STUDIES OF BURROWS IN RECENT SUBLITTORAL FINE SEDIMENTS OFF THE WEST COAST OF SCOTLAND

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The feeling of inadequacy, once it emerges from its burrow, is hard to kill or to drive back underground. It worms its way into your consciousness in the middle of the night and obstinately refuses to listen to reason.

Mike Brearley

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Summary

The burrows of the smaller macrofauna, principally polychaetes, bivalves and echinoderms are described from aquarium studies and from X-ray radiographs of boxcore subsamples obtained with a Reineck boxcorer from both sealochs and open marine sites encompassing a range of depths from 25-216m and sediments from sandy to fine muds. A model relating burrow types to depth is presented. Shallow sea loch sites are characterised by the deep U-burrows of the bivalve Thracia, deep sea lochs by a paucity of burrows due to the low oxygen levels found in the overlying waters. Shallow marine sites display a diverse suite of polychaete burrows and tubes and the burrows of the ophiuroid Amphiura . Two deep marine areas (>100m) have been sampled, each characterised by capitellid polychaetes: in the Firth of Clyde the wavy burrows of Dasybranchus are found whereas in the Sound of Jura the spiral burrows of Notomastus are abundant.

Trophic group amensalism does not occur in these muds; the suspension feeding bivalves Thracia, Mya and Arctica are found as there is no tidal resuspension of the sediment.

From boxcores obtained in the vicinity of the Garroch Head Sludge Dumping Ground, Firth of Clyde and near a pulp-paper mill situated between Lochs Linnhe and Eil, a model relating burrow types to organic enrichment of the sediment is presented. In the transitory zone there is an increased number of burrows compared to the normal situation. In the polluted zone the normal fauna is replaced by opportunistic polychaetes, chiefly Capitella capitata and the upper layers of the sediment are riddled with their burrows.

The method developed of serially X-raying boxcores allows quantitative studies of the density and depth distribution of burrows. The total length of burrows in a boxcore shows a peak of around 250cm in shallow sea loch and deep marine sites. The reduced length of burrows in shallow marine sites may be due to the presence of the burrowing echinoid Brissopsis which does not create a distinctive biogenic trace in these fine grained sediments. On average, burrows occupy 0·1% by volume of the top 5cm of the sediment but represent an increase in surface area of 10%.

Studies of the spatial distribution of burrow entrances, an important diversity regulating mechanism, reveal patches of various dimensions at some sites especially in the Arran Deep.

This ichnocoenose is compared to others from Recent sublittoral, fine sediments inhabited by brittle star communities in the Atlantic, Mediterranean and North Sea and to the ichnocoenoses of sheltered, intertidal sandflats in the U.S.A. The results of this study are used to suggest the possible producers of trace fossils commonly found in fine grained sediments: Chondrites and Planolites are ascribed to polychaetes, Scolicia to gastropods and Thalassinoides to crustaceans.

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Chapter 1 : Introduction

1.1.1 The biological modification of sediments

Animals affect the physical and chemical properties of the sediment by burrowing, ingesting and defecating it and by binding it into tubes; this has been termed sediment processing by Myers (1977a). Depositional sedimentary structures are destroyed (Moore & Scruton 1957) or prevented from forming (Featherstone & Risk 1977), bottom topography altered (Heezen and Hollister 1971, McCave 1976) and biogenic structures formed (Dörjes & Hertweck 1975).

The shear strength of the sediment may be either decreased by burrowing and irrigating (Rowe 1974), making it easily resuspendible (Rhoads 1970, Eagle 1975), or increased by tube building, pelleting or algal binding (Rhoads 1974). The particle size distribution may be affected by selective feeding (Rhoads 1967) or incorporation of material into tubes (Fager 1964) or by biodeposition (Hagmeier 1930). Clay minerals are altered by passage through the animal's gut (Anderson, Jonas & Odum 1958, Pryor 1975).

An infauna produces aerobic sediments moving the redox potential discontinuity from a few millimetres to several centimetres below the sediment surface (Rhoads 1974). The pumping of water through a burrow alters the chemistry of the surrounding sediment (Aller & Yingst 1978) and promotes the exchange of nutrients with the overlying water column (Davies 1975, Aller 1978).

Measurements of sediment turnover made on many species have been summarised by Cadée (1976, table II): on average the top 2 cm of sediment are reworked each year. The depth distribution of radioactive isotopes in the sediment also reveals intense mixing in the top 2-4 cm (Aller & Cochran 1976, Benninger et al. 1979) and has provided the basis for mathematical models of bioturbation (Guinasso & Schink 1975, Goreau 1977).

This thesis describes the types of burrows produced in a Recent sublittoral fine sediment and quantifies their distribution with depth. Estimates of the total length of burrows in a boxcore are made and the spatial distribution of burrow entrances is examined. Environments sampled range from sea-lochs to open marine sites and include glacially overdeepened hollows. Sea-lochs represent a low energy environment with a high organic input mainly from terrestial detritus (Ansell 1974), and so may prove useful in the interpretation of ancient enclosed sedimentary basins.

From a measure of the total length of burrows in the sediment the increase in the effective area of the sediment-water interface can be calculated and the effect on nutrient exchange quantified.

The spatial distribution of burrow entrances provides a measure of the area occupied by each species, a factor which helps to determine the diversity of the benthic community occupying a particular environment.

1.1.2 History of the uniformitarian approach in the study of trace fossils

The traces produced by animals in Recent environments were first used by Hancock (1858) and Nathorst (1873) as supporting evidence for the animal origin of structures previously classified as fucoids (fossil algae). The producers of trace fossils are rarely preserved.

Following this approach Richter (1927) realised that a study of the production of modern traces could yield explanations as to the function of various trace fossils. The establishment of the Senckenberg marine laboratory at Wilhelmshaven in 1925 enabled him and subsequent German workers to investigate the biogenic structures found on the extensive intertidal mud flats (Schäfer 1972). Such observations have been used to make hypotheses about the mode of life of the producers of trace fossils (Bromley & Asgaard 1975) and the palaeoenvironment (Weimar & Hoyt 1964). More recently the ichnocoenoses of sheltered intertidal sand flats have been described from both the Atlantic coast (Myers 1977a, b, Risk & Tunnicliffe 1978) and Pacific coast (Ronan 1977) of North America.

Sublittoral environments are less accessible and investigation of their biogenic structures in order to evaluate the bathymetric zonation of trace fossils proposed by Seilacher (1967) has had to await technological advances such as the invention of the boxcorer (Reineck 1963), bottom cameras (Rhoads & Cande 1971, Heezen & Hollister 1971) and SCUBA and submersible diving.

Resin casting of the large burrows of fish and crustaceans has been carried out by SCUBA divers on the Bahama Banks (Shinn 1968), Aldabra Atoll (Farrow 1971) and in the muds off the west coast of Scotland (Chapman, Johnstone & Rice 1975).

A Reineck boxcorer recovers an intact block of sediment of surface area 20 x 30 cm and up to 45 cm deep and so cannot completely sample the large burrows of fish and crustaceans. It is suitable for retaining the burrows of the smaller macrofauna such as polychaetes, bivalves and echinoderms. Ichnofacies have been described from boxcore transects from the supralittoral to sublittoral environments of the north German coast (Reineck et al. 1967), southern Italy (Hertweck 1973) and Georgia coastal region, U.S.A. (Hertweck 1972) and from the Georgia estuaries (Dörjes & Howard 1975). This study extends this work to the sublittoral muds off the west coast of Scotland.

Animal-sediment relations have also been investigated in the shallow sublittoral muds off Massachusetts, U.S.A. by SCUBA divers and bottom cameras (Rhoads 1970, Rhoads & Young 1971) and their observations are compared to those of this survey.

1.2 Method

1.2.1 Cruises (Table 1.1, fig 1.1)

From reconnaissance cruises in the Firth of Clyde (December 1977) and Argyll sea-lochs (May 1978) nine principal sites were chosen for more detailed study. These sites were selected to represent the full range of depths and environmental conditions (enclosed sea-loch to open sea). They comprise three sea-loch sites, in Lochs Creran, Etive and Riddon, three shallow marine sites (less than 70 m) in Cemas Nathais and Ardmucknish Bays and the Sound of Mull, and three deep sites (between 100 and 250 m deep) in Kilbrannan Sound, the Arran Deep and the Sound of Jura.

The sites in Lochs Etive and Creran were chosen to coincide with those of Gage (1972) so that the abundant information on the benthic fauna of these sites could be employed to interpret the producers of burrows found in the boxcores.

Loch Riddon and Cemas Nathais Bay are being used for studies on the larger burrowing crustacea and fish by R. Nash and Dr. R. J. A. Atkinson of the Millport Marine Station and so afforded an opportunity for joint study of the complete burrowing fauna.

An offer by Dr. Gage of a place on the R.R.S. Challenger cruise 79/11 provided an opportunity to obtain samples from bathyal sites on the Hebrides Terrace and in the Whittard Canyon in the south west Approaches. Unsuccessful attempts were made to sample abyssal sites in the Rockall Trough and Porcupine Sea Bight but the corer either failed to trigger or triggered prematurely on each occasion.

Table 1.1

Table of cruises

DATE	SHIP	AREA	NO. OF BOXCORES	NO. OF SITES
Dec. 1977	R.R.S.John Murray	Firth of Clyde	17	17
May 1978	R.V.Calanus	Argyll Sea Lochs L. Etive, L. Creran Firth of Lorne	12	4
July 1978	R.R.S.Shackleton	Sound of Jura Sound of Mull	8	2
Oct. 1978	R.V.Calanus	North Firth of Clyde	15 (8 X-rayed)	4
June 1979	R.V.Calanus	Loch Creran	5	1
Aug. 1979	R.R.S.Challenger	Hebrides Terrace Whittard Canyon	2 1	2
Sept. 1979	R.V.Calanus	Firth of Lorne	8	1
Oct. 1979	R.V. Calanus	Firth of Clyde	4	4
Nov. 1979	R.V.Calanus	Loch Eil/Linnhe	11 (9 X-rayed)	6
Jan. 1980	R.V.Calanus	Loch Creran	3	1

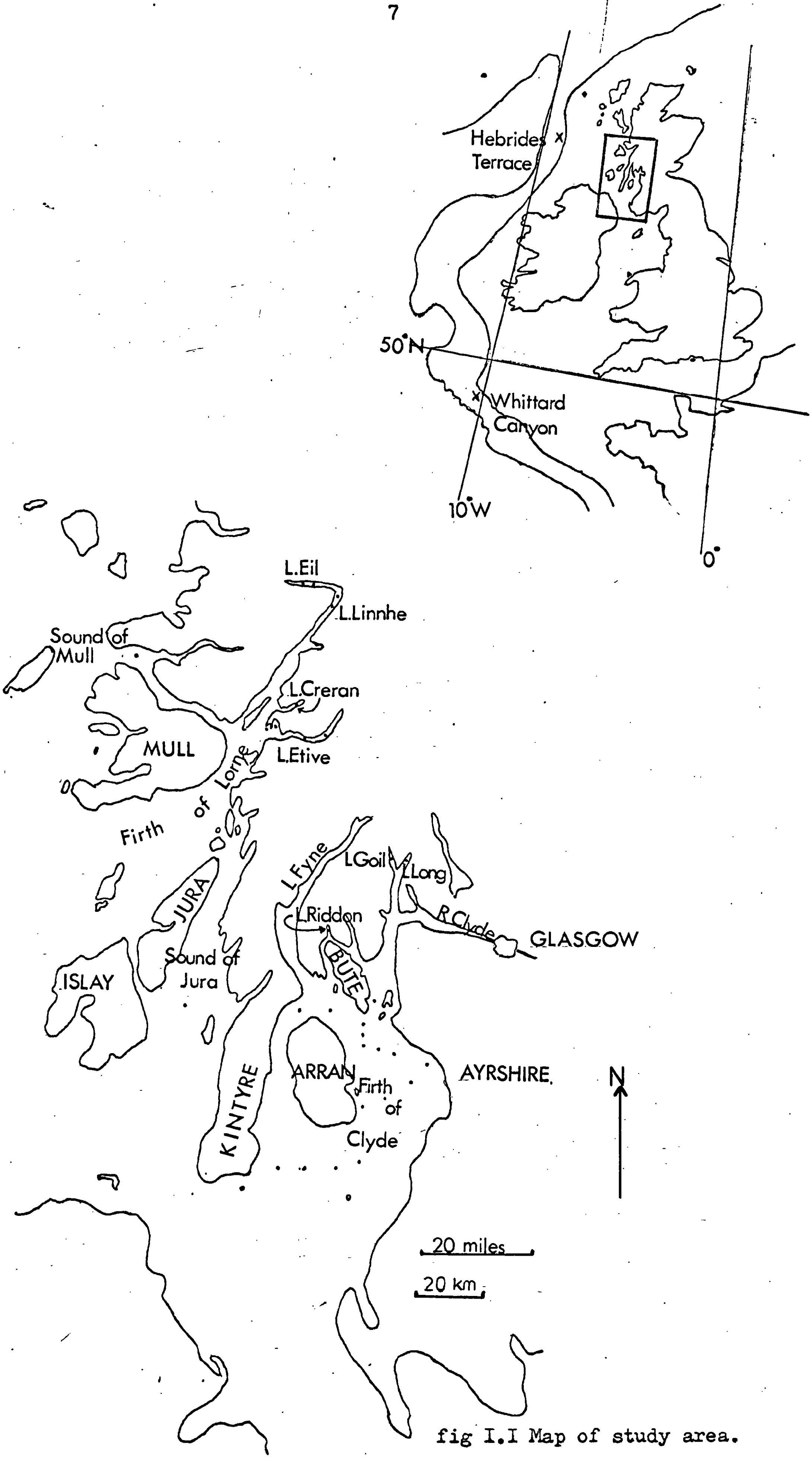


fig I.I Map of study area.

Studies of burrowing at sites of high organic loading around a pulp-paper mill in Loch Linnhe and Loch Eil and around the Garroch Head Sludge Dumping Ground in the Firth of Clyde have been carried out in conjunction with Dr. T. Pearson and the Organic Degradation Group of the Dunstaffnage Marine Laboratory.

1.2.2 Processing the sample

Intact sediment samples of surface area 20 x 30 cm and up to 45 cm deep were obtained with a Reineck Box Corer (fig 1.2) (Reineck 1963, Bouma 1969, p. 332). The sampler is described in Appendix I.

Hertweck and Reineck (1966) examined boxcores by careful excavation, casting with polyester resin burrows greater than 1 cm in diameter and X-raying a 1 cm-thick subsample. In this study the complete boxcore was divided into serial sections and X-rayed. Quantitative studies of the depth distribution of burrows, estimates of their total length and analysis of the spatial pattern of burrow entrances can then be made.

The sample, contained in a stainless steel box with a baseplate held in place by two springs, was transported to the laboratory (fig 1.3). Here it was allowed to drain for several days so that the sediment solidified and did not flow when the boxcore was subsampled. An alternative method to solidify the sediment would be to freeze it. Facilities for the freezing of a large number of boxcores were not available for this study. While the boxcore was draining any animals which emerged were removed, recorded and preserved in formalin. With the exception of the echinoderms animals came to the surface along their burrows and no "death-thro" bioturbation occurred. The echinoid Brissopsis may have destroyed the burrows of other animals as it emerged and the burrows of the ophiuroid Amphiura were not recorded on radiographs from sites where Amphiura was found, probably because they collapsed as the animals came to the surface. Surface trails in boxcores were ignored as they were created by the writhings of dying animals; the bow wave of the sampler erased any original surface markings.

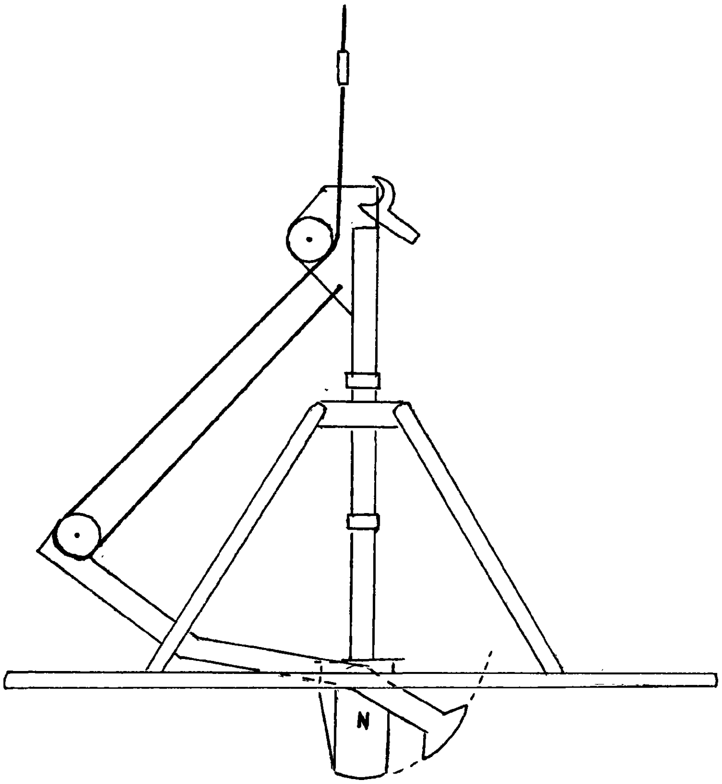


fig I.2 The Reineck Box Corer (×0·04)

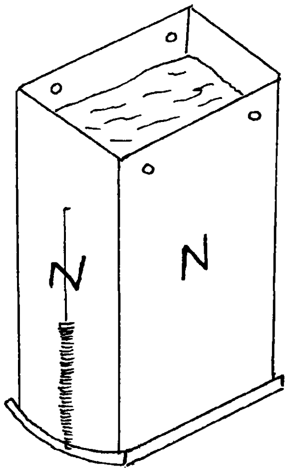


fig I.3 The boxcore ready for transport to the laboratory (×0·1)

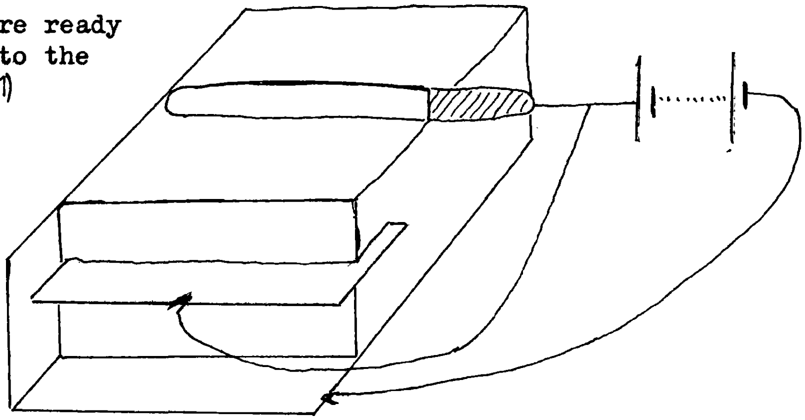


fig I.4 Subsampling an opened boxcore using the electrophoretic plate and knife in conjunction.

1.2.2.1 Examination of the boxcore

The box was laid on its side and the springs removed; the base plate was then slid off. The box was unscrewed, separating into two L-shaped pieces. The sediment was then divided into subsamples for X-raying. Subsample size is governed by the size of X-ray film available. Kodak Industrex X-ray film in three sizes (10 x 24 cm, 13 x 18 cm and 18 x 24 cm) has been used; the larger the radiograph the more of a burrow system is revealed in each picture. The thickness of the subsample is governed by the ability of X-rays to penetrate the sediment.

In initial surveys boxcores were divided into 10 x 24 x 4 cm or 13 x 13 x 4 cm subsamples oriented either vertically or horizontally in the sediment to reveal the full three dimensional nature of the burrows. In later work horizontal sectioning was abandoned as burrow configurations could be ascertained from vertical sections alone; the boxcores were divided into six or seven, 18 x 24 x 3 cm vertical slices. It was found possible to X-ray thicker subsamples using longer exposures so the number of subsamples was reduced to four, each 5 cm thick. This greatly increased the speed at which boxcores could be processed and reduced the amount of X-ray film required.

The subsample was removed using a modified form of the electrophoretic knife (fig 1.4) (Bouma 1969, p. 375). As the cut through the sediment tended to close up behind the narrow knife blade, a metal plate of greater surface area than the intended subsample was used. One terminal of a 12V car battery or 12V D.C. transformer was connected to the metal plate, the other to the segment of the stainless steel box on which the sediment was resting. Gas bubbles, formed on the metal plate by electrolysis, eased its passage through the sediment.

No sediment stuck to the metal plate but smearing was sufficient, however, to prevent any burrows less than 1 cm in diameter being exposed on the cut surface.

Subsamples were contained in open perspex boxes of base area 20 x 10 cm and depth 4 cm which were pushed into the sediment and then cut out using the charged metal plate. Sidewalls to subsample containers were found to be unnecessary and the open perspex boxes were replaced by perspex sheets. An electrophoretic knife attached to the same terminal of the battery as the metal plate, was used in conjunction with the metal plate to cut the subsample out. The subsample, resting on the metal plate was removed and a perspex sheet placed on top of it. The 'sandwich' thus formed was flipped over and the metal plate prised away leaving the subsample resting on the perspex sheet ready for X-raying.

1.2.2.2.1 X-ray radiography

The X-ray machine used in this study was a former hospital machine, a WATSON 90/30 Trolley Set Type C (Power Mobilix-Austerity Model) housed in the basement of the Department of Natural Philosophy, University of Glasgow. It developed a potential 90kV and a tube current of 30-40mA. The X-ray beam was directed downwards from the tube which was situated 1 metre above the floor. The sample was placed on the floor with the film contained in a lightproof plastic envelope underneath it.

2 cm thick mud samples require an exposure of 10 seconds
4 cm thick mud samples require an exposure of 15-20 seconds
5 cm thick mud samples require an exposure of 30-40 seconds.

Exposure also depends on the grain size of the sediment and its water content.

Stereopair radiographs can be taken by slightly tipping the sample so that there is an angle of 5° between the sample and the film in the second exposure.

It was found that the additional information on the three dimensional nature of the burrows available from stereopairs was insufficient to justify doubling the number of radiographs required.

1.2.2.2.2 Development

X-ray film was developed in standard photographic developer requiring five minutes at $20^{\circ}C$. It must be turned during development as the film is coated on both sides. Fixing was also done in standard photographic fix for three minutes after which the radiograph was washed and dried.

1.2.2.3 Other techniques used on boxcores

1.2.2.3.1 Resin casting (Shinn 1968, Farrow 1975, p. 547)

Polyester resin was poured onto the surface of a boxcore and left to harden. The box was unscrewed and the mud gently hosed away.

The resin had penetrated the shallow burrows of the ophiuroid *Amphiura filiformis* but had failed to penetrate the deeper and narrower polychaete burrows.

1.2.2.3.2 Resin peels

The technique of Bull (1977) was tried but the polyurethane varnish failed to penetrate the dried sediment. It seems that this technique is unsuitable for marine silts and clays as salt renders the dried sediment impervious.

1.2.2.3.3 Transmitted infra-red radiation

The technique of Rhoads and Stanley (1966) was followed but 5 mm thick mud sections failed to show any structures when photographed using Kodak infra-red film.

1.2.2.3.4 Staining

The technique of Pantin (1960) was attempted but both methyl blue and ink failed to penetrate fine sediment since it dried to an impervious block. The stains were found to penetrate dried sandy muds resulting from an aquarium experiment: no recognizable biogenic structures were revealed.

1.2.3 Faunal samples (Appendix 3)

In co-operation with R. Nash (Marine Station, Millport), Van Veen grab samples (Holme & McIntyre 1971, p. 98) were taken in Irvine Bay and Loch Riddon and sieved through a 2 mm sieve. The fauna, both live and dead, was extracted and preserved or used in aquarium experiments.

1.2.4 Aquarium studies

1.2.4.1 Tanks of unsieved mud

Samples of mud obtained either with a Naturalist dredge (Holme & McIntyre 1971, p. 86) or a Van Veen Grab were tipped into tanks and allowed to settle. The tanks were placed under the flowing seawater aquarium system at Millport Marine Station. Observations were made of animal activities visible at the mud surface. After several weeks the tanks were drained and subsampled for study by X-ray radiography in the same manner as boxcores.

Tanks of unsieved mud contain an enriched fauna as the samplers used scrape off the more densely populated top few centimetres of the sediment. By leaving the tanks for several weeks all escape traces produced by animals during the settling up of the tanks were destroyed by further burrowing.

1.2.4.2 Narrow Aquaria

Perspex aquaria, 20 cm long, 15 cm deep and 4 cm thick were constructed. These were filled with sieved mud containing no macrofauna and allowed to settle overnight. One or two animals of the same species were then introduced and the mud-filled aquaria placed under the flowing seawater system either at Millport Marine

Station or in the Department of Zoology, University of Glasgow.

The aquaria were X-rayed but radiographs failed to record any details of the burrow systems produced in the sediment by the animals. It is assumed that the density difference between a water-filled burrow and moist sediment is insufficient to be recorded on X-ray film. Drawings and photographs were made to record the burrow systems visible through the perspex walls.

An animal introduced to a narrow aquarium will explore the full extent of its confinement and may produce deep burrows which it would not normally construct. It may also produce a greater density of burrows as it is forced to reburrow the same sediment in search of food.

In order to study the disruption of sediment by burrowing animals (bioturbation) mud filled aquaria containing laminae of lead filings were set up as described by Ronan (1977). However all animals placed in these aquaria died. This may have been caused by interruptions in the flow of seawater which meant that insufficient dissolved oxygen was available in the water to sustain the benthos.

1.2.5 Particle Size Analysis of Sediments (Table 1.2)

Particle size analysis of sediments was obtained from the I.G.S. for sites in the Firth of Clyde (Deegan pers. comm. 1977), Gage (1972) for sites in Lochs Etive and Creran and Pearson (1970) for sites in Lochs Linnhe and Eil. Sediment from boxcores taken in the Sounds of Jura and Mull, Cemas Nathais and Ardmucknish Bays, the Hebrides Terrace and Whittard Canyon were analyzed by wet sieving and pipette methods as described by Holme and McIntyre (1971, p. 32).

Table 1.2 Particle size

Particle size	Ø values	Particle diameter
Sand	less than 4 Ø	greater than 0.0625 mm diameter
Silt	4 - 8 Ø	0.0625 mm - 0.0039 mm diameter
Clay	greater than 8 Ø	less than 0.0039 mm diameter

1.3 Area Description

1.3.1 Firth of Clyde

1.3.1.1 Bathymetry (fig 1.5)

A bathymetric map of the Firth of Clyde has been compiled by the I.G.S. (Deegan et al. 1973) from echo sounder traces and Admiralty soundings.

A deep trough extends from Loch Fyne around the east coast of Arran and terminates against a rock bar at a depth of 40 m which extends from Kintyre to the Ayshire coast. The trough is asymmetric, being steeper on the Arran side and consists of a series of basins separated by ridges, a topography produced by water flowing beneath an ice sheet, which Recent sedimentation has yet to mask. Greatest depths (200 m) are found to the north east of Arran shallowing to 100 m east of Brodick.

Kilbrannan Sound, the channel forming the west side of Arran, reaches depths of only 140 m and again shallows to the south.

Loch Riddon, at the junction of the east Kyle of Bute with the more deeply incised West Kyle, has a depth of 30 m.

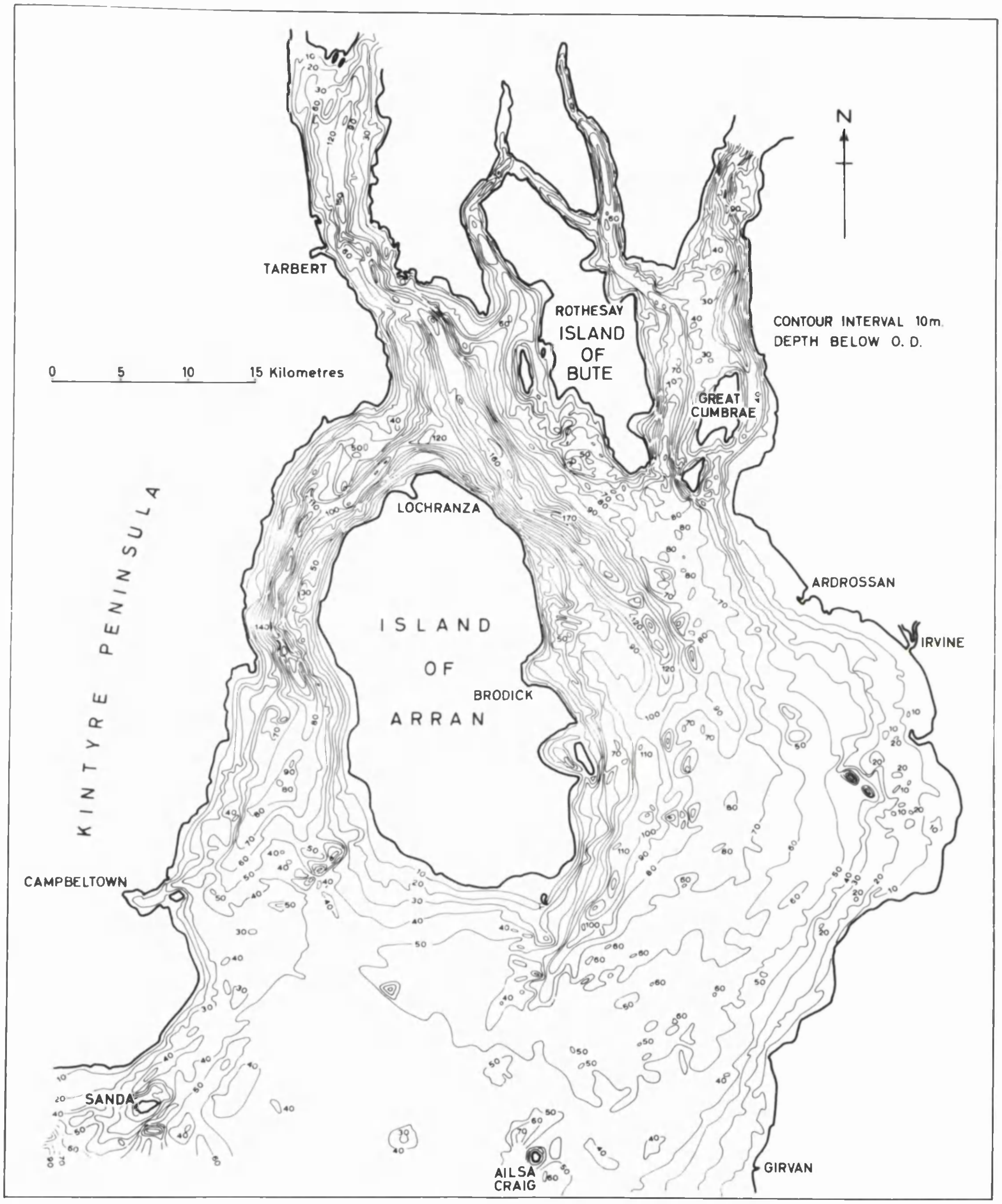


fig 1.5 Bathymetry of the Firth of Clyde.
(from Deegan et al. 1973)

A channel extending from Loch Striven deepens to 120 m between the Cumbraes and Bute while the main channel from the River Clyde and Loch Long swings east and shallows to form the Fairlie Channel (40 m) to the east of the Cumbraes.

The Ayshire coast shelves to a depth of 80 m before descending rapidly into the trough.

1.3.1.2 Surface Deposits (fig 1.6)

The Institute of Geological Sciences recognise three sedimentary facies whose distribution is closely related to bathymetry: a coarse littoral facies, a transitional facies and a silty clay facies (Deegan et al. 1973, p. 7).

The following account combines their observations with those of this study and contains unpublished particle size analysis supplied by the I.G.S.

The coarse littoral facies consists of clean sand and all sediments with a gravel fraction. It is restricted to depths of less than 40 m and includes the gravelly mud of the Fairlie Channel. No boxcores were taken in this facies but observations have been made on animals obtained from the Fairlie Channel in aquaria.

The transitional facies, deposits of sandy mud and muddy sand, comprises only a narrow strip in most of the area as the coarse littoral facies passes rapidly offshore into the silty mud facies. It forms a broad band between Ailsa Craig and the mainland and floors Kilbrannan Sound and the Cumbrae Deep (all three areas have been boxcored). The

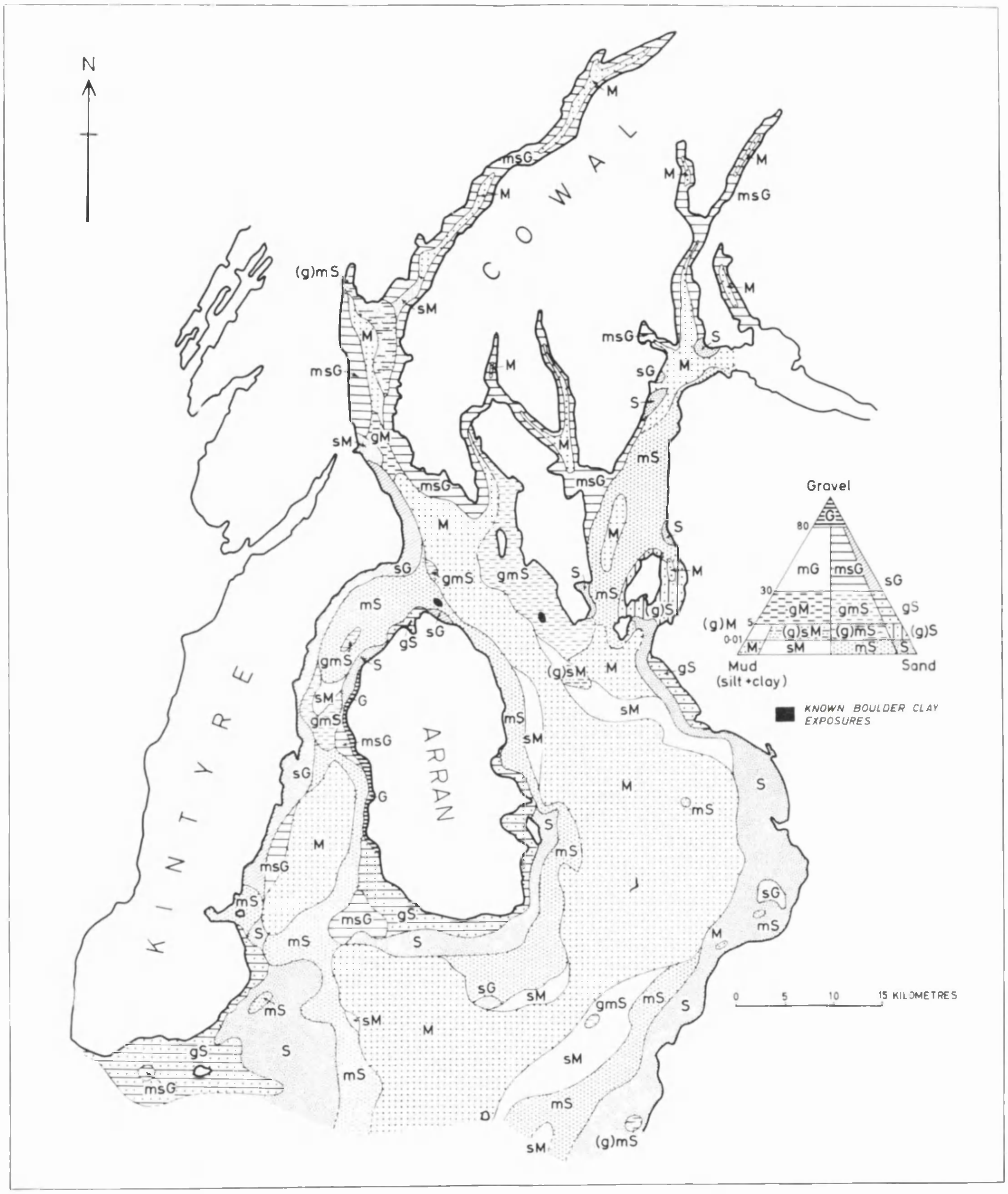


fig 1.6 Surface sediment distribution in the Firth of Clyde (from Deegan et al. 1973)

sand fraction of the Kilbrannan Sound sediment is probably derived from erosion of the Arran granite (Boyd pers. comm. 1980) giving a much coarser sediment than is found in other parts of the Firth of Clyde at this depth.

The Cumbrae Deep forms part of the main shipping channel between Glasgow and the sea and the coarse fraction of its sediment is in part derived from dredging spoils and slag from ships' boilers.

The silty clay facies is the most extensive sediment type forming a broad mud plain off the coast of Ayshire and flooring the deep trough which runs from Loch Fyne around the east coast of Arran. This connects with a further area of mud to the south of Arran. Mud is also found in the deep central parts of Loch Long and Loch Goil and at the southern end of Kilbrannan Sound.

Sediments from the south and east of Arran (boxcore sites: Firth of Clyde 1-9) show a decrease in sand content from 30% at 40 m to zero at 75 m concomitant with an increase in the clay fraction from 30% to 65%. The finest sediment is found at the bottom of the Arran Deep at 180 m and consists of 30% silt, 70% clay. This seems surprising in view of the proximity of the trough to the island of Arran; however, it receives very little direct fluvial input as it lies in the rain-shadow of the mountains which are drained by predominantly westward flowing rivers (Mill 1892).

The dominant clay minerals are illite, chlorite and kaolin with subordinate amounts of montmorillonite and mixed layer clays (Lennie pers. comm. 1978). Erosion of boulder clay is the principal source of these sediments. In Loch Riddon and Loch Fyne the sand fraction of the mud is highly micaceous. Manganese occurs as nodules in Loch

Fyne (Murray & Irvine 1894, Calvert & Price 1970) and as coatings on the shells of living molluscs (Allen 1960).

The top 0.5 cm of the sediment is an orange-brown oxidized layer; below it is a dark cohesive mud displaying no apparent lamination. Oxidized sediment extends into the underlying anaerobic sediment around burrows forming a zone several millimetres thick. The top 5 cm of the sediment has a water content above 80% (Moore 1931). Sedimentation rates measured by sedimentation jar (Moore 1931) and by the naturally occurring isotope Lead-210 (Swan 1978) are of the order of 1-5 mm/year, which, allowing for compaction, means that the top 40 cm (the average penetration of a boxcore) was deposited in the last 100-600 years.

Moore (1931) found that most material reaching the bottom was in the form of zooplankton faecal pellets produced mainly during the spring plankton bloom. These breakdown at the sediment surface and are converted into more compact faecal pellets by the deposit feeding benthos.

I consider the bands of peaty sediment revealed in sediment cores left in the sunlight by Moore (1931, fig 9) and interpreted by him as marking the spring diatom increase recorded in the sediment, to be graded beds formed by the settling out of material resuspended in the coring tube of the sampler (Moore & Neill 1930).

1.3.1.3 Hydrography

The Firth of Clyde has a small tidal range (0.3-2.5 m)* and weak tidal currents (Admiralty 1973). Salinity below 10 m is normally around 34^{o}/oo with a minimum of 31^{o}/oo. Oxygen saturation may drop from 80% to 40% during the summer (Craig 1959).

Bottom temperatures range from 6^{o}C (April) to 12^{o}C (September) at a depth of 50 m, south of Arran and from 5^{o}C (April) to 11^{o}C (November) in the Arran Deep (180 m). The mean annual temperatures for these two sites are 9^{o}C and 7^{o}C respectively (Mill 1894). In Loch Riddon the minimum temperature is 6.5^{o}C (April) and the maximum 11.5^{o}C (September) with a mean of 9^{o}C (Mill 1894).

Exchange of deep water occurs only during the winter and complete replacement of the Firth's waters by the Irish Sea takes around nine months (Craig 1959).

* Spring tides 2.5m
Neap tides 0.3m

1.3.2 Argyll Sea Lochs and Inshore Sounds

1.3.2.1 Bathymetry (fig 1.7)

The irregular bottom topography of this area is a product of the Pleistocene glaciation (Binns et al 1974) and is characteristic of recently glaciated shelves (Shep~~h~~ard 1959).

Elongate overdeepened hollows up to 200 m deep are found in the Sound of Jura and Firth of Lorne (Evans & Ruckley 1980). The coastline is embayed with fjords; these have shallow sills at their entrances and overdeepened basins. Loch Etive consists of three basins, the deepest of which has a depth of over 150 m, separated by rock sills, the shallowest only 10 m deep at the loch entrance. Loch Creran has an entrance sill also 10 m deep but has only been eroded to a depth of 50 m (Gage 1972).

