. The differences between medium and no turbulence and between medium and high turbulence were statistically significant.

*Corophium* spent longer pointing towards water of medium turbulence than towards water of lesser or greater turbulence. All these differences were statistically significant.

Effect of different degrees of turbulence on the percentage of time animals spent beating their pleopods, when pointing towards the right (table 58a and b).

As the Kruskal-Wallis test showed that there was significant between treatment heterogeneity in experiments on Lembos ($\chi^2 = 13.54$, 3d.f., $P < 0.01$) and Corophium ($\chi^2 = 34.74$, 3d.f., $P < 0.001$), further analysis was conducted on both species.

With increasing turbulence, the percentage of time *Lembos* spent beating its pleopods remained approximately the same, until the animals were exposed to high turbulence, whereupon it fell. The reaction of *Lembos* to highly turbulent conditions was significantly different from their reaction to all less turbulent conditions.

The percentage of time *Corophium* spent beating its pleopods decreased as turbulence increased. Their reaction to high turbulence was significantly different from their reaction to all less turbulent conditions. In addition, their reaction to medium turbulence was significantly different from their reaction to still water.

The effect of different types of suspended particles on the percentage of time animals spent beating their pleopods, when pointing towards the right (table 59a and b).

As Friedman's method showed that there was significant variation between treatments for Corophium ($\chi^2 = 10.72$, 2d.f., $P<0.01$) but not Lembos ($\chi^2 = 0.74$, 2d.f., $P>0.05$), further analysis was only conducted on Corophium.

Corophium reacted in the same way to suspended detritus and to suspended clay. In addition, Corophium beat their pleopods for longer in the presence of both types of suspended particles than in filtered sea water. However, only the difference between suspended detritus and filtered sea water was statistically significant.

The effect of different concentrations of suspended clay on the percentage of time animals spent beating their pleopods, when pointing towards the right (table 60a and b).

As Friedman's method showed that there was no significant variation between treatments for Corophium ($\chi^2 = 4.44$, 2d.f., $P>0.05$), whilst there was for Lembos ($\chi^2 = 7.5$, 2d.f., $P<0.05$), further analysis was only conducted on Lembos.

Lembos reacted in the same way to suspended boulder clay, at concentrations of 0.1 and 1.0$gl^{-1}$. Lembos beat its pleopods for slightly longer in the presence, than in the absence, of suspended clay (as did Corophium). However, neither differences were statistically significant.

## E. THE EFFECT OF SEDIMENTATION ON LEMBOS AND COROPHIUM.

### Materials and Methods.

Individuals were left overnight to build tubes of fine sand and detritus. For most experiments only those tubes which were built in the angle of the dish and had both entrances touching the vertical walls were used. In one series of experiments with Corophium, only those tubes which were built away from the angle of the dish were used.

The clay was the same as that used in the turbidity survival experiments. Complete clay sedimentation covered Corophium tubes to a depth of 3 mm, whilst Lembos tubes were only covered to a depth of 2 mm. This was due to Lembos tubes being c. 1 mm higher than those of Corophium. The sand was collected from the Laminaria zone in Fintray Bay (the top few cm of sand). This sand, in February 1976, consisted of grains which were 5% (by volume) $>500\mu m$, 80% 250-500$\mu m$ and 15% $<250\mu m$. Tubes were individually covered with sand to a depth of 3 mm.

24 h after sedimentation the number of individuals still occupying their original tubes, which had at least one entrance in contact with the overlying water, were counted.

During these experiments the water temperature ranged from 10-12.75°C.

### Results (table 64)

### Clay sedimentation.

### Comparison 1. *Corophium* versus *Lembos*. All tubes against the walls of the dish.

No Lembos but most Corophium had at least one entrance in contact with the overlying water. This difference was statistically significant.

### Comparison 2. *Corophium* (against wall) versus *Corophium* (away from wall).

The proportion of tubes, which had at least one entrance in contact with the overlying water, was significantly higher for tubes against the walls of the dish than for those away from the walls.

### Sand sedimentation.

### Comparison 3. *Corophium* versus *Lembos*. All tubes against the walls of the dish.

Although the proportion of individuals, with at least one entrance in contact with the overlying water, was higher for Corophium than for Lembos, the difference was not statistically significant.

# TABLE 64

## PERCENTAGE OF ANIMALS WITH AT LEAST ONE TUBE ENTRANCE IN CONTACT WITH THE OVERLYING WATER 24 HOURS AFTER SEDIMENTATION.

| COMPARISON | SPECIES | SEX | TUBES AGAINST OR AWAY FROM WALL | SEDIMENT | NO. ANS. TESTED | °/o | $\chi^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | COROPHIUM | FEMALE | AGAINST | CLAY | 35 | 94.3 | 69.15 | $< 0.001$ |
| | LEMBOS | MALE + FEMALE | AGAINST | CLAY | 46 | 0 | | |
| 2 | COROPHIUM | FEMALE | AGAINST | CLAY | 35 | 94.3 | 6.43 | $< 0.05$ |
| | COROPHIUM | FEMALE | AWAY | CLAY | 45 | 68.9 | | |
| 3 | COROPHIUM | FEMALE | AGAINST | SAND | 12 | 100 | 1.06 | $> 0.05$ |
| | LEMBOS | MALE + FEMALE | AGAINST | SAND | 27 | 74.1 | | |
| 4 | LEMBOS | FEMALE | AGAINST | SAND | 12 | 75.0 | † | $> 0.3380$ |
| | LEMBOS | MALE | AGAINST | SAND | 15 | 73.3 | | |
| 5 | LEMBOS | MALE + FEMALE | AGAINST | SAND | 27 | 74.1 | 42.60 | $< 0.001$ |
| | LEMBOS | MALE + FEMALE | AGAINST | CLAY | 46 | 0 | | |
| 6 | COROPHIUM | FEMALE | AGAINST | SAND | 12 | 100 | † | $> 0.5503$ |
| | COROPHIUM | FEMALE | AGAINST | CLAY | 35 | 94.3 | | |

† NO $\chi^2$ VALUE FOR EXACT TEST (SEE BAILEY, 1964, P.61)

### Comparison 4. *Lembos* (male) versus *Lembos* (female). All tubes against the walls of the dish.

There was no difference between male and female *Lembos*, in the percentage of individuals, which had at least one entrance in contact with the overlying water.

### Sand versus clay sedimentation.

### Comparison 5. *Lembos*. All tubes against the walls of the dish.

The percentage of tubes with at least one entrance in contact with the overlying water was significantly higher after burial by sand than by clay.

### Comparison 6. *Corophium*. All tubes against the walls of the dish.

There was no difference in the percentage of tubes with at least one entrance in contact with the overlying water, between animals buried under clay and animals buried under sand.

## F. DISCUSSION.

Sedimentation was a problem in the turbidity survival experiments. At the end of the experiments with oscillating plates, only the suspensions of kaolin and silica, with initial concentrations of $1.0 gl^{-1}$ and boulder clay, with initial concentrations of $0.5 gl^{-1}$, were still quite turbid. As the weight of inorganic particles in suspension, at the end of the experiment, is not known, the results only provide a *suggestion* as to the real relationship between turbidity and survival. With the exception of *Lembos*, in the presence of silica, the survival of *Lembos* and *Corophium* appeared to be independent of exposure (ten days) to suspended inorganic particles up to an initial concentration of $6.8 gl^{-1}$. In order to test this hypothesis an experimental design (rotating propellers), which was more effective in reducing sedimentation, was employed. These experiments showed that the survival of *Corophium* was independent of exposure (ten days) to suspended boulder clay, up to a concentration varying between 6.6 and c. $1.7 gl^{-1}$.