The Loch Linnhe-Loch Eil system is connected to the Firth of Lorne via the Corran Narrows (11 m deep) and Loch Eil is separated from Loch Linnhe by the Annat Narrows (5.5 m deep). The maximum depths in Loch Linnhe and Loch Eil are 153 m and 72 m respectively (Pearson 1970).

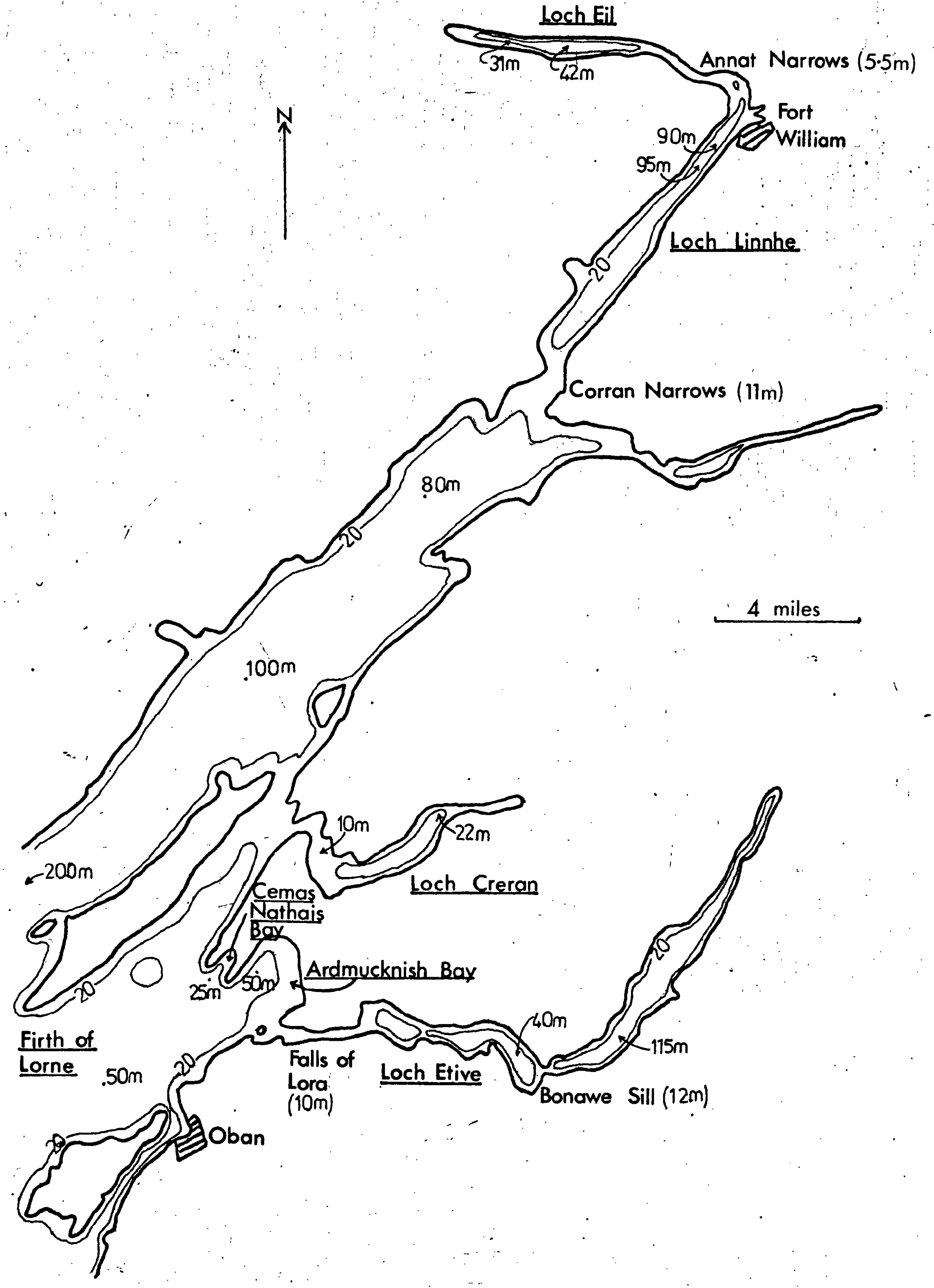


fig I.7 Bathymetry of the Argyll Inshore Sounds and Sea Lochs.

1.3.2.2 Surface Deposits (fig 1.8)

Muddy sediments predominate in deep water throughout the inshore area. They extend often to within 30 m of the shore before grading rapidly into beach gravels (Binns et al 1974). In Ardmucknish Bay at 50 m the sediment contains 60% clay but at 25 m in neighbouring Cemas Nathais Bay the sediment has already coarsened to comprise 56% silt grade material. Sediment from a deep site in the Sound of Jura (216 m) is surprisingly coarse (47% silt) when compared to sediment from similar depths in the Firth of Clyde (70% clay). This may be due to the strong tidal currents which are thought to be responsible for the formation of these deep elongate troughs (Evans & Ruckley 1980).

The sills at the loch entrances are associated with strong currents and are floored by gravels or bare rock surfaces (Gage 1972). The loch sediments themselves are predominantly silty, most markedly in Loch Linnhe and Loch Eil where one station contains 94% silt grade material.

Studies of organic sedimentation in Loch Etive and Creran (Ansell 1974) stress the importance of terrestial detritus. Rates of deposition of 247 g Carbon/m^2/year were recorded at station E-6 (Loch Etive) at a depth of 54 m; two-thirds of which accumulated during the autumn and winter (September-February) (Ansell 1974, table 2).

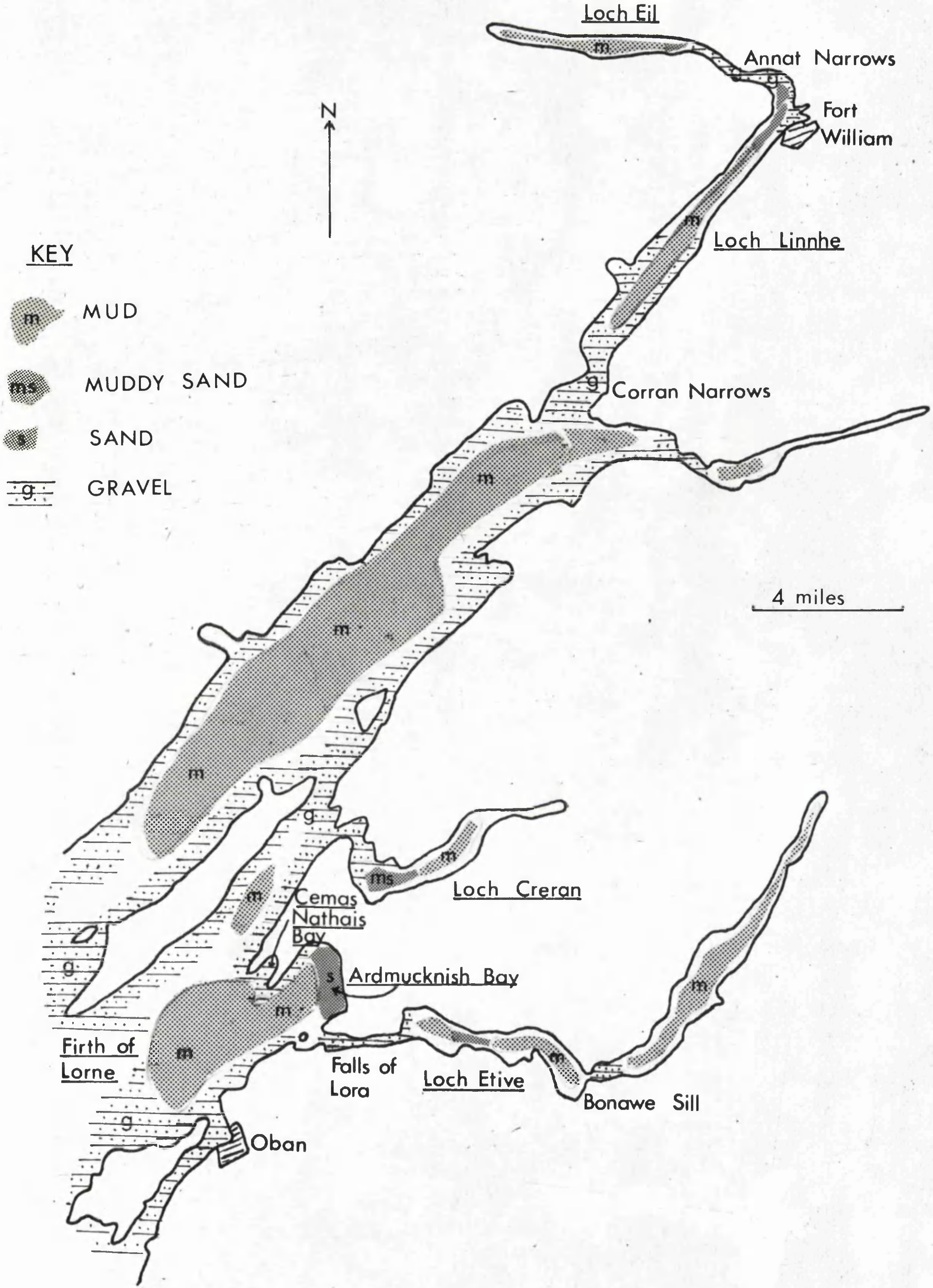


fig I.8 Surface sediment distribution in the Argyll Inshore Sounds and Sea Lochs.

1.3.2.3 Hydrography

Freshwater runoff reduces salinity in the surface water especially in the sea-lochs where the water column is stratified for most of the year. Loch Etive, with its large catchment, has surface salinities between 1 and 26^{o}/oo. At depths greater than 20 m salinity remains constant at 28^{o}/oo, temperature ranges between 6^{o}C (February) to 14^{o}C (August) and oxygen saturation may fall to 40% (Gage 1972).

Loch Creran has a less restricted circulation with salinity at depth around 32^{o}/oo and oxygen concentration does not fall below 80%. Temperatures are similar to those of Loch Etive.

Both salinities in Loch Eil range from $25\text{-}30^{o}$/oo and in the less restricted Loch Linnhe from $31\text{-}33^{o}$/oo, bottom temperatures from $6\text{-}12^{o}$C (Pearson 1970). Oxygen concentrations have been affected by the effluent from a pulp and paper mill situated between the two lochs. In Loch Eil bottom waters are now 50-60% saturated compared to 70% saturated before the discharge started. Loch Linnhe is less affected with oxygen saturation remaining close to the pre-discharge level of 90% (Pearson 1975).

1.3.3 The Relationship between depth and particle size in the study area

When particle size is plotted against depth for the complete area studied (fig 1.9 in back pocket) it is apparent that the simple model of sediment fining with depth is complicated by source factors e.g. high silt content in Loch Linnhe-Loch Eil and in the case of the sandy mud found at a depth of 216 m in the Sound of Jura by the assumption inherent in the simple model that energy levels decrease with depth.

1.4 Fauna of the fine sediments

1.4.1 Firth of Clyde

The Scottish Marine Biological Association, while based at the Millport Marine Station (1897-1971), compiled species lists for each of the important benthic groups (except for the echinoderms) relevant to this study, the Polychaeta (Clark 1960), the Mollusca (Allen 1962) and the decapod Crustacea (Allen 1967). These surveys updated and extended previous dredgings in the area made by Sir John Murray (Chumley 1918).

Further species records have been provided by Clark and Dawson (1963) and Comely (1972). Clark (1952) pointed out the Mediterranean affinities of the polychaete fauna.

Unpublished benthic data obtained by the Department of Agriculture and Fisheries for Scotland, Aberdeen, have also been made available to me.

The current state of knowledge of the benthos of this area has been reviewed by Barnett (1974). It could be described as belonging to the _Amphiura_ community of Thorson (1957), the boreal offshore mud association of Jones (1950) or to the _Nucula sulcata_ - _Brissopsis lyrifera_ sandy mud community composed of stenothermal and boreal species adapted to the temperature régime of the open sea étage (range less than 10°C, mean 10°C) of Glémarec (1973).

Surveys of the Garroch Head Sludge Dumping Ground which receives a million tons of sewage sludge from the Glasgow connurbation annually, have been carried out by Halcrow, Mackay and Thornton (1973) and Pearson (1980 in prep.).

An area of highly reducing sediment, 3 sq. miles in extent, has been formed in which the normal fauna is replaced by one of few opportunistic polychaete species (mainly Capitella and Scolelepis) with very high biomass (up to 1Kg/m^2, ten times normal wet weight biomass, Pearson pers. comm. 1980). This is surrounded by a zone up to a mile wide in which the fauna is enriched, both in terms of biomass and number of species. Boxcores from both areas are described in Chapter 3.

1.4.2 Argyll Sea Lochs and Inshore Sounds

The benthos of Loch Etive, Loch Creran and the Firth of Lorne has been surveyed by Gage (1972). Further studies were made on the spatial distribution of species (Gage & Geekie 1973a) and large and small scale patchiness of the fauna (Gage & Geekie 1973b, Gage & Toghill 1977) in which comparisons were made of the various statistical approaches to these phenomena.

The fauna could be described as belonging to the same communities and associations as the Firth of Clyde benthos. However, in sea-lochs the distinctions between communities are blurred, possibly because of the entrapment of planktonic larvae within the sea-loch system (Pearson 1970, Gage 1972).

The fauna of Loch Linnhe and Loch Eil has also been ascribed to the Amphiura community (Pearson 1970). The absence of the irregular echinoid Brissopsis lyrifera is thought to be due to the high silt content of the sediment (Glénmarec 1973). In the immediate vicinity of the pulp-paper mill situated between the two lochs the normal fauna has been replaced by one dominated by the polychaetes Capitella and Scolelepis (Pearson 1975), common indicators of pollution (Pearson & Rosenberg 1978).

In the remainder of Loch Eil the fauna has become enriched, having a larger number of species and biomass than at sites unaffected by the effluent (Pearson & Stanley 1979).

The distribution of live and dead organisms in the northern part of the Sound of Jura has been described by Brown (1979).

Chapter 2 : Burrows and biogenic structures constructed by animals living in the study area

2.1 Introduction

The observations presented in this chapter are derived from either boxcores where the animal was recovered from a burrow or from narrow aquaria containing only animals of one species.

A key to burrows is presented in section 2.9.

2.1.1 Types of burrow

The simplest form of burrow is a vertical shaft which allows an animal to withdraw from the sediment surface, away from predators or unfavourable environmental conditions; coelenterates such as pennatulids and cerianthid sea anemones construct burrows of this type. Many polychaete species have evolved specialised organs with which to feed from the shaft entrance. Terebellids and ampharetids have also developed gills in the anterior region; other polychaetes respire through the body wall. Inhalent and exhalent currents must be maintained in the shaft for respiration and to remove the products of excretion.

In order that the burrow does not become fouled by the animal's faeces these must be ejected from the burrow. This poses no problem for sea anemones since waste products are passed through the mouth; however, polychaetes which have an anus situated at the opposite end of the body from the mouth must turn around in a burrow with a single entrance in order to defecate.

The vertical shaft has also been used by the maldanid polychaetes and some holothurians to feed at depth and defecate at the surface. These animals create considerable bioturbation and have been termed "conveyor-belt" organisms by Rhoads (1974).

The U-burrow allows feeding from the sediment surface or overlying water to take place from one entrance and defecation from the other. Its advantage over the vertical shaft is that a single unidirectional current for the purposes of respiration and excretion will suffice.

Alternatively surface sediment may be allowed to slump into one arm of the U-burrow and this may be ingested in safety at depth while respiration is maintained along the open arm. The irrigating activities of the animal involved create aerobic conditions in otherwise anaerobic sediment encouraging the growth of digestable microorganisms, an additional source of food. This has been termed "gardening" by Hylleberg (1975) and is practised by the lugworm Arenicola and various crustacea.

The horizontal spiral burrows constructed by the capitellid polychaete Notomastus latericeus may be a modification of the basic U-burrow to accommodate the complete worm in the basal portion of the burrow.

Interlinked U-burrows are used by errant polychaetes such as Nephtys and Glycera to lie in wait for prey passing over the burrow entrances.

Many animals secrete mucus to bind the sediment forming the burrow walls. Some use mucus to cement material into a tube, discrete from the sediment, which may protrude above it, giving access to higher levels in the overlying water for suspension feeders such as the sabellids (fan-worms). Movement in the tube is by peristaltic contraction, the same method as used by burrowers but the parapodia are reduced and the walls are gripped by modified unicinate setae (Barnes 1974, p. 484). This means that the worm's body is not in contact with the tube wall allowing a free circulation of water around the animal.

Shafts and U-burrows would be termed domichnia and fodinichnia (dwelling and feeding structures) under the behavioural classification of trace fossils proposed by Seilacher (1953).

2.1.2 Other biogenic structures

Instead of creating a burrow some animals plough through the sediment either at the surface or at a fixed depth beneath it, maintaining contact with the surface for respiration purposes. Their passage through the sediment may be detected by the formation of a distinctive biogenic structure (fodinichnia, Seilacher 1953) or the disruption of pre-existing sedimentary structures.

Most bivalves and some polychaetes and crustaceans feed from positions buried in the sediment but create no permanent burrow. Some vagile species bury themselves in the sediment to avoid predation during periods of inactivity. The sediment may be firm enough to retain an impression of their bodies which would be termed domichnia if created by a sedentary species or cubichnia (resting traces) if created by a vagile species.

2.2 Vertical shafts

2.2.1 Unlined shafts

2.2.1.1 Pennatulids (fig 2.1)

Three species of pennatulid are found off the west coast of Scotland, Virgularia mirabilis, Funiculina quadrangularis and Pennatula phosphorea (Marshall and Marshall, 1882). All three species construct vertical mucus-lined burrows up to 30 cm deep and 5 mm in diameter into which they can withdraw rapidly, using their muscular peduncle (Hoare and Wilson, 1977). They are filter feeders and do not feed in the sediment in the manner suggested by Bradley (1972) to produce the trace fossil Zoophycos. The axial calcareous rod orientated vertically in the sediment was found in boxcores and is a potential fossil although no record of its occurrence in ancient sediments could be found. The fossil pennatulids Pennatulites and Protovirgularia are now interpreted as a feeding burrow and a trail respectively (Häntzschel, 1975); their producers are unknown.

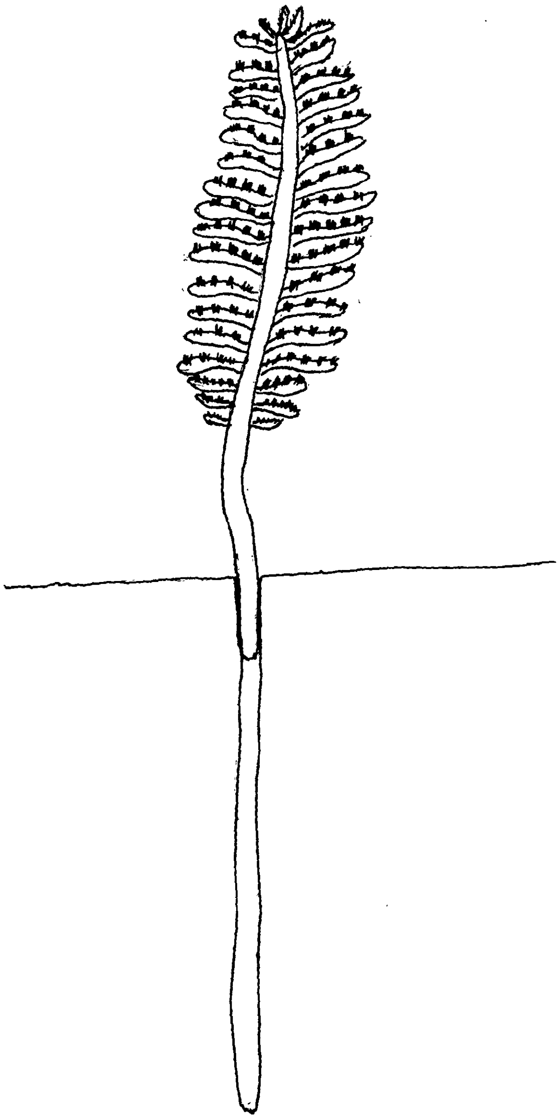


fig 2.I Pennatulid burrow (x1)

2.2.1.2 Golfingia vulgaris (de Blainville) (fig 2.2)

(Plate 5B,p.237)

This sipunculid constructs a tapering J-shaped burrow 2-5 mm in diameter to a depth of 2 cm at station C-12, Loch Creran and in the Fairlie Channel, Firth of Clyde (Comely 1972). It feeds from the sediment surface by extending its introvert, the anterior end of which contains the mouth surrounded by tentacles. Gibbs (1977) reports that Golfingia vulgaris builds vertical burrows to depths of 30-50 cms.

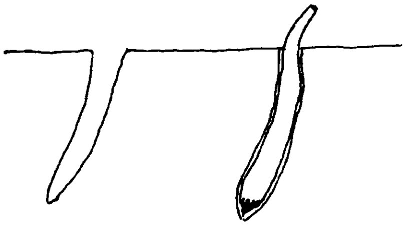


fig 2.2 Burrow of Golfingia vulgaris (x1)

2.2.2 Tube dwellers

Tubes are constructed by members of several polychaete families and cerianthid anemones by cementing the substrate with mucus. If a preferred material is available in sufficient quantities, selection may be practised. Tubes are utilised by surface deposit feeders, filter feeders and subsurface deposit feeders; the latter pair have vertical or near vertical tubes. Amongst surface deposit feeders tube orientation may be a function of food availability (Fauchald and Jumars, 1979) as horizontal tube building across the sediment surface allows access to new areas for feeding.

Vertical tubes would be ascribed to the trace fossil, genus *Skolithos*, those deflecting sediment laminae to *Monocraterion* (Hallam and Swett, 1966). Tubes running obliquely through the sediment would probably be ascribed to the unbranched burrow *Planolites*. It is important to distinguish tubes from burrows in a geological context since tubes can be allochthonous.

Tubes may be up to 10 times the length of the worm which built them and extend to depths far in excess of those required to escape the attention of predators. MacGinitie and MacGinitie (1949, p. 205) suggest that some long tubes may act as a source of microorganisms which can be fed on. Alternatively dissolved organic compounds may diffuse into them from the sediment and these can be absorbed through the body wall of many invertebrate species (Southward and Southward, 1972).

2.2.2.1 Cerianthus lloydi Gosse (fig 2.3)

(Campbell and Nicholls 1976, p. 86)

This burrowing anemone lives in a vertical leathery tube, 1.5 cm in diameter extending to a depth of 20 cm (Reineck et al 1967). The tube is constructed from mud woven into a felt by threads from the cnidoblasts (Baçescu 1972). The animal feeds by spreading its tentacles across the sediment surface and burrows by means of introversion and eversion of a modified base or physa (Ansell and Trueman 1966). This species is common in the Fairlie Channel, Firth of Clyde and was also found in a boxcore from Loch Linnhe. Hallam (1960a) describes a trace fossil, Kulindrichnus langi from the Blue Lias which he considers to have been created by a cerianthid anemone although of greater girth than Cerianthus burrows.

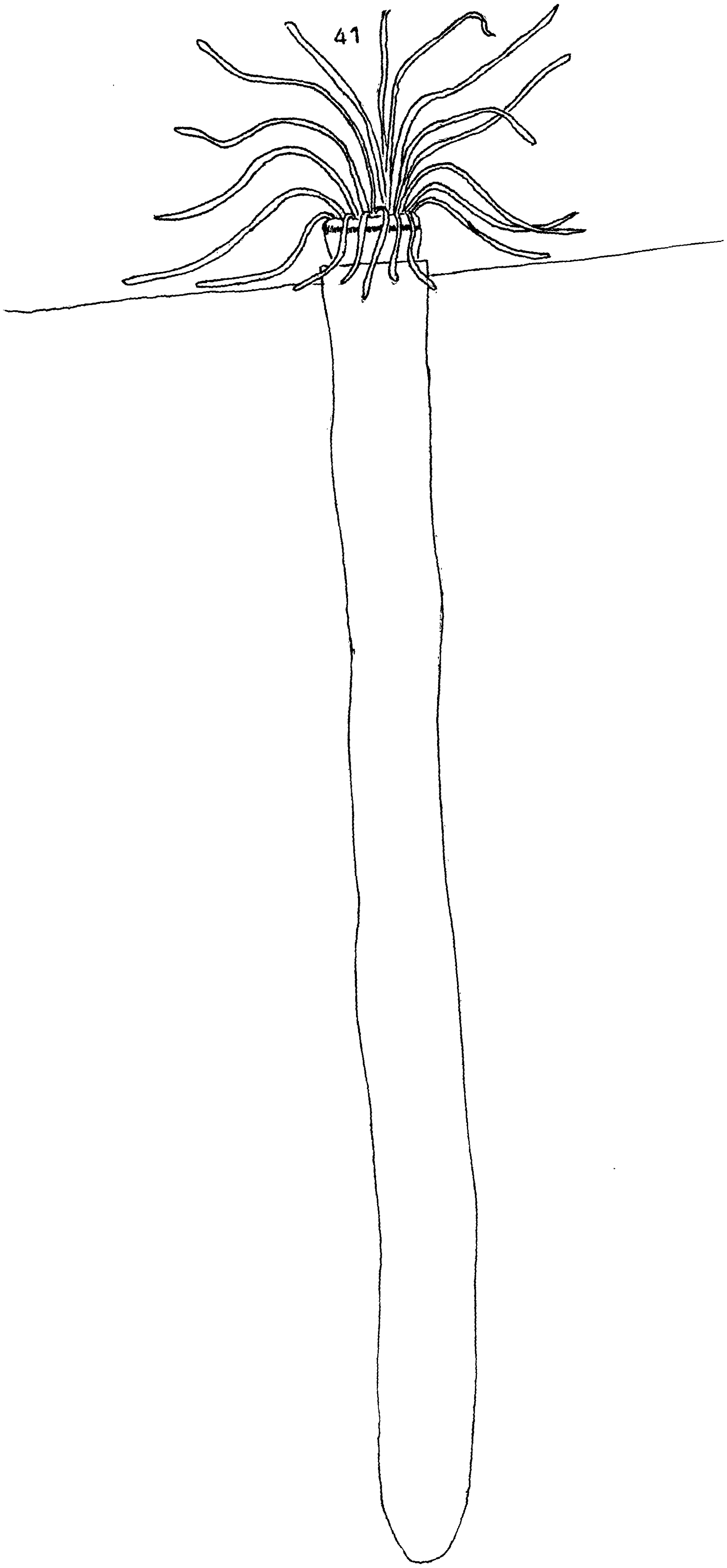


fig 2.3 Tube of Cerianthus lloydi (x1)

2.2.2.2 *Spionidae* chiefly *Spiophanes bombyx* (Claparede) (fig 2.4) (Fauvel 1927, p. 42)

(Plates 1A,1B,p233.Plate 2B,p234.Plate 3A,p235)

Clusters of 2 mm diameter tubes of mucus impregnated mud (5 tubes in 20 sq cm) extending to depths of 10 cm in the sediment were found in boxcores from deeper (> 80 m) parts of the Firth of Clyde. However, more exotic materials may be used (Pearce 1971). Spionids feed using their long peristomial tentacles or "palps" to gather food from the sediment surface (Day 1967, p. 460). Particles are selected on the basis of specific gravity and surface texture (Self and Jumars 1978). They are also capable of swimming if disturbed in a series of translational figure-of-eight contortions (Myers 1977b). If the surrounding sediment becomes depleted in food, spionids can leave their tubes and build a new one in a more favourable location (Fauchald and Jumars 1979).

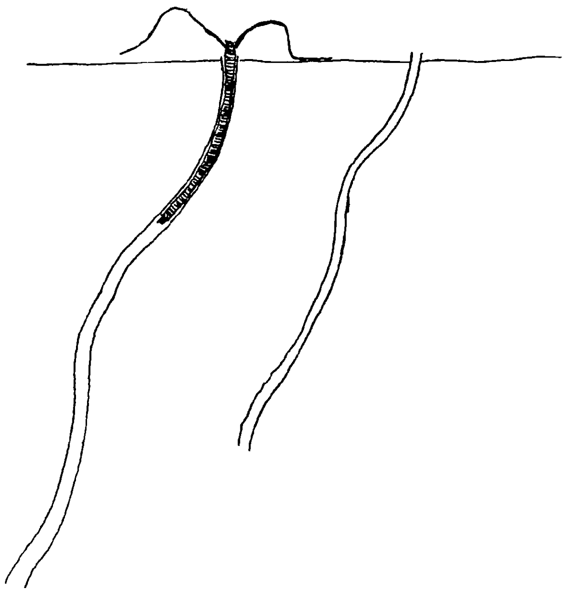


fig 2.4 Tube of *Spiophanes bombyx* (x1)

2.2.2.3 Spiochaetopterus typicus Sars (fig 2.5)

(Fauvel 1927, p. 82)

This chaetopterid constructs an annulated tube of mucus impregnated mud, 2 mm in diameter and up to 10 cm long in the very fine muds found in the deep water to the east of Arran (Clark 1960). Feeding and tube building have been described for S. oculatus by Barnes (1964): it feeds by creating a current down the tube by means of membranelles (cilia) which line 3 ring-like openings formed by the foliaceous notopodia on the first 13 segments. The middorsal ring on each segment secretes mucus and the mucus and particles from the current entrapped in it, are caught and rolled into a ball by a cupule, then passed up the middorsal groove to the mouth.

In contrast to the spionids the palps are not directly involved in feeding but are used to remove detritus from the tube. Faecal pellets are carried from the anus, up the middorsal groove and ejected by the palps although the worm can turn around in its tube. The tube is secreted a half-cylinder at a time by epidermal glands which cover the ventral surface of the anterior body region. Each secretion is marked off by an annulation (Howard and Frey 1975, fig 2D, p. 33).

The feeding method is more typical of the chaetopterids than the single mucus bag utilised by Chaetopterus variopedatus (Barnes 1965).

Annulated tubes are ascribed to the trace fossil genus Tigillites.

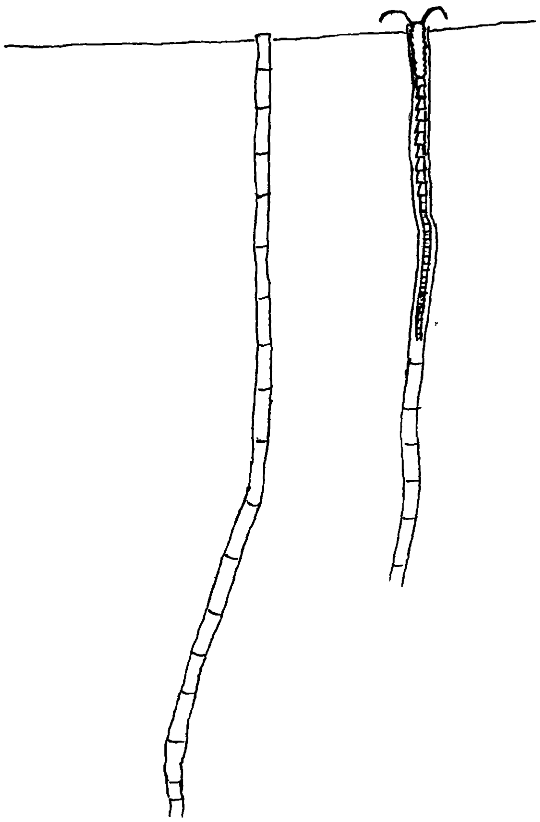


fig 2.5 Tube of <u>Spiochaetopterus typicus</u> (x1)

2.2.2.4 Sabella pavonina Savigny (fig 2.6) (Fauvel 1927, p. 298)

The mud tubes constructed by this species may extend 8-10 cm above the sediment surface. Specimens were recovered from the head of Loch Goil. Clark (1960) records this species from muds throughout the area but it would appear that its distribution is now much more restricted.

The sabellids or fan worms filter feed by means of their tentacular crown (Nicol 1930).

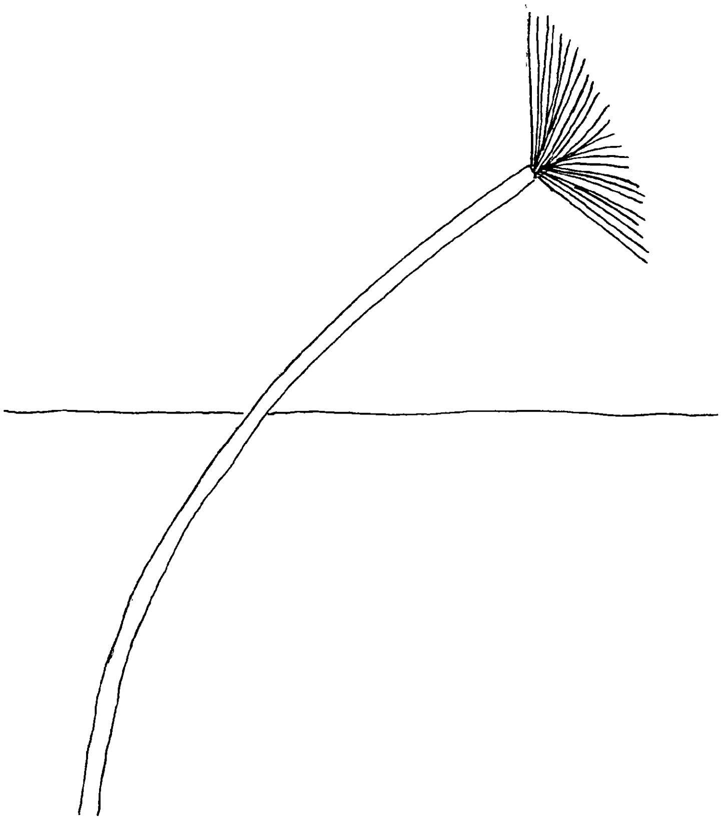


fig 2.6 Tube of Sabella pavonina (x1)

2.2.2.5 Terebellidae

Terebellides stroemi	Sars	(Fauvel 1927, p. 291)
Thelepus cincinnatus	(Fabricus)	(Fauvel 1927, p. 271)
Nicolea venustula	(Montagu)	(Fauvel 1927, p. 260)
Amaea trilobita	(Sars)	(Fauvel 1927, p. 285)

(Plate 8A,p240)

Terebellides stroemi was the most common terebellid occurring at a density of 10/m^2 throughout the area. Thelepus and Nicolea were found in the Fairlie Channel, Firth of Clyde and Amaea trilobita, a species not previously recorded from the Firth of Clyde, was found in a grab sample from Irvine Bay.

Terebellids construct tubes. Thelepus may incorporate shell material in it (McIntosh 1894). Most tubes are oriented vertically in the sediment except that of T. stroemi which runs obliquely through the sediment in the manner of ampharetids from which it can be distinguished by its larger diameter (5 mm) (fig 2.7). Some intertidal terebellids construct U-burrows (Rhoads 1967, Ronan 1977); in areas where food is scarce feeding from either entrance allows access to a greater area of the sediment surface.

Most terebellids use their grooved buccal tentacles to collect food particles and convey them to the mouth (Day 1967, p. 706) but T. stroemi has been observed to use its expanded upper lip as a scoop and then sort through the excavated sediment with its fine feeding tentacles (Fauchald and Jumars 1979).

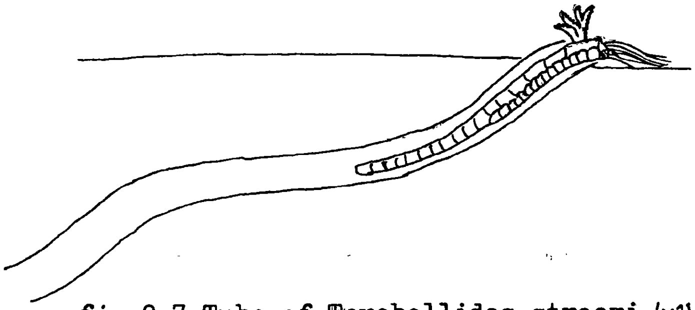


fig 2.7 Tube of Terebellides stroemi (x1)

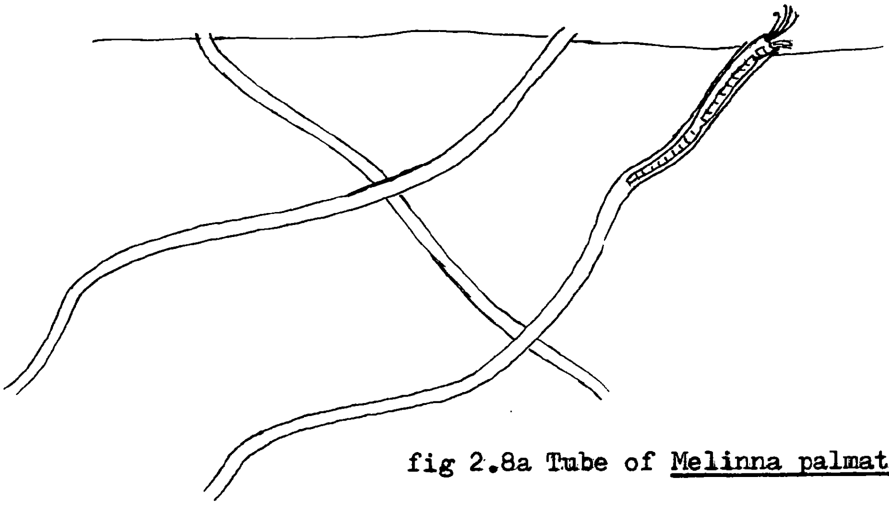


fig 2.8a Tube of Melinna palmata (x1)

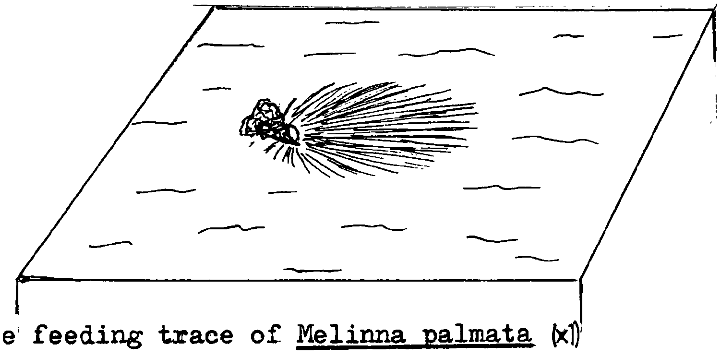


fig 2.8b Surface feeding trace of Melinna palmata (x1)

2.2.2.6 Ampharetidae

Melinna palmata	Grube	(Fauvel 1927, p. 239)
Amage adspersa	(Grube)	(Fauvel 1927, p. 234)
Amphicteis gunneri	(Grube)	(Fauvel 1927, p. 231)

(Plate 58,p237)

Two species were encountered in large numbers; Melinna palmata at station C-12, Loch Creran and around the island of Cumbrae in the Firth of Clyde (Clark & Milne 1955) and Amage adspersa in Loch Riddon, Firth of Clyde. Clark (1960) correlates their presence with the occurrence of decomposing algae in the sediment. Amphicteis gunneri was found in small numbers in Kilbrannan Sound.

Tubes of mucus impregnated mud up to 5 mm in diameter extending obliquely from the sediment surface to depths of 10-15 cms were revealed in radiographs of boxcore subsamples from the sites mentioned above (fig 2.8a). In shelly muds around the island of Cumbrae Melinna augmented its tube with shell fragments, placed in an imbricate manner along the portion of the tube exposed on the sediment surface.

The worm feeds by emerging from its tube and raking the sediment surface with its buccal tentacles while the branchiae are held up in the water (Dragoli 1961). In aquaria this produced a distinctive feeding trace on the sediment around the tube entrance consisting of a cicular area of smoothed sediment 5 cm in diameter with faint radiating grooves as well as a small pile of thread-like faeces (fig 2.8b). This resembled the Lower Cambrian trace fossil Oldhamia. The bow-wave created by the sampler must have been sufficient to remove this trace from the surface of boxcores. Extension of the tube above the sediment surface with the worm arching over to rake the sediment as illustrated by Baçescu (1972, fig 7-14) and claimed as characteristic for the ampharetids by Fauchald and Jumars (1979) was not observed.

2.2.2.7 Owenia fusiformis Delle Chiaje (fig 2.9)

(Fauvel 1927, p. 203)

This species was taken in large numbers in Kilbrannan Sound and Cumbrae Deep; Clark (1960) describes it as a widespread, often abundant, sublittoral species.

It lives inside a tube of imbricate sand grains (Watson 1900) which is normally oriented upright in the sediment although it can be moved about. It can feed by ciliary means on suspended particles or bend over and feed from the sediment surface (Dales 1957).