The highest concentration of suspended solids, used in these experiments, was larger than the average, of $0.001gl^{-1}$, for inshore waters (Chester and Stoner, 1972) and larger than the maximum value, of $0.3gl^{-1}$, which Moore (1972) recorded in his turbid water area. Values of several $gl^{-1}$ are only reached intermittently, along eroding shores and in certain estuarine situations (Moore, in press).

We may therefore conclude that the survival of Corophium and possibly also Lembos is independent, over short periods, of natural levels of inorganic turbidity. The high density of Corophium in the turbid waters off Redcar (Moore, 1973b) supports this conclusion.

Before inorganic turbidity can be described as a non-lethal factor further experiments need to be conducted, especially on Lembos. The most ecologically relevant experimental design would be to use sea water and suspended solids from Moore's turbid water sites. Some important questions include, (1) Are suspended solids from Redcar less deleterious than those from other sites? (2) Is survival affected by variables combining in a synergistic manner with turbidity? For instance, DDT is very effective at controlling Simulid larvae when added to muddy waters, where it becomes adsorbed to the suspended particles (Hynes, 1970). (3) Is survival independent of the length of exposure to turbid water?

The sub-lethal effects of inorganic turbidity were also investigated. Exposure to suspended boulder clay, for ten days, at concentrations of up to $2.3\text{-}6.5gl^{-1}$ had no effect on the general activity of Corophium, as measured by the speed taken to build tubes. In both clear and turbid water, both species often rubbed their gnathopods (excluding Corophium's second pair) over various parts of their bodies. Attached particles have been seen to be removed from the antennae and in the case of Lembos, from the flexed abdomen. No marked build-up of silica, kaolin or boulder clay was found on either species at the end of turbidity survival experiments. Some particles, especially boulder clay, did accumulate on Corophium's fifth pair of pereopods, being trapped by the setae of each basal article. In contrast, a marked accumulation of particles was found, on both species, after exposure to suspended ferric oxide for five hours.

In beakers, which were still turbid at the end of the ten day turbidity survival experiments, boluses of inorganic particles and organic detritus were sometimes found in the marsupia of female Lembos and Corophium. This was most frequent after the animals were exposed to clay, at an initial concentration of $6.75 gl^{-1}$, which was maintained in suspension with an oscillating plate. The percentage of mature females with clay and organic detritus in their marsupia was 17% for Corophium (n=41) and 64% for Lembos (n=36). The quantity present varied from virtually nothing to a bolus, which nearly filled the entire brood pouch. Of the females with particles in their marsupia 86% of Corophium and 17% of Lembos also carried embryos. Some embryos shared a marsupium with a considerable quantity of extraneous material. For instance, one female Lembos had a thin layer of clay between the brood plates and the underlying embryos. The co-occurrence of inorganic particles and embryos is probably deleterious to the latter. For instance, it probably (1) reduces the efficiency of brood pouch irrigation and (2) provides a source of irritation and facilitates microbial infection. As both species can reach into their marsupia with their gnathopods, they probably are able to remove entrapped particles. The resultant effect of brood pouch contamination and cleaning on hatching success needs to be studied. However, it seems likely that this is one means by which inorganic turbidity acts as a deleterious factor. In addition, faecal pellets were occasionally found in the marsupia of Corophium (but never in the marsupia of Lembos) after exposure to turbid water. This might have been due (1) to Lembos, with its highly developed refection behaviour, releasing fewer faecal pellets than Corophium and/or (2) to the more open brood pouch of Corophium facilitating the entry of these large particles. The latter explanation is supported by the fact after several days in a bowl, which was tilted c. 18 $min^{-1}$, swilling large particles of organic detritus over the bottom, several Corophium but no Lembos had detritus in their marsupia. It is thought that large particles are forced into the marsupium when an individual somersaults round in its tube. Extraneous material, eg. sand grains or organic detritus, is found very rarely in the marsupia of Corophium and never in the marsupia of Lembos, collected from Fintray Bay.

The proportion of time Lembos spent beating its pleopods was not affected to any marked extent, by the presence of organic or inorganic particles in suspension. The same result was obtained, in one experiment, with Corophium. However, in another experiment, the proportion of time Corophium spent beating its pleopods increased by c. 35%, in the presence of suspended particles (inorganic and organic). Enequist (1949, p.377) observed that Corophium beat its pleopods more energetically, for short periods, when the water was made turbid with suspended detritus. Whilst Foster-Smith and Shillaker (in press) did not find a marked increase in the proportion of time Corophium pumped water through its tube, on transfer from clear to turbid water (c.0.8-0.6$gl^{-1}$ clay), they do report a 20% increase in the pumping rate. Under the same experimental conditions, Foster-Smith and Shillaker report that there was no marked effect on either the percentage of time spent pumping or the pumping rate of Lembos. Current evidence therefore suggests that turbidity has a more marked influence on the pleopod activity of Corophium than Lembos. However, these effects of turbidity were neither very spectacular, ie. they resulted in less than a 100% change in activity, nor were they normally inhibiting. Furthermore, in the presence of suspended clay, at a concentration of 1.0$gl^{-1}$, no abnormal behaviour patterns were observed. Therefore, these experiments do not provide an explanation for the general absence of Corophium and Lembos from Moore's turbid water sites.

In beakers which were still turbid at the end of the turbidity survival experiments, most individuals of both species had material in their guts and had produced a large number of faecal pellets. Therefore, both species appear to feed in water made turbid with inorganic particles. In addition, Corophium has been observed to filter off and ingest suspended clay particles. Moore (in press) states,

> "Suspended inert particles present large surface areas for adsorption of detritus (Fox, 1950), dissolved organic matter (Bader, Hood and Smith, 1960) and colonization by microorganisms, eg. bacteria and fungi (reviewed by Rheinheimer, 1971)"

Suspended inorganic particles are therefore of potential nutritional value to the suspension feeding species, Lembos and Corophium. If these particles can be covered with such a calorie-rich film, why are these two species normally rare in turbid waters? Although this paradox has not been investigated a few pertinent comments can be made.

(1) An electronic particle size analysis (by a Coulter Counter) of sea water collected from Robin Hood's Bay (a turbid water site) in January 1975 showed that c. 40% of the particles had a diameter $\geqslant 2\mu m$. Only Corophium can efficiently filter particles as small as c. 1-2$\mu m$.

(2) Wiebe and Pomeroy (1972) point out that there is very little evidence to support the widespread belief that suspended particles in the sea are richly covered with bacteria. After studying particles

collected from deep and surface waters of the sea they conclude, "In almost no case do bacteria cover a significant portion of the total surface area of particles." A similar conclusion was reached for estuarine waters, "Whilst occasional samples had high densities of attached bacteria, the vast majority of particles did not contain many recognisable bacteria."

(3) Did the high concentration of nutrients in the sea off Redcar promote a richer than normal bacteria film on the suspended particles? This might have been particularly beneficial to *Corophium*, the more efficient small particle feeder, allowing it to flourish at this turbid water site.

(4) One of the two main mineral components of kaolin is kaolinite. Kaolinite has very poor ion-exchange properties (Probert, 1975) and is therefore almost inert, from the point of view of adsorption. Particles of kaolin may therefore be less calorie-rich than other particles.

(5) *Lembos* and *Corophium* will ingest freshly powdered chalk within minutes of the chalk being added to water. There must have been very little organic material on the surface of these particles. Are *Lembos* and *Corophium* unselective particle feeders? Meadows (1964), when discussing burrowing in *Corophium volutator*, reports that removal or alteration of the primary film on particles renders the substratum unattractive.

(6) If unselective feeding occurs, does the ingestion of particles of low nutritional value reduce the animals assimilation efficiency?

The effect of turbidity on complete emergence from the tube needs to be investigated. If light intensity is important in controlling this behaviour in male *Lembos*, turbidity, by reducing the light intensity, may alter the timing of this event. Meadows and Reid (1966) report that in turbid water very small *Corophium volutator* swim for much longer than is usual (see the discussion in Chapter II for further comments). In this context, it ought to be mentioned that Bellan-Santini (1971) and Leung Tack Kit (1972) considered that *Lembos* was common in parts of the turbid old Port of Marseille because it was a shade-loving species.

The brief investigation into the effect of sedimentation produced some interesting results. Soon after burial by sand *Corophium* (always) and *Lembos* (sometimes) started to extend their tubes, one shaft at a time, to the sediment surface. Both species employed the same technique of forcing themselves upwards (head first) into the sand, consolidating the sand by knitting with their first two pairs of pereopods, before moving upwards a little further. Lembos sometimes left its tube completely, by burrowing quickly upwards to the sediment surface. After burial by clay Corophium normally remained in its tube and relied upon its pleopod current to flush out two vertical shafts to the sediment surface. No attempt was made to consolidate the sediment by knitting with the first two pairs of pereopods. Lembos never succeeded in using its pleopod current to flush out two vertical shafts and always vacated its tube, by burrowing upwards to the sediment surface. The greater pumping rate of Corophium (Foster-Smith and Shillaker, in press) probably accounted for its ability to clear sediment from its tube. Although the animals were not measured, Corophium was often smaller than Lembos.

The ecological significance of these results is uncertain as the sedimentation rate and particle size distribution of settling particles, in Laminaria holdfasts, are not known. However, it does show that (1) Corophium is better able, than Lembos, to cope with fine particle sedimentation and (2) that both species will be able to cope with slight sand burial, as at Fintray Bay.

Reineck (1958) reports that heavy sedimentation (size of particles?) causes Corophium volutator to leave its tube. If sedimentation is slight the animal remains in its tube and either pushes the settling particles out of its tube or washes them away with a strong pleopod current.

The ability of both species to withstand sedimentation is dependent on their own activity, which is, in turn, temperature dependent. A combination of high sedimentation and very low temperatures, something littoral populations might experience in winter, might prove to be extremely deleterious. Crisp (1964) reports that some bivalves died in the very cold winter of 1962/63, as a result of their inability to clear mud from the mantle cavity. Lembos, with its more southerly centre of distribution, might be particularly susceptible at the northern part of its range.

Both species mostly build their tubes in the angle of a dish. One advantage of this is that following burial by clay, significantly more Corophium, in tubes against the wall of the dish, formed vertical shafts to the sediment surface, than Corophium in tubes which were away from the walls. An upright solid surface restricts the number of directions from which unstable sediment can cascade into the incipient burrow.

Finally, the effect of turbulence was investigated. These experiments were designed to see if the behaviour of Lembos and Corophium was affected by turbulence up to a level, which was still too weak to dislodge their detritus tubes. Whilst both species spent just as long pointing towards the most turbulent water, as they did towards unagitated water, they spent a significantly shorter proportion of the time beating their pleopods, when pointing towards the turbulent water. The latter behavioural change was particularly marked in Corophium. Corophium and Lembos beat their pleopods for, respectively, 8.7 and 1.3 times longer in still than in highly turbulent water. Further experiments are required to identify the factor(s), which caused this change in behaviour. The possibilities are, (1) water movement outside the tube, (2) the propeller - induced through tube current, (3) factors correlated with (1) and (2), for instance the availability of suspended particles and vibration of the animal's tube.

Although poor visibility restricted observations on feeding behaviour it appeared that whilst Lembos removed and worked over particles from the propeller induced current Corophium rarely did so. Therefore, the marked decrease in Corophium's pleopod activity in very turbulent water was probably not due to animals relying on the propeller induced current to provide them with food (suspended particles). Corophium mostly remained well inside its tube and as a result, was probably not directly affected by turbulence outside its tube. In contrast, Lembos held its antennae outside its tube for long periods. Even in the most turbulent water the antennae, with the exception of their distal tips, maintained their rigidity and could catch passing particles. The conclusion that may be drawn from these experiments is that the highest level of turbulence used was more inhibitory to the normal activity of Corophium, than that of Lembos. Assuming that, in the sea, natural water movement can force water through Corophium's tube, this may partially explain why Corophium is more abundant in Laminaria holdfasts at sheltered than at exposed localities.

The effect of water movement on partial and complete tube emergence would seem to be another useful topic for further research.

## REFERENCES

Achuthankutty, C.T., K.K.C. Nair and K.S. Purusham, (1973) A shoal of sergestid shrimp Acetes in association with a swarm of gammarid amphipods in the south-west coast of India. Current Science, 42, 840.

Agrawal, V.P., (1963) Studies on the physiology of digestion in Corophium volutator. Journal of the Marine Biological Association of the U.K., 43, 125-128.

Alexander, D.W., (1969) The study of the biology of animals living on and in littoral sponges with species reference to Halichondria panicea (Pallas). Ph.D. thesis, University of London.

Andres, H.G., (1970) Zur biologie und ökologie des amphipoden Corophium volutator Pallas (Corophiidae). Dipl. Arbeit (Biologie), University of Hamburg.

Armstrong, F.A.S. and W.R.G. Atkins, (1950) The suspended matter of sea water. Journal of the Marine Biological Association of the U.K., 29, 139-143.

Austin, A.B. and K.H. Williams, (1972) A ten-year study of meroplankton in north Carolina estuaries : amphipods. Chesapeake Science, 13, 175-192.

Bacescu, M.C., (1970) 7. Substratum 7.3. Animals. In, Marine Ecology, Ed. O. Kinne, J. Wiley, London, 1, 1291-1322.

Bacescu, M.C., E. Dumitrescu, A. Marcus, G. Paladian and R. Mayer, (1963) Données quantitatives sur la faune pétricole de la Mer Noire à Agigea (Secteur Roumain), dans les conditions spéciales de l'année 1961. Travaux du Muséum d'histoire naturelle 'Gr. Antipa', 4, 131-155.

Bader, R.G., D.W. Hood and J.B. Smith, (1960) Recovery of dissolved organic matter in sea-water and organic sorption by particulate material. Geochimica et cosmochimica acta, 19, 236-243.

Bailey, N.T.J., (1964) Statistical methods in biology. Hodder and Stoughton, London, 198pp.

Barnard, J.L., (1969a) Gammaridean Amphipoda of the rocky intertidal of California : Monterey Bay to La Jolla. Bulletin U.S. National Museum, No. 258, 230pp.

Barnard, J.L., (1969b) The families and genera of marine Gammaridean Amphipoda. Bulletin U.S. National Museum, No. 271, 535pp.