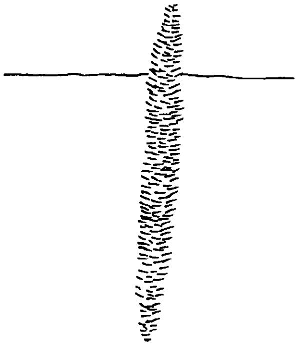


fig 2.9 Tube of Owenia fusiformis in feeding position(x1)

2.2.2.8 Onuphis conchylega Sars (fig 2.10) (Fauvel 1923, p. 415)

The animal was found in a grab sample from Kilbrannan Sound. It had constructed a rough tube of shell debris attached to a dead Chlamys septemradiata shell from which it was observed to partially emerge in order to search the sediment surface for food. Day (1967, p. 406) claims that the tube may be dragged about like that of a caddis-fly larva.

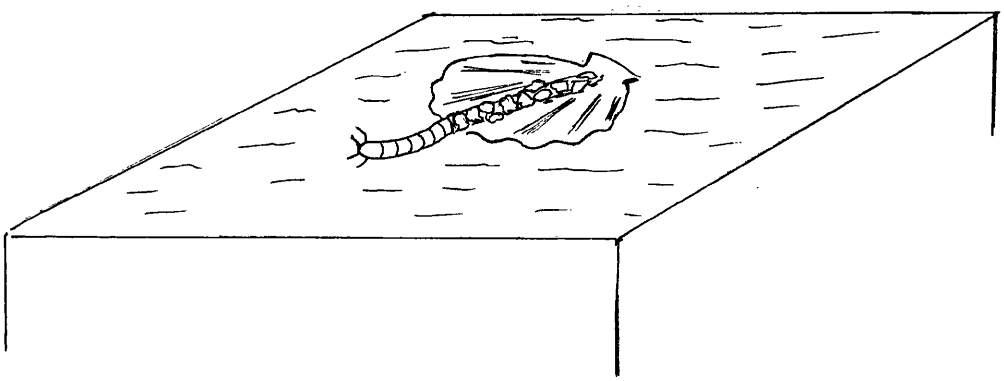


fig 2.10 Tube of Onuphis conchylega attached to a dead Chlamys septemradiata shell (x1)

2.2.2.9 Amphipoda (Campbell and Nicholls 1976, p.206)

Specimens of Ampelisca sp. were recovered in grab samples from the Cumbrae Deep but when introduced to aquaria they neither burrowed nor built tubes. Allen (1953) reports a community of the tube dwelling amphipods Haploops in the Cumbrae Deep but amphipods were not encountered in this survey in sufficiently large numbers to justify designating them a community.

2.2.3 "Conveyor-belt" organisms (sensu Rhoads 1974)

2.2.3.1 Maldanidae (fig 2.11)

Clymene sp.		(Fauvel 1927, p. 170-181)
Maldane sarsi	Malmgren	(Fauvel 1927, p. 197)

Several species were encountered but never in the numbers reported by Moore (1931). Clark (1960) does not record any maldanid species as being abundant in the Firth of Clyde.

The maldanids or bamboo-worms, so-called because their parapodia resemble cane-joints, are tubicolous and feed by means of an eversible pharynx (Kudenov 1977). Feeding at the base of the tube creates a void into which fresh sediment falls (Rhoads 1967) although in areas of low food content the tube is probably continuously extended (Fauchald & Jumars 1979).

Material is ejected onto the sediment surface, a vulnerable manoeuvre since maldanid 'tails' are frequently cropped by fish.

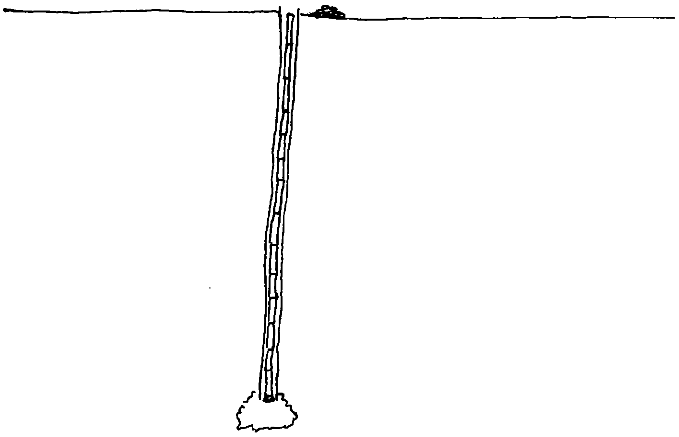


fig2.II Tube of Maldane sarsi (x1)

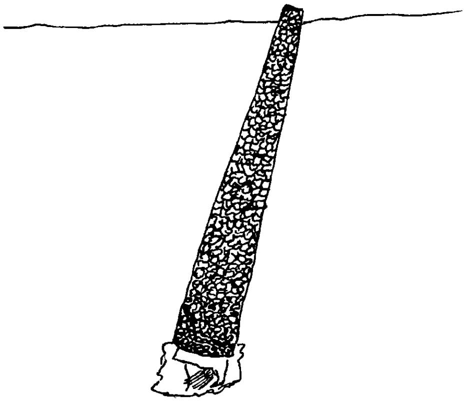


fig 2.I2 Tube of Pectinaria belgica (x1)

2.2.3.2 Pectinaria belgica (Pallas) (fig 2.12)

(Fauvel 1927, p. 220)

In common with all pectinariids this species builds a tapering tube of cemented sand grains up to 12 cm long in which it lives (McIntosh 1894, Vovelle 1973). The tube is oriented vertically in the sediment and the animal feeds at the bottom whilst excreted material is ejected from the top onto the sediment surface resulting in an annual turnover of 6-8.6 Kg dry sediment/m^2 (Gordon 1966, Nichols 1974). It digs using stout flattened setae (palae) and sorts the particles with numerous buccal tentacles (Whitlach 1974).

The animal can move laterally through the sediment keeping the tube vertical but Fauchald and Jumars (1979) conclude that mobility and sediment turnover by these animals is dependent on the organic content of the sediment. Animals in high organic content sediment remain stationary and create a headshaft through their feeding activities.

In the Firth of Clyde this species has a density of less than 30/m^2 and does not dominate the biomass as reported for pectinariids from other areas. No live Pectinaria were recovered in a boxcore but the tubes were often found preserved at depth. However since these serve an exoskeletal function they are not true trace fossils in the sense of Seilacher (1953).

2.2.3.3 Scaphopoda (Phylum:Mollusca)

(Campbell and Nicholls 1976, p. 166)

Dentalium entalis (fig 2.13)

Several specimens were recovered from the sandy muds in Kilbrannan Sound. Allen (1962) records this species as common in sandy sediments. The tusk-like shell is oriented vertically in the sediment in the manner of Pectinaria and the animal feeds selectively at depth on foraminifera, diatoms and other microorganisms (Schäfer 1972, p. 245).

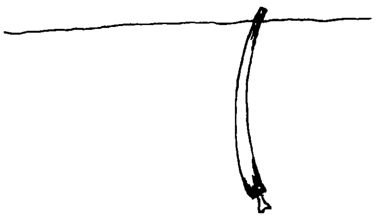


fig 2.I3 Tube of Dentalium entalis (x1)

2.3 U-burrows

Vertical U-burrows without spreiten are referred to the trace fossil *Arenicolites*, whilst those with spreiten are referred to *Corophioides*, *Diplocraterion* or *Rhizocorallium*, the latter normally occurring oblique to the bedding. In the fine sediments, on which this study is based, no spreiten were observed, although later diagenetic changes in the sediment may render them visible.

2.3.1 *Chaetopterus variopedatus* (Renier) (fig 2.14)

(Fauvel 1927, p. 77)

This species constructs a U-burrow with a tough leathery lining up to 1 cm in diameter and up to 30 cm deep. The tube extends about 1 cm above the sediment surface and tapers to an opening 0.5 cm in diameter (MacGinitie 1939, fig 1). Feeding is by means of a single mucus bag secreted by the long wing-like 12th segment.

The volume of water contained in this larger tube is too great to be moved by cilia (cf. *Spiochaetopterus*); instead 3 disc-like segments in the middle region of the body create a current through the tube. In a U-burrow a uni-directional flow can be maintained and large particles are allowed to pass right through the tube (Brown 1975, fig 8). The smaller palps reflect their reduced role in the manipulation of particles compared to *Spiochaetopterus* (Barnes 1964).

Clark (1960) records *Chaetopterus variopedatus* as widespread and moderately common throughout the Firth of Clyde especially in gravelly muds. A tube was recovered intact in a boxcore from Loch Riddon and a worm in its tube was found in a grab sample from Ardmucknish Bay in the Firth of Lorne.

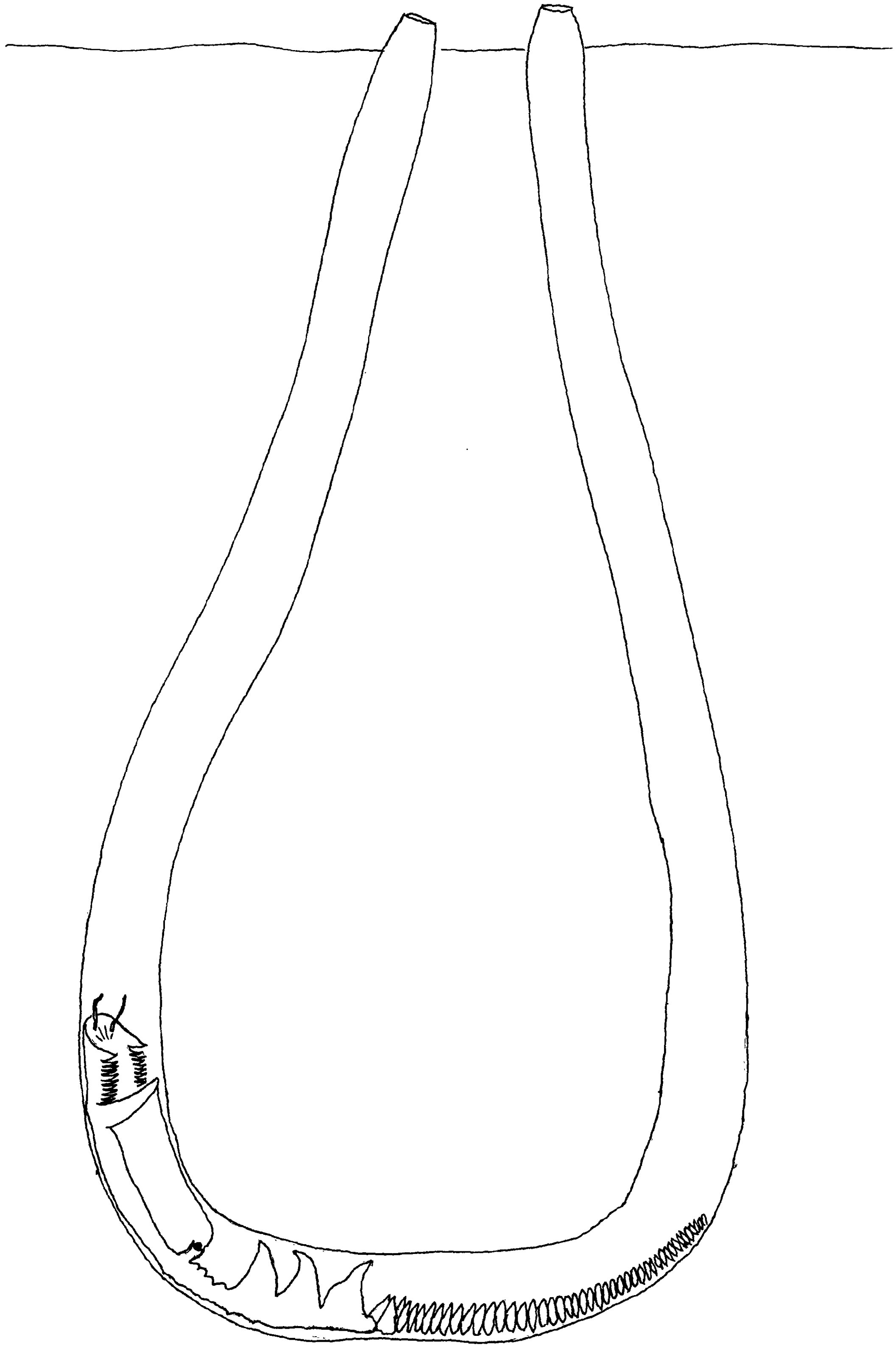


fig 2.I4 Tube of <u>Chaetopterus variopedatus</u> (after MacGinitie I939)
(x1)

2.3.2 Scalibregmidae

Scalibregma inflatum	Rathke	(Fauvel 1927, p. 123)
Lipobranchius jeffreysi	(McIntosh)	(Fauvel 1927, p. 127)

Scalibregmids have sac-like eversible pharynges which they use to burrow in the mud; they do not form tubes. Day (1967) considers them to inhabit the surface layer of silt but Ashworth (1901) claims that they burrow to depths of 60 cm. When sampled in a boxcore, scalibregmids appear on the mud surface within half an hour of sampling which would seem to indicate that they are shallow burrowers (to depths of less than 10 cm).

Their guts are filled with mud and Fauchald and Jumars (1979) suspect that the degree of selectivity in their feeding is related to the productivity of the area.

In the Firth of Clyde, both Scalibregma and Lipobranchius are found across the complete depth range that muddy bottoms occupy, from 10 to 200 metres (Clark 1960). Scalibregma is more abundant in shallow waters, Lipobranchius in deep water (greater than 80 m). Lipobranchius is rare in the sea-lochs and sounds further north.

2.3.2.1 Scalibregma inflatum (fig 2.15)
(Plate 3A,p235.Plate 8A,p240)

This species seldom survived for more than a few days in aquaria during which time a 1 mm diameter burrow comprising a series of shallow interconnected U-burrows was constructed in the top 2 cm of the sediment. Ashworth (1901) and Hertweck & Reineck (1966) found galleries constructed by this species to depths of 30-60 cm below the sediment surface.

2.3.2.2 Lipobranchius jeffreysi (fig 2.16) (Plate 3B,p235)

In an aquarium a 4 mm diameter shallow U-burrow extending to a depth of 1.5 cm below the sediment surface was constructed. This was the only burrow produced in an aquarium by this species. When sieved from the sediment and placed in an aquarium the animal remained at the surface and never lived for longer than one day. When mud from a site where this species was found was tipped into a tank unsieved, Lipobranchius appeared at the surface within a few hours and died within twenty four hours.

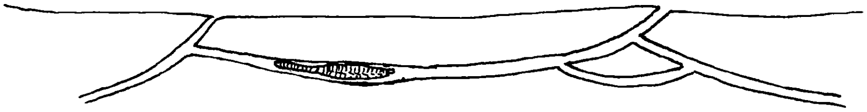


fig 2.15 Burrow of Scalibregma inflatum (x1)

fig 2.16 Burrow of Lipobranchius jeffreysi (x1)

2.3.3 Holothuria

Most sea cucumbers are deposit or suspension feeders sweeping their mucus-bearing tentacles about them to entrap particles. The tentacles are then placed in the pharynx one at a time and the mucus and particles wiped off (Barnes 1974). In soft sediments many species create a U-shape burrow from which to feed while others construct vertical shafts and feed at depth in the same manner as maldanid polychaetes (Rhoads 1974, Heezen & Hollister 1971, fig 2.51).

2.3.3.1 *Cucumaria elongata* Duben & Koren (fig 2.17)

(Mortensen 1927, p. 399)

In an aquarium this species constructs a 4 mm diameter U-burrow to a depth of 2 cm. Both ends of the animal were extended from the burrow and the species is probably a plankton feeder. This animal occurs in densities of less than 10/m^2 in Loch Riddon, Firth of Clyde. In a population of *Cucumaria elongata* off the Northumberland coast Fish (1965) found that this species concentrated all its growth into the summer months and did not feed at all in the winter.

fig 2.17 Burrow of *Cucumaria elongata* (x1)

2.3.3.2 Psolus phantapus Strussenfelt (fig 2.18)

(Mortensen 1927, p. 415)

This species constructs a 6 mm diameter U-burrow to a depth of 3 cm. It is a deposit feeder inhabiting the gravelly muds of the Fairlie Channel, Firth of Clyde (Comely 1972). The sole is used in some Psolus species to anchor the animal to stones or shell debris in the sediment.

2.3.3.3 Thyone fusus (O. F. Muller) (fig 2.19)

(Mortensen 1927, p. 407)

This species constructs a 1 cm diameter U-burrow to a depth of 5 cm and inhabits the gravelly muds of the Fairlie Channel. It is a suspension feeder.

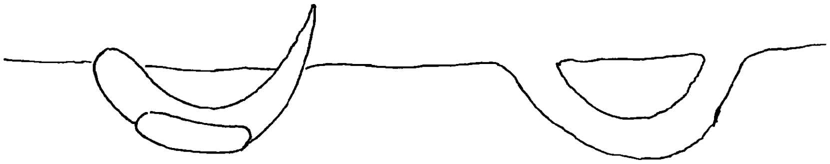


fig 2.I8 Burrow of Psolus phantapus (x1)

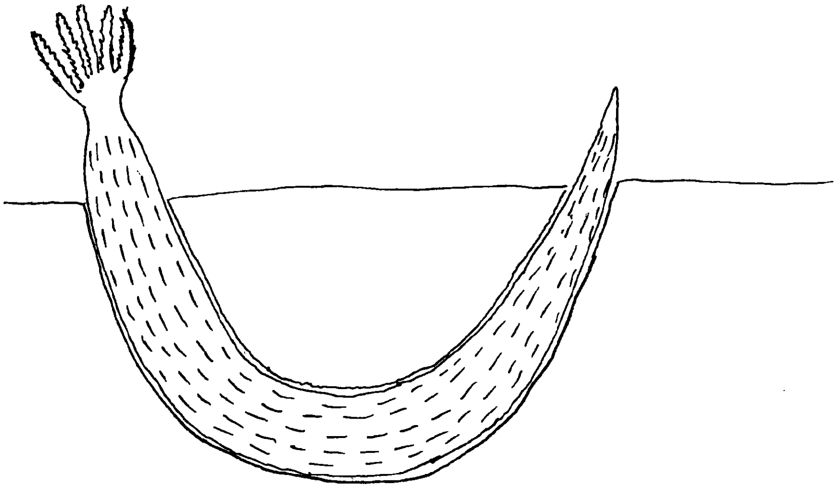


fig 2.I9 Burrow of Thyone fusus (x1)

2.3.3.4 Leptosynapta inhaerens (O. Fr. Muller) (fig 2.20)

(Mortensen 1927, p. 427)

This species constructs a deep U-burrow with a diameter of 4 mm extending to a depth of 10 cm. It is a deposit feeder occurring in small numbers (less than $10/m^2$) in the muds to the east of Arran.

Leptosynapta tenuis forms irregular U-burrows to depths of 27 cm in sand in the shallow sublittoral environment of the east coast of the U.S.A. (Hertweck 1972) and is the dominant sediment processing animal in that benthic community (Myers 1977a).

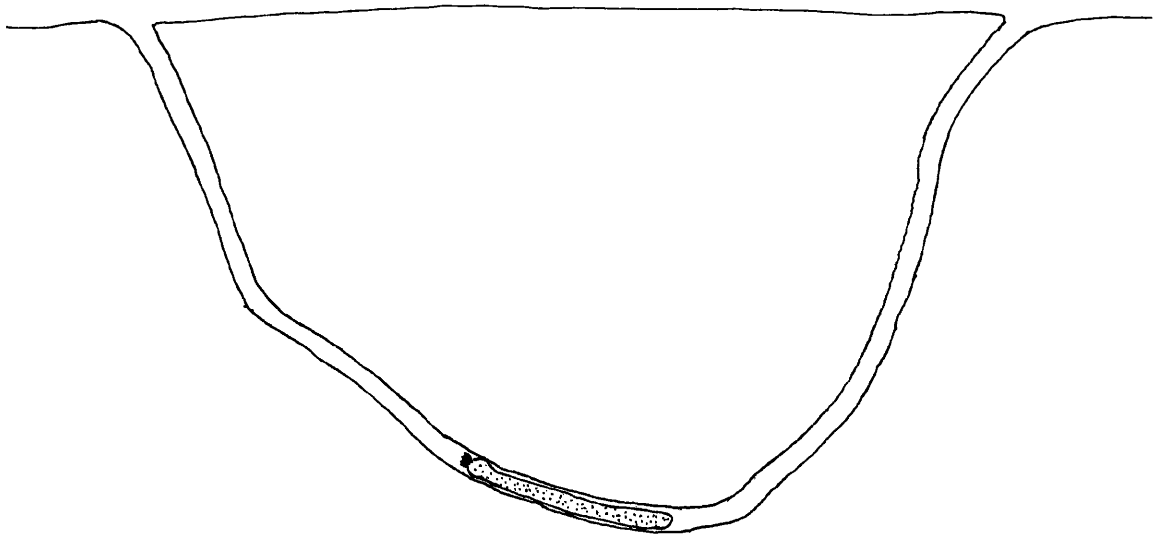


fig 2.20 Burrow of Leptosynapta inhaerens (×1)

2.3.4 Ophiuroidea

Amphiura chiajei Forbes (fig 2.21a)
(Mortensen 1927, p. 212)
Amphiura filiformis (O. F. Muller) (fig 2.21a)
(Mortensen 1927, p. 214)
(Plate 4A,4B,p236 Plate 5A,p237)

In aquaria Amphiura burrowed using its tube feet until its disc was situated about 5 cm below the sediment surface. Connection to the surface for respiration, feeding and the removal of waste products was maintained by one or two arms. The remaining arms either probed the sediment or remained coiled adjacent to the disc. A zone of orange oxidized sediment, 1-2 cm in diameter was formed around each burrow. These observations agree with those of Woodley (1975) and Ockelmann and Muus (1978). Concentrations of faecal pellets similar to those attributed to maldanids by Moore (1931, fig 11) were observed in aquaria containing only Amphiura.

Amphiura filiformis can suspension feed by trapping particles in mucus on an arm held up in the water; Amphiura chiajei feeds from the surface around the burrow entrance (Buchanan 1964). The exposed tips of the arms may be eaten by bottom-feeding fish and frequently show signs of regeneration. A. filiformis will tolerate a range of muddy sediments and is one of the characterising species of Petersen's Echinocardium-filiformis community whilst Amphiura chiajei prefers finer deposits and characterises Petersen's Brissopsis-chiajei community (Petersen 1918). Both species were found throughout the area with A. chiajei predominating only in the fine sediments of the Arran Deep.

In radiographs of boxcores from Loch Riddon Amphiur~~i~~a burrows were observed but in most boxcores Amphiur~~i~~a emerged at the surface as the boxcore drained so destroying its burrow. In boxcores from station E-6, Loch Etive, horizontal galleries made by lateral migrations of Amphiur~~i~~a chiajei through the sediment were found (fig 2.20b).

Shallow Amphuria burrows may be assigned to the stellate trace fossil Asteriacites and deeper burrows to Volkichnium (Häntzschel 1975).

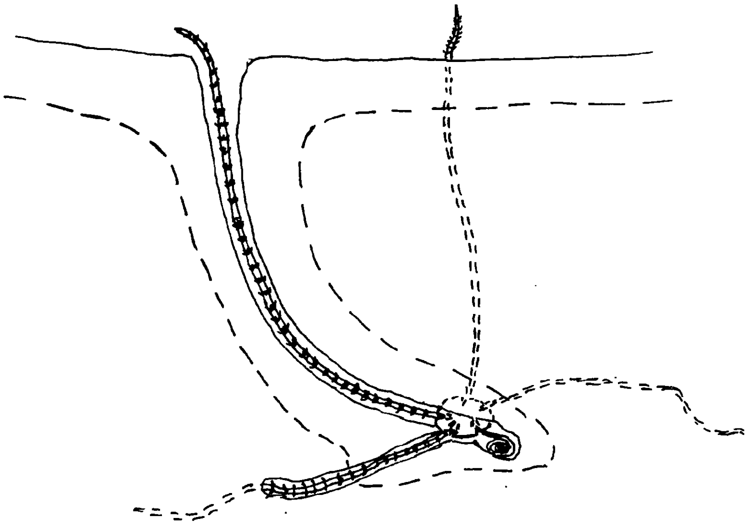


fig 2.21a Burrow of Amphiura (x1)

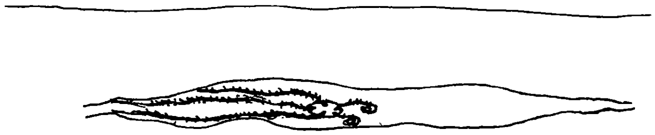


fig 2.21b Horizontal galleries created by Amphiura (x1)

2.3.5 Bivalvia

Thracia convexa (W Wood) (fig 2.22) (Allen 1961, p. 723) (Plate 7A,p239)

This species was found buried at depths of 10-20 cm in the mud in Loch Riddon and Loch Creran. Occasional specimens were also found in Irvine Bay. The depth at which it lives is below the bite of most grabs and dredges and its presence has been underestimated in past surveys (Allen 1962, Gage 1972).

It constructs a U-tube of mucus impregnated mud through which it filters particles from the overlying water. The method of tube construction by the siphons has been described for Thracia phaseolina (Yonge 1937a).

The globose fragile shell lies with the anterior-posterior axis horizontal in the sediment and with the umbo uppermost and not as might be expected by analogy with Mya truncata vertically in the sediment with posterior end uppermost. This latter assumption appears to be the basis for the erroneous interpretation by Duff (1975, p. 460) that Thracia depressa found resting flat on the bedding plane in the lower Oxford clay is evidence for the erosion of the sediment exhuming the shell.

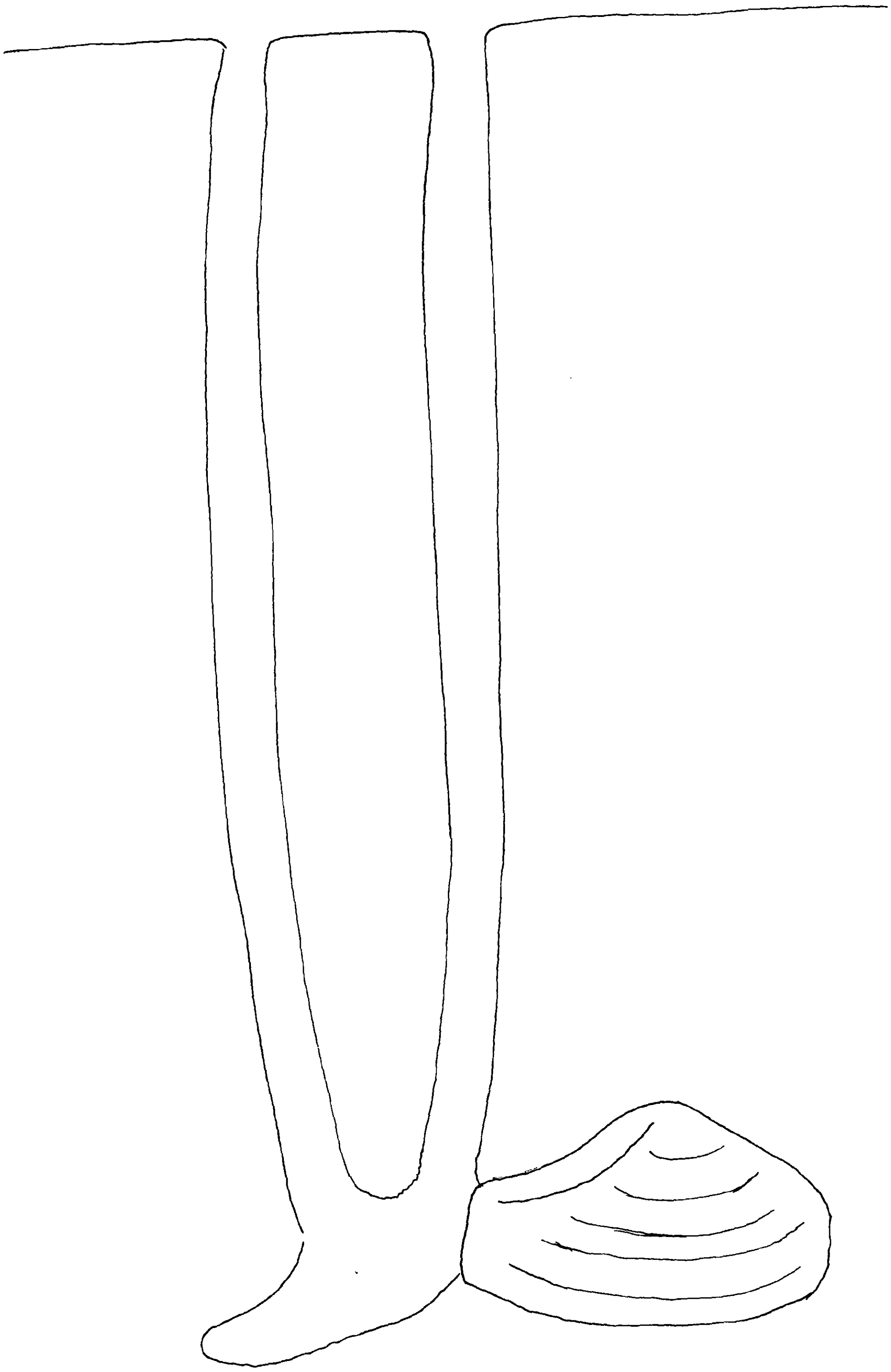


fig 2.22 Burrow of Thracia convexa (x1)

2.3.6 *Thyasira flexuosa* (Montagu) (fig 2.23)

(Tebble 1966, p. 79)

This species was found in the Cumbrae Deep in small numbers but Allen (1962) records it as more widely distributed.

It burrows to a depth of several centimetres and then uses its foot to construct a mucus lined tube through which an inhalent current is maintained (Allen 1958, fig 26).

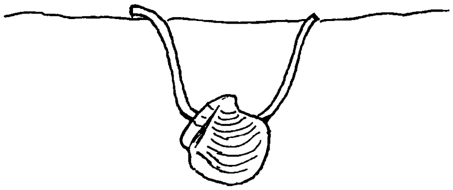


fig 2.23 Burrow of *Thyasira flexuosa* (x1)

2.4 Deep burrowing capitellid polychaetes

Notomastus latericeus is common and abundant throughout the area except in the deeper parts of the Firth of the Clyde where it is replaced by Dasybranchus caducus (Clark 1960).

Mediomastus fragilis, newly recorded from British waters by Warren (1979) is also present in this region.

In the polluted muds of the Garroch Head Sludge Dumping Ground, Capitella capitata occurs in large numbers (Clark & Dawson 1963; Halcrow, Mackay & Thornton 1973, fig 7).

2.4.1 Notomastus latericeus Sars (fig 2.24) (Fauvel 1927, p. 43) (Plate 6A,p238)

Notomastus latericeus' burrow has been described as a U-burrow with a basal spiral portion (Reineck et al 1967). Hertweck (1972) states that the burrow may have straight and spiral portions but does not mention branching.

In aquaria a 2 mm diameter burrow was formed, extending vertically from the sediment surface to the bottom of the aquarium (depth 10 cm). (The absence of shallow burrows distinguished the system from those of Nephtys and Glycera). Branching occurred both at depth and near the surface to produce several burrow openings. No spiral portions were observed in aquaria perhaps as none were constructed adjacent to the aquarium wall. However, radiographs of boxcores showed spiral burrows at depths of 10-20 cms. Since no burrows linking these spirals to the surface were apparent, it may be that this connection is not maintained at all times. Burrows of a similar form are produced in estuarine muds in Georgia, U.S.A. (Howard & Frey 1975, figs 4B, 48).

These spiral burrows resemble the trace fossil Helicodromites (Häntzschel 1975) and vertical spiral burrows constructed in intertidal sediment on the eastern seaboard of the U.S.A. by Notomastus lobatus have been compared to the trace fossil Gyrolithes by Powell (1977).

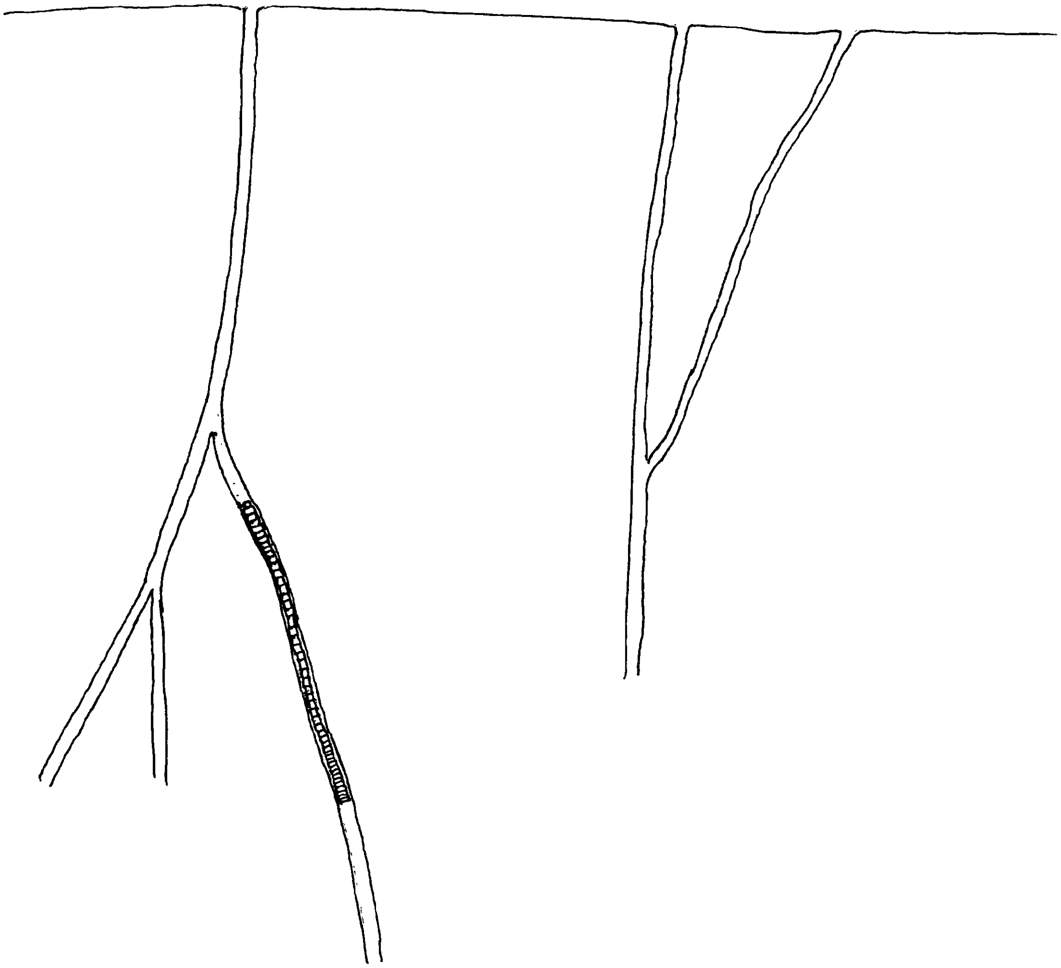


fig 2.24 Burrow of <u>Notomastus latericeus</u> (in aquarium)
(x1)

2.4.2 Dasybranchus caducus (Grube) (fig 2.25

(Fauvel 1927, p. 148)
(Plate 68,p238)

2 mm diameter wavy burrows found at depths of 10-20 cm in the sediment in boxcore samples from the Arran Deep and Kilbrannan Sound, Firth of Clyde, are attributed to this species. No burrow was seen to branch and the overall form of each burrow is probably a U with surface entrances about 30 cm apart. This wavy burrow resembles the flysch trace fossil Cochlichnus (Häntzschel 1975).

Burrows infilled with faecal pellets resembling the trace fossil Granularia (Häntzschel 1975, fig 40,3), found at depths of more than 20 cm in the sediment in boxcores from the Arran Deep, were probably formed by this species as the posterior portion of the worm's body was frequently observed to be full of such pellets (fig 2.25b).

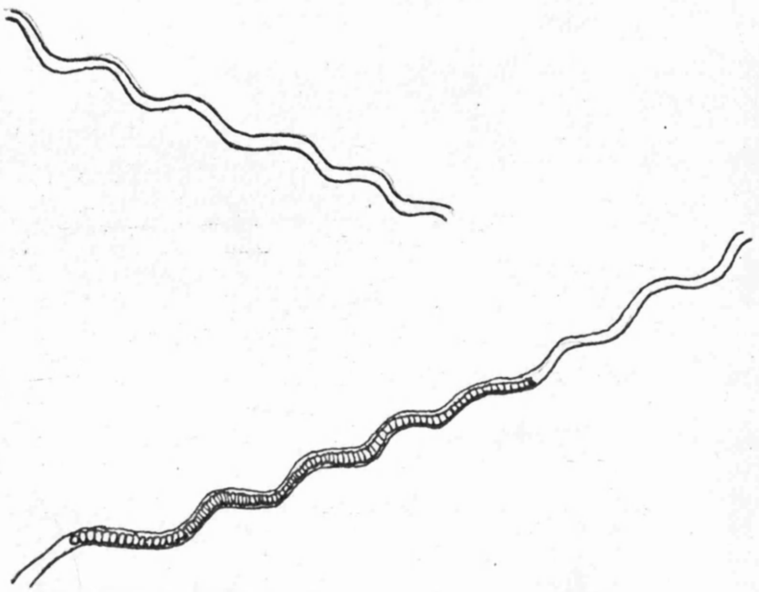


fig 2.25a Burrow of Dasybranchus caducus (x1)

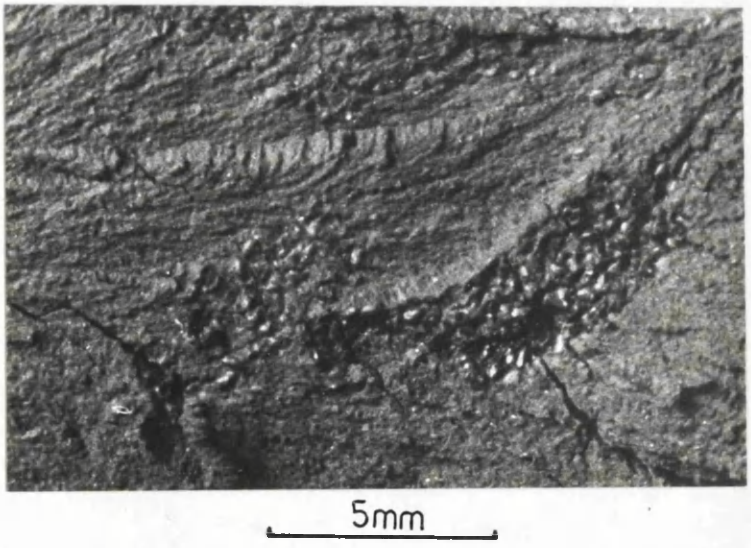


fig 2.25b Faecal pellet infilled burrow of Dasybranchus caducus.

2.5 Branching burrows

Complex branching burrow systems were produced in aquaria by the polychaetes *Nephtys hombergi* and *Glycera sp.* and the priapulid *Priapulus candatus*. *Nephtys* and *Glycera* both produced a burrow system which comprised a network of shallow U-burrows with occasional deeper burrows. *Nephtys* burrows have a maximum diameter of 2 mm, some glycerid are wider. *Priapulus* produced a dense network of burrows to a depth of 10 cm. The producers of these burrows search for prey in the sediment or lie in wait for it to pass above a burrow entrance. The burrowing activities of these animals cause little mixing of the sediment as particles are displaced only a few millimetres in the construction of the burrow.

Dense burrow networks might be ascribed to the trace fossil genus *Chondrites*, more open ones to *Megagrapton*.

2.5.1 *Glycera alba* Rathke (fig 2.26) (Fauvel 1923, p. 385)

In aquaria this species produced a 3 mm diameter complex branching burrow extending to the bottom of the tank.

Similar burrows have been produced in aquaria by *Glycera alba* (Ockelmann and Vahl 1970, fig 1) and *Glycera americana* (Frey & Howard 1972, fig 7). *Glycera alba* feeds by capturing animals passing above the burrow entrances (Ockelmann and Vahl 1970) and constructs a permanent burrow in which it lies in wait for passing prey. *Glycera americana* appears to feed on animals both in the sediment and passing above the burrow entrances, since it constructs (in aquaria) a permanent burrow with ephemeral offshoots produced whilst foraging for individual prey (Frey & Howard 1972).

MacGinitie & MacGinitie (1949) state that glycerids burrow continuously in search of food. This is true for species searching for prey in the sediment in mobile substrates where permanent burrows are difficult to maintain, e.g. the unbranched burrows of *Glycera sp.* from the upper offshore of Sapelo Island, Georgia, described by Hertweck (1972, fig 4).

The predominant glycerid in the Firth of Clyde is *Glycera rouxi* occurring in muds at all depths (Clark 1952, 1960). *Glycera alba* is present in subordinate numbers and *Goniada maculata* was found in grab samples from Irvine Bay. All 3 species occur in the Argyll sea-lochs (Gage 1972).

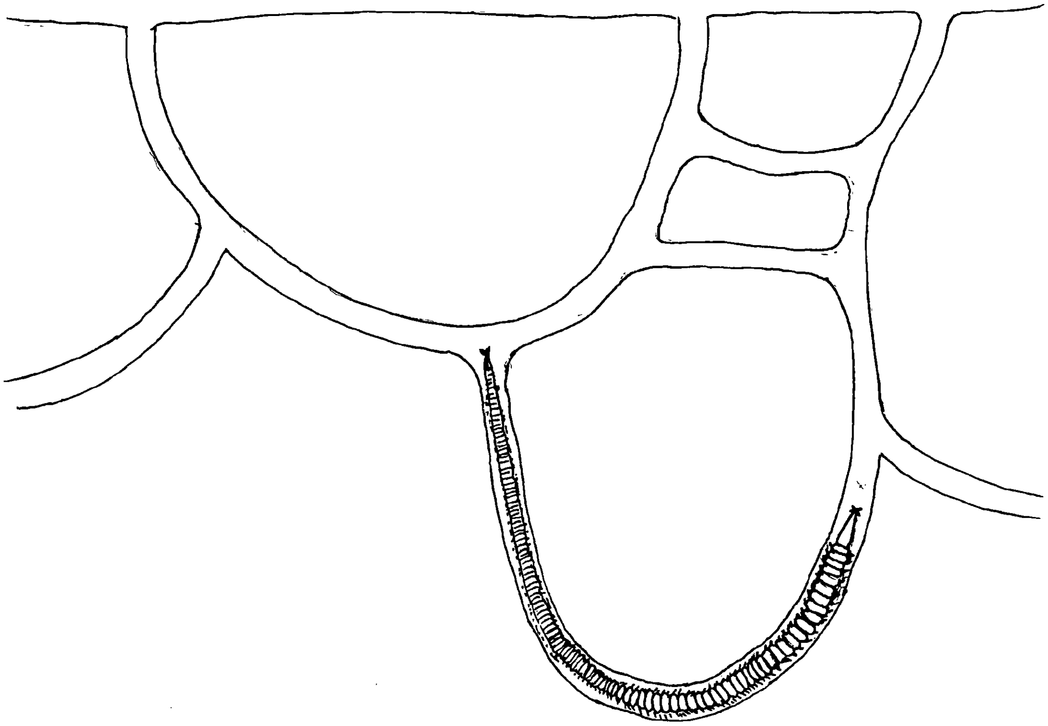


fig 2.26 Burrow of Glycera alba (x1)

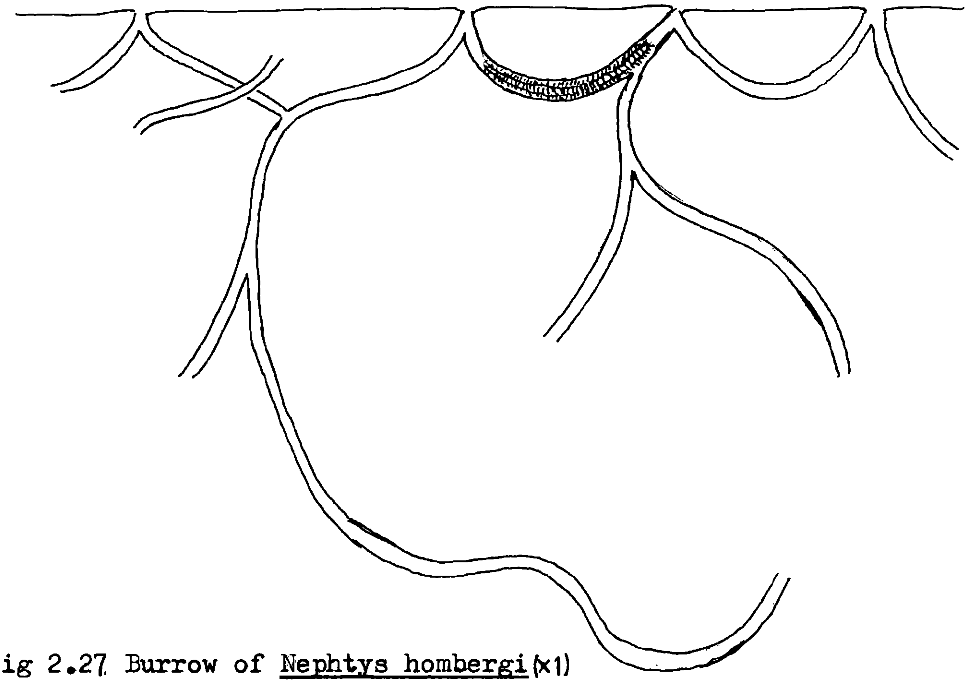


fig 2.27 Burrow of Nephtys hombergi (x1)

2.5.2 *Nephtys hombergi* Audouin & Milne-Edwards (fig 2.27)

(Fauvel 1923, p. 367)

(Plate 1B,p233,Plates 2A,2B,p234)

In narrow aquaria a series of linked U-burrows, 2 mm in diameter, was constructed in the top 2 cm with occasional deeper burrows which penetrated to the bottom of the tank (12 cm).

The burrow of *Nephtys hombergi* has also been described by Hertweck (1973, fig 3) from sublittoral muds in the Mediterranean (Gulf of Gaeta, Italy).

Nephtys hombergi is the commonest species in the benthic community inhabiting the sublittoral muds of the Firth of Clyde. *Nephtys hystricis* occurs in small numbers in the Firth of Clyde (Clark 1960) but in the sea lochs to the north it is as abundant as *N. hombergi* (MacIntyre 1960, Gage 1972).

2.5.3 Priapuloidea

Priapulus caudatus Lamark (fig 2.27)

(Campbell & Nicholls 1976, p. 136)

A 2 mm diameter, complex branching burrow system, which was continuously extended through the sediment was constructed in an aquarium by a juvenile Priapulus, 1 cm in length. Priapulus caudatus grows to lengths of 8 cm but unfortunately no large specimens were obtained during sampling for aquarium studies.

Lang (1948) claims that this species produces a vertical burrow while Hammond (1970) and Schäfer (1972, p. 239) state that the animal does not live in a distinct burrow but moves vigorously in all directions through the sediment apparently feeding on any suitable prey encountered. The presence or absence of a burrow may depend on sediment composition (Fauchald & Jumars 1979, p. 245).

This species occurs throughout the Firth of Clyde in small numbers. Around Millport Priapulus is heavily preyed upon by the gastopod Neptunea antiqua (Taylor 1978).

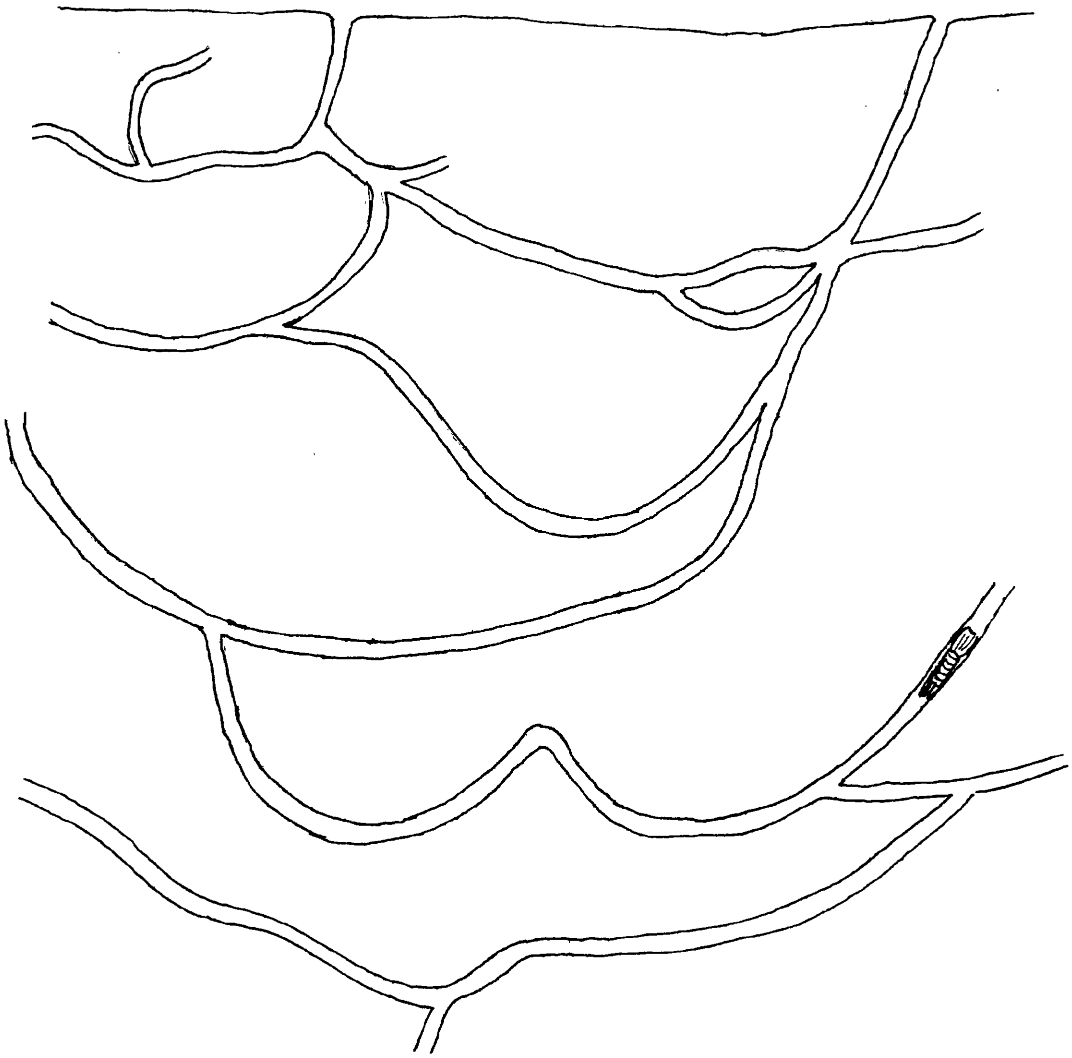


fig 2.28 Burrow of Priapulus caudatus (x1)

2.5.4 Lumbrinereis hibernica McIntosh (McIntosh 1910, p. 383)

When sieved from the sediment and placed in a mud filled aquarium this species died without producing a burrow. However, Fauchald & Jumars (1979, fig 12) state that some lumbrinereids are burrowers.

L. hibernica differs only slightly from L. impatiens (Clark 1952). It was found in small numbers in grab samples from Irvine Bay and around the Isle of Cumbrae (Clark 1960). Gage (1972) records it from the Argyll sea-lochs but McIntyre (1960) could only find L. impatiens in the sea-lochs further to the north.

2.5.5 Orbinia latreilli (Audouin & Milne-Edwards) (fig 2.29) (Fauvel 1927, p. 11)

This species produced infrequently branching burrows in mud tanks filled with gravelly mud from the Fairlie Channel, Firth of Clyde. Occasional specimens were found in grab samples from Irvine Bay; Clark (1960) records it as most abundant interdially in Balloch Bay, Isle of Cumbrae at densities of $35/m^2$.

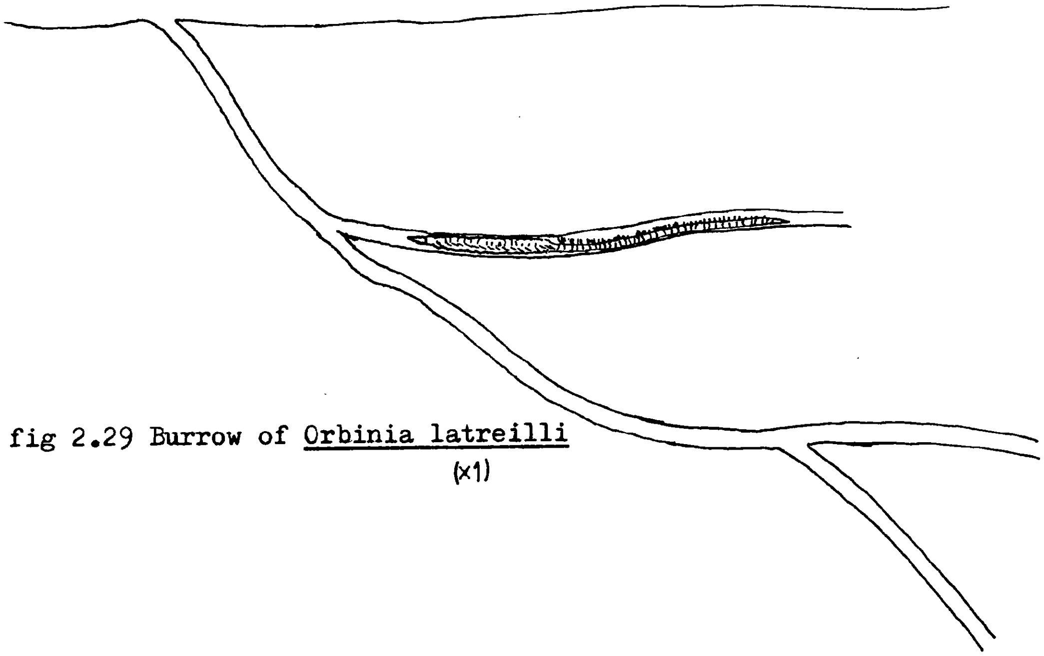


fig 2.29 Burrow of Orbinia latreilli

(x1)

2.5.6 Crustacean burrows

Decapod crustacean burrows have a diameter an order of magnitude greater than polychaetes (with the exception of *Chaetopterus*).

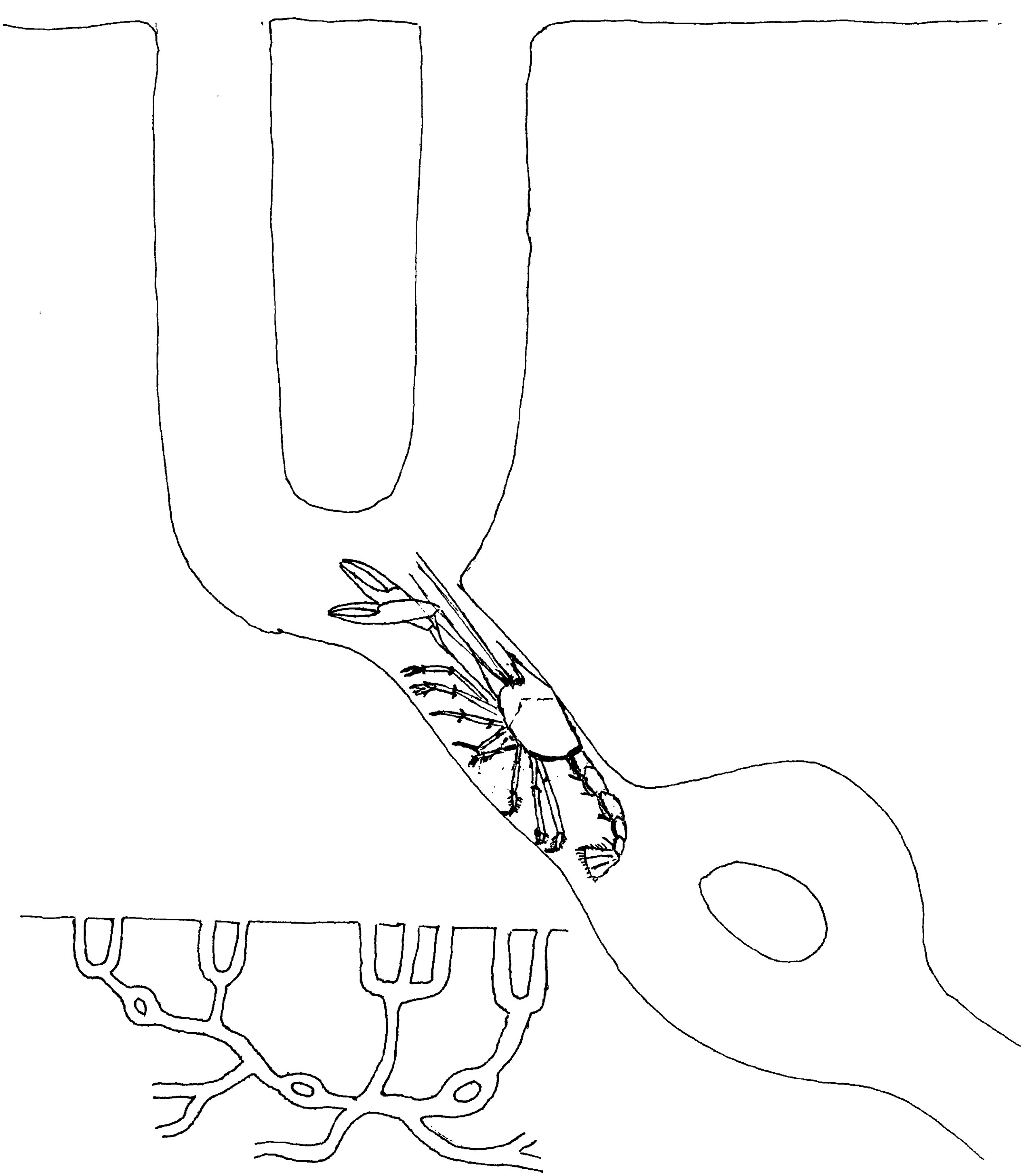
The trace fossil *Thalassinoides* is generally regarded as being produced by thalassinoid crustaceans (Häntzschel 1975).

2.5.6.1 Calocaris macandreae Bell (fig 2.30) (Allen 1967, p. 17)

This species constructs an extensive burrow system with several surface entrances. It has a diameter of 2 cm and may reach depths of 30 cm. Only a portion of the burrow system can be contained in a boxcore.

It seems that this species may "garden" (sensu Hylleberg 1975) since Buchanan (1963) has observed that Calocaris will readily grasp food particles for burial in its burrow. It could then feed on the microbial fauna involved in the decomposition of this buried organic matter. A similar hypothesis has been made about the feeding biology of Upogebia littoralis by Ott et al (1976) and by Farrow (1971) for Neaxius sp. .

Calocaris macandreae is recorded throughout the area (Allen 1967, Gage 1972).



Complete burrow (x0·1)

fig 2.30 Burrow of Calocaris macandreae (x1)

2.5.6.2 The large burrowing crustacea and fish

These construct burrows too large to be incorporated in a boxcore but they have been studied by resin casting of the burrows by SCUBA divers. Their burrows are described by:-

Crustacea

Nephrops norvegicus	Rice & Chapman (1971)	Farmer (1974)	Atkinson (1974a)
Goneplax rhomboides	Rice & Chapman (1971)	Atkinson (1974b)	

Fish

Lesueriqobius freesii	Rice & Johnstone (1972)
Cepola rubescens	Atkinson, Pullin & Dipper (1977)

All these species are recorded as common from muddy grounds throughout the area (Allen 1967, Bagenal 1965, Gage 1972) except for *Cepola* which is restricted to a small area of Irvine Bay, Firth of Clyde (Atkinson pers. comm. 1978).

2.6 Animals ploughing through the sediment

Surface trails are destroyed in boxcores by resuspension of sediment during sampling but trails of large gastropods (mainly Buccinum undatum) do occur on the deeper muds and have been observed from submersibles (Eden et al 1971, p. 8).

2.6.1 Aphrodite aculeata (L.) (fig 2.31) (Fauvel 1923, p. 33)

In tanks of mud obtained from the Fairlie Channel, Firth of Clyde, this species ploughed through the top centimetre of the sediment creating a trail as recorded by Reineck et al (1967) from the North Sea.

It is present in small numbers throughout the Firth of Clyde (Clark 1960) and Argyll sea-lochs (Gage 1972).

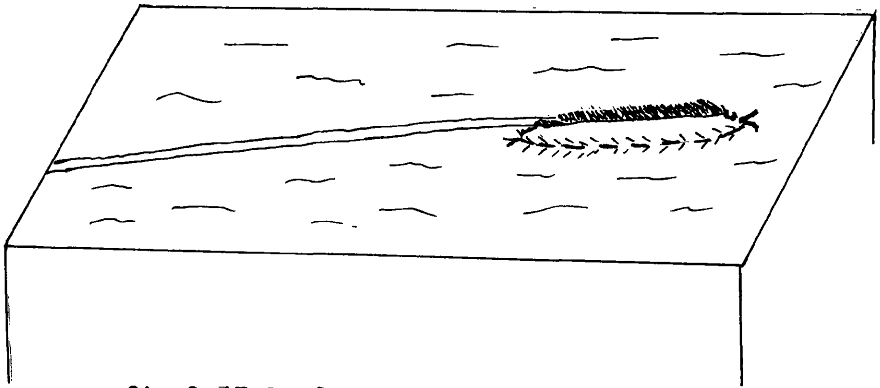


fig 2.31 Surface trail of Aphrodite aculeata (x1)

2.6.2 Echinoidea

Brissopsis lyrifera (Forbes) (fig 2.32)
(Mortensen 1927, p. 338)
Echinocardium flavescens (O. Fr. Muller) (fig 2.32)
(Mortensen 1927, p. 334)
(Plate 5A,p237)

These irregular echinoids burrow horizontally through the mud at a depth of around 5 cm. No tunnel is created behind the animals and the sedimentary structures produced by *Echinocardium cordatum* in sands (Bromley & Asgaard 1975) are not seen in these finer grained sediments. Unsuccessful attempts were made to render structures visible with dyes, resins and peels.

The calcareous tests of these species were found at depth in boxcores not filled by sediment. Their fossilisation potential is reduced by their habit of emerging at the surface whenever stress is experienced, where predators and scavengers may attack the animal.

Echinocardium flavescens is found in Loch Riddon; *Brissopsis lyrifera* is a conspicuous member of the benthonic community of the Firth of Clyde often occurring in dense concentrations (Mortensen 1927, R. Nash pers. comm. 1978).

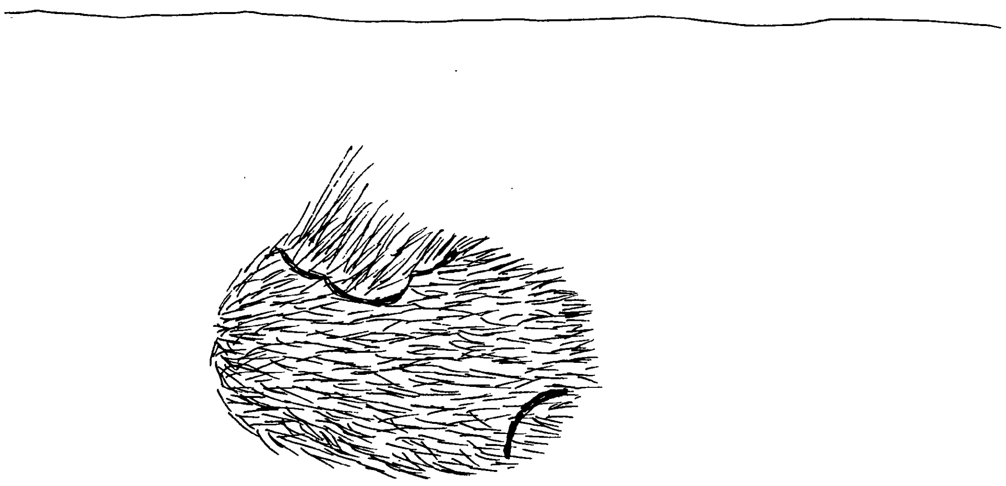


fig 2.32 Position of *Brissopsis lyrifera* in the sediment (x1)

2.7 Burial in the sediment - no burrow created

Ammotrypane aulogaster	Rathke	(fig 2.33)
	(Fauvel 1927, p. 133)	
Cirratulus cirratulus	(O. F. Muller)	(fig 2.34)
	(Fauvel 1927, p. 94)	
Diplocirrus glauca	Haase	(fig 2.35)
	(Fauvel 1927, p. 117)	
Stylarioides flabellata	(Sars)	(fig 2.36)
	(Fauvel 1927, p. 120)	

None of these species constructed burrows in aquaria; it is suggested that they bury themselves in the sediment and feed from this position.

2.7.1 *Ammotrypane aulogaster* (fig 2.33)

This species is common and widespread in the Firth of Clyde (Clark 1960) and Argyll sea-lochs (Gage 1972). It was often found in dense concentrations (Thomas & Davidson 1962) especially in the Cumbrae Deep.

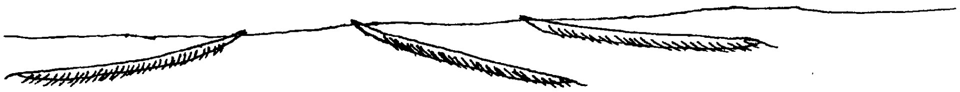


fig 2.33 *Ammotrypane aulogaster* in life position (x1)

2.7.2 Cirratulus cirratulus (fig 2.34)

This species is found throughout the area (Clark 1960, Gage 1972, Halcrow et al 1973, fig 6A) and was observed in aquaria buried in the sediment but with its grooved tentacular filaments spread on the sediment surface. This is similar to the 'mudball' cirratulid Tharyx luticastellus described by Jumars (1975a) from the abyssal north Pacific. However some cirratulids do produce burrows: Cirriformia spirabrancha was found to construct a J-shaped burrow to a depth of 20 cm in intertidal sediments in California (Ronan 1977).

2.7.3 Diplocirrus glauca (fig 2.35)

This species was found in Loch Riddon, Firth of Clyde.

2.7.4 Stylarioides flabellata (fig 2.36)

This species was found in the gravelly muds of the Fairlie Channel.

Both D. glauca and S. flabellata are members of the polychaete family Chloraemidae or Flabelligaridae and are thought to be surface deposit feeders (Fauchald & Jumars 1979).

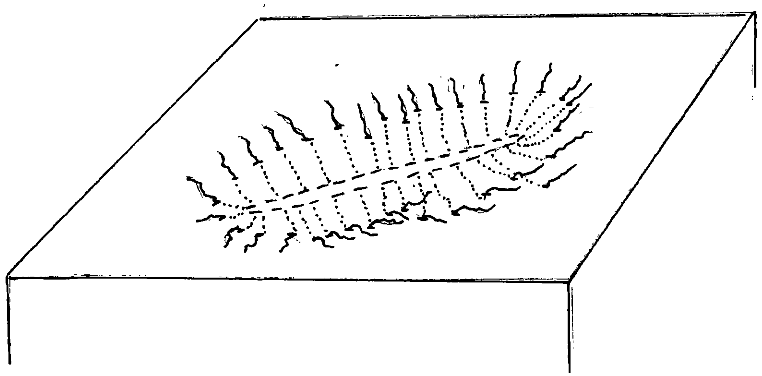


fig 2.34 Cirratulus cirratulus in life position (x1)

fig 2.35 Diplocirrus glauca in life position (x1)

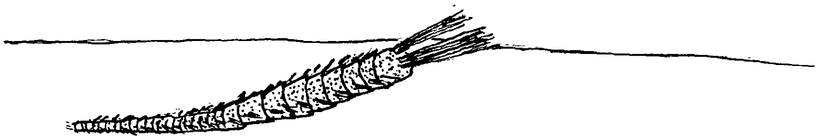


fig 2.36 Stylarioides flabellata in life position (x1)

2.7.5 Bivalvia

Nuculidae

In aquaria Nucula burrowed, either burying itself completely or leaving only its umbo exposed. Shell orientation in the sediment is variable (Stanley 1970, plate 1, Trevallion 1966, fig 11). Traces of lateral movement were seen in boxcore radiographs. It feeds within the sediment using its palps, and its irrigating activities may make the sediment easily resuspendible; this can exclude suspension feeders and has been termed trophic group amensalism by Rhoads & Young (1970).

The valves remain articulated after death as their taxodont dentition binds them together.

2.7.5.1 Nucula sulcata Bronn (fig 2.37) (Allen 1954, p. 471)
(Plate 1B,p233.Plate 3A,p235.Plate 7A,p239)

This species was recorded throughout the area. Deposits of manganese on the shells (Allen 1960) were found, and damage to the umbones by crustaceans was also common.

2.7.5.2 Nucula turgida Leckenby & Marshall (Allen 1954, p. 471)

Specimens of this species were found in Irvine Bay, the Cumbrae Deep and Loch Riddon.

2.7.5.3 Nucula tenuis (Montagu) (Allen 1954, p. 471)

This species was found only in Irvine Bay.

2.7.6 Bivalvia

Nuculanidae

Nuculana minuta (Muller) (fig 2.38) (Tebble 1966, p. 27)

This species was recorded from Kilbrannan Sound and the Cumbrae Deep (Ansell & Parulekar 1978, fig 1). It is a shallow burrower, feeding by means of short siphons.

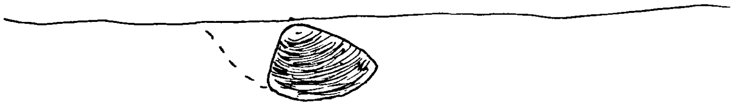


fig 2.37 Nucula sulcata in life position (×1)

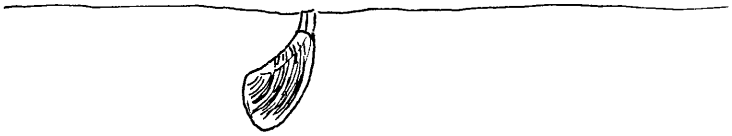


fig 2.38 Nuculana minuta in life position (×1)

2.7.7 Bivalvia

Abra alba (Wood) (fig 2.39) (Tebble 1966, p. 151) (Plate 8A,p240)

When placed in an aquarium Abra alba burrowed to a depth of several centimetres and used its siphons to feed from the sediment surface. It has a thin shell which is easily crushed by crustacean predators. Dead shells were often found disarticulated in the sediment.

This species was found throughout the Firth of Clyde in depths of 20-200 metres, and sometimes occurred in large numbers (60 were found in a single grab sample taken at a depth of 80 m, south of Garroch Head, Bute).

2.7.8 Bivalvia

Corbula gibba (Olivi) (fig 2.40) (Tebble 1966, p. 171)

Corbula gibba burrows to a depth of several centimetres and uses byssal threads attached to stones or shell fragments in the sediment to remain in position. It has short siphons through which it suspension feeds from the overlying water (Yonge 1946a). The shell tends to remain articulated after death.

This species was found in small numbers in Loch Riddon, Cumbrae Deep and Irvine Bay.

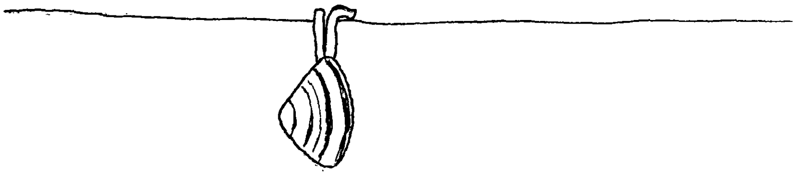


fig 2.39 Abra alba in life position (×1)

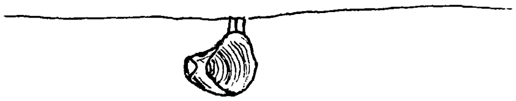


fig 2.40 Corbula gibba in life position (×1)

2.7.9 Bivalvia

Chlamys septemradiata (Müller) (fig 2.41)

(Tebble 1966, p. 61)

This species lives partially buried in the sediment and is able to adjust its position by flapping its valves and swimming. It is common on muds deeper than 70 m (Allen 1953) and its disarticulated valves are common in the sediment from these depths.

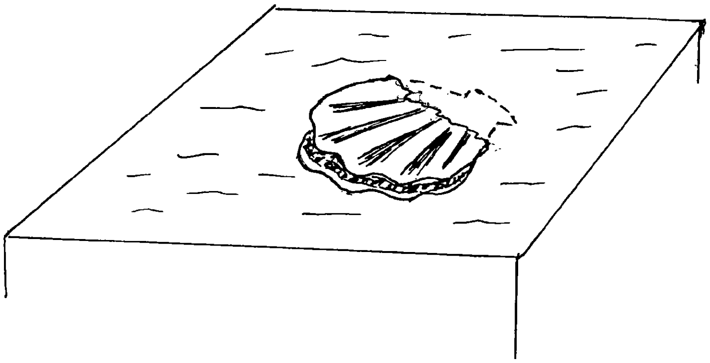


fig 2.41 Chlamys septemradiata in life position (x1)

2.7.10 Gastropoda

Turritella communis Risso (fig 2.42) (Graham 1971, p. 74) (Plate 7B,p239)

This species buries itself just below the sediment surface with the shell horizontal. Connection to the surface is maintained by means of two shafts through which it respires and feeds from suspended particles, as described by Yonge (1946b). When kept in aquaria this species was found to be more active than claimed by Yonge (1946b). The animals ploughed through the surface sediment producing trails.

The shells of this species occur in considerable numbers at depth in boxcores, often in large aggregations, with the shells displaying no preferred orientation.

Turritella shells from the Firth of Clyde, south of Arran, were encrusted by Serpulid worm tubes and several had been bored by the predatory gastropod Natica.

The dead shells of Turritella are frequently occupied by the sipunculid Phascolion strombi which prevents them from becoming buried (Hylleberg 1970). They are also used by young hermit crabs (Pagurus bernhardus).

fig 2.42 Turritella communis in life position (x1)

fig 2.43 Aporrhais pespelicani quadrifidus in life position (x1)

2.7.11 Gastropoda

Aporrhais pespelicani quadrifidus Da Costa 1778 (fig 2.43)

(Graham 1971, p. 78)

This animal buries itself in the sediment just below the surface as described by Yonge (1937b). However some specimens from the Firth of Clyde have been found to be encrusted by barnacles (*Balanus crenatus*) and hydroids suggesting time spent at the surface (Barnes & Bagenal 1952). Perron (1978) studying the American species *Aporrhais occidentalis* discovered it fed epifaunally from January to August and then buried itself and did not feed from September to January. In aquaria this animal frequently moved around the tank suggesting a more active mode of life than that proposed by Yonge (1937b).

This species is widespread throughout the area but never occurs in large numbers. Shells occupied by the sipunculid *Phascolion strombi* were found.

2.8 Temporary burial in the sediment by vagile animals

Harmothoë lunulata	(Delle chiaje)	(Fauvel 1923, p. 70)
Polynoë kinbergi	(Malmgren)	(Fauvel 1923, p. 82)
Halosydna gelatinosa	(M. Sars)	(Fauvel 1923, p. 84)

All three species were recovered in boxcores and grabs from muddy sites. *Harmothoë* may occupy the burrows or tubes of other species since the grab samples it was recovered in included the coelenterate *Cerianthus* and the holothurian *Leptosynapta* (Clark 1956). *Polynoë kinbergi,* redescribed from Clyde specimens by Clark (1952), was the only species recovered from a boxcore in Loch Riddon. Subsequent sampling in the area to obtain specimens that could be observed in narrow aquaria failed to find this species. *Halosydna gelatinosa* was found in grab samples from Irvine Bay.

In addition, the deep water prawns *Pandalus montagui* and *Crangon allmani*, common in this area (Allen 1967), are known to bury themselves temporarily in the bottom sediment (Schäfer 1972, p. 389).

2.9 Key to burrows

		Producing Species	Trace Fossil
1.	The burrow branches	2	
	The burrow does not branch	5	
2.	Burrow diameter is greater than 1 cm	*Calocaris*	*Thalassinoides*
	Burrow diameter is less than 1 cm	3	
	Burrow diameter varies between 2-5 mm	*Amphiura*	
3.	The burrow system is predominately in the top 5 cm with only occasional deeper burrows	4	
	The burrow system is not concentrated in just the top 5 cm	*Priapulus*	*Chondrites* or *Megagrapton*
4.	Burrow diameter greater than 3 mm	*Glycera*	*Chondrites* or *Megagrapton*
	Burrow diameter less than 3 mm	*Nephtys*	*Chondrites* or *Megagrapton*
5.	The burrow spirals	6	
	The burrow does not spiral	7	
6.	The spirals overlap	*Notomastus*	*Helicodromites*
	The spirals are open, having a wavy form	*Dasybranchus*	*Cochlichnus*
7.	The burrow has one surface entrance	8	
	The burrow has two surface entrances	16	

		Producing Species	Trace Fossil
8.	The burrow is vertical in the sediment	9	
	The burrow runs obliquely through the sediment	15	
9.	The burrow wall is cemented to form a tube	10	
	The burrow wall is unlined	14	
10.	The tube wall has annulations	Spiochaetopterus	Tigillites
	The tube wall does not have annulations	11	
11.	The tube is composed predominately of sand grains	18	
	The tube is not composed of sand grains	12	
12.	Diameter of tube greater than 0.5 cm	Cerianthus	Skolithos
	Diamter of tube less than 0.5 cm	13	
13.	Cavity at base of tube	Maldanids	Skolithos
	No cavity at base of tube	Spionids	Skolithos
14.	Burrow diameter less than 1 mm	Pennatulids	
	Burrow diameter greater than 1 mm	Golfingia	
15.	Burrow diameter less than 2 mm	Ampharetids	
	Burrow diameter greater than 2 mm	Terebellides	
16.	Burrow lined with a tube	Chaetopterus/Thracia	
	Burrow unlined	17	

		Producing Species	Trace Fossil
17.	Burrow diameter less than 2 mm	Scalibregma/ Leptosynapta	
	Burrow diameter greater than 2 mm	Lipobranchius/ Cucumaria/ Thyone/ Psolus	Arenicolites
18.	Sand grains arranged imbricately along tube	Owenia	
	Sand grains arranged in non-imbricate fashion	Pectinaria	

2.10.1 Key to burrows without spreiten

1.	Does the burrow branch?	- Yes	2
		- No	3
	Burrow diameter greater than 1 cm		*Thalassinoides*
	Burrow diameter less than 1 cm		2
2.	Is the branching	- regular?	*Chondrites*
		- occasional?	*Megagrapton*
		- rare?	*Planolites*
3.	Is it a	- U-burrow?	*Arenicolites*
		vertical shaft?	4
		helical burrow?	*Helicodromites*
4.	Is the tube annulated?	- Yes	*Tigillites*
		- No	5
5.	Are the sediment laminae deflected around it?	- Yes	*Monocraterion*
		- No	*Skolithos*

2.10.2 Key to U-burrows with spreiten

1.	Vertical to bedding	2
	Oblique to bedding	*Rhizocorallium*
2.	Short squat U-burrow	*Corophioides*
	Deep U-burrow	*Diplocraterion*

Chapter 3 : Distribution of Burrow Types and of Organisms with a high fossilisation potential

Twelve burrow types (Table 3.1) can be recognised from boxcores and their distribution is described in the following section.

3.1 Firth of Clyde (fig 3.1)

3.1.1 Shallow Marine Sites (40-80 m depth) (Table 3.2)

3.1.1.1 Site West of Ardrossan

Depth : 74 m
Sediment : 40% silt; 60% clay
(fig 3.2)

A boxcore taken at this site contained tubes, U-burrows and spiral burrows. The 1 mm diameter tubes were oriented obliquely in the sediment and extended to depths of around 5 cm. They were constructed by the spionid polychaete Spiophanes bombyx.

2 mm diameter U-burrows extending to depths of 6-9 cm were constructed by the polychaete Scalibregma inflatum.

Two burrows with spiral portions were found: one had an overall U-shape, the other consisted of a spiral portion oriented horizontally in the sediment at a depth of 3 cm linked to a vertical burrow which extended to a depth of 15 cm before turning to form a horizontal gallery.