Barnard, J.L., and D.J. Reish, (1959) Ecology of Amphipoda and Polychaeta of Newport Bay, California. Occasional Papers of the Allan Hancock Foundation, 21, 106pp.

Barnes, H., (1955) Climatological and salinity data for Millport, Scotland. Glasgow Naturalist, 17, 193-204.

Barrett, B.E., (1966) A contribution to the knowledge of the amphipodous crustacean Amphithoe valida Smith, 1873. Ph.D. thesis, University of New Hampshire.

Bassindale, R., (1940) Studies on the biology of the Bristol Channel IV. The invertebrate fauna of the southern shores of the Bristol Channel and Severn estuary. Proceedings of the Bristol Naturalists' Society, 9, 143-201.

Bate, C.S. and J.O. Westwood, (1863) A history of the British sessile-eyed Crustacea. 2 Vols. John Van Voorst, London.

Bellan-Santini, D., (1971) Amphipodes des milieux portuaires. Tethys, 3, 255-264.

Bellan-Santini, D., and M. Ledoyer, (1973) Check list of gammaridean Amphipoda collected in the area of Marseille. Tethys, 4, 899-934.

Bousfield, E.L., (1963) Shallow-water gammaridean Amphipoda of New England. Cornell University Press, Ithaca, 312pp.

Bousfield, E.L., and A.H. Leim, (1958) The fauna of Minas Basin and Minas Channel. Bulletin. National Museum of Canada, No. 166, 1-30.

Bradfield, R.E.N., R.W.S.M. Kingsbury and C.P. Rees, (1976) An assessment of the pollution of Cornish coastal waters. Marine Pollution Bulletin, 7, 187-193.

Bregazzi, P.K., (1972) Life cycles and seasonal movements of Cheirimedon femoratus (Pfeffer) and Tryphosella kergueleni (Miers) (Crustacea : Amphipoda). British Antarctic Survey Bulletin, 30, 1-34.

Bruce, J.R., J.S. Colman and N.S. Jones, (1963) Marine fauna of the Isle of Man. Liverpool University Press, 307pp.

Campbell, J.I. and P.S. Meadows, (1974) Gregarious behaviour in a benthic marine amphipod (Corophium volutator). Experimentia, 30, 1396-1397.

Carriker, M.R., (1967) Ecology of estuarine benthic invertebrates : a perspective. In, Estuaries Ed. G.H. Lauf, American Association for the Advancement of Science, No. 83, 442-487.

Chapman, J.W. and J.A. Dorman, (1975) Diagnosis, systematics and notes on Grandidierella japonica (Amphipoda : Gammaridea) and its introduction to the Pacific coast of the United States. Bulletin Southern California Academy of Sciences, 74, 104-108.

Chardy, P., (1970) Ecologie des crustaces peracarides des fonds rocheux de Banyuls-sur-Mer. Thesis, University of Paris, 78pp.

Chester, R. and J. Stoner, (1972) Concentration of suspended particulate matter in surface sea water. Nature, London, 240, 552-553.

Chevreux, E. and L. Fage, (1925) Amphipodes. Faune de France, 9, 488pp.

Clarke, G.M., (1969) Statistics and experimental design. Edward Arnold, London, 161pp.

Clay, E., (1965) Literature survey of the common fauna of Estuaries. No. 15. Corophium volutator (Pallas). Imperial Chemical Industries, Paint Division, 17pp.

Colman, J., (1940) On the faunas inhabiting intertidal seaweeds. Journal of the Marine Biological Association of the U.K., 24, 129-183.

Connell, J.H., (1963) Territorial behaviour and dispersion in some marine invertebrates. Researches on Population Ecology, 5, 87-101.

Costa, S., (1960) Recherches sur les fonds à Halarachnion spatulatum de la baie de Marseille. Vie et milieu, 11, 1-68.

Coustalin, J.B., (1972) Méthodologie expérimentale en vue de la création de recifs artificiels. Tethys, 3, 827-840.

Crawford, G.I., (1937a) A review of the amphipod genus Corophium, with notes on British species. Journal of the Marine Biological Association of the U.K., 11, 589-630.

Crawford, G.I., (1937b) Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. Journal of the Marine Biological Association of the U.K., 11, 631-646.

Crisp, D.J., (1964) The effects of the winter of 1962/63 on the British marine fauna. Helgoländer wissenschaftliche Meeresuntersuchungen, 10, 313-327.

Croker, R.A., (1968) Return of juveniles to the marsupium in the amphipod Neohaustorius schmitzi Bousfield. Crustaceana, 14, 215.

Crothers, J.H., (Editor) (1966) Dale Fort marine fauna. 2nd Ed., 169pp.

Dahl, E., (1946) The Amphipoda of the Sound. Part 2. Undersökningar Över Öresund, 30, 1-49.

Dahl, E., (1948) On the smaller Arthropoda of marine algae especially in polyhaline waters off the Swedish west coast. Undersökningar Över Öresund, 35, 1-193.

Dahl, E., H. Emanuelsson and C. von Meckelburg, (1970) Pheromone reception in males of the amphipod Gammarus duebeni Lilljeborg. Oikos, 21, 42-47.

Davis, C.C., (1968) Hatching of aquatic invertebrate eggs. Oceanography and Marine Biology Annual Review, 6, 325-376.

Della Valle, A., (1893) Gammarini del Golfo di Napoli. Fauna Flora Golf Neapel, 20, 948pp.

Dennell, R., (1934) The habits and feeding mechanism of the amphipod Haustorius arenarius. Journal of the Linnean Society, 38, 363-388.

Dommasnes, A., (1968) Variations in the meiofauna of Corallina officinalis L. with wave exposure. Sarsia, 34, 117-124.

Duhig, M., (1960) The Amphipoda of Dalkey Island and its neighbouring waters. Proceedings of the Royal Irish Academy, 61, B, 59-77.

Ekman, S., (1953) Zoogeography of the sea. Sidgwick and Jackson, London, 417pp.

Embody, G.C., (1911) A preliminary survey of the distribution, food and reproductive capacity of some freshwater amphipods. Internationale Revue der gesamten Hydrobiologie u Hydrographie, Biol. Suppl., 3, 1-33.

Emmart, E.W., (1936) Studies on the effect of temperature on the embryo of Carcinogammarus mucronatus Say. Journal of Experimental Zoology, 74, 353-379.

Enequist, P., (1949) Soft bottom amphipods of the Skagerak. Zoologiska Bidrag Fran Uppsala, 28, 297-492.

Fage, L., (1954) Les Amphipodes pélagiques du genre Rhabdosoma. Compte rendu hebdomadaire des séances de l'Académie des sciences, 239, 661-663.

Faletans, N. de., (1958) Morphologie et ecologie de Corophium lacustre Vanhöffen. Mémoires de la Société nationale des sciences naturelles et mathématiques de Cherbourg, 47, 62-85.

Feeley, J.B. and M.L. Wass, (1971) The distribution and ecology of the Gammaridea (Crustacea : Amphipoda) of the lower Chesapeake estuaries. Special Papers in Marine Science, No. 2, Virginia Institute of Marine Science, 58pp.

Fenchel, T., (1970) Studies on the decomposition of organic detritus from Turtle Grass Thalassia testudinum. Limnology and Oceanography, 15, 14-20.

Fenchel, T., (1972) Aspects of decomposer food chains in marine benthos. Verhandlungsbericht der Deutschen Zoologischen Gesellschaft, 65, 14-23.