Table 3.1 Burrow types identified from boxcore radiographs

		Producers	Trace Fossil
Tubes			
Type 1	⩽ 2 mm diameter	Spionids/Ampharetids/ *Spiochaetopterus*/Maldanids	*Skolithos*
Type 2	> 2 mm diameter	Terebellids, *Cerianthus*	*Skolithos*
Type 3	Pectibaria tubes	*Pectinaria*	-
U-burrows			
Type 4	⩽ 2 mm diameter	*Scalibregma*/*Leptosynapta*	*Arenicolites*
Type 5	> 2 mm diameter	*Lipobranchius*/*Holothurians*	*Arenicolites*
Type 6	~1 cm diameter deep burrows	*Thracia*/*Chaetopterus*	*Arenicolites*
Type 7	Amphiura burrows	*Amphiura*	*Asteriacites*
Deep burrowing capitellid polychaetes			
Type 8	2 mm spiral burrows	*Notomastus latericeus*	*Helicodromites*
Type 9	2 mm wavy burrows	*Dasybranchus caducus*	*Cochlichnus*
Branching burrows			
Type 10	⩽ 2 mm diameter	*Nephtys*/*Glycera*/*Priapulus*	*Chondrites*
Type 11	2-5 mm diameter	*Glycera*/*Priapulus*	*Chondrites*
Type 12	~1 cm diameter	*Calocaris*	*Thalassinoides*

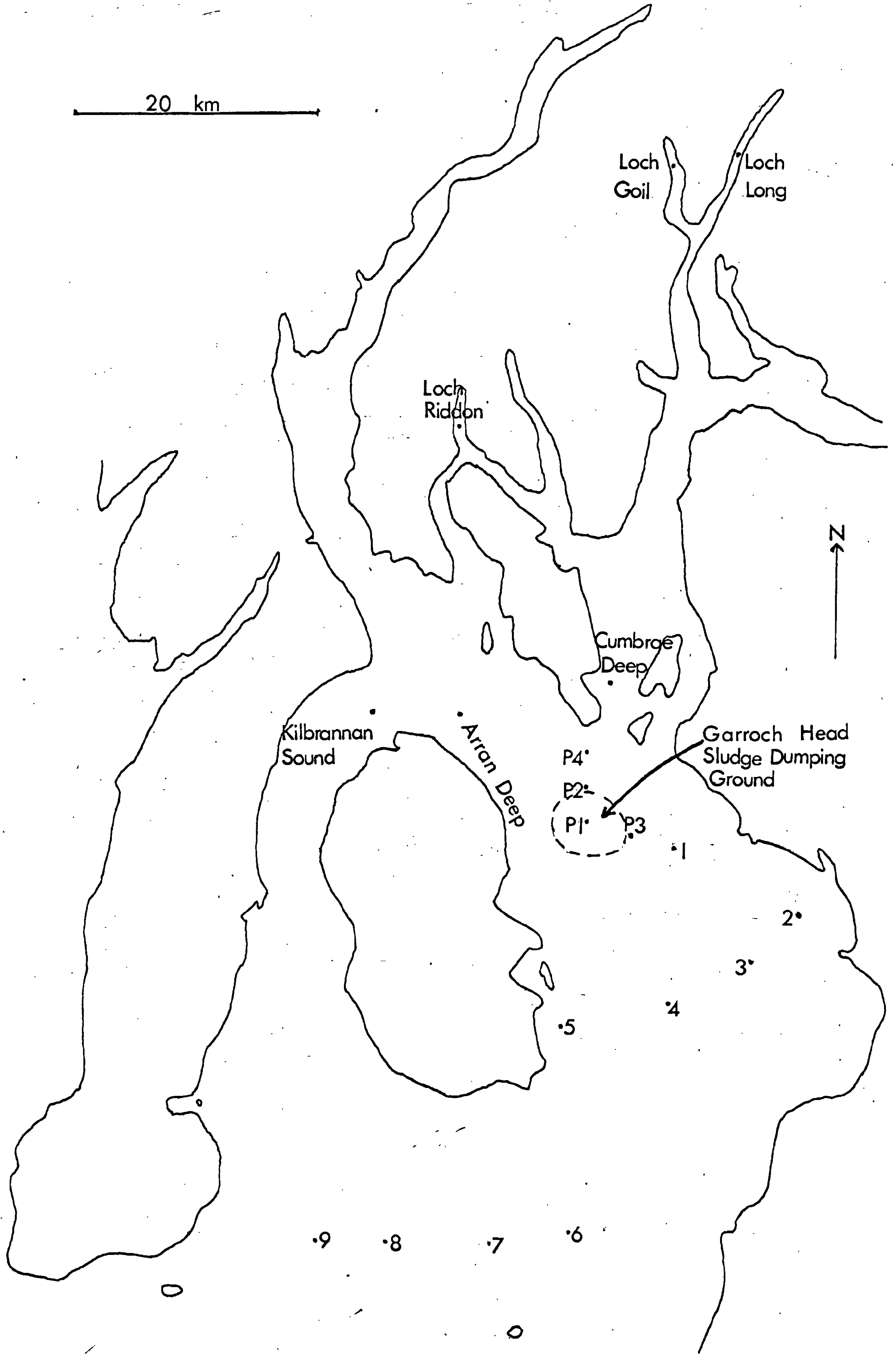


fig 3.I Sample sites in the Firth of Clyde.

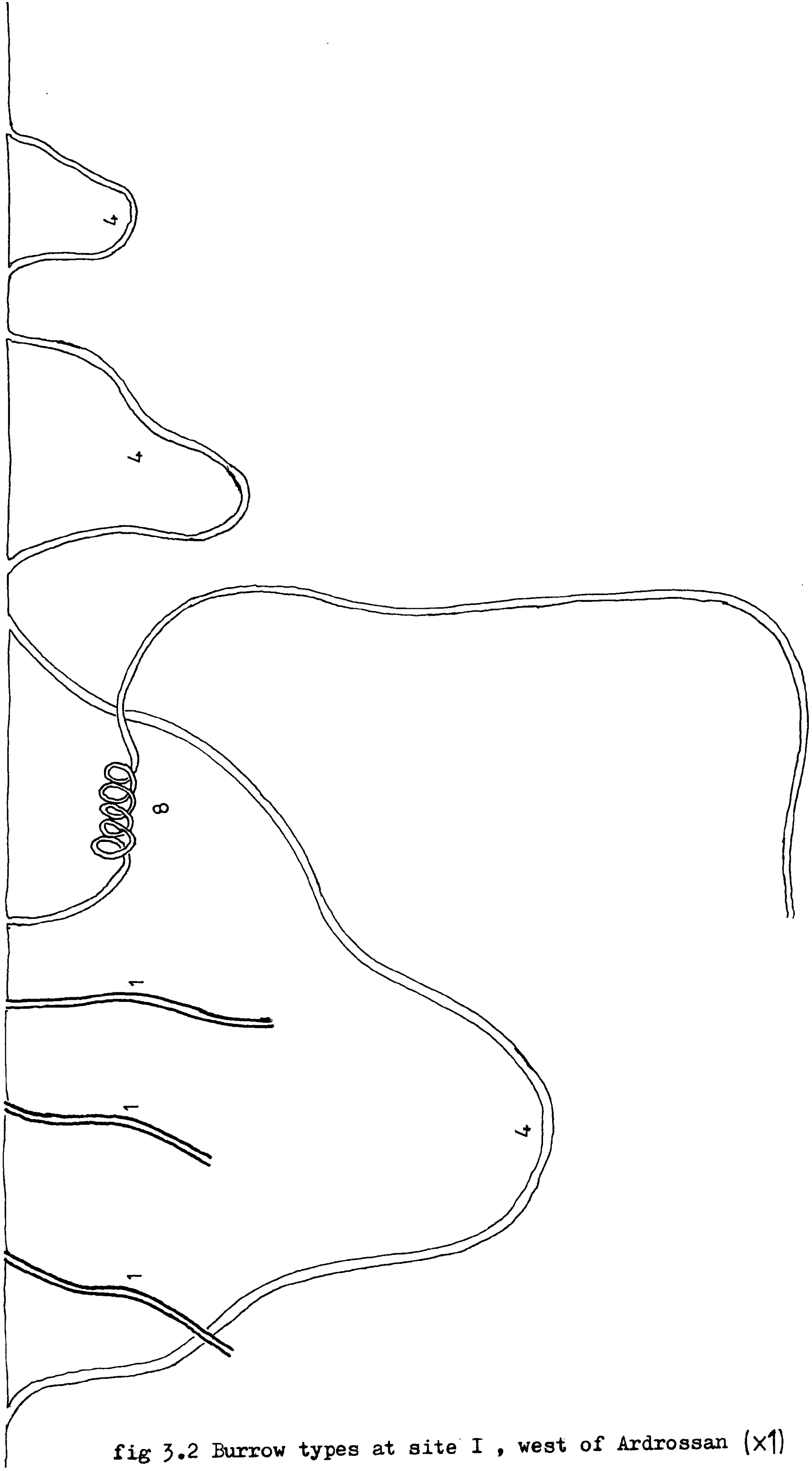


fig 3.2 Burrow types at site I , west of Ardrossan (X1)

3.1.1.2 Irvine Bay - Holy Island Transect

	Depth	Sand	Silt	Clay	
site 2	43 m	35	35	30	(fig 3.3) (Plate 2A, p234)
site 3	47 m	15	42	43	(fig 3.4)
site 4	76 m	-	32	68	(fig 3.5)
site 5	47 m	30	36	34	(fig 3.6)

In the top 4 cm of sediment all four cores contained 1 mm diameter tubes of mucus impregnated mud probably those of the spionid polychaete Spiophanes bombyx as well as branching burrows, 2 mm in diameter, constructed by the errant polychaete Nephtys hombergi.

Burrows at depths of 10 cm or more in the sediment were recorded from three cores; at sites 2 and 4 these were the wavy burrows of the capitellid polychaete Dasybranchus caducus but at site 5 a spiral burrow constructed by the capitellid Notomastus latericeus was found.

The irregular echinoid Brissopsis lyrifera was found at all four sites at a density of one/boxcore.

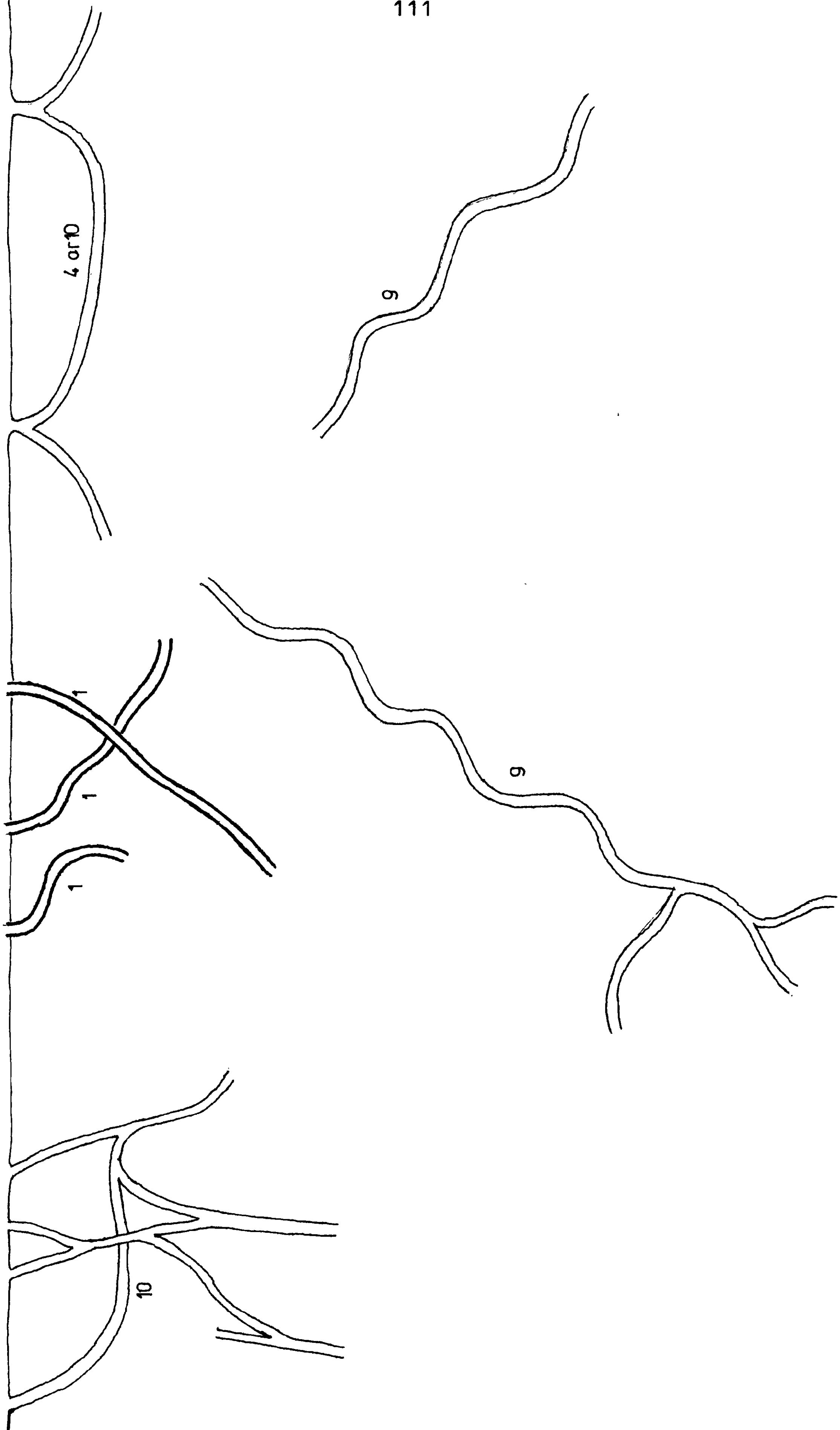


fig 3.3 Burrow types at site 2 (x1)

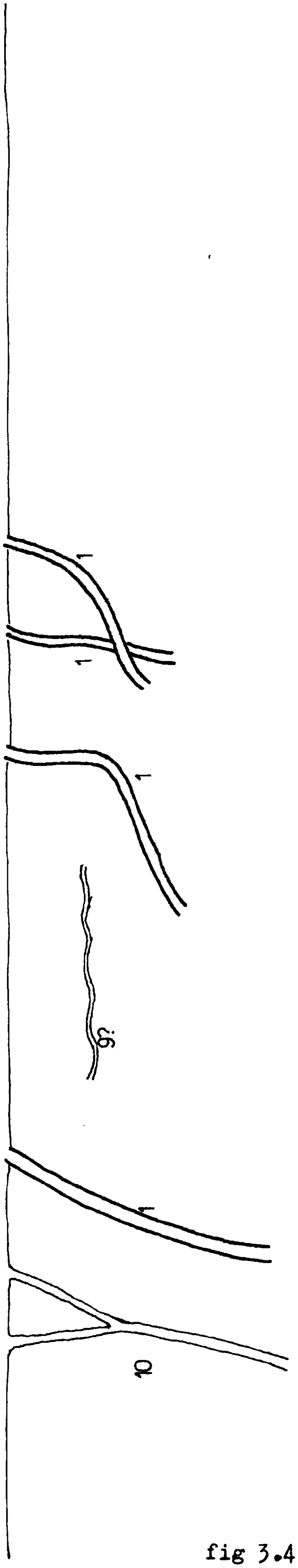


fig 3.4 Burrow types at site 3 (×1)

fig 3.5 Burrow types at site 4 (×1)

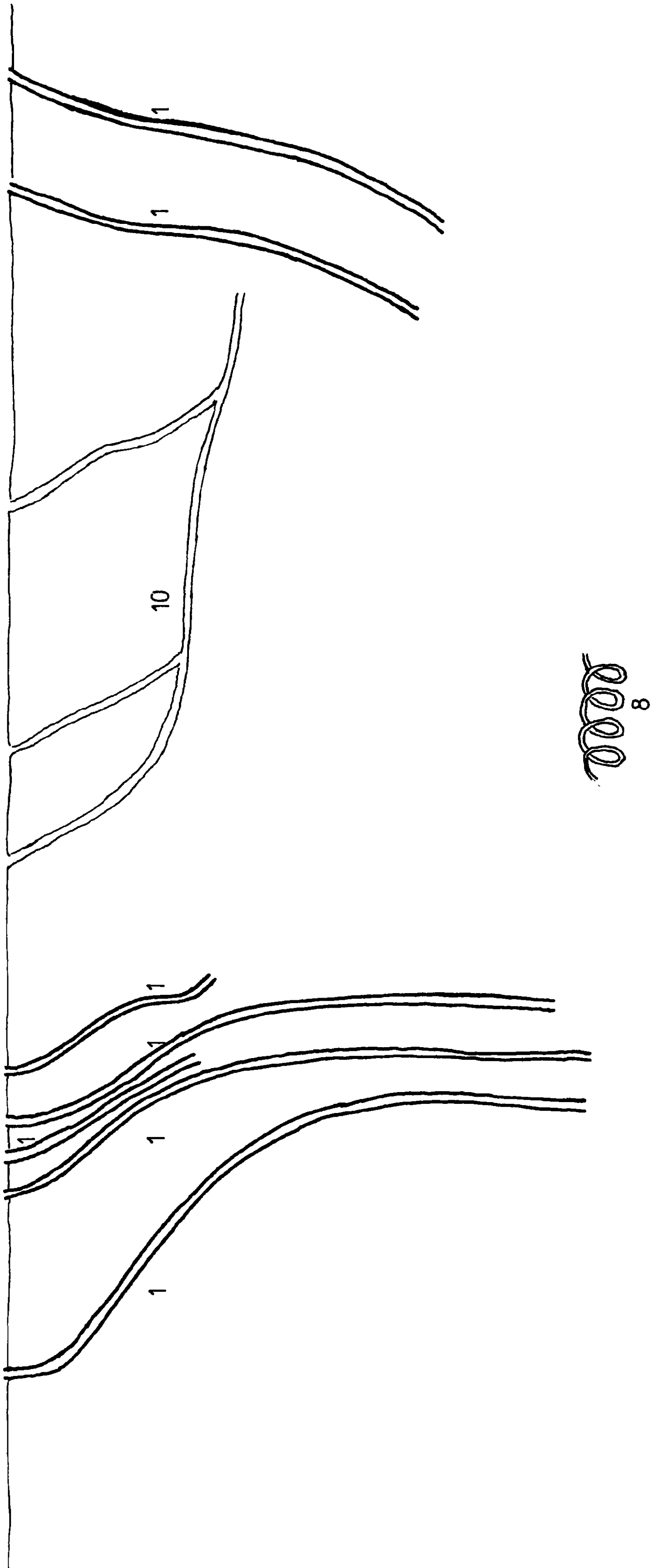


fig 3.6 Burrow types at site 5 (x1)

3.1.1.3 Mud plateau south of Arran

	Depth	Sand	Silt	Clay	
site 6	56 m	-	54	46	(fig 3.7)
site 7	54 m	5	48	47	(fig 3.8)
site 8	50 m	8	50	42	(fig 3.9)
site 9	47 m	30	42	28	(fig 3.10) (Plate 7B,p239)

The commonest type of burrow recorded from these boxcores was 2 mm branching burrows constructed by the errant polychaete Nephtys hombergi. Shallow U-burrows built by the polychaete Scalibregma inflatum or the holothurian Leptosynapta inhaerens were found in small numbers. Tubes were comparatively rare and the deep wavy burrows of the capitellid Dasybranchus caducus were found only at site 6.

The sandy mud at site 9 contained the bivalve Mya truncata and large numbers of shells of the burrowing gastropod Turritella communis. The dead shells were oriented in all directions in the sediment and sometimes occurred in dense concentrations.

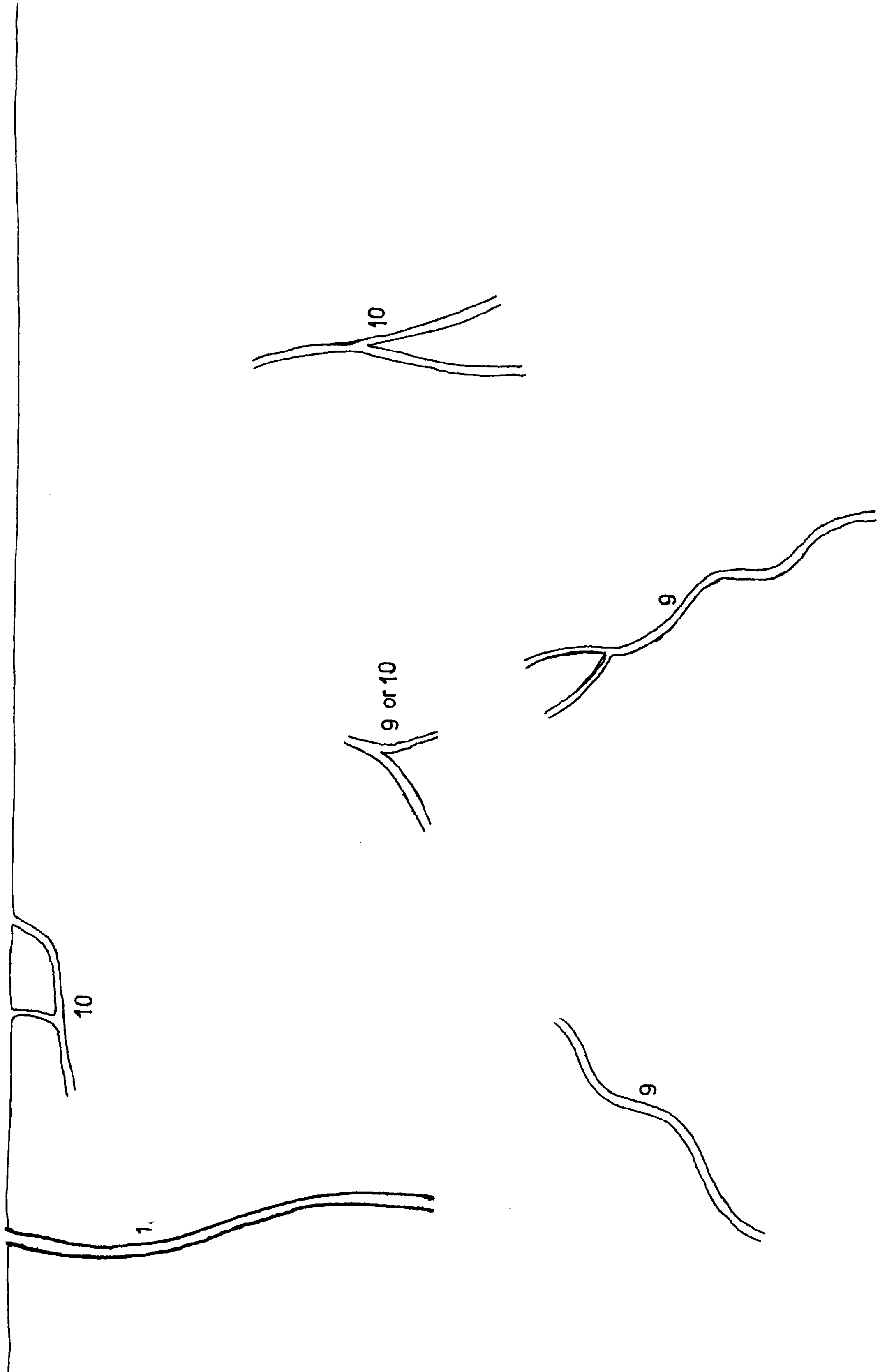


fig 3.7 Burrow types at site 6 (x1)

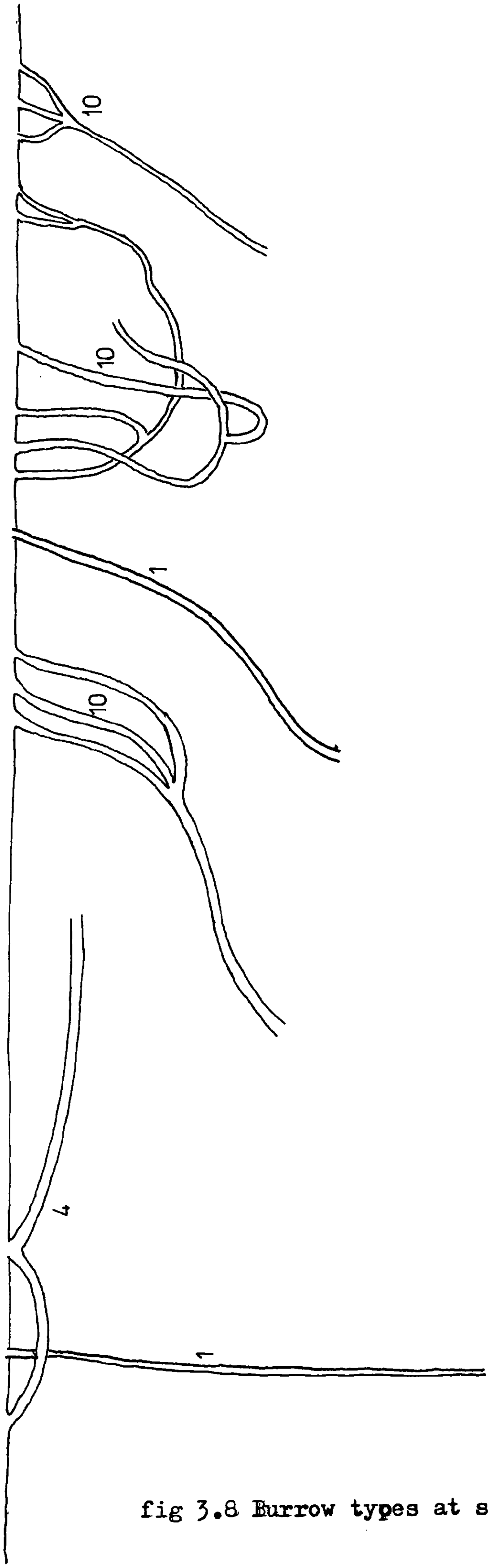


fig 3.8 Burrow types at site 7 (x1)

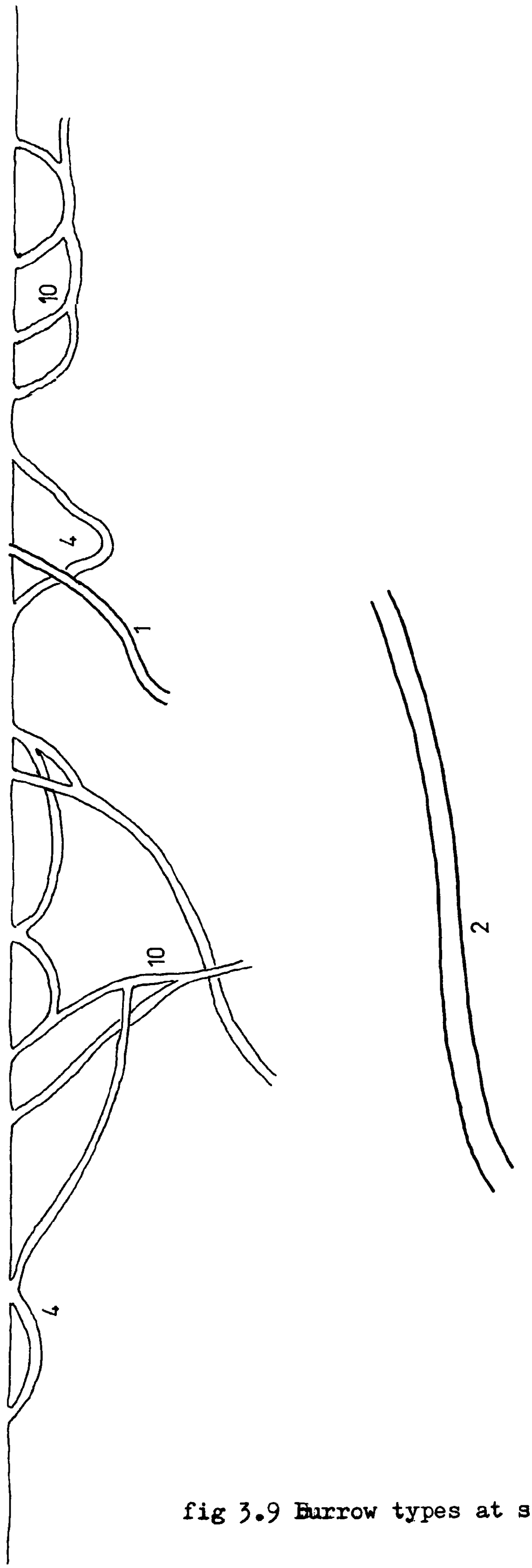


fig 3.9 Burrow types at site 8 (x1)

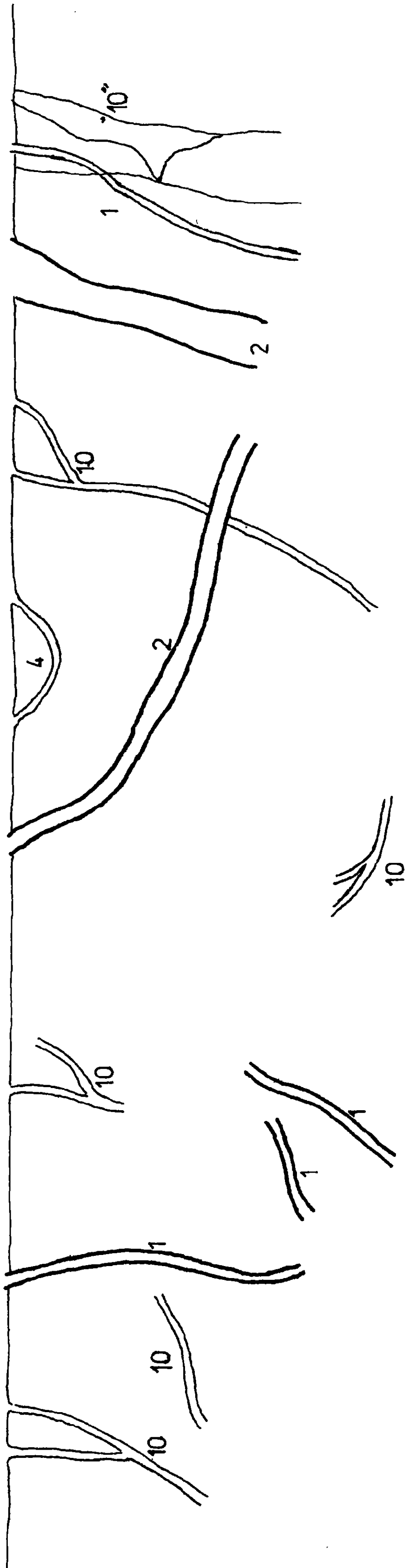


fig 3.10 Burrow types at site 9 (x1)

Table 3.2 Distribution of Burrow Types

Firth of Clyde - Shallow Marine Sites

Burrow Types

	TUBES			U BURROWS				SPIRALS		BRANCHING			Totals
	1	2	3	4	5	6	7	8	9	10	11	12	
site 1	X			X				X					3
site 2	X								X	X			3
site 3	X									X			2
site 4	X								X	X			3
site 5	X							X		X			3
site 6	X								X	X			3
site 7	X			X						X			3
site 8	X	X		X						X			4
site 9	X	X		X						X			4
Totals	9	2		4				2	3	8			

3.1.2 Deep Marine Sites (greater than 70 m depth) (Table 3.3)

3.1.2.1 Kilbrannan Sound

Depth: 124 m
Sediment: 53% sand, 15% silt, 31% clay
(fig 3.11)
(Plate 1A,p233.Plate 6B,p238)

In the three boxcores obtained from the sandy mud at this site burrows of three types were abundant:-

1. 1 mm diameter tubes oriented predominantly vertically in the sediment extending from the surface to a depth of around 6 cm. They often occurred in small aggregations with five tubes occurring in an area of 20 sq. cm. These tubes were constructed by the polychaetes Spiophanes bombyx and Owenia fusiformis.

2. 2 mm branching burrows mostly confined to the top 5 cm of sediment constructed by Nephtys hombergi and glycerids.

3. Portions of wavy burrows at depths of 10-15 cm below the sediment surface produced by the capitellid polychaete Dasybranchus caducus.

In addition:-

(a) Part of the burrow system of the crustacean Calocaris macandreae was found in one boxcore.
(b) A Pectinaria tube was found lying almost horizontally in the sediment at a depth of 10 cm.
(c) The ophiuroid Amphiura chiajei was recovered from boxcores but it destroyed its burrow on emerging at the sediment surface.

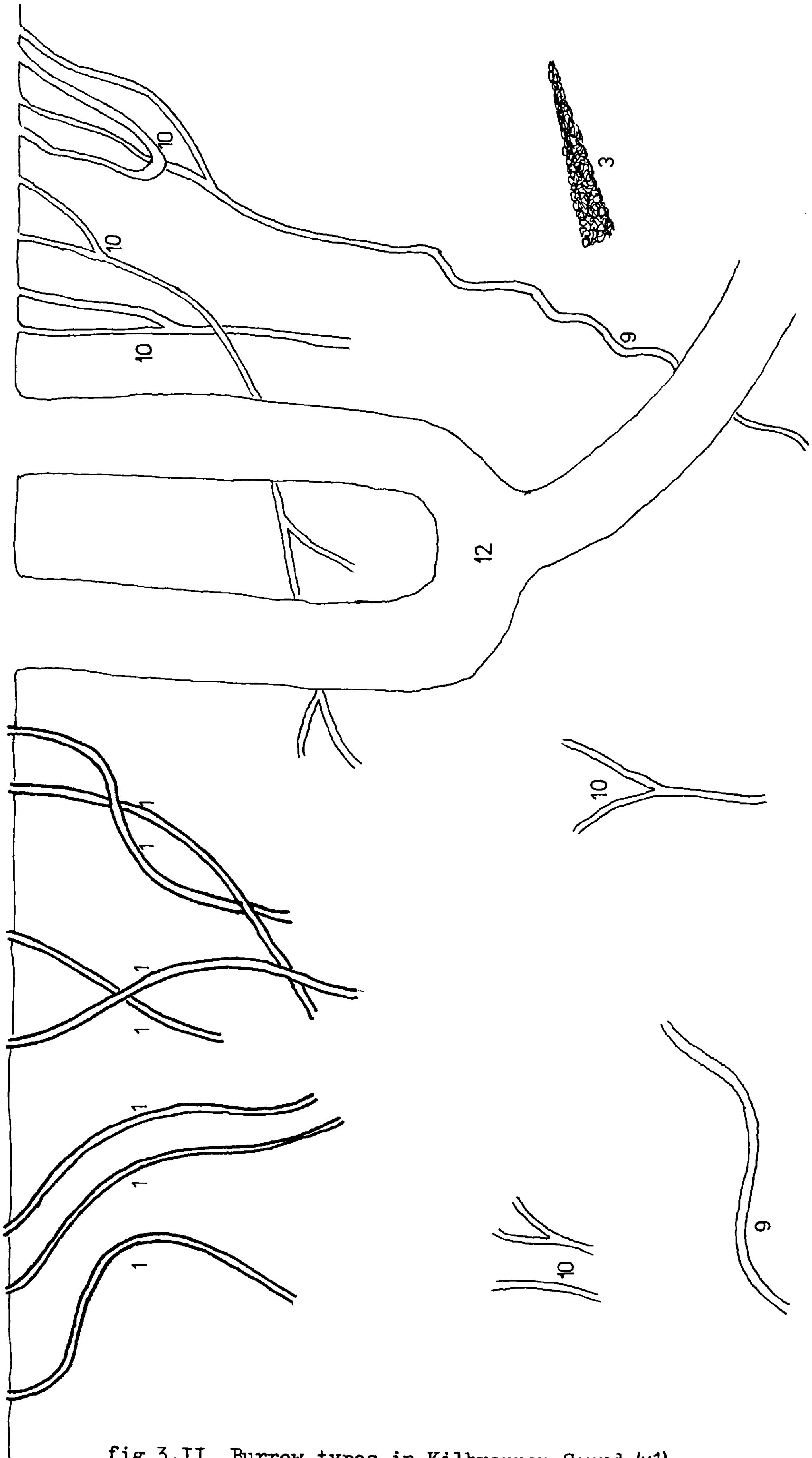


fig 3.II Burrow types in Kilbrannan Sound (x1)

3.1.2.2 Cumbrae Deep Depth: 105 m

Sediment: 26% coarser than sand, 34% sand

16% silt, 24% clay

(fig 3.12)

A boxcore from this site contained several burrows of the ophiuroid *Amphiura*, a few sections of branching burrows, several tubes and a shallow U-burrow. *Nephtys hombergi*, *Spiophanes bombyx* and *Scalibregma inflatum* are the probable builders of the latter three burrow types.

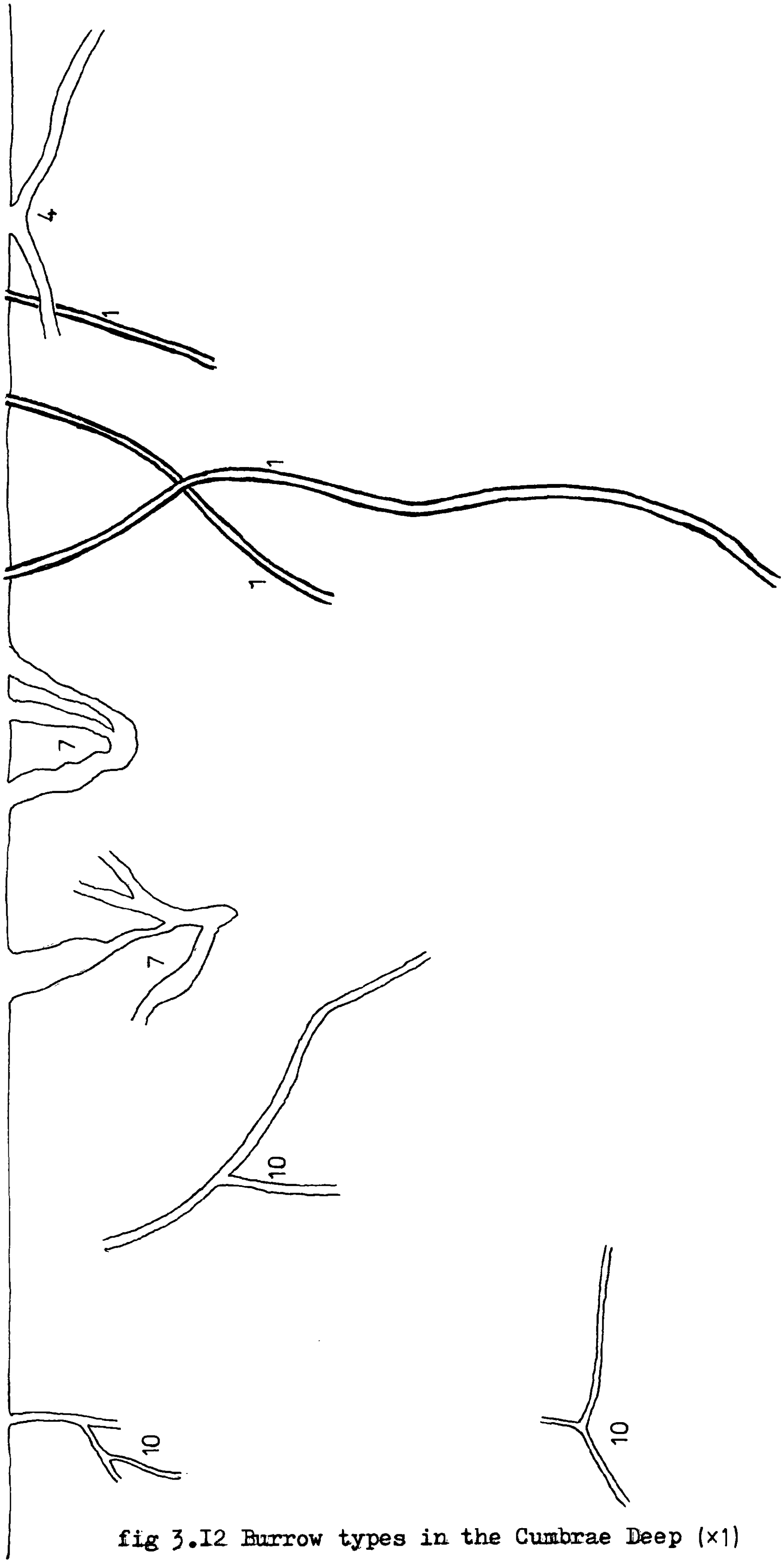


fig 3.12 Burrow types in the Cumbrae Deep (×1)

3.1.2.3 Arran Deep Depth : 170 m

Sediment : 30% silt, 70% clay

(fig 3.13)

(Plate 1B,p233.Plate 2B,p234.Plate 3A,3B, p235)

In the six boxcores obtained from the very fine sediment found at this site burrows of three types were abundant:-

1. 1 mm diameter tubes with a variety of forms: some run horizontally along the surface before turning vertical; others run vertically down from the surface and turn horizontal at a depth of 2-3 cm in the sediment; others run obliquely through the sediment.

   The tubes are produced predominantly by the spionid polychaete Spiophanes bombyx and the remainder by Spiochaetopterus typicus and maldanids.

2. 1 mm diameter branching burrows; some branch to give several surface entrances, others branch at depth from a single surface entrance. The probable producer is the errant polychaete Nephtys hombergi.

   Two examples of 1 mm diameter burrows which intersected at a depth of several centimetres from surface entrances 1-1.5 cm apart may represent a separate burrow type.

3. Sections of 2 mm diameter wavy burrows were found at depths of 10-20 cms in the sediment. They are produced by the deep burrowing capitellid polychaete Dasybranchus caducus.

In addition:-

(a) One boxcore contained a 4 mm diameter branching burrow system with many surface entrances. This was probably produced by the errant polychaete *Glycera alba*.

(b) Two types of U-burrow:-

  (i) Two 4 mm diameter U-burrows, one extending to a depth of 4 cm, the other to 1 cm, were probably built by the polychaete *Lipobranchius jeffreysi*.

  (ii) A 1 mm diameter U-burrow extending to a depth of 4 cm from surface entrances 8 cm apart was constructed by either the polychaete *Scalibregma inflatum* or the holothurian *Leptosynapta inhaerens*.

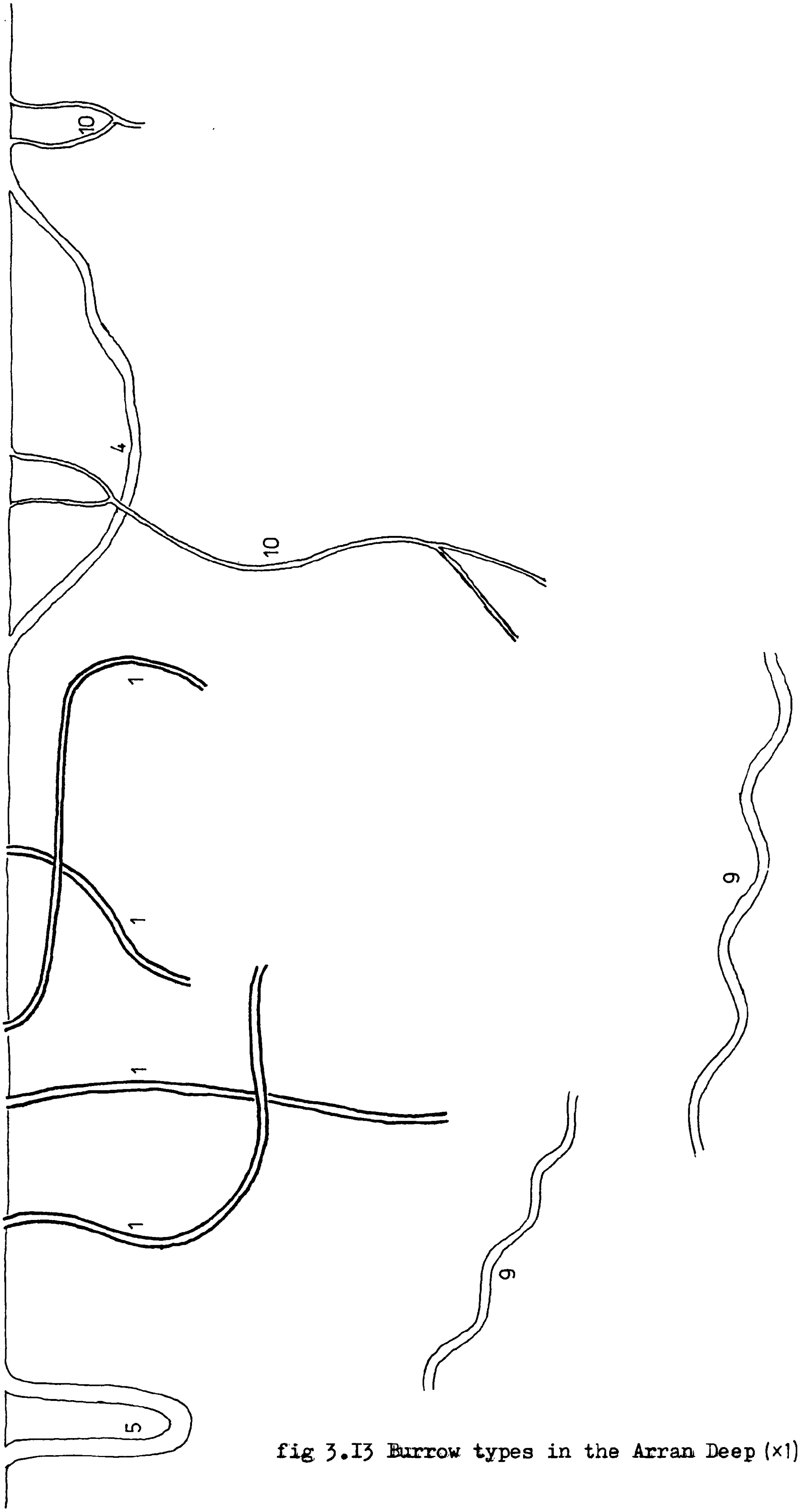


fig 3.13 Burrow types in the Arran Deep (×1)

Table 3.3 Distribution of Burrow Types:

Firth of Clyde - Deep Marine Sites

Burrow Types

	TUBES			U-BURROWS				SPIRALS		BRANCHING BURROWS			
Sample Sites	1	2	3	4	5	6	7	8	9	10	11	12	Total
Kilbrannan Sound (3 boxes) 1	X		X						X	X			4
2	X								X	X			3
3	X						X		X	X		X	5
Arran Deep (6 boxes) 1	X									X			2
2	X								X	X			3
3	X								X	X	X		4
4	X			X	X				X	X			5
5	X			X					X	X			4
6	X								X	X			3
Cumbrae Deep	X			X			X			X			4
Total	10		1	3	1		2		8	10	1	1	

3.1.3 Sea Loch Sites (Table 3.4)

3.1.3.1 Loch Riddon

Depth : 30 m

Sediment : sand 35%, silt 35%, clay 30%

(fig 3.14)

(Plate 4A,p236.Plate 5A,p237.
Plate 7A,p239)

The commonest burrow type in the four boxcores taken at this site was 1 mm diameter tubes of mucus impregnated mud oriented predominantly vertically in the sediment and extending to depths of 10 cm below the sediment surface. These are constructed mainly by the ampharetid polychaete Amage adspersa.

Subhorizontal 2 mm diameter tubes, confined to the top 5 cm of sediment, constructed by the terebellid polychaete Terebellides stroemi, were recorded from two boxcores.

Branching 2 mm burrows consisting predominantly of vertical burrows in the top 8 cm of the sediment were probably constructed by Nephtys hombergi.

One shallow U-burrow extending to a depth of 2 cm, was recorded. This was constructed by the holothurian Cucumaria elongata.

Deep, 2 cm diameter, leathery U-tubes, extending to depths of 30 cm, produced by the polychaete Chaetopterus variopedatus, were found in two boxcores. U-burrows, built by the bivalve Thracia convexa to depths of 10-20 cm, were found in two boxcores.

Complex systems of vertical shafts sloping galleries built by Amphiura chiajei to depths of 10 cm below the sediment surface, were found in the sediment at this site.

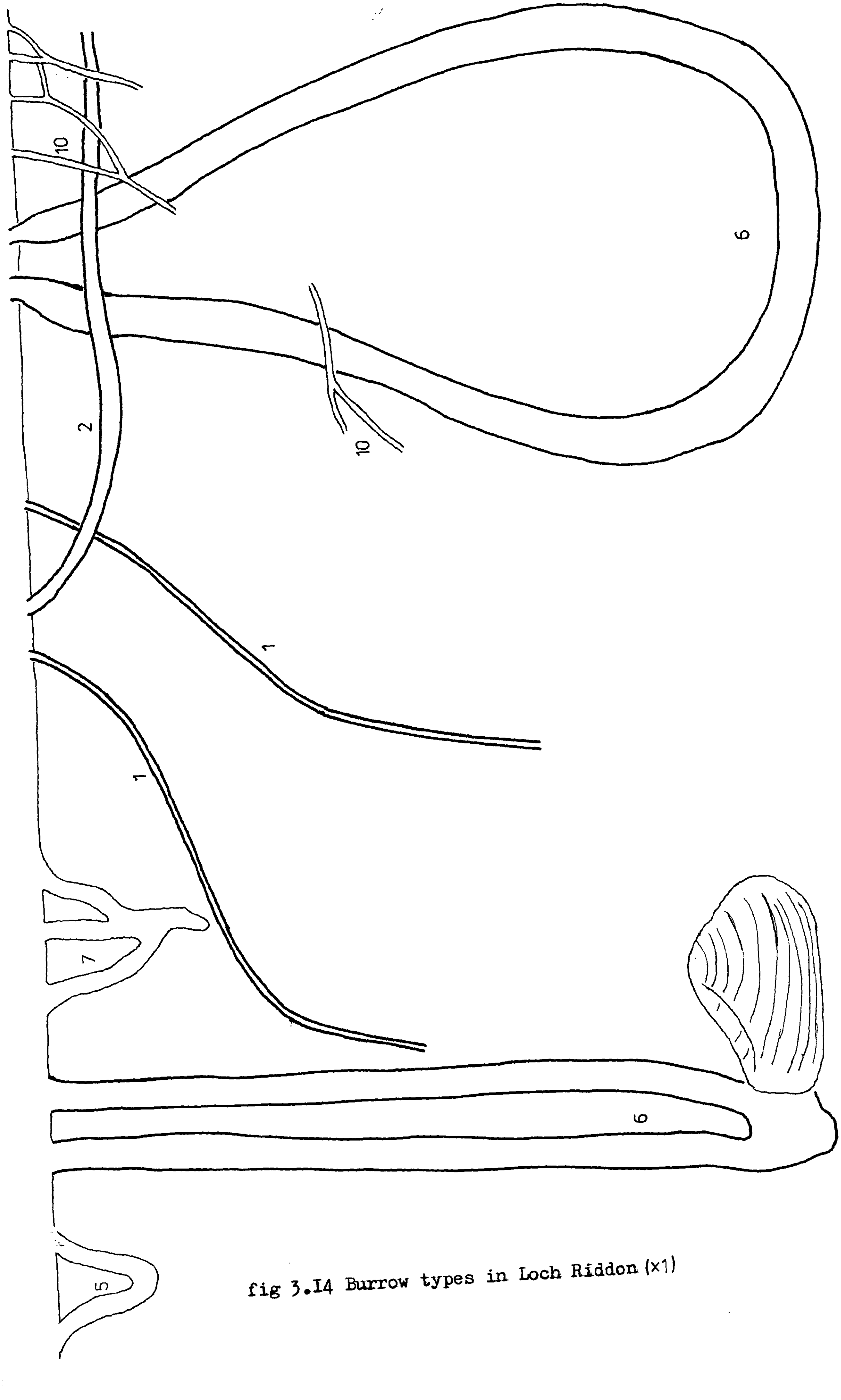


fig 3.14 Burrow types in Loch Riddon (x1)

3.1.3.2 Loch Goil

Depth : 77 m

Sediment : 8% sand, 70% silt, 22% clay

(fig 3.15)

A boxcore from this site contained 1 mm diameter tubes and 1 mm branching burrows in the top 8 cm. The tubes were oriented obliquely in the sediment and were probably built by ampharetid polychaetes. The branching burrows were of two forms: one set consisted of linked shallow U-burrows; the other of vertically oriented Y-burrows. *Nephtys hombergi* and glycerids were the probable producers.

3.1.3.3 Loch Long (fig 3.16)

Subsamples of boxcores taken with a length of gravity core liner from sites along the length of the Loch, contained portions of tubes and branching burrows.

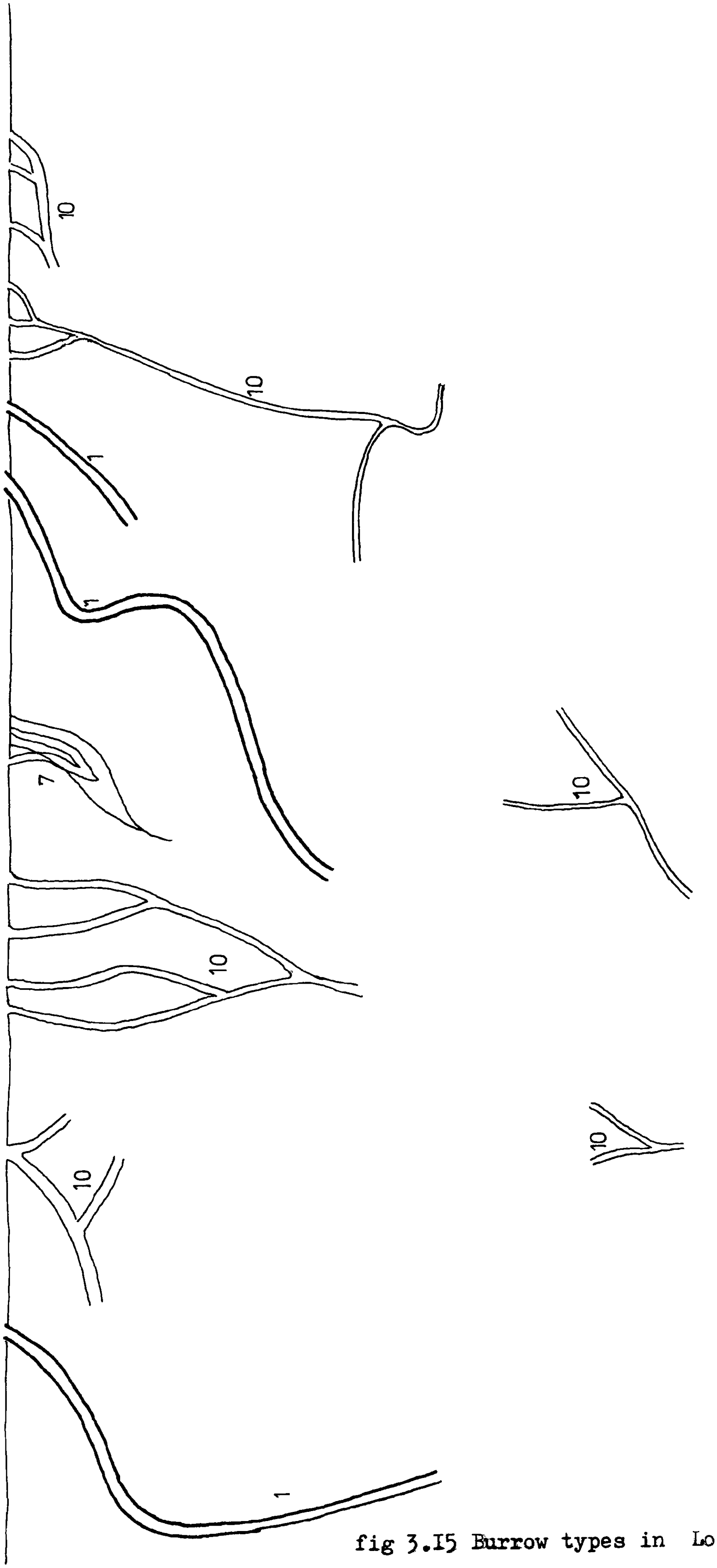


fig 3.I5 Burrow types in Loch Goil (x1)

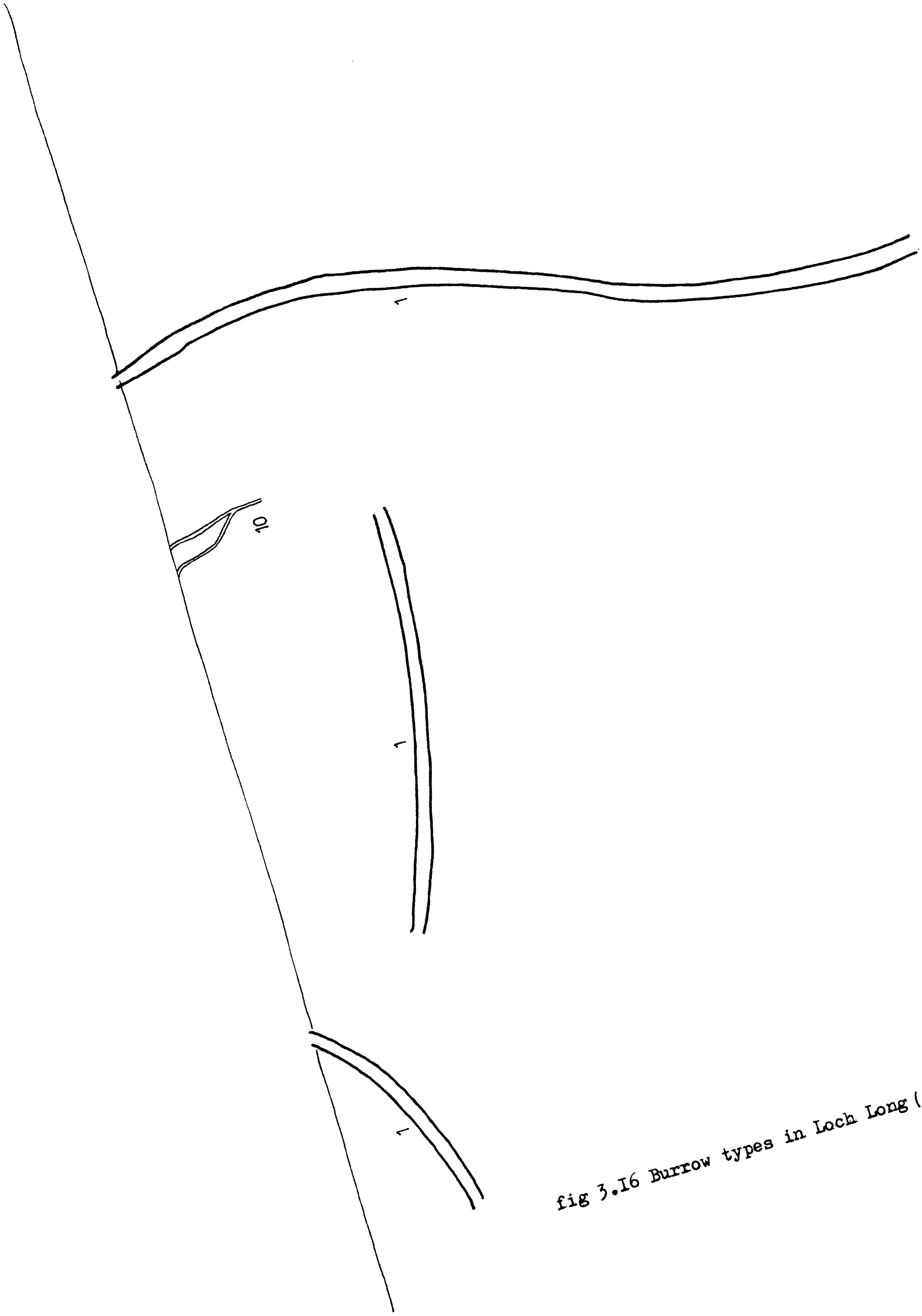


fig 3.16 Burrow types in Loch Long (x1)

Table 3.4 Distribution of Burrow Types:

Firth of Clyde - Sea Loch Sites

	TUBES			U-BURROWS				SPIRALS		BRANCHING BURROWS			
Sample Sites	1	2	3	4	5	6	7	8	9	10	11	12	Total
Loch Riddon (4 boxes) 1	X	X				X				X			5
2	X	X				X				X			4
3	X			X			X			X			4
4	X					X	X			X			4
Loch Goil	X						X			X			3
Loch Long	X									X			2
Total	6	2		1		3	3			6			

Table 3.5 Distribution of Burrow Types:

Firth of Clyde - Polluted Sites

	TUBES			U-BURROWS				SPIRALS		BRANCHING BURROWS			
Sample Sites	1	2	3	4	5	6	7	8	9	10	11	12	Total
Firth of Clyde P1										X			1
P2	X	X		X			X						4
P3		X		X						X			3
P4	X									X			2
Total	2	2		2			1			3			

3.1.4 Polluted Sites (Garroch Head Sludge Dumping Ground) (Table 3.

3.1.4.1 Site P1 Centre of new dump site Depth: 79 m (fig 3.17)

(Plate 8B,p240)

The dark anaerobic sediment was riddled with a network of 1 mm diameter burrows to a depth of 4 cm. These were constructed by *Capitella capitata*, a common indicator of polluted sediments (Pearson & Rosenberg,1978).

3.1.4.2 Site P2 Between old and new dump sites Depth: 74 m (fig 3.18)

The dominant burrow type at this site was 1 mm diameter vertical tubes built by the spionid polychaete *Spiophanes bombyx*. The other conspicuous burrow type was 3 mm diameter horizontal tubes in the top 2 cm of the sediment constructed by the terebellid polychaete *Terebellides stroemi*. In addition, an *Amphiura* burrow and a 2 mm diameter U-burrow were also found.

3.1.4.3 Site P3 Edge of new dump site Depth: 72 m (fig 3.19)

(Plate 8A,p240)

A boxcore from this site contained shallow U-burrows and horizontal tubes; spionid tubes were noticeably absent. 2 mm U-burrows in the top 5 cm of the sediment were produced by the polychaete *Scalibregma inflatum*. Subhorizontal tubes, 4 mm in diameter, were probably constructed by *Terebellides stroemi*.

3.1.4.4 <u>Site P4</u> Old dump site Depth: 83 m (fig 3.20)

A layer of dense solids at a depth of 2-4 cm showed up clearly on X-ray radiographs. This layer was penetrated by tubes and U-burrows which extended to depths of 6-10 cm in the sediment.

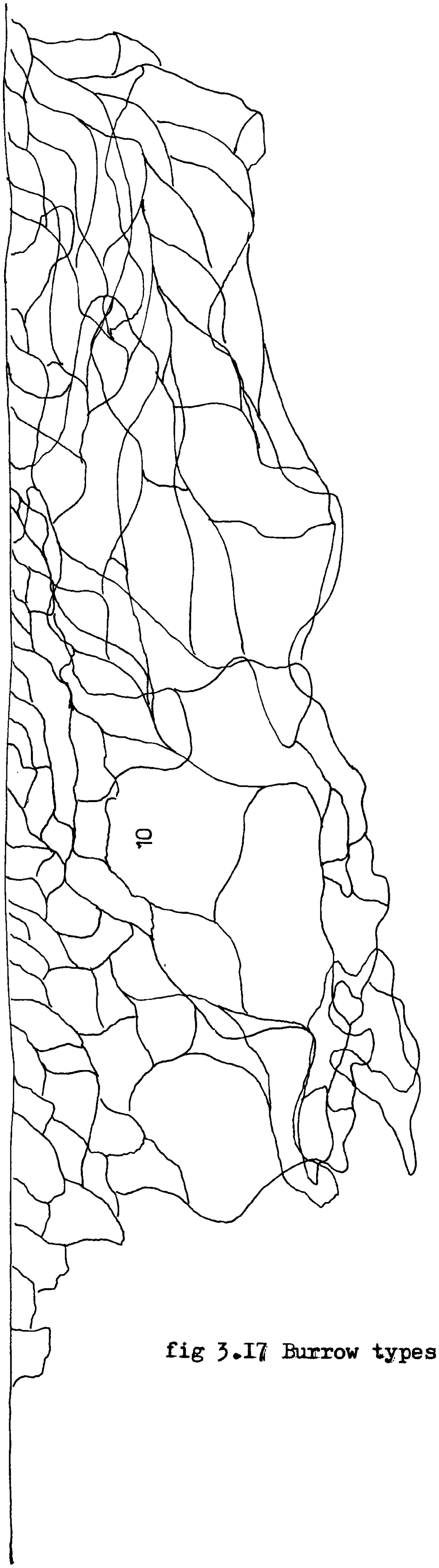


fig 3.17 Burrow types at site P1 (×1)

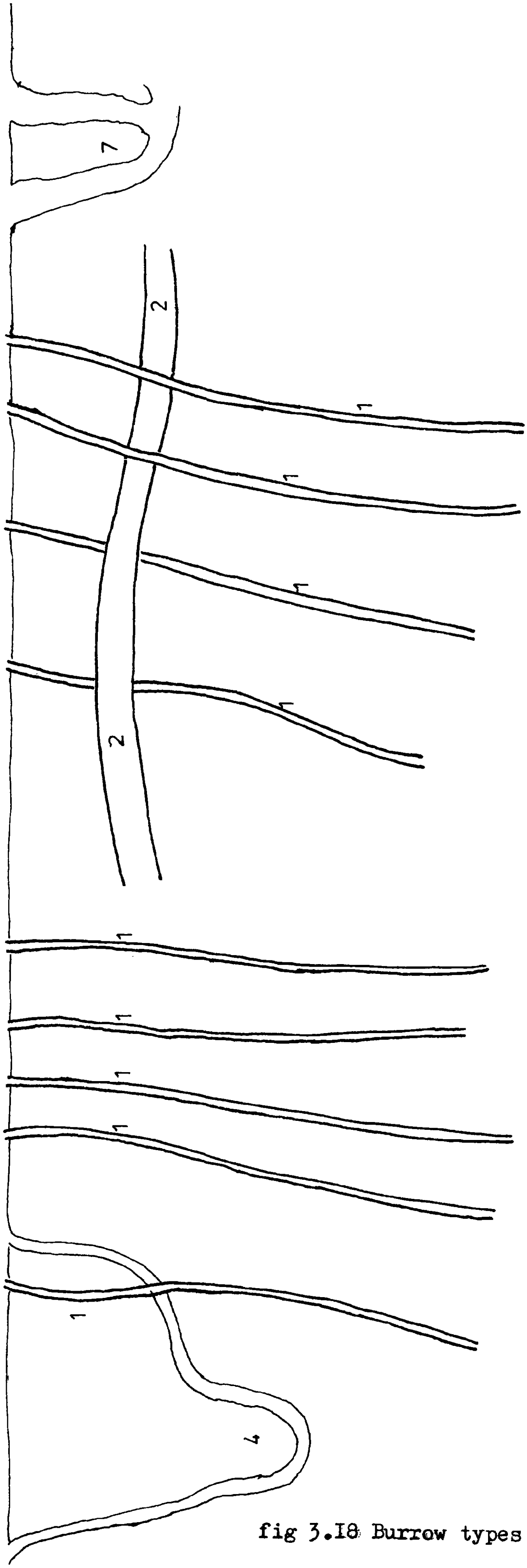


fig 3.18 Burrow types at site P2 (×1)

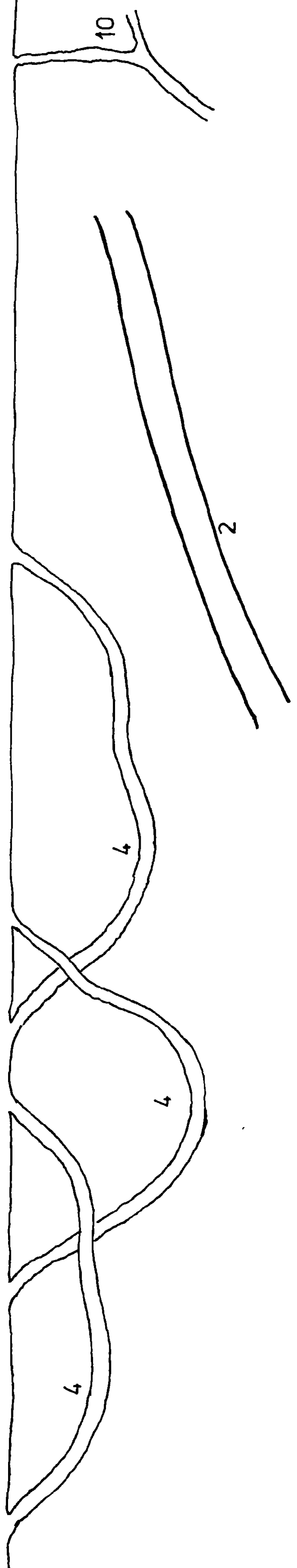


fig 3.19 Burrow types at site P3 (×1)

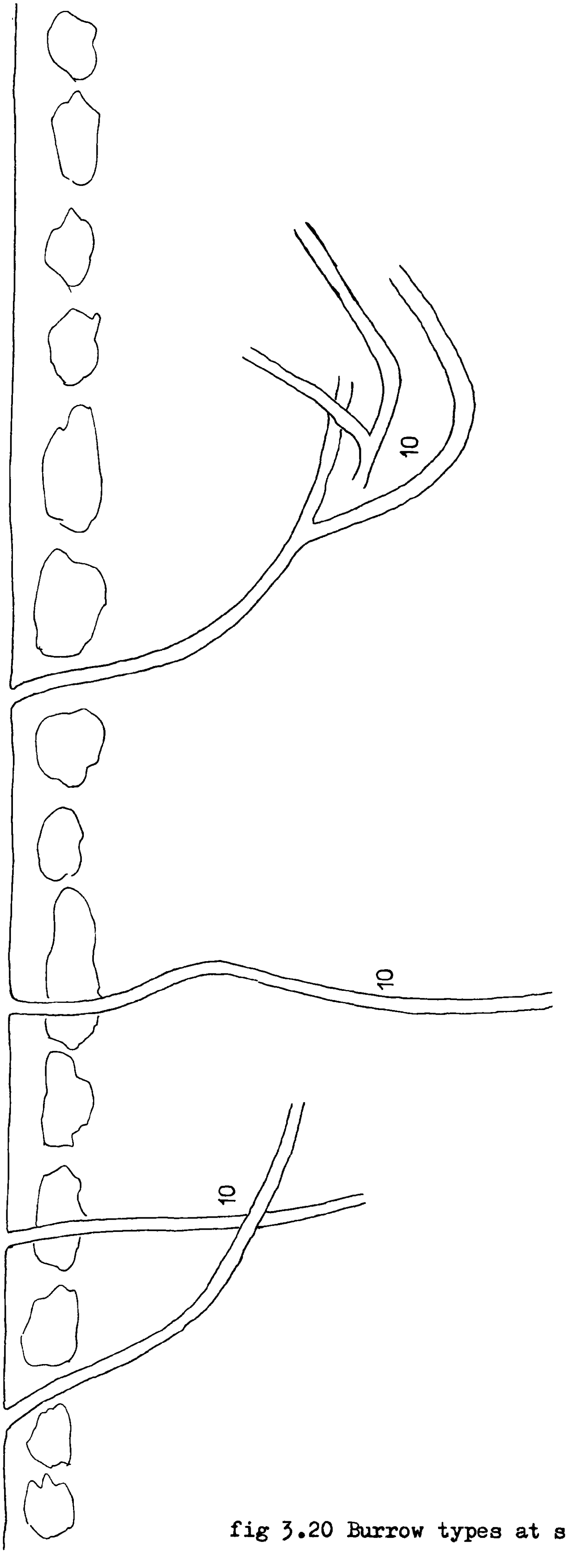


fig 3.20 Burrow types at site P4 (x1)

3.2 Argyll Sea Lochs and Sounds

3.2.1 Argyll Open Marine Sites (Table 3.6)

3.2.1.1 Ardmucknish Bay Depth: 50 m Sediment: 10% sand, 30% silt, 60% clay

(figs 3.21, 3.22)

Burrows were not abundant in the eight boxcores taken at this site.

Seven burrow types were identified:-

1. 1 mm diameter subvertical tubes extending to depths of 10-13 cm in the sediment probably produced by the maldanid polychaete *Rhodine gracilior*.
2. 2 mm diameter subvertical tubes extending to depths of 11 cm probably produced by the spionid polychaete *Spiophanes kroyeri*.
3. 2 mm diameter branching burrow systems with many surface entrances confined to the top 2 cm of sediment constructed by *Nephtys hystricis* and *Glycera alba*.
4. Intensive 0.5 mm burrow networks confined to the top 4 cm of the sediment possibly produced by the hesionid polychaete *Ancistrosyllis groenlandica*.
5. 1 mm diameter U-burrows extending to depths of 4.5-7 cm produced by the holothurian *Leptosynapta inhaerens*.

6. Vertical burrows with a diameter between 2 and 3 mm and extending to depths of 4-8 cm. They branch to give several surface entrances. The shallow ones are produced by the ophiuroid *Amphiura chiajei* and the deep ones may in part be the tubes constructed by the deep burrowing bivalve *Thracia convexa*.

7. Spiral burrows, 2 mm in diameter at depths of 6-14 cm, produced by the capitellid polychaete *Notomastus latericeus*.

The distribution of these burrows amongst the boxcores taken at this site is shown in Table 3.6.

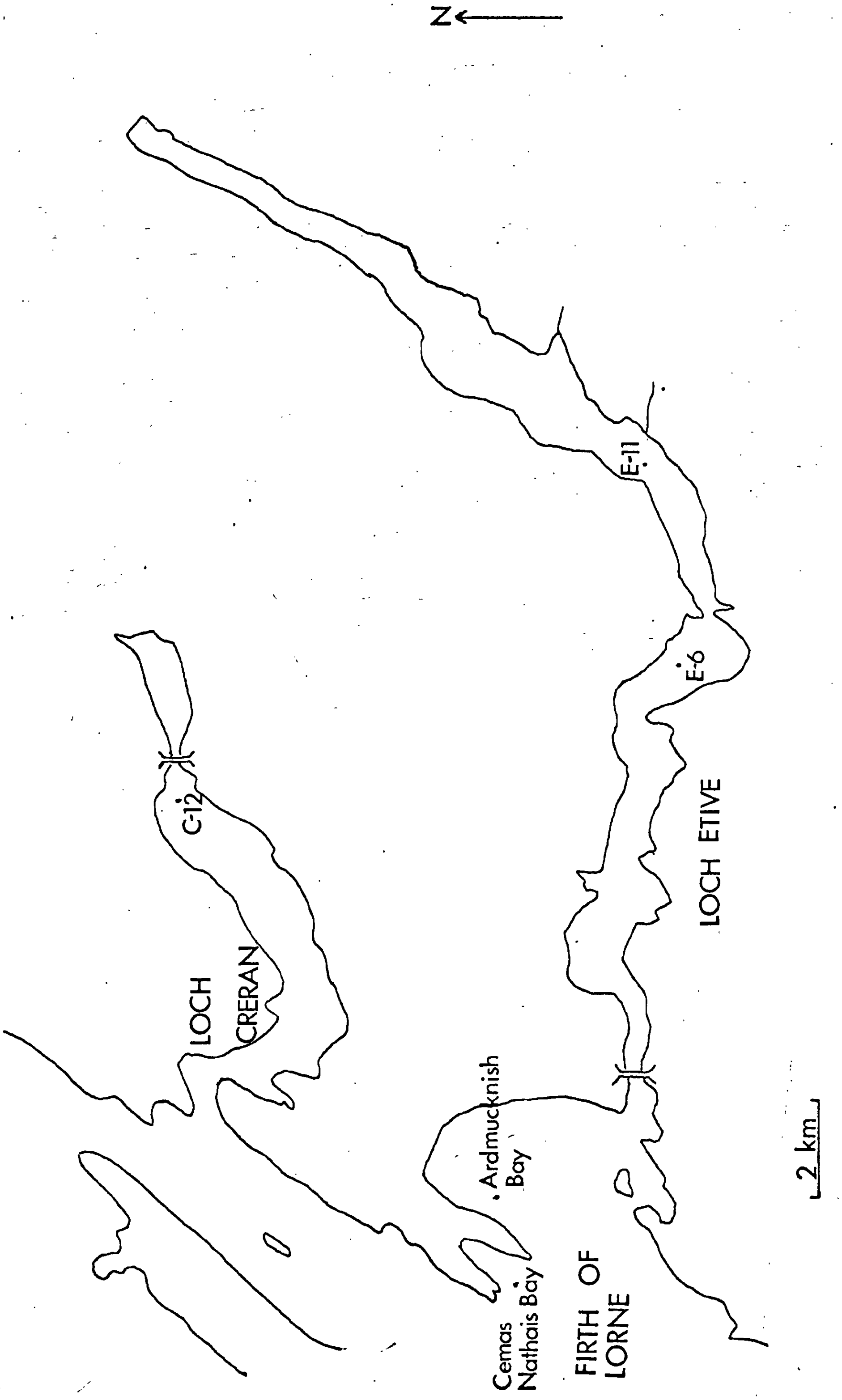


fig 3.21 Sample sites in Loch Etive, Loch Creran and the Firth of Lorne redrawn from Gage (1972)

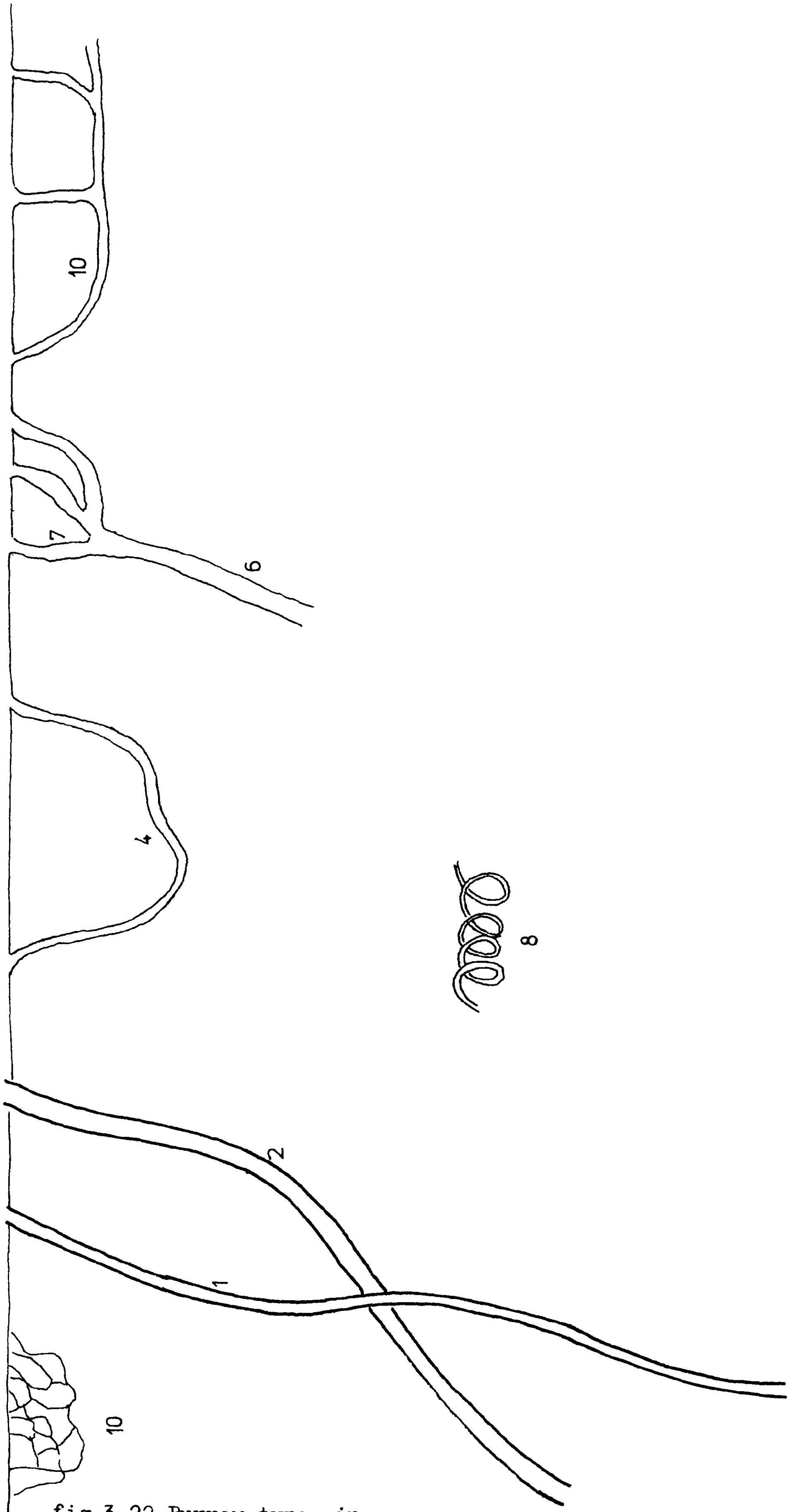


fig 3.22 Burrow types in Ardmucknish Bay (x1)

3.2.1.2 Cemas Nathais Bay Depth: 25 m Sediment: 27% sand, 17% clay
56% silt
(figs 3.21, 3.23)
(Plate 4B,p236)

Two boxcores taken at this site contained the seven burrow types described from the neighbouring Ardmucknish Bay. In addition, shells of the infaunal gastropod Turritella communis were abundant.