Fenchel, T., L.H. Kofoed, A. Lappalainen, (1975) Particle size-selection of two deposit feeders ; the Amphipod Corophium volutator and the Prosobranch Hydrobia ulvae. Marine Biology, 30, 119-128.

Fenwick, G.D., (1976) The effect of wave exposure on the amphipod fauna of the alga Caulerpa brownii. Journal of Experimental Marine Biology and Ecology, 25, 1-18.

Fincham, A.A., (1968) The ecology of some inshore and intertidal amphipods. Ph.D. thesis, University of Liverpool.

Fish, J.D., (1975) Development, hatching and brood size in Bathyporeia pilosa and B. pelagica (Crustacea : Amphipoda) Journal of the Marine Biological Association of the U.K., 55, 357-368.

Forsman, B., (1956) Notes on the invertebrate fauna of the Baltic. Arkiv för zoologi (series 2), 9, 389-419.

Forsman, B., (1970) Small animals in algal belts and drifting seaweeds. Zoologisk revy, 32, 3-8.

Foster-Smith, R.L. and R.O. Shillaker, (in press) Tube irrigation by Lembos websteri and Corophium bonnellii (Crustacea : Amphipoda). Journal of Experimental Marine Biology and Ecology.

Fox, D.L., (1950) Comparative metabolism of organic detritus by inshore animals. Ecology, 31, 100-108.

Gage, J., (1972a) Community structure of the benthos in Scottish sea lochs 1. Introduction and species diversity. Marine Biology, 14, 281-297.

Gage, J., (1972b) A preliminary survey of the benthic macrofauna and sediments in Loch Etive and Crenan, sea-lochs along the West coast of Scotland. Journal of the Marine Biological Association of the U.K., 52, 237-276.

Gauld, D.T., T.B. Bagenal and J.H. Connell, (1953) The marine fauna and flora of St. Kilda, 1952. The Scottish Naturalist, 65, 29-49.

Gauthier, H., (1941) Sur l'éthologie d'un amphipode qui vit dans une coquille. Bulletin de la Société d'histoire naturelle de l'Afrique du Nord, 32, 245-266.

Ghelardi, R.J., (1971) Species structure of the holdfast community. In, The biology of giant kelp beds (Macrocystis) in California. Ed. W.J. North, J. Cramer, Lehre, pp381-420.

Gidney, A.R., (1969) The light sensitivity and light environment of Corophium volutator. Ph.D. thesis, University of Aberdeen.

Gomoiu, M.-T. and G.I. Müller, (1962) Studies concerning the benthic association dominated by Barnea candida in the Black Sea. Revue de biologie, 7, 255-271.

Goodhart, C.B., (1939) Notes on the bionomics of the tube building Amphipod, Leptocheirus pilosus Zaddach. Journal of the Marine Biological Association of the U.K., 23, 311-325.

Goss-Custard, J.D., (1966) The feeding ecology of Redshank Tringa tutanus L. in winter, on the Ythan estuary, Aberdeenshire. Ph.D. thesis, University of Aberdeen.

Greve, L., (1967) On the tube building of some Tanaidacea. Sarsia, 29, 295-298.

Greze, I.I., (1968) Feeding habits and food requirements of some Amphipods in the Black Sea. Marine Biology, 1, 316-321.

Greze, I.I., (1970) Biology of the amphipod Ericthonius difformis M. Edw. in the Black Sea. In, Ecologo - Morfologicheskie Issledovaniya Donnykh Organizmov, Ed., V.A. Vodyanitskii, Kiev, pp 36-51.

Greze, I.I., (1971) A comparative study of feeding of some similar and closely related amphipod species in the Mediterranean and Black Seas. Ekspeditsionnye Issledovaniya v Sredizemnom more V Mae-Iyule 1970, Kiev, pp 52-63.

Greze, I.I., (1973) Feeding of Amphipoda in the Black Sea. Trofologiya Vodnykh Zhivotnykh Moscow, pp 183-205.

Gurjanova, E., (1951) The marine amphipods of USSR and adjacent waters. Amphipoda. Gammaridea. Academy of Sciences of the USSR., Opredel. Faun. SSSR 41, 1029pp.

Haldane, J.B.S., (1945) The use of chi-square as a test of homogeneity in a (nx2)-fold table when expectations are small. Biometrika, 33, 234-238.

Hamond, R., (1967) The Amphipoda of Norfolk. Cahiers de biologie marine, 8, 113-152.

Hardy, A.C., (1956) The open sea its natural history : Part 1, The world of Plankton. Collins, London, 335pp.

Harrison, R.J., (1940) On the biology of the Caprellidae. Growth and moulting of Pseudoprotella phasma Montagu. Journal of the Marine Biological Association of the U.K., 24, 483-493.

Hart, T.J., (1930) Preliminary notes on the bionomics of the amphipod Corophium volutator Pallas. Journal of the Marine Biological Association of the U.K., 16, 761-789.

Heller, S.P., (1968) Some aspects of the biology and development of Amphithoe lacertosa (Crustacea : Amphipoda). M.Sc. Thesis, University of Washington.

Hiscock, K. and R. Hoare, (1975) The ecology of sublittoral communities at Abereiddy Quarry, Pembrokeshire. Journal of the Marine Biological Association of the U.K., 55, 833-864.

Holmes, S.J., (1901) Observations of the Habits and Natural History of *Amphithoe longimana* Smith. Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 2, 165-193.

Hughes, R.G., (1975) The distribution of epizoites on the hydroid *Nemertesia antennina* (L.). Journal of the Marine Biological Association of the U.K., 55, 275-294.

Hynes, H.B.N., (1970) The ecology of running waters. Liverpool University Press, 555pp.

Ingle, R.W., (1966) An account of the burrowing behaviour of the amphipod *Corophium arenarium*. Annals and Magazine of Natural History, Series 13, 9, 309-317.

Ingle, R.W., (1969) The crustacean amphipod genus *Corophium* Latreille; a morphological and taxonomic study. Ph.D. Thesis, University of Reading.

Ingle, R.W., (1972) The proposed suppression of the name *Oniscus bicaudatus* Linnaeus, 1761, the earliest available name for *Corophium volutator* (Pallas, 1766); the selection of neotypes for *C.volutator* and for *C.bonnellii* H.Milne Edwards, 1830 (Amphipoda, Corophiidae). Crustaceana, Supplement 3, 326-328.

Issel, R., (1912) Richerche di etologia sull' Isopodo tubiculo : *Zenobiana prismatica* (Risso). Archives de Zoologie Experimentale, 51, 479-500.

Johannes, R.E., (1964) Uptake and release of phosphorus by a benthic marine amphipod. Limnology and Oceanography, 9, 235-242.

Jones, N.S., (1948) The ecology of the Amphipoda of the South of the Isle of Man. Journal of the Marine Biological Association of the U.K., 27, 400-439.

Jones, D.A., N. Peacock and O.F.M. Phillips, (1973) Studies on the migration of *Tritaeta gibbosa*, a subtidal benthic amphipod. Netherlands Journal of Sea Research, 7, 135-149.

Jones, D.J., (1973) Variation in the trophic structure and species composition of some invertebrate communities in polluted kelp forests in the North Sea. Marine Biology, 20, 351-365.

Just, J., (1970) Amphipoda from Jørgen Brønlund Fjord, North Greenland. Meddelelser om Grønland, 184, 1-39.

Kaestner, A., (1970) Invertebrate Zoology. Vol. 3. Crustacea. Wiley - Interscience, New York, 523pp.

Kanneworf, E and W. Nicolaisen, (1969) The stomach (foregut) of the amphipod Bathyporeia sarsi Watkin. Ophelia, 6, 211-229.

Kitching, J.A., T.T. Macan and H.C. Gilson, (1934) Studies in sublittoral ecology I. A submarine gulley in Wembury Bay, South Devon. Journal of the Marine Biological Association of the U.K., 19, 677-705.

Kitching, J.A., F.J. Ebling, J.C. Gamble, R. Hoare, A.A.Q.R. Mcleod and T.A. Norton, (1976) The ecology of Lough Ine XIX. Seasonal changes in the western trough. Journal of Animal Ecology, 45, 731-758.

König, D., (1966) Aus der entsthungszeit des naturschultz-gebietes 'Rantumbecken' auf Sylt. Faun.-Okol. Mitt., 3, 32.

Krapp-Schickel, G., (1960) Zur ökologie der amphipoden aus dem phytal der Nordadria. Zoologische Jahrbucher. Systomatik, Ökologie und Geographie der Tiere. 96, 265-448.

Krapp-Schickel, G., and F. Krapp, (1975) Quelques traits de l'écologie d'amphipodes et de pycnogonides provenant d'un ilot Nord-Adriatique. Vie et milieu, 25, 1-32.

Krishnan, L. and P.A. John (1974) Observations on the breeding biology of Melita zeylanica Stebbing, a brackish water amphipod. Hydrobiologia, 44, 413-430.

Kristensen, J.H., (1972) Carbohydrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates studied. Marine Biology, 14, 130-142.

Kühne, H. and G. Becker, (1964) Der Holz - Flohkrebs Chelura terebrans Philippi (Amphipoda, Cheluridae). Beihefte der Zeitschrift für angewandte Zoologie, No 1, 141pp.

Lakshmana Rao, M.V. and K. Shyamasundari, (1963) Tube-building habits of the fouling amphipod Corophium triaenonyx Stebbing at Visakhapatnam harbour. Journal of the Zoological Society of India, 15, 134-140.

Laverack, M.S. and M. Blackler, (1974) Fauna and Flora of St. Andrews Bay. Scottish Academic Press, Edinburgh, 310pp.

Ledoyer, M. (1962) Étude de la faune vagile des herbiers superficiels de Zostéracées et de quelques biotopes d'algues littorales. Recueil des travaux de la Station marine d'Endoume, Faculté des sciences de Marseille, 25, 119-235.

Ledoyer, M., (1964a) La faune vagile des herbiers de *Zostera marina* et de quelques biotopes d'algues infralittorales dans la zone intertidale en Manche et comparaison avec les milieux Méditérranéens identiques. Recueil des travaux de la Station marine d'Endoume, Faculté des sciences de Marseille, *34*, 227-240.

Ledoyer, M., (1946b) Les migrations nycthémérales de la faune vagile au sein des herbiers de *Zostera marina* de la zone intertidale en manche et comparaison avec les migrations en Méditerranée. Recueil des travaux de la Station marine d'Endoume, Faculté des sciences de Marseille, *34*, 241-247.

Ledoyer, M., (1968) Écologie de la faune vagile des biotopes Méditerranéens accessibles en scaphandre autonome (region de Marseille principalement). (IV) Synthèse de l'étude ecologique. Recueil des travaux de la Station marine d'Endoume, Faculté des Sciences de Marseille, *44*, 126-295.

Ledoyer, M., (1969) Aperçu sur la faune vagile des quelques biotopes de substrat due de Méditerranée orientale. Comparison avec les mêmes biotopes en Méditerranée occidentale. Tethys, *1*, 281-290.

Le Roux, M.L. (1933) Récherches sur la sexualité des gammariens. Croissance, reproduction, determinisme des characteurs sexuels secondaires. Bulletin biologique de la France et de la Belgique, Suppl. 16, 1-138.

Leung Tack Kit, D., (1972) Etude d'un milieu pollué : le vieux port de Marseille. Influence des conditions physico-chimiques sur la physionomie du peuplement de quai. Tethys, *3*, 767-826.

Lewis, J.R., (1964) The ecology of rocky shores. English Universities Press, London, 323pp.

L'Hardy, J.P., (1962) Observations sur le peuplement épiphyte des lames de *Laminaria saccharina* (Linné) Lamouroux en Baie de Morlaix (Finistère). Cahiers de biologie marine, *3*, 115-127.

Lie, U., (1961) On the growth and food of O-group coalfish, *Pollachius virens* (L.), in Norwegian waters. Sarsia, *3*, 1-36.

Lim, K.H. and W.D. Williams, (1971) Ecology of *Austrochiltonia subtenuis* (Sayce) (Amphipoda, Hyalellidae). Crustaceana, *20*, 19-24.

McCloskey, L.R., (1970) The dynamics of the community associated with a marine scleractian coral. Internationale Revue der gesamten Hydrobiologie u Hydrographie, *55*, 13-81.

MacDonald, R., (1945) The Crustacea Amphipoda of County Down. Annals and Magazine of Natural History, 11th Series, *12*, 528-535.

MacDonald, R., (1954) The Crustacea, Amphipoda of Belfast and Strangford Loughs. Annals and Magazine of Natural History, 12th Series, 4, 280-288.

McLusky, D.S., (1971) Some aspects of salinity on the mud-dwelling euryhaline amphipod Corophium volutator. Vie et milieu, Suppl. 22, 135-143.

Macquart-Moulin, C., (1968) Les amphipodes bentho-planctoniques du golfe Marseille. Analyse des captures faites au cours de pêches nocturnes régulières (année 1963-64) Recueil des travaux de la Station marine d'Endoume, Faculté des Sciences de Marseille, 43, 311-332.

Marine Biological Association (1957) Plymouth Marine Fauna. 3rd Edition, Plymouth, 453pp.

Marshall, S.M. and A.P. Orr, (1958) Some uses of antibiotics in physiological experiments in sea water. Journal of Marine Research, 17, 341-346.

Martin, A.L., (1966) Feeding and digestion in two intertidal gammarids : Marinogammarus obtusatus and M. pirloti. Journal of Zoology, 148,515-525.

Mathais, J.A., (1971) Energy flow and secondary production of the amphipods Hyallela azteca and Crangonyx richmondensis occidentalis in Marion Lake, British Columbia. Journal of the Fisheries Research Board of Canada, 28, 711-726.

Mather, K., (19~~66~~51) Statistical analyses in biology. Methuen, London, 267pp.

Mathews, L.H., (1923) Notes on the fauna of the Bristol Channel. Proceedings of the Bristol Naturalists' Society, 6, 46-48.

Meadows, P.S., (1964) Experiments on substrate selection by Corophium species : Films and bacteria on sand particles. Journal of Experimental Biology, 41, 499-511.

Meadows, P.S., (1967) Discrimination, previous experience and substrate selection by the amphipod Corophium. Journal of Experimental Biology, 47, 553-559.

Meadows, P.S., and A. Reid, (1966) The behaviour of Corophium volutator. Journal of Zoology, 150, 387-400.

Mills, E.L. (1963) A new species of liljeborgiid amphipod with notes on its biology. Crustaceana, 4, 158-162.

Mills, E.L. (1967) The biology of an ampeliscid amphipod crustacean sibling species pair. Journal of the Fisheries Research Board of Canada, 24, 305-355.