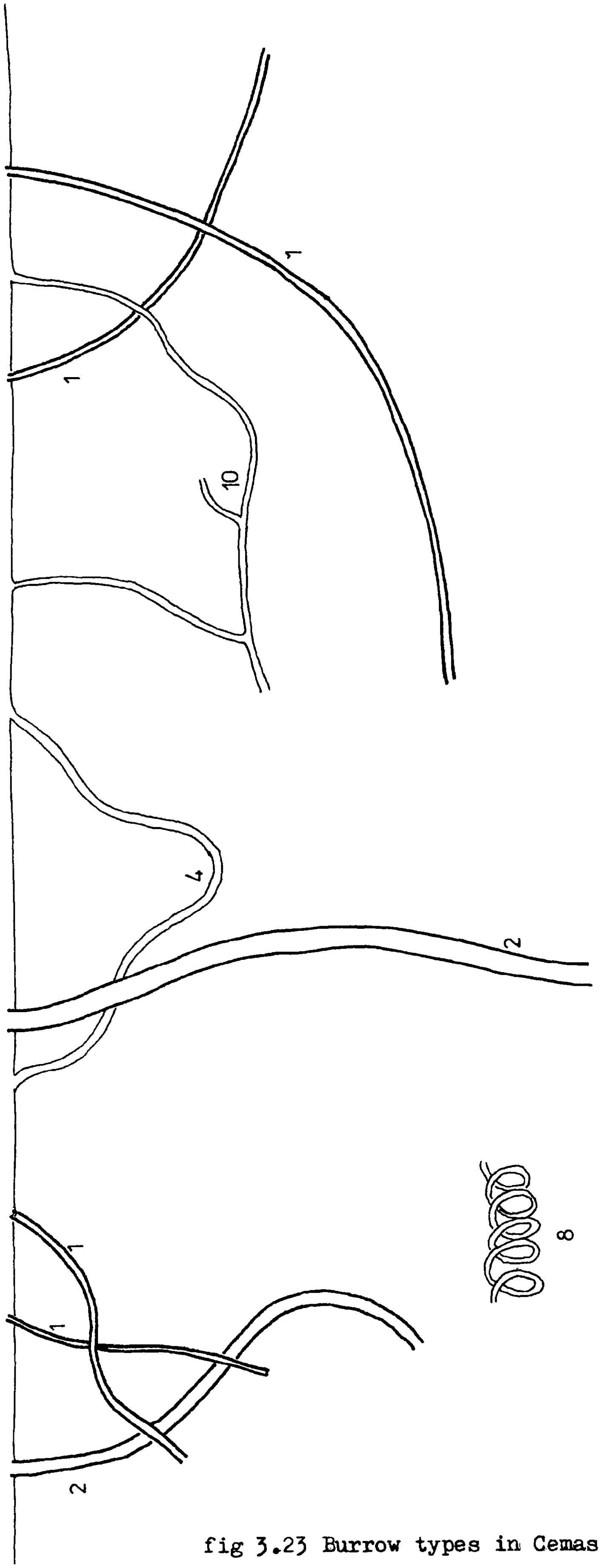


fig 3.23 Burrow types in Cemas Nathais Bay (x1)

3.2.1.3 Sound of Mull Depth: 66 m Sediment: 17% sand, 47% silt, 36% clay (figs 1.1, 3.24)

In the three boxcores taken at this site very few burrows were found. Several tubes running obliquely through the sediment, one to a depth of 10 cm and the remainder to depths of 5-6 cm, were found. The producers were probably Owenia fusiformis and spionid polychaetes.

A few spiral burrows produced by the capitellid polychaete Notomastus latericeus were found at depths of 12-18 cm below the sediment surface.

One boxcore contained part of the burrow system of the crustacean Calocaris macandreae and sloping shafts produced by the ophiuroid Amphiura filiformis were also observed.

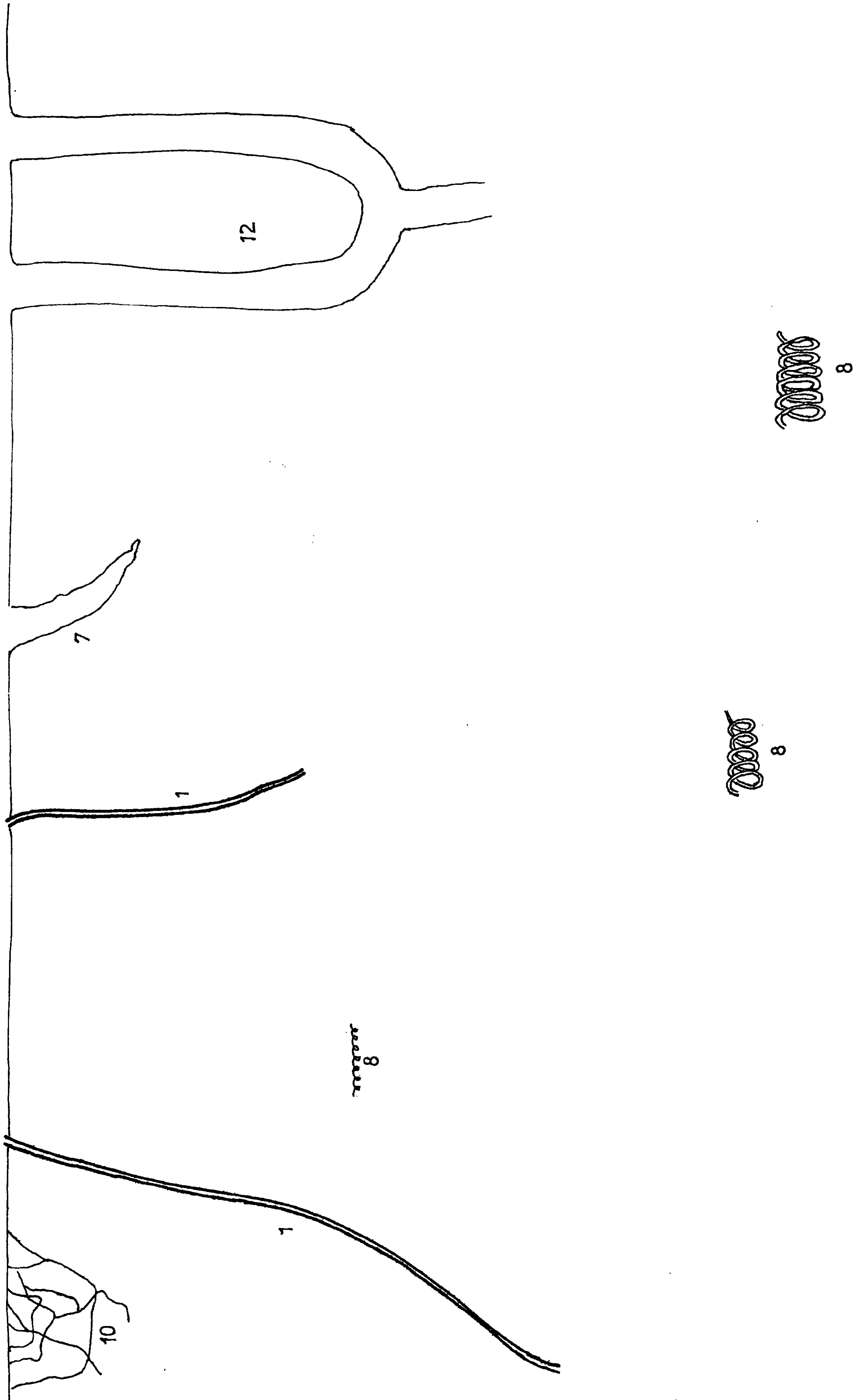


fig 3.24 Burrow types in the Sound of Mull (×1)

3.2.1.4 Sound of Jura Depth: 216 m Sediment: 33% sand, 47% silt, 20% clay

(figs 1.1, 3.25)

(Plate 6A,p238)

The only burrow type common to all four boxcores taken at this site was 2 mm diameter branching burrows extending to depths of 8 cm in the sediment. They were produced by Nephtys hombergi or N. hystricis.

Two boxcores contained large numbers of spiral burrows at depths of 5-24 cms in the sediment. These were constructed by the capitellid polychaete Notomastus latericeus.

5 mm diameter unbranched burrows running subhorizontally through the sediment up to 20 cm below the sediment surface were found in two boxcores (one of which also contained spiral burrows). The producer of these burrows is unknown; the priapulid Priapulus caudatus is tentatively suggested.

Two 5 mm diameter tubes with shell debris placed in an imbricate manner along the tube which ran for up to 8 cm along the sediment surface were found. The eunicid polychaete Onuphis conchylega is a possible producer of such tubes. 1 mm diameter tubes were rare; portions of the burrow of the ophiuroid Amphiura were also observed.

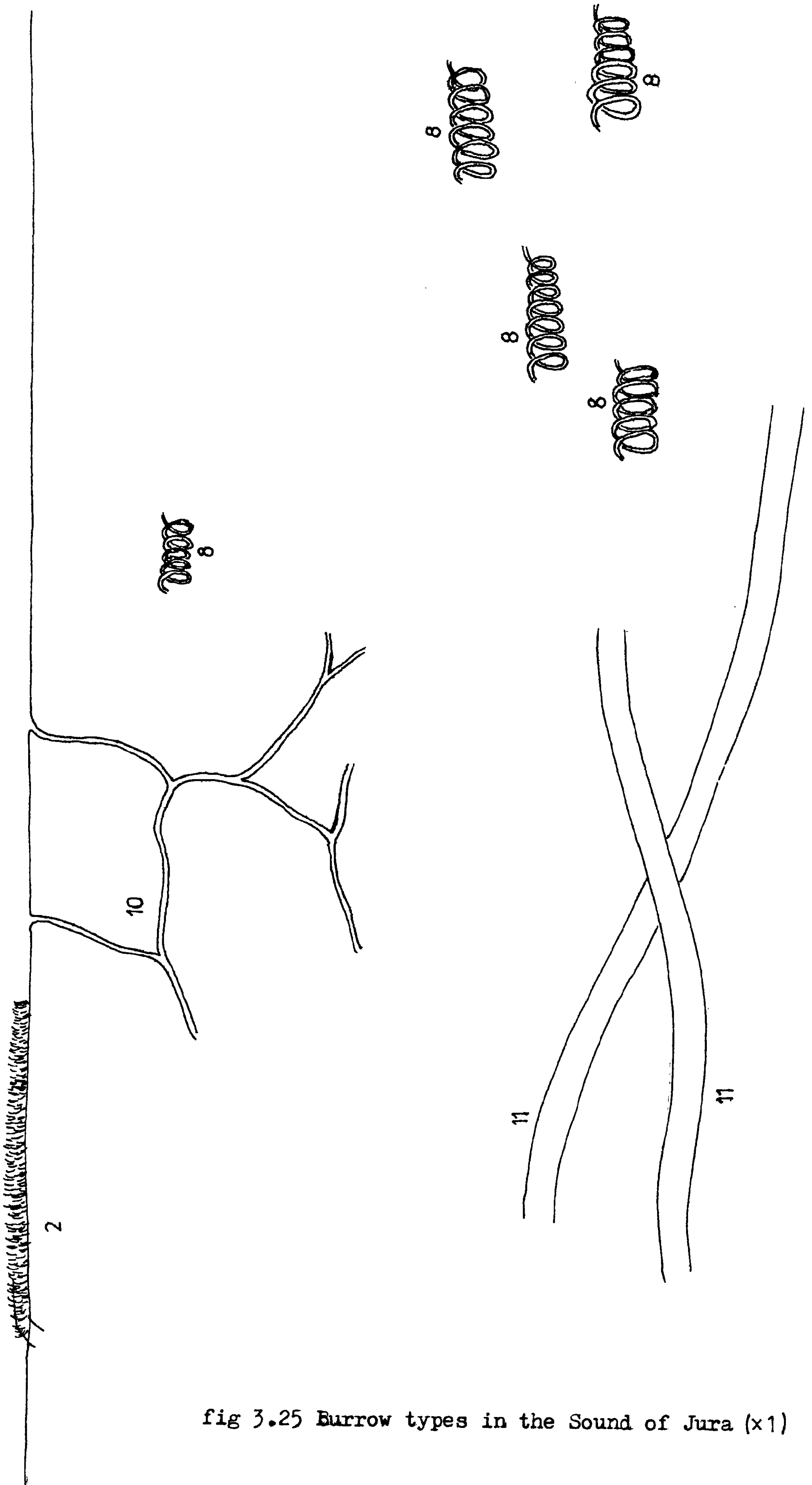


fig 3.25 Burrow types in the Sound of Jura (x1)

Table 3.6 Distribution of Burrow Types:

Argyll Open Marine Sites

Burrow Types

		TUBES			U-BURROWS				SPIRALS		BRANCHING BURROWS			
Sample sites		1	2	3	4	5	6	7	8	9	10	11	12	Total
Ardmucknish Bay (8 boxes)	1		X						X		X			3
	2	X	X		X			X	X		X			6
	3	X			X									2
	4										X			1
	5	X			X			X	X					4
	6	X	X						X					3
	7	X						X			X			3
	8	X			X			X	X		X			5
Cemas Nathais Bay (2 boxes)	1	X	X		X				X		X			5
	2	X	X		X			X			X			5
Firth of Lorne (3 boxes)	1										X			1
	2							X			X			2
	3		X					X			X			3
Sound of Mull (3 boxes)	1	X							X		X			3
	2	X							X		X			3
	3							X	X				X	3
Sound of Jura (4 boxes)	1								X		X			2
	2	X	X					X			X			4
	3		X									X		2
	4	X							X		X	X		4
Total		11	9		6			9	11		15	2	1	

3.2.2 Argyll Sea Lochs (Table 3.7)

3.2.2.1 Loch Creran Station C-12 Depth: 22 m Sediment: 35% sand, 44% silt, 21% clay (figs 3.21, 3.26) (Plate 5B,p237)

Eleven boxcores were taken at this site and the most abundant type of burrow observed was 1 mm diameter tubes of mucus impregnated mud extending to 10 cm below the sediment surface. Their orientation varied from vertical to subhorizontal and the majority were constructed by the ampharetid polychaete Melinna palmata. Some of the vertical tubes may have been constructed by maldanid polychaetes.

Less common were 2 mm diameter tubes constructed by the terebellid polychaetes Amphrite cirrata, Scionella lornesis and Thelepus setosus.

The second commonest burrow type was 2 mm diameter branching burrows which occurred in 75% of the samples. They are confined to the top 5 cm of the sediment and were produced by Nephtys hystricis and glycerids.

Shallow 1 mm diameter U-burrows recorded from two boxcores were probably produced by the holothurian Cucumaria elongata.

The U-tubes constructed by the siphons of the deep burrowing bivalve Thracia convexa were recorded from two boxcores although live Thracia were found at densities of 2 or 3/boxcore (= 30-50/m^2) at depths of between 10 and 25 cms below the sediment surface.

Both Amphiura chiajei and Amphiura filiformis are found at this site and their burrows were found in three boxcores.

Spiral burrows produced by the capitellid polychaete Notomastus latericeus were recorded from two boxcores.

Boxcores taken in the winter contained only two burrow types; tubes and branching burrows.

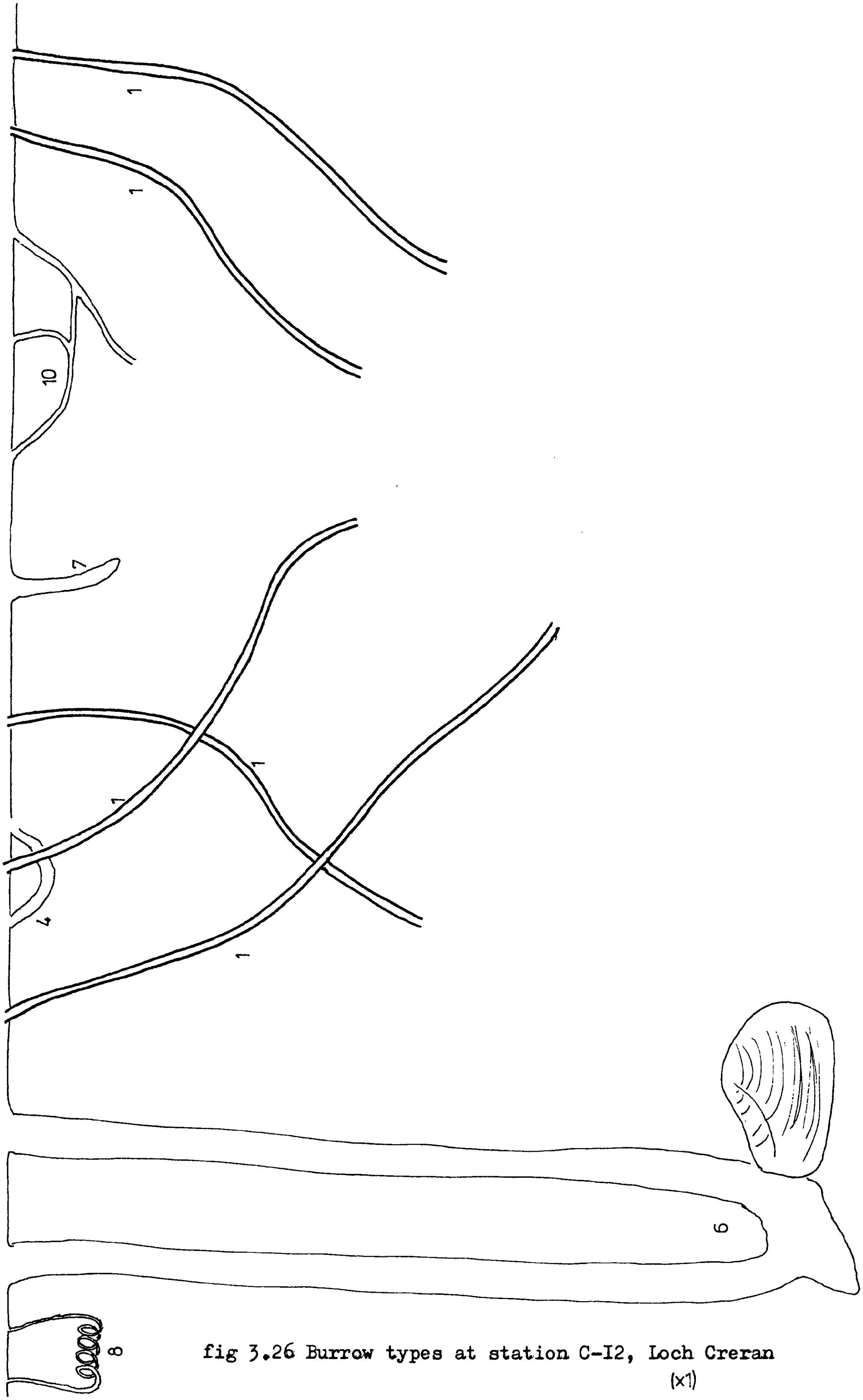


fig 3.26 Burrow types at station C-I2, Loch Creran
(x1)

3.2.2.2 Loch Etive Station E-6 Depth: 40 m Sediment: 18% sand, 51% silt, 31% clay (figs 3.21, 3.27)

The commonest burrow type recorded from the three boxcores taken at this site was 2 mm diameter branching burrows. Branching in the top 5 cm of the sediment gave multiple surface entrances linked to deeper portions of the burrow systems which extended to depths of 12 cm below the sediment surface. These burrows are probably produced by Nephtys hombergi or Glycera alba.

The shallow 2 mm diameter U-burrows which occur both singly and in chains may also be produced by Nephtys or by Scalibregma inflatum.

The vertical tubes linking the bivalve Thracia convexa to the surface were recorded from one boxcore.

3.2.2.3 Loch Etive Station E-11 Depth: 115 m Sediment: 17% sand, 51% silt, 32% clay (figs 3.21, 3.28)

The principal burrow type found in the three boxcores from this site was 1 and 2 mm diameter tubes in the top 10 cm of the sediment. Gage (1972) records the following tube dwelling polychaetes from this site:- Spiochaetopterus typicus, the spionid Nerine sp. and the malanids Praxillura longissima and Rhodine gracilior.

The conical tubes of sand grains constructed by Pectinaria belgica were found in two boxcores from this site.

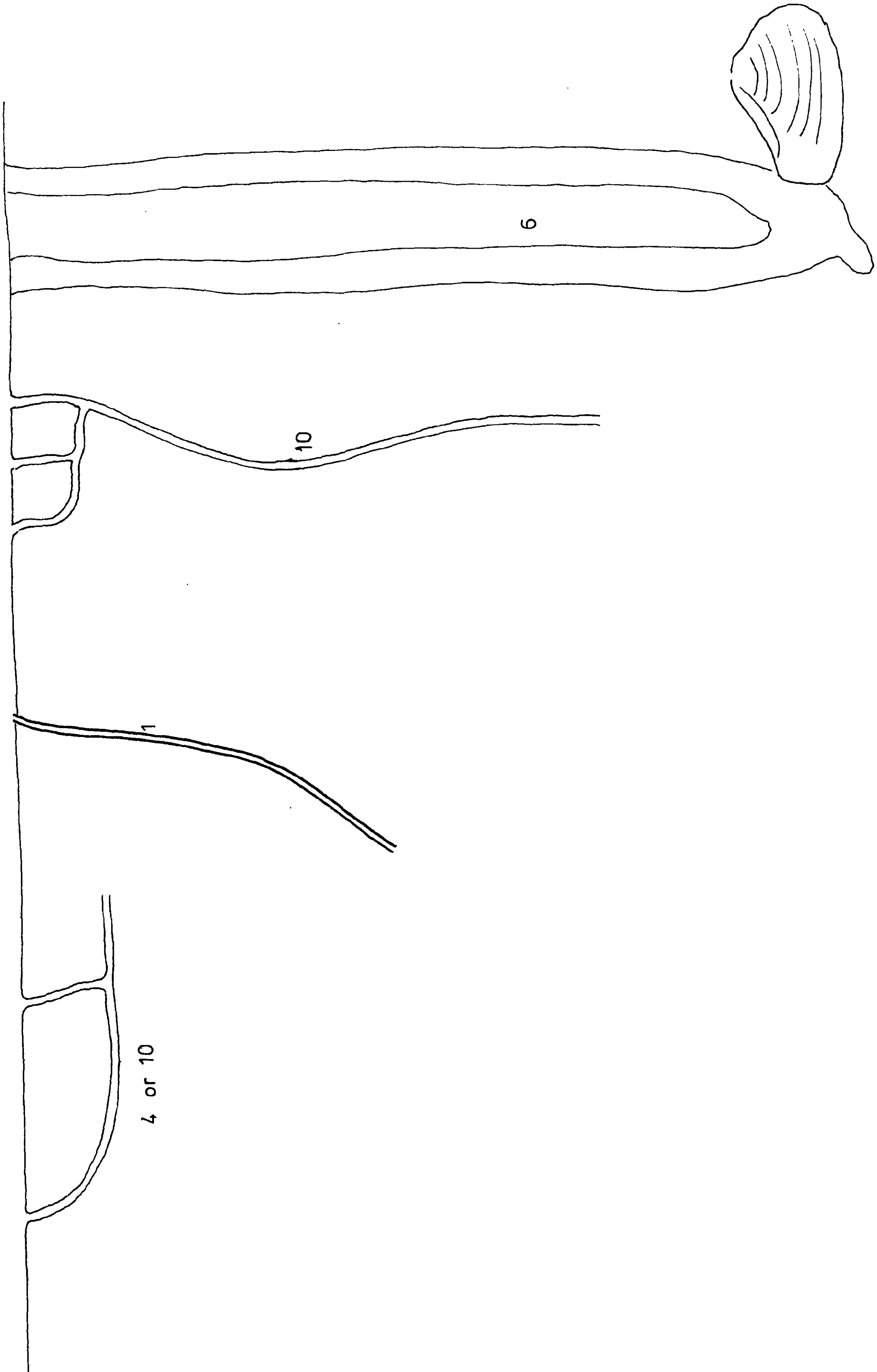


fig 3.27 Burrow types at station E-6 , Loch Etive (x1)

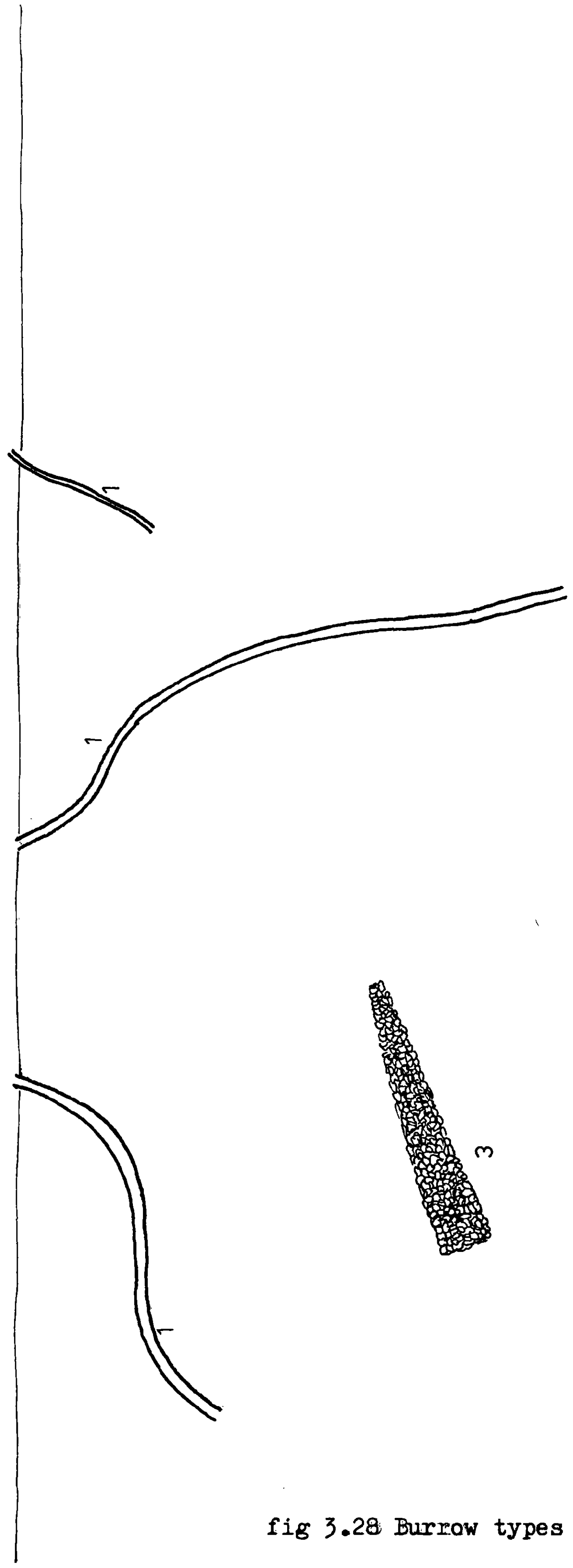


fig 3.28 Burrow types at station E-II, Loch Etive
(x1)

3.2.2.4 Loch Linnhe - Loch Eil (fig 3.29)

			Sediment			
		Depth	Sand	Silt	Clay	
Loch Eil	Station 24	31 m	2	94	4	(fig 3.30)
	Station 1	42 m	11	71	18	(fig 3.31)
Loch Linnhe	Station 10	90 m	30	67	3	(fig 3.32)
	Station 11	95 m	12	83	5	(fig 3.33)

The commonest burrow type in these boxcores was 1 mm diameter tubes, some of which were oriented vertically, others obliquely in the sediment. At station 1, Loch Eil, tubes extended to 18 cm below the sediment surface; at other sites they were found down to 10 cm. They were built by the ampharetid polychaete Melinna palmata, the spionid Prionospio cirrifera and the maldanid Praxillura affinis (Pearson & Stanley 1979).

4-6 mm diameter subhorizontal tubes found up to 9 cm below the sediment at station 24, were probably built by Terebellides stroemi. A 2 cm diameter leathery tube extending to a depth of 30 cm in the sediment occupied by the sea anemone Cerianthus lloydi was also found at this site.

The deep burrowing bivalves Thracia convexa and Lucinoma borealis were found at depths of 10-15 cms below the sediment surface at stations 24 and 1 respectively.

1 mm branching burrows produced by *Nephtys hystricis*, *Glycera sp.* and *Goniada maculata* and 2 mm spiral burrows of capitellids were both common.

Amphiura chiajei was recovered from boxcores from all four stations but its burrow was comparatively rare as in most cases it was destroyed by the emerging animal.

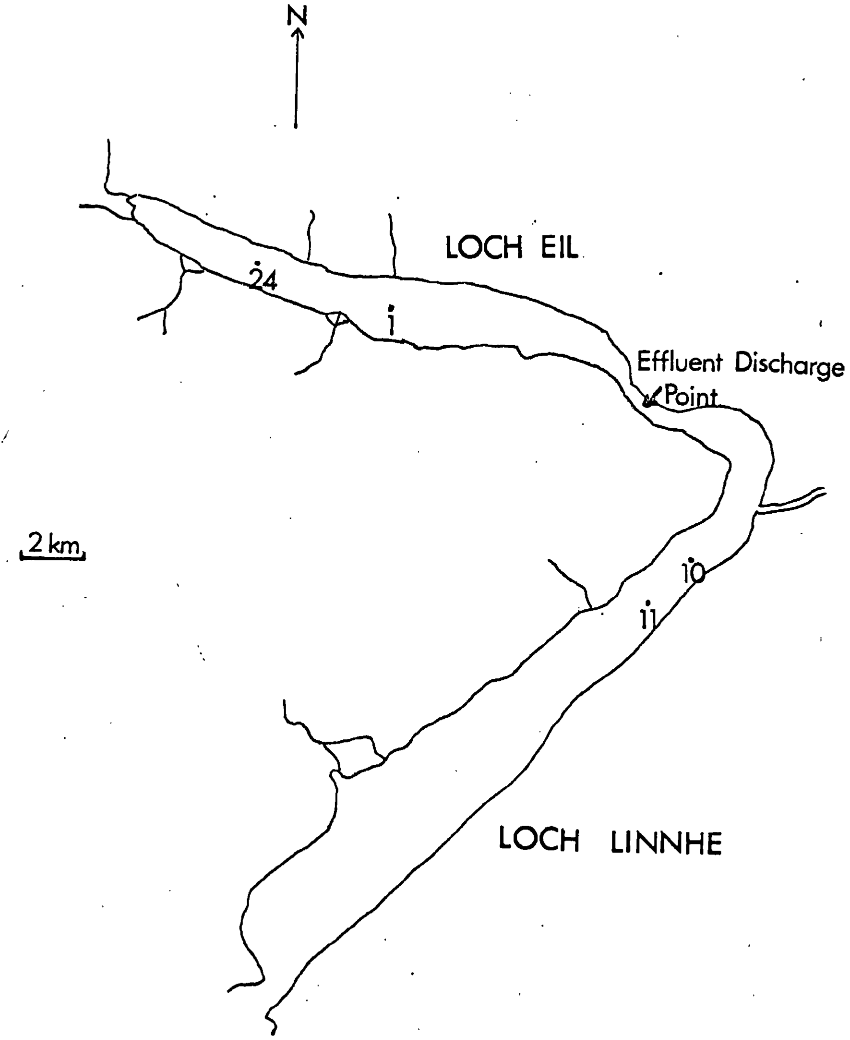


fig 3.29 Sample sites in Loch Linnhe and Loch Eil redrawn from Pearson (1975)

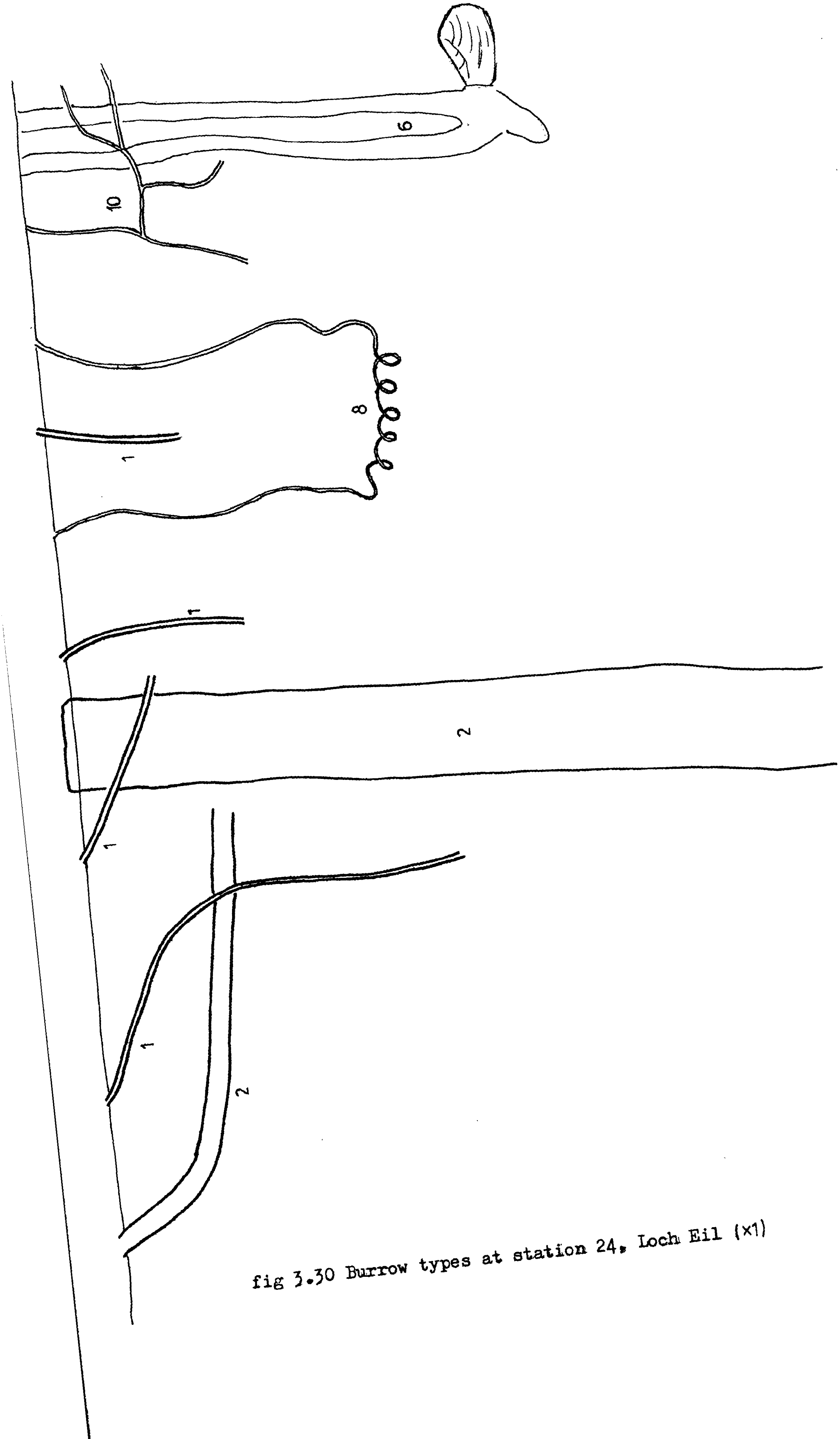


fig 3.30 Burrow types at station 24, Loch Eil (x1)

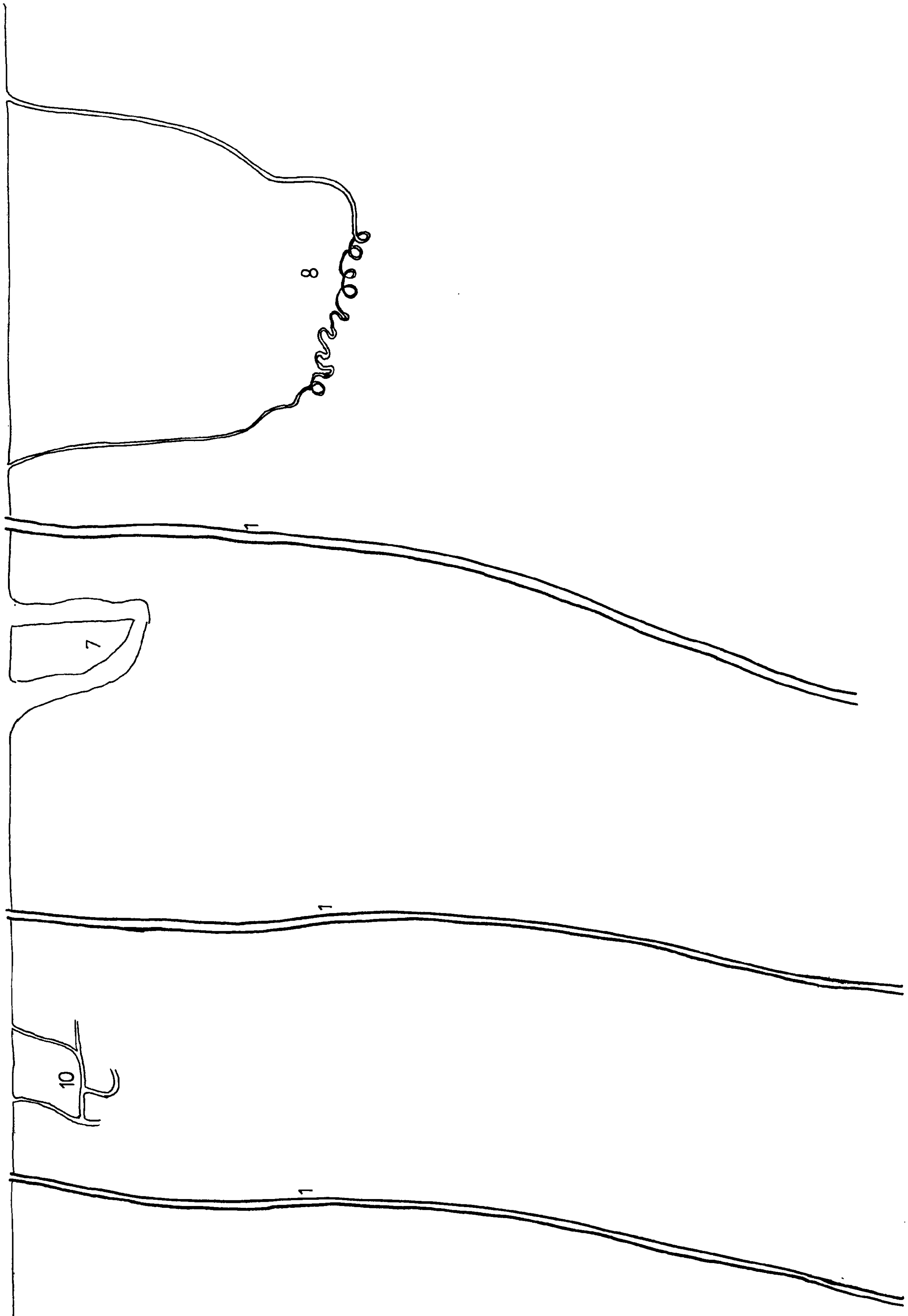


fig 3.31 Burrow types at station I, Loch Eil (×1)

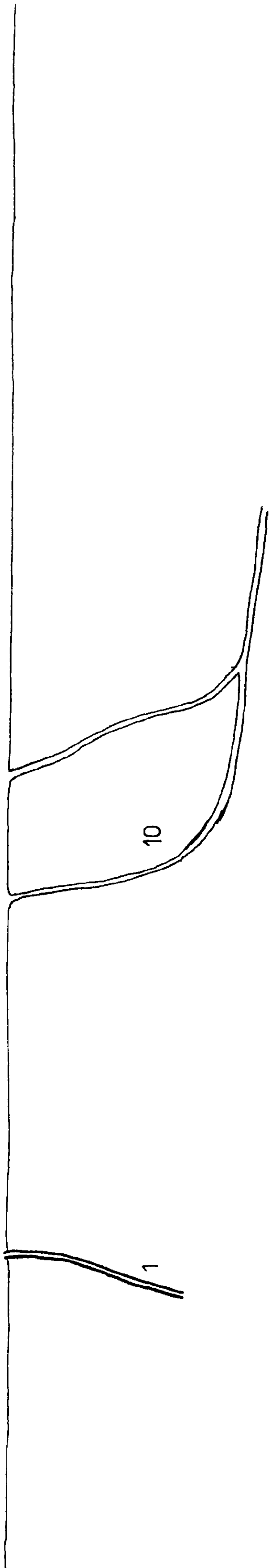


fig 3.32 Burrow types at station IO , Loch Linnhe (×1)

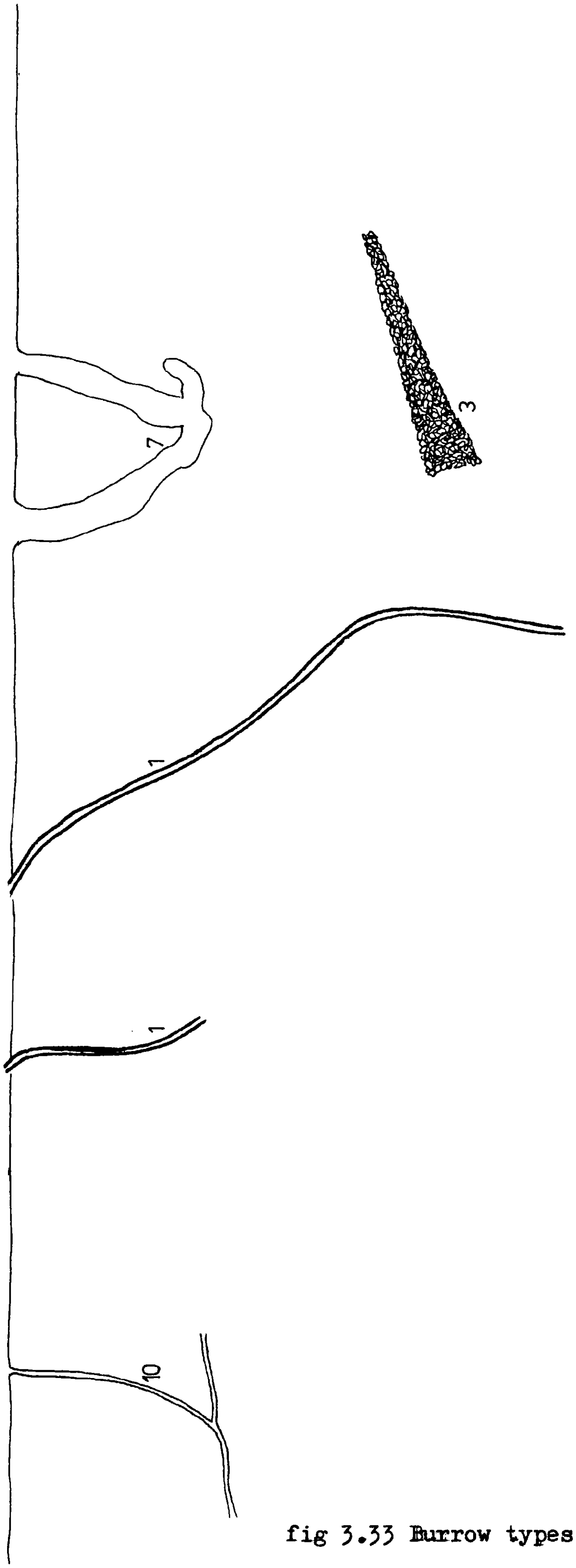


fig 3.33 Burrow types at station II, Loch Linnhe
(x1)

Table 3.7 Distribution of Burrow Types:

Argyll Sea Loch Sites

Burrow Types

		TUBES			U-BURROWS				SPIRALS		BRANCHING BURROWS			
Sample Sites		1	2	3	4	5	6	7	8	9	10	11	12	Total
Loch Creran	1	X	X		X									3
C-12	2	X						X			X			3
June 5 boxes	3	X	X						X		X			4
	4	X			X						X			3
	5	X					X	X			X			4
Loch Creran	6	X									X			2
C-12 (3 boxes)	7	X												1
January	8	X									X			2
Loch Creran	9	X	X				X				X			4
C-12	10	X									X			2
May (3 boxes)	11	X						X	X					3
Total		11	3		2		2	3	2		8			
Loch Etive	1	X									X			2
E-6	2				X		X				X			3
(3 boxes)	3				X						X			2
Loch Etive	1	X		X										2
E-11	2	X		X										2
(3 boxes)	3	X												1
Loch Linnhe Stn	10	X									X			2
Stn 11	1	X		X							X			3
(2 boxes)	2	X						X						2
Loch Eil Stn 24	1	X	X								X			3
(2 boxes)	2	X							X					2
Loch Eil Stn 1	1	X						X						2
(2 boxes)	2	X						X	X		X			4

3.3 Continental Slope Sites (Table 3.8) (figs 1.1, 3.34)

3.3.1 Hebrides Terrace

Depth: 1173 m 56° 46.7' N 9° 13' W
Depth: 1260 m 56° 46.7' N 9° 16' W
Sediment: 17% sand, 50% silt, 33% clay
(Plate 9B,p241)

The most distinctive burrow type at this site was 2 mm diameter U-burrows extending to depths of 4 cm. Surface entrances were less than 1 cm apart and the burrow resembled those produced by the amphipod *Corophium volutator* in intertidal sediments. The producer of these burrows is unknown but one of the large amphipod species found at these depths is suspected.