Miloslavaskaya, N.M., (1939) On the ecology of Black Sea Gammaroidea in connection with the origin of their fauna. Trudy Karadahs' koyi Biolohichnoyi Stantsiyi, 5, 152-174.

Mohan Joseph, M., (1972) Tidal rhythm in the feeding activity of the intertidal amphipod Hyale hawaiensis (Dana). Proceedings of the Indian Academy of Sciences (B), 38, 456-461.

Moore, P.G., (1971) A study of pollution in certain marine ecosystems. Ph.D. thesis, University of Leeds.

Moore, P.G., (1972) Particulate matter in the sublittoral zone of an exposed coast and its ecological significance with special reference to the fauna inhabiting kelp holdfasts. Journal of Experimental Marine Biology and Ecology, 10, 59-80.

Moore, P.G., (1973a) The kelp fauna of northeast Britain. I. Introduction and physical environment. Journal of Experimental Marine Biology and Ecology, 13, 97-125.

Moore, P.G., (1973b) The kelp fauna of northeast Britain. II. Multivariate classification : turbidity as an ecological factor. Journal of Experimental Marine Biology and Ecology, 13, 127-163.

Moore, P.G., (1973c) The larger Crustacea associated with holdfasts of kelp (Laminaria hyperborea) in North East Britain. Cahiers de biologie marine, 14, 493-518.

Moore, P.G., (1974) The kelp fauna of northeast Britain. III. Qualitative and quantitative ordinations, and the utility of a multivariate approach. Journal of Experimental Marine Biology and Ecology, 16, 257-300.

Moore, P.G., (in press) Inorganic particulate suspensions in the sea and their effects on marine animals. Oceanography and Marine Biology Annual Review.

Morgan, E., (1965) The activity rhythm of the amphipod Corophium volutator (Pallas) and its possible relationship to changes in hydrostatic pressure associated with the tides. Journal of Animal Ecology, 34, 731-746.

Movaghar, C.-A., (1964) Verbreitung und ökologie der amphipoden im Elbe-Aestuar. Archiv für Hydrobiologie, Supplement 29, 97-179.

Muus, B.J., (1967) The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Meddelelser fra Danmarks Fiskeu-og Havundersøgelser, 5, 1-316.

Nagata, K., (1966) Studies on the marine gammaridean Amphipoda of the Seto Island sea. IV. Publications of the Seto Marine Biological Laboratory, 8, 327-348.

Nagle, J.S., (1968) Distribution of the epibiota of macroepibenthic plants. Contributions in Marine Science, University of Texas, 13, 105-144.

Nayar, K.N., (1956) The life history of a brackish water amphipod Grandidierella bonnieri Stebbing. Proceedings of the Indian Academy of Sciences (B), 43, 178-189.

Noble, W., (1962) Studies on the life cycle and habitat requirements of the amphipod Corophium volutator Pallas. B.Sc. Thesis, University of Aberdeen.

Nuttal, P.M. and G.H. Bielby, (1973) The effect of china-clay wastes on stream invertebrates. Environmental Pollution, 5, 77-86.

Odum, W.E. and E.J. Heald, (1972) Trophic analyses of an estuarine mangrove community. Bulletin of Marine Science, 22, 671-738.

Parker, R.H., (1975) The study of benthic communities, a model and a review. Elsevier, Amsterdam, 260pp.

Peacock, N.A., (1972) Some aspects of the ecology and behaviour of the amphipod Tritaeta gibbosa (Bate). M.Sc. thesis, University of Wales.

Pearse, A.G.E., (1968) Histochemistry theoretical and applied. Vol.I. 3rd Edition, J. and A. Churchill, London, 759pp.

Pickard, G.L., (1975) Descriptive physical oceanography. 2nd Edition, Pergamon, Oxford, 214pp.

Probert, P.K., (1973) The bottom fauna of china clay waste deposits in Mevagissey Bay. Ph.D. thesis, University of London.

Probert, P.K., (1975) The bottom fauna of china clay waste deposits in Mevagissey Bay. Journal of the Marine Biological Association of the U.K., 55, 19-44.

Rasmussen, E., (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia, 11, 1-507.

Reid, D.M., (1951) Report on the Amphipoda (Gammaridea and Caprellidea) of the coast of tropical west Africa. Atlantide Report, 2, 189-291.

Reineck, H.-E., (1958) Wühlbau-gefüge in abhängigkeit von sediment-umlagerungen. Senckenbergiana lethaea, 39, 1-23.

Remane, A., (1971) The ecology of brackish water. In, Remane, A. and C. Schlieper, The biology of brackish water. J. Wiley, New York, pp.1-210.

Rheinheimer, G., (1971) . Turbidity. .1. Bacteria, fungi and blue-green algae. In, Marine Ecology, ed., O.Kinne, J.Wiley,London,1, 1167-1175.

Rhoads, D.C., (1974) Organism-sediment relations on the muddy sea floor. Oceanography and Marine Biology Annual Review, 12, 263-300.

Rhoads, D.C., and D.K. Young, (1970) The influence of deposit feeding organisms on sediment stability and community trophic structure. Journal of Marine Research, 28, 150-178.

Robertson, D., (1888) A contribution towards a catalogue of the Amphipoda and Isopoda of the Firth of Clyde. Transactions of the Natural History Society of Glasgow, 2, 9-99.

Rossi, L, A. Manassero and G.V. Tadini, (1975) Control of parental 'marsupia' in Asellus aquaticus (L.) (Crustacea, Isopoda). Atti dell' Accademia nazionale dei Lincei. Rendiconti, 58, 443-440.

Round, F.E., J.F. Sloane, F.J. Ebling and J.A. Kitching, (1961) The ecology of Lough Ine. X. The hydroid Sertularia operculata (L.) and associated flora and fauna : Effects of transference to sheltered water. Journal of Ecology, 49, 617-629.

Sars, G.O., (1890) An account of the Crustacea of Norway. Vol I. Amphipoda. Alb. Cammermeyer, Copenhagen, 711pp.

Sars, G.O., (1899) An account of the Crustacea of Norway. Vol. II. Isopoda. Bergen Museum, 270pp.

Scarratt, D.J., (1961) The Fauna of Laminaria holdfasts. Ph.D. thesis, University of Wales.

Schellenberg, A., (1942) Amphipoda. In Die Tierwelt Deutschlands und der angrenzenden meeresteile; krebstiere oder Crustacea IV, 40, 1-252.

Schiecke, U., (1973) Ein beitrag zur kenntnis der systematikk, biologie und aütokologie mariner Peracarida (Amphipoda, Isopoda, Tanaidacea) des Golfes von Neapel. Dissertation, University of Kiel, 409pp.

Schodduyn, M., (1926) Observations faits dans la baie d'Ambleteuse (Pas de Calais). Bulletin de l'Institut océanographique, 482, 1-64.

Schultz, G.A., (1969) How to know the marine isopod crustaceans. W.C. Brown, Dubuque, Iowa, 359pp.

Scott, A., (1922) On the food of young Plaice Pleuronectes platessa. Journal of the Marine Biological Association of the U.K., 12, 678-687.

Segerstrale, S.G., (1959) Synopsis of data on the crustaceans Gammarus locusta, G. oceanicus, Pontoporeia affinis and Corophium volutator. Commentationes biologicae, 20, 1-23.

Sexton, E.W. and A. Mathews, (1913) Notes on the life history of Gammarus chevreuxi in laboratory conditions. Journal of the Marine Biological Association of the U.K., 9, 546-556.

Sexton, E.W. and G.M. Spooner, (1940) An account of Marinogammarus (Schellenberg) gen. nov. (Amphipoda) with a description of a new species, M. pirloti. Journal of the Marine Biological Association of the U.K., 24, 633-682.

Sexton, E.W. and D.M. Reid, (1951) The life history of the multiform species Jassa falcata (Montagu) (Crustacea, Amphipoda) with a review of the bibliography of the species. Journal of the Linnean Society, 42, 29-91.

Sheader, M., (1973) North Sea hyperiid amphipods. Ph.D. thesis, University of Newcastle.

Sheader, M., and F-S. Chia, (1970) Development, fecundity and brooding behaviour of the amphipod Marinogammarus obtusatus. Journal of the Marine Biological Association of the U.K., 50, 1079-1099.

Shoemaker, C.R., (1947) Further notes on the amphipod genus Corophium from the east coast of America. Journal of the Washington Academy of Sciences, 37, 47-63.

Shyamasundari, K., (1973) Studies on the tube-building amphipod Corophium triaenonyx Stebbing from Visakhapatnam harbour : effect of temperature and salinity. Biological Bulletin. Marine Biological Laboratories, Woods Hole, Mass., 144, 503-510.

Shyamasundari, K., and K. Hanumantha Rao, (1974) Effect of temperature on embryonic and post-embryonic stages of Corophium triaenonyx Stebbing (Crustacea, Amphipoda). Broteria, 43, 187-194.

Sikora, W.B., R.W. Heard and M.D. Dahlberg, (1972) The occurrence and food habits of two species of Hake, Urophycis regius and U. floridanus in Georgia estuaries. Transactions of the American Fisheries Society, 101, 513-525.

Skogsberg, T. and G.H. Vansell, (1928) Structure and behaviour of the amphipod, Polycheira osborni. Proceeding of the California Academy of Sciences, 17, 267-295.

Skutch, A.F., (1926) On the habits and ecology of the tube building amphipod, Amphithoe rubricata Montagu. Ecology, 7, 481-502.

Sloane, J.F., R. Bassindale, E. Davenport, F.J. Ebbing and J.A. Kitching, (1961) The ecology of Lough Ine. IX. The fauna and flora associated with the undergrowth-forming algae in the rapids area. Journal of Ecology, 49, 353-368.

Smallwood, M.E., (1905) The salt-marsh amphipod Orchestia pallustris. Cold Spring Harbour Monographs, No.3.

Smith, S.I., (1882) On the amphipodous genera, Cerapus, Unciola and Lepidactylis described by Thomas Say. Transactions of the Connecticut Academy of Arts and Sciences, 4, 268-284.

Snedecor, G.W. and W.G. Cochran, (1967) Statistical methods. Iowa State University Press, 593pp.

Sokal, R.R. and F.J. Rohlf, (1969) Biometry. W.H. Freeman, San Francisco 776pp.

Stebbing, T.R.R., (1906) The amphipodes. 1. Gammaridea. Das Tierreich, 21, 806pp.

Steele, J.H., (1976) Comparative studies of beaches. Philosophical Transactions of the Royal Society (B), 274, 401-415.

Stephensen, K., (1929) Marine Crustacea. Amphipoda. Zoology of the Faroes, No. 13, 1-40.

Stephensen, K., (1940a) Marine Amphipoda. Zoology of Iceland, 3, 1-111.

Stephensen, K., (1940b)=1929 Amphipoda. In, Die tierwelt der Nord-und Ostsee, Ed. G. Grimpe and E. Wa ler, Akademische Verlagsges, Leipzig, pp1-183.

Stephensen, K., (1942) The Amphipoda of North Norway and Spitsbergen with adjacent waters. Tromsø museums skrifter, 3, 363-526.

Stephensen, K, (1944) The zoology of East Greenland. Amphipoda. Meddelelser om Grønland, 121, 1-165.

Stock, J.H. and A.E.M.H. Bloklander, (1952) Notes on adventive Amphipoda (Crustacea, Malacostraca) on the Dutch coast. Beaufortia, 10, 1-9.

Tait, R.V., (1968) Elements of marine ecology. Butterworths, London, 272pp.

Tenore, K.R., M.G. Browne and E.J. Chesney, (1974) Polyspecies aquaculture systems : the detrital trophic level. Journal of Marine Research, 32, 425-432.

Thamdrup, H.M., (1935) Beitrage zur oekologie der wattenfauna auf experimenteller grundlage. Meddelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser, Ser. Fiskeri, 10, 1-125.

Toulmond, A. and J.-P. Truchot, (1964) Inventaire de la faune marine de Roscoff. Amphipodes, Cumacées. Travaux de la Station biologique de Roscoff, 3, 289-306.

Trewin, N.H. and W.Welsh, (1976) Formation and composition of a graded estuarine shell bed. Palaeogeography, Palaeoclimatology, Palaeoecology, 19, 219-230.

Truchot, J.-P., (1963) Etude faunistique et écologique des amphipodes des faciès rocheux intertidaux de Roscoff. Cahiers de biologie marine, 4, 121-176.

Turquier, Y, (1964) Une nouvelle station du Corophium insidiosum Crawford (Crustacea, Amphipoda) avec une remarque sur les espèces Francaises du genre Corophium. Bulletin de la Société linnéenne de Normandie, 10th Série, 5, 133-140.

Turquier, Y, (1965) A propos des Corophium (Crustacea : Amphipoda) des cotes Francaises de la Manche. Bulletin de la Société linnéenne de Normandie, 10th Série, 6, 133-139.

Ussing, H. and K. Stephensen, (1924) Corophium bonelli (M.-Edw.?) G.O. Sars, ny for Danmark, med noter om andre Corophium - arter. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn, 78, 69-79.

Vaughan, A.K., (1938) Studies on the biology of certain species of the amphipod genera Corophium and Bathyporeia. M.Sc. thesis University of Wales.

Vlasblom, A.G., (1969) A study of a population of Marinogammarus marinus (Leach) in the Oosterschelde. Netherlands Journal of Sea Research, 4, 317-338.

Watkin, E.E., (1941a) The yearly life cycle of the amphipod Corophium volutator. Journal of Animal Ecology, 10, 77-93.

Watkin, E.E., (1941b) The male of the amphipod Haustorius arenarius Slabber. Journal of the Marine Biological Association of the U.K., 25, 303-305.

Weygoldt, D., (1958) Die embryonalentwicklung des amphipoden Gammarus pulex pulex (L.) Zoologische Jahrbücher, Anatomie und Ontogenie de Tiere, 77, 51-110.

Wiebe, W.J. and L.R. Pomeroy, (1972) Microorganisms and their association with aggregates and detritus in the sea : a microscope study. Memorie dell' Istituto italiano di idrobiologia Dott. Marco de Marchi, Suppl. 29, 325-352.

Williams, G., (1954) Fauna of Strangford Lough and neighbouring coasts. Proceedings of the Royal Irish Academy, 56, B, 77-82.

Zaitsev, Y.P., (1970) Marine neustonology. Israel Program for Scientific Translations, Jerusalem, 1971, 207pp.

Zenkevitch, L., (1963) The biology of the seas of the U.S.S.R. George Allen and Unwin, London, 955pp.