1 mm diameter branching burrow systems extending to depths of 8 cm were common in both boxcores. 2 mm tubes, running horizontal in the sediment just below the surface before turning vertical and extending up to 4 cm below the surface, were abundant in one boxcore and a single, horizontal spiral burrow, diameter 2 mm, was found at a depth of 4 cm.

The branching burrows were produced either by *Glycera mimica* or *Lumbrinereis sp*., the tubes by *Spiophanes kroyeri* and the spiral burrow by *Notomastus latericeus*. All four species have been recorded from these depths by Gage (unpublished records 1973-6).

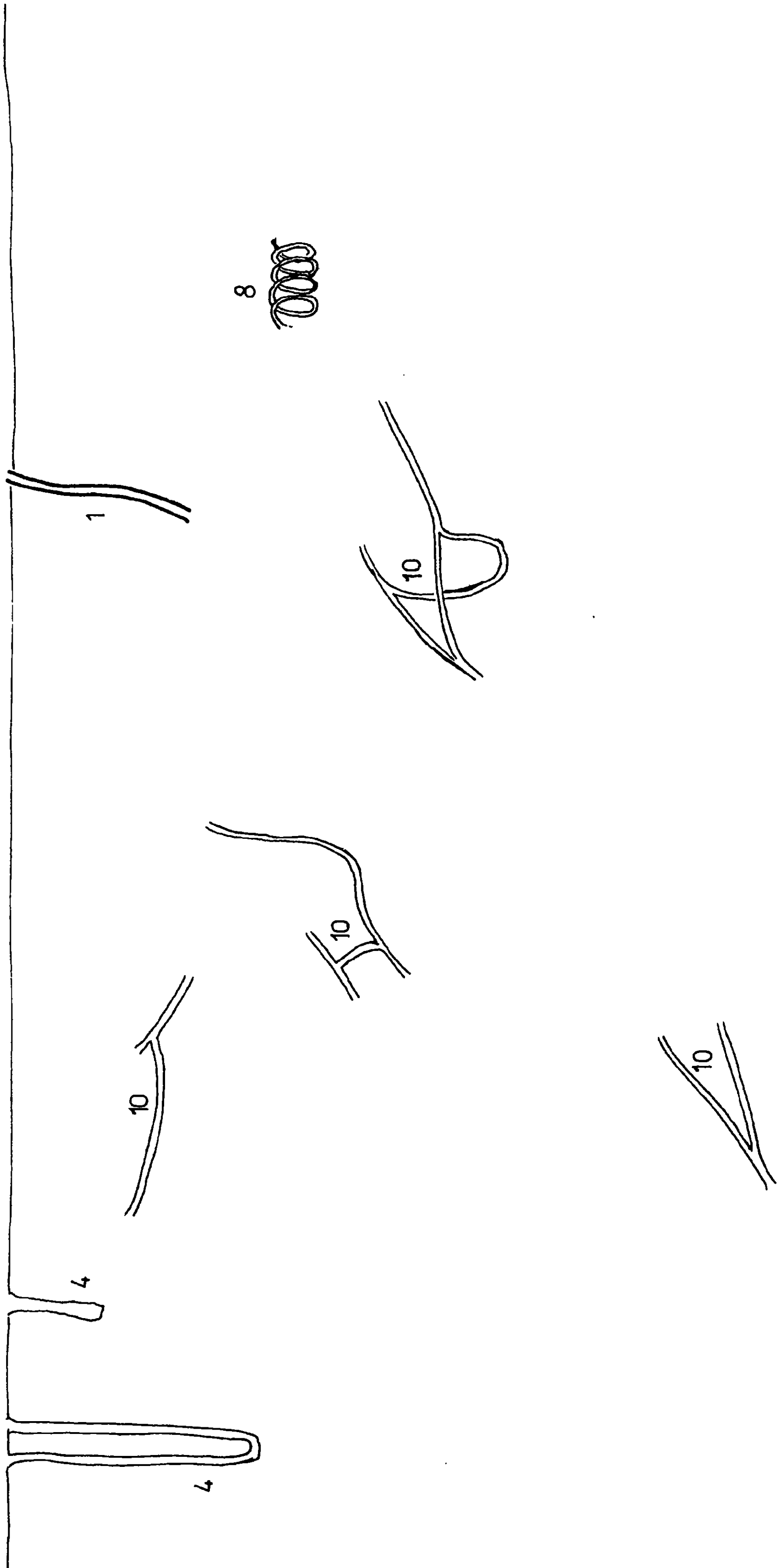


fig 3.34 Burrow types on the Hebrides Terrace (x1)

3.3.2 Whittard Canyon (S.W. Approaches) Depth: 1330 m

Sediment: 24% sand, 48% silt, 28% clay
(figs 1.1, 3.35) 48° 28'N 10° 21'W
(Plate 9A,p241)

A boxcore from the muddy sediment found at this site contained 2 mm diameter tubes, 1 mm diameter branching burrows, 2 mm diameter spiral burrows and a horizontal 5 mm diameter branching burrow at a depth of 10 cm.

The tubes ran vertically from the surface turning horizontal at depths of 6-8 cm and were built by Siboglinum sp., a member of the phylum Pogonophora (Southward & Southward 1958a). Pogonophorans are long worm-like creatures (10-85 cm long) which have no mouth or digestive tract; dissolved organic matter is absorbed directly through the body wall (Barnes 1974, p. 675). They live in long chitinous tubes which act as imperfect semi-permeable membranes allowing the passage of gases but not larger molecules (Southward & Southward 1963).

The producers of the burrows found at this site are unknown; the polychaetes Eunice pennata and E. oerstedii and the holothurian Psolus squamatus are recorded from this locality by Southward & Southward (1958b).

Table 3.8

	TUBES			U-BURROWS				SPIRALS		BRANCHING BURROWS			
Sample Sites	1	2	3	4	5	6	7	8	9	10	11	12	Total
Whittard Canyon	X							X		X	X		4
Hebrides Terrace 1173 m 1	X			X				X					3
Hebrides Terrace 1330 m 2	X			X						X			3
Total	3			2				2		2	1		

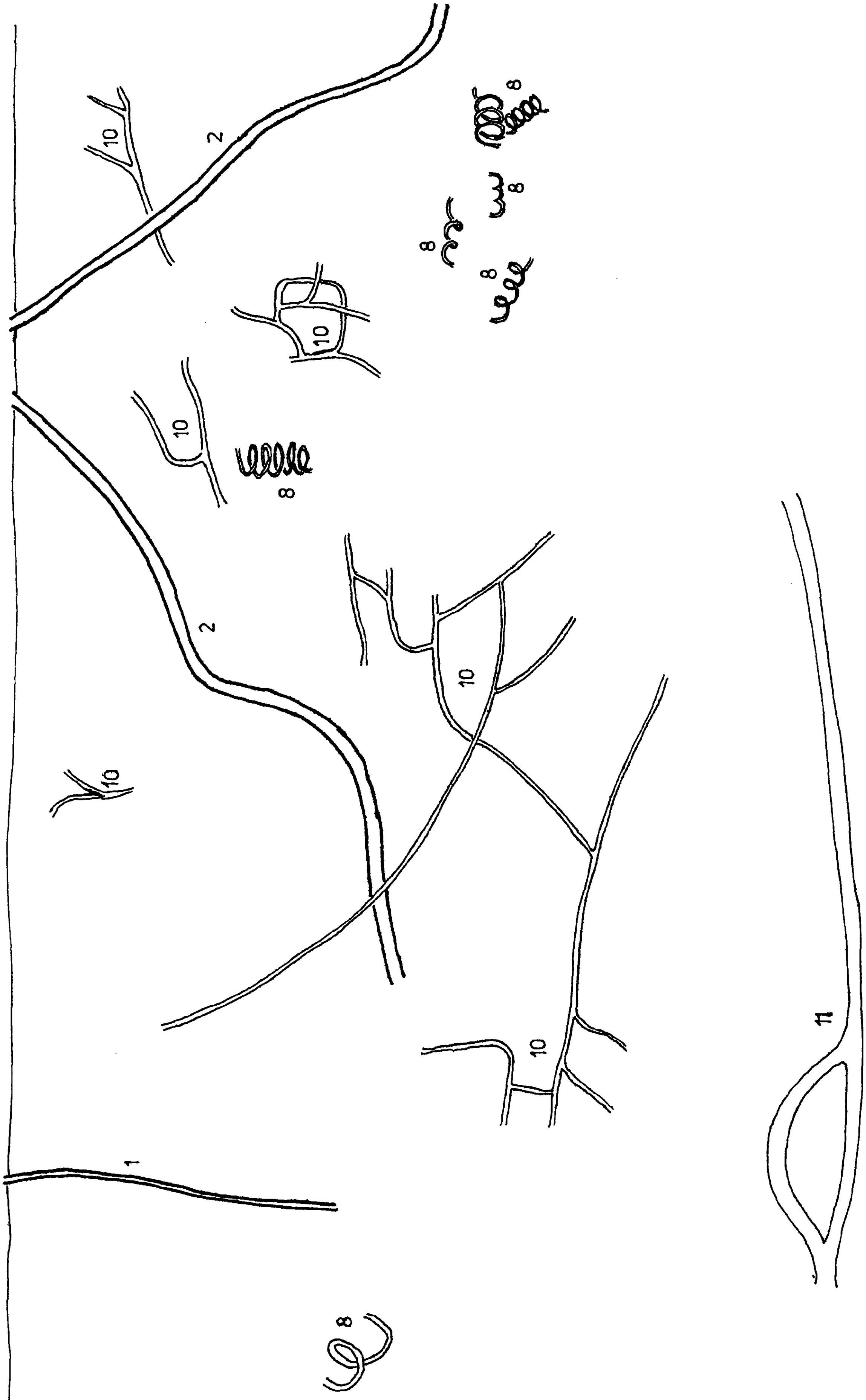


fig 3.35 Burrow types in the Whittard Canyon (x1)

3.4 Distribution of organisms with a high fossilisation potential

The animals most likely to be preserved as fossils are those with hard parts. In the study area these consisted of species of bivalves, gastropods and echinoids; their distribution is shown in Table 3.9. (in back pocket).

Nucula sulcata and Abra alba were the most common species occurring at densities of greater than 10/m^2 throughout the area. Corbula and Thyasira were similarly widespread but at lower densities. The large shallow burrowing bivalves Arctica islandica and Glossus humanus, the gastropod Aporrhais pes pelicani and the scaphopod Dentalium entalis also displayed wide distributions.

Thracia convexa and another deep burrowing bivalve Lucinoma borealis were almost exclusive to sea-lochs. At depths of less than 50 m a diverse mollusc fauna was found, consisting of the bivalves Acanthocardium echinatum, Dosinia lupinus, Mysia undata, Mya truncata, Venus ovata and V. striatula and the gastropod Natica montagui. Large numbers of Turritella communis occurred in sediments containing more than 30% sand and the irregular echinoid Brissopsis lyrifera was abundant (around 20/m^2) at depths of between 40 and 60 m in the Firth of Clyde. The epifaunal bivalve Chlamys opercularis was most abundant at shallower sites; below 70 m it was progressively replaced by Chlamys septemradiata. Deep water muds contained populations of Abra alba and the protobranchs Nucula sulcata, N. tenuis and Nuculana minuta.

Chapter 4 : Distribution of burrows with depth in the sediment and their total length/boxcore

4.1 Introduction

Moore (1931) and Mare (1942) studied the distribution with depth of the meiofauna of sublittoral fine sediments, using a 3 cm diameter gravity corer (Moore & Neill 1930). Investigations of the distribution of the macrofauna with depth in the sediment has had to await the invention of a sampler capable of obtaining a large enough block of sediment to contain sufficient numbers of animals for quantitative studies to be carried out. The boxcorer (Reineck 1963) fulfils this requirement; Rosenberg (1974) found 64% of all individual animals and 74% of the biomass concentrated in the top 5 cm of the sediment of a Swedish estuary. The smaller animals inhabiting bathyal environments have been studied by Jumars (1978) from cores taken by an unmanned submersible at a depth of 1200 m off southern California; 82% of the polychaetes lived in the top 1 cm of the sediment.

No previous studies of the distribution with depth of the number of burrows appear to have been made in spite of the need for such information in order to model the increased flux of nutrients from the sediment to the overlying water brought about by the increase in the sediment-water interface which these burrows represent (Aller & Yingst 1978).

4.2 Method

Radiographs were viewed against a grid of lines, 1 cm apart, placed so that the top line of the grid corresponded to the sediment surface as revealed in the radiograph.

The number of burrows intersecting each line was recorded and the total number of burrows at that depth in the boxcore was calculated by adding the figures obtained from radiographs of each boxcore subsample. The results were plotted as graphs of the number of burrows against depth. Average values for the number of burrows at each depth were calculated for each site.

4.3 Results

4.3.1 Firth of Clyde excluding polluted sites

4.3.1.1

Boxcores from Kilbrannan Sound, the Arran Deep and Loch Riddon had between 30 and 40 burrows in the top 2 cm. This figure declined in a linear fashion to less than 10 at a depth of 13 cm (fig 4.1).

4.3.1.2

Boxcores from sites 1-9 had between 15 and 25 burrows in the top 2 cm declining to 10 at a depth of 7 cm (fig 4.2), except for site 6 where the profile was similar to those described from Ardmucknish Bay below.

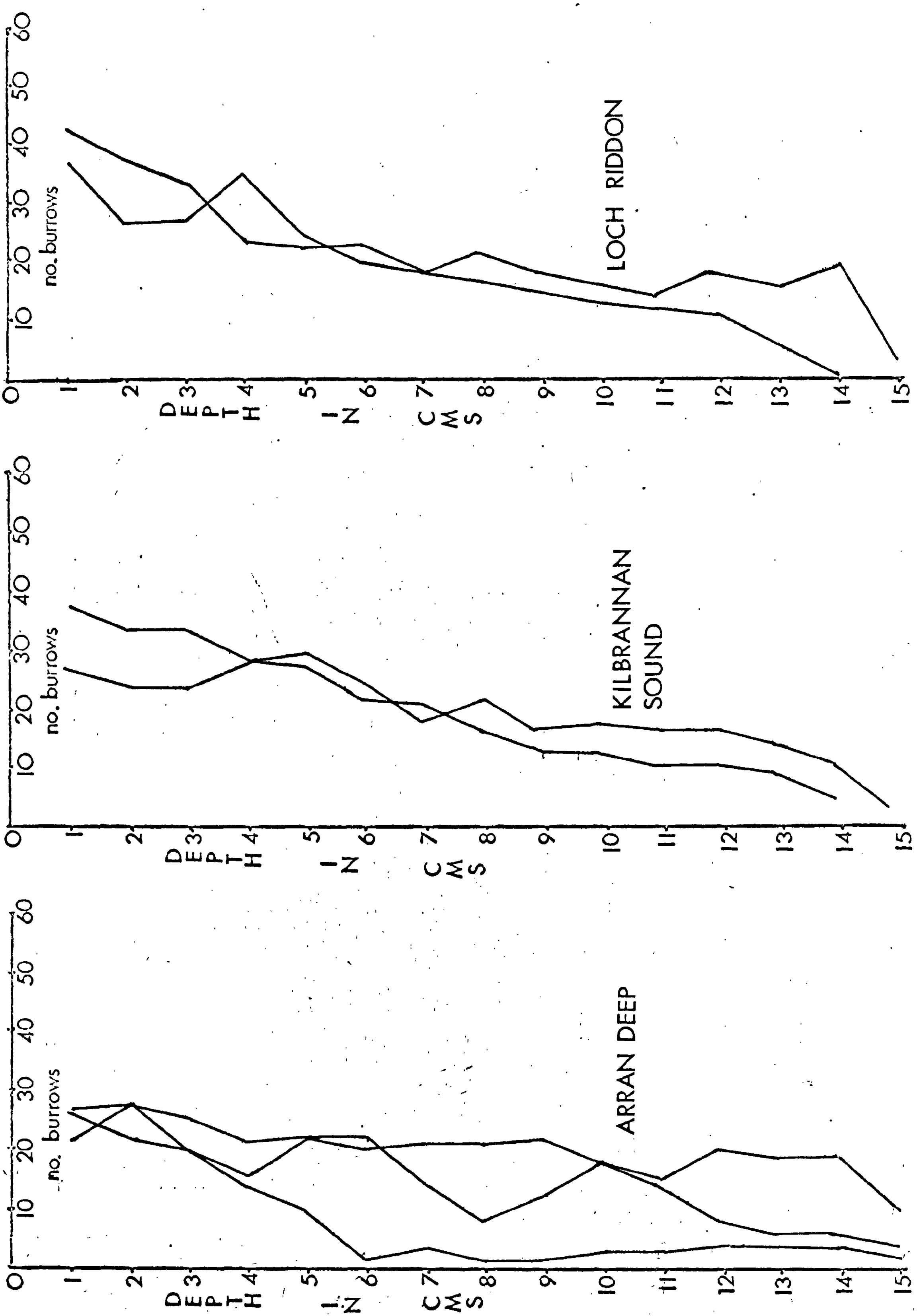


fig 4.I Depth distribution of burrows in the Arran Deep, Kilbrannan Sound and Loch Riddon.

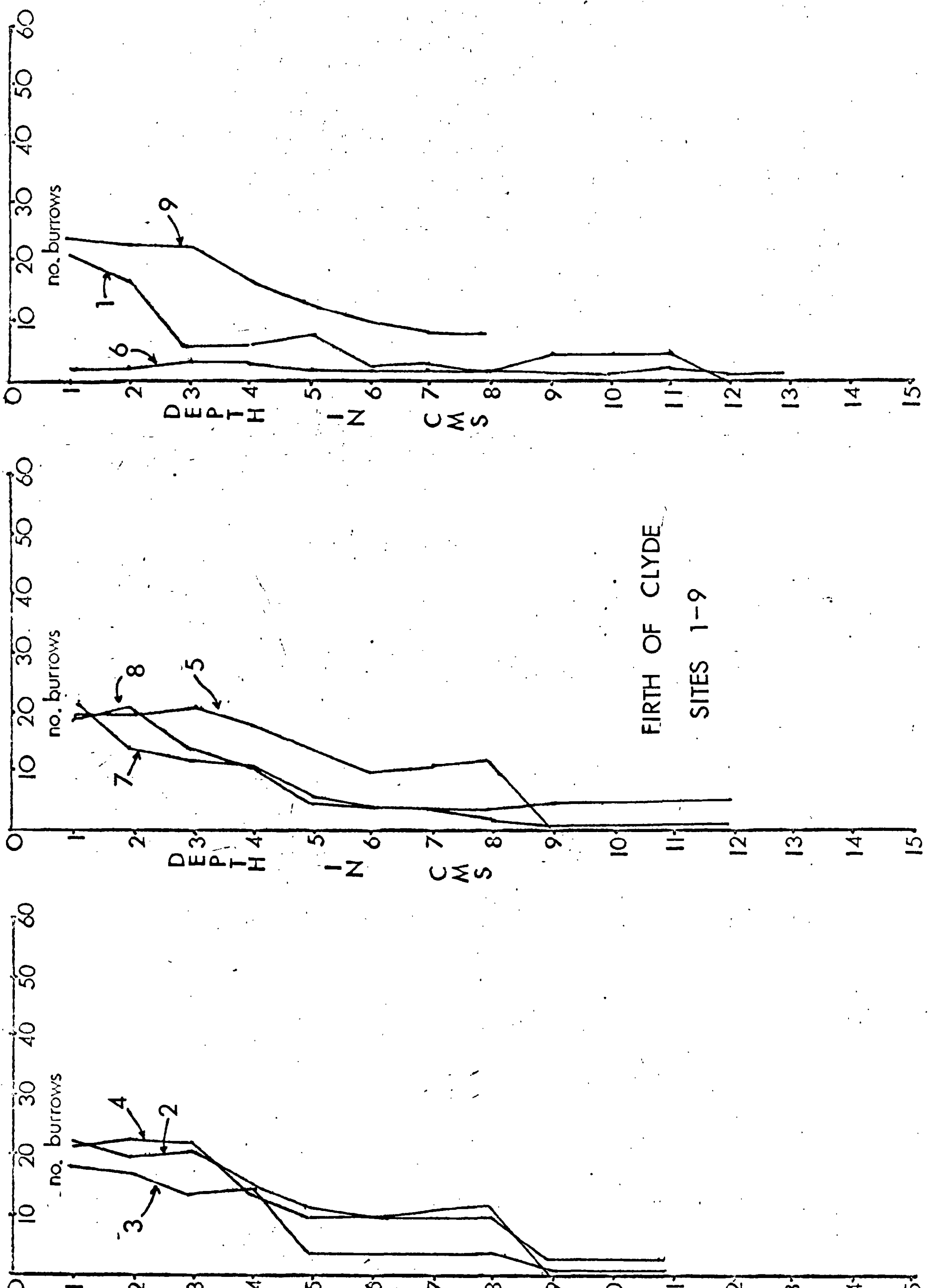


fig 4.2 Depth distribution of burrows at sites I-9, Firth of Clyde.

4.3.1.3

One boxcore from the Arran Deep and those from the Cumbrae Deep and Loch Goil showed considerable differences in their distribution of burrows with depth from the other Firth of Clyde sites. The Arran Deep and Loch Goil cores displayed a much more rapid decline in burrow numbers with depth from a surface maximum of 68 and 42 respectively to less than 10 at a depth of 7 cm. The Cumbrae Deep core was similar to the first group of cores described above but had a higher number of burrows in the top 2 cm (greater than 50) (fig 4.3).

4.3.2 Polluted sites in the Firth of Clyde and station C-12 Loch Creran (fig 4.4)

At these sites the number of burrows decreased rapidly from a maximum of around 30 in the top 2 cm to less than 10 at a depth of 5 cm.

4.3.3.1 Ardmucknish Bay, Sound of Mull, Loch Linnhe, Loch Eil and Loch Etive (fig 4.5)

The number of burrows rarely exceeded 10 and showed a tendency to decrease with depth.

4.3.3.2 Cemas Nathais Bay

Two boxcores from Cemas Nathais Bay showed widely divergent profiles, on average paralleling the profile obtained from neighbouring Ardmucknish Bay but with burrows twice as abundant (between 10 and 20 at each depth) (fig 4.6).

Two boxcores from the Sound of Jura had profiles similar to one

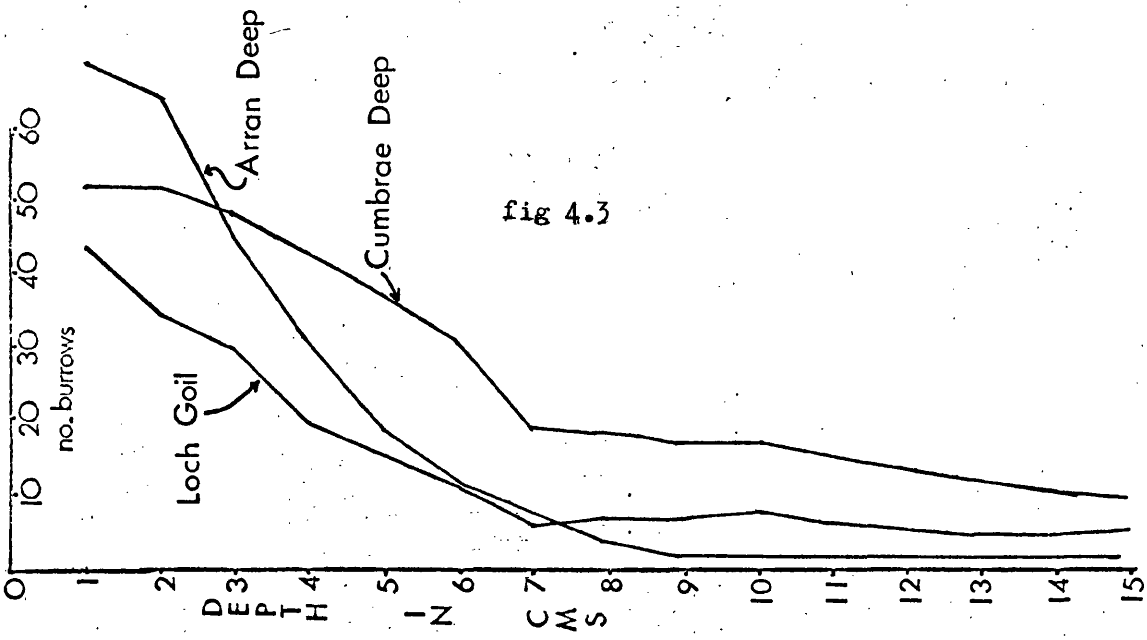


fig 4.3

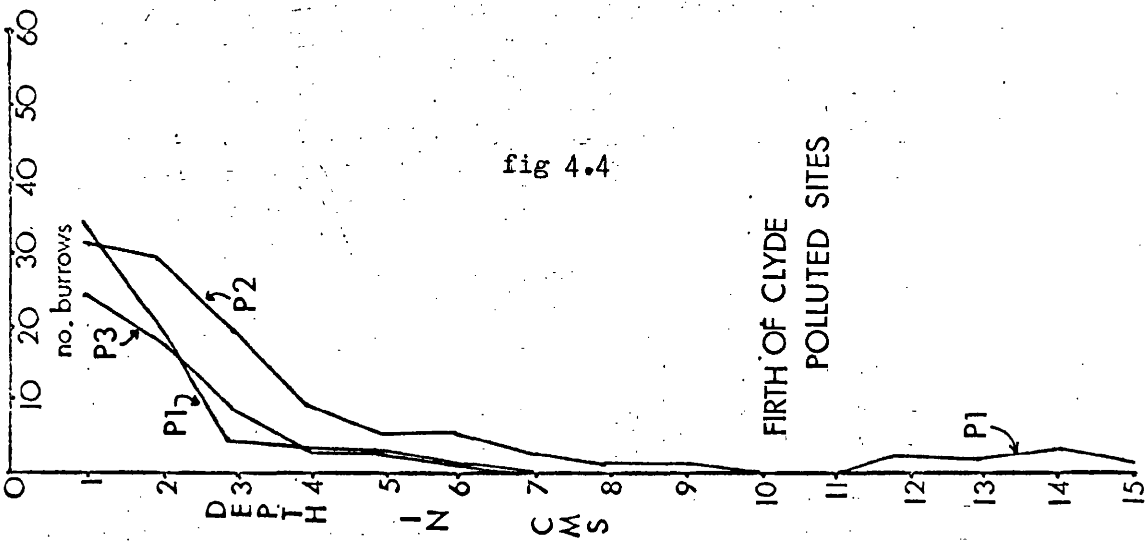


fig 4.4

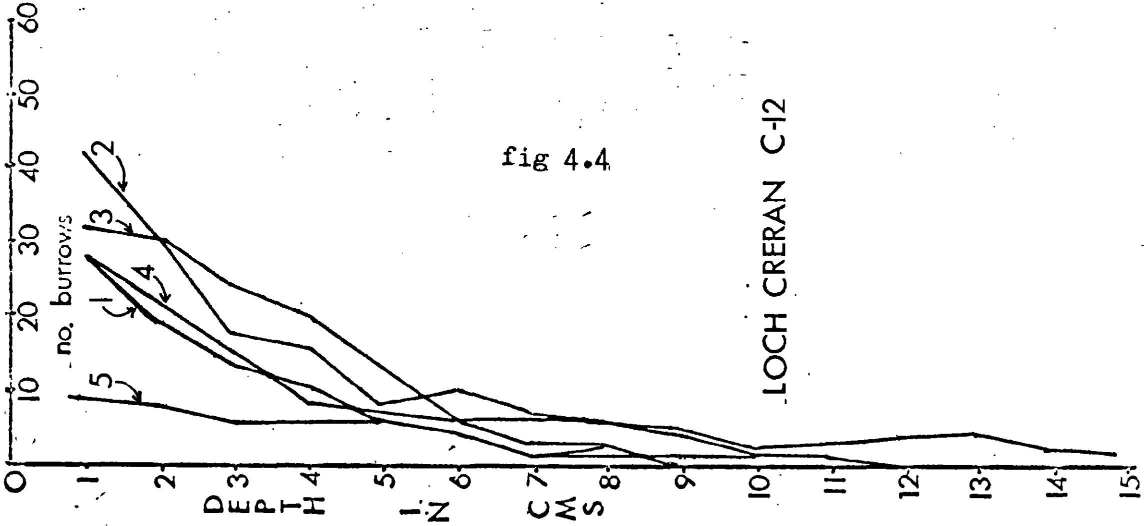


fig 4.4

fig 4.3 Depth distribution of burrows in the Cumbrae Deep, Loch Goil, and the Arran Deep.

fig 4.4 Depth distribution of burrows at station C-I2, Loch Creran and Firth of Clyde polluted sites I-3.

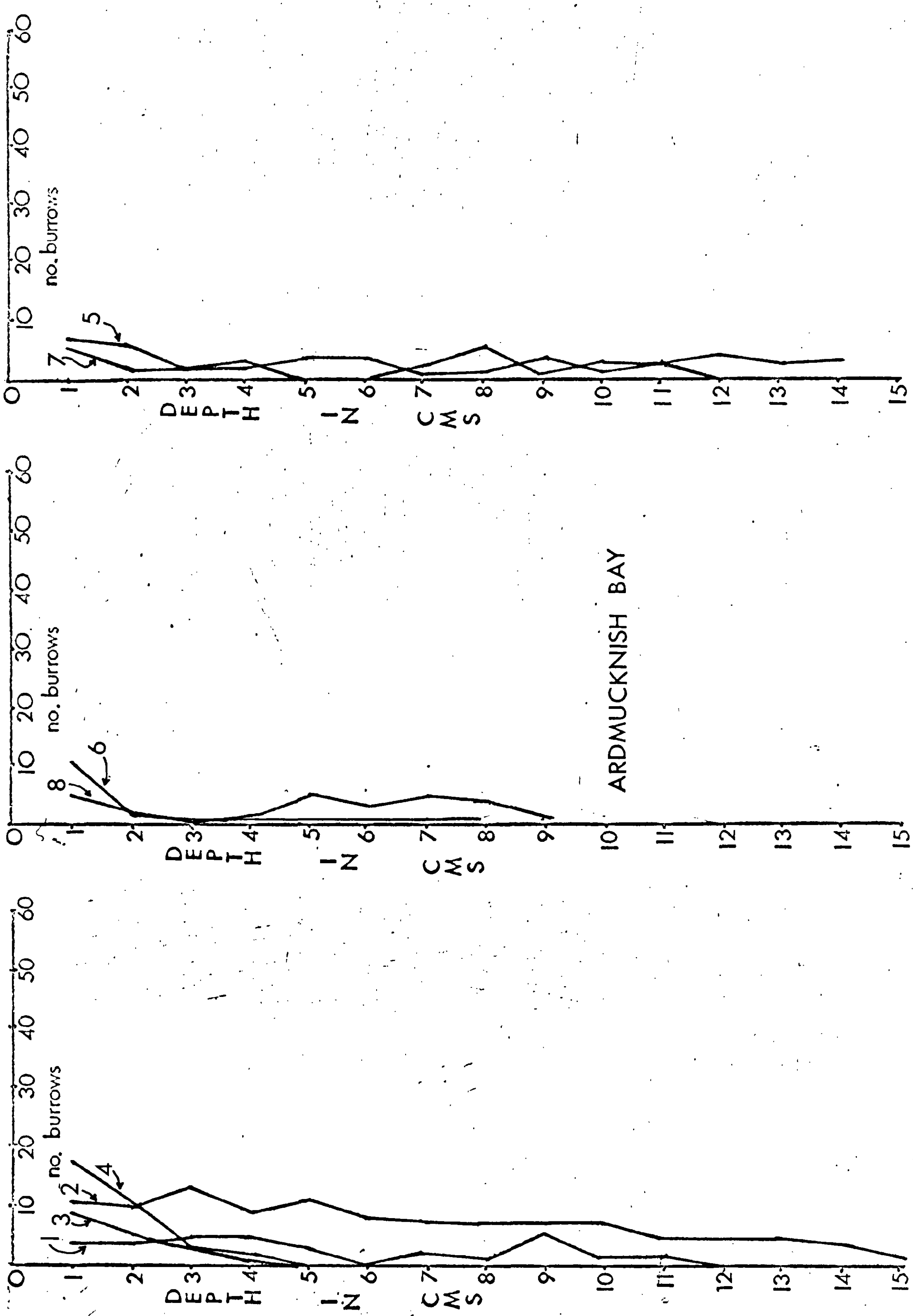
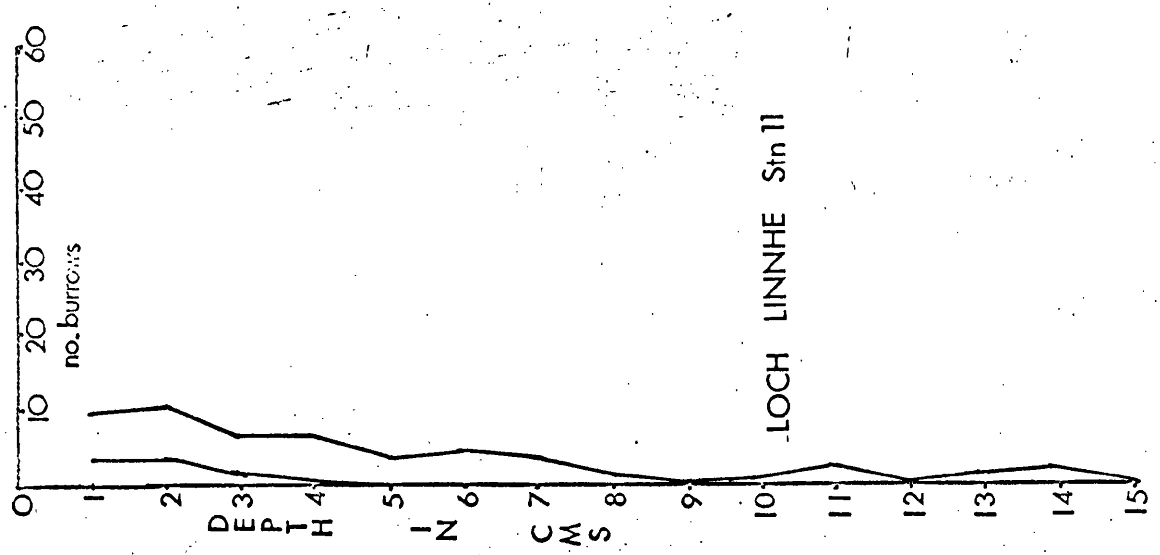
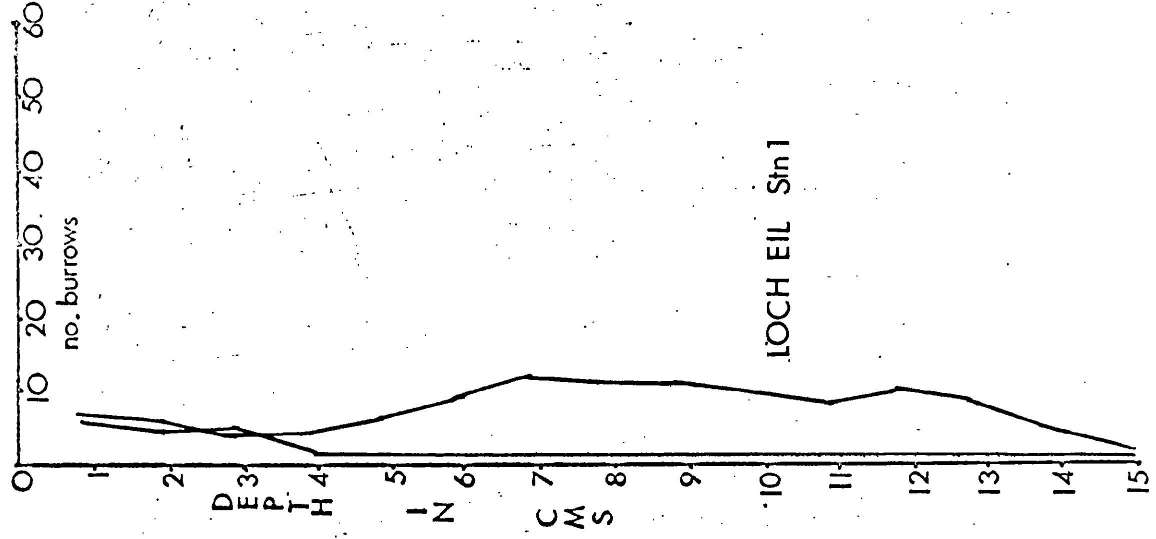


fig 4.5 Depth distribution of burrows in Ardmucknish Bay, the Sound of Mull and Lochs Linnhe, Eil and Etive.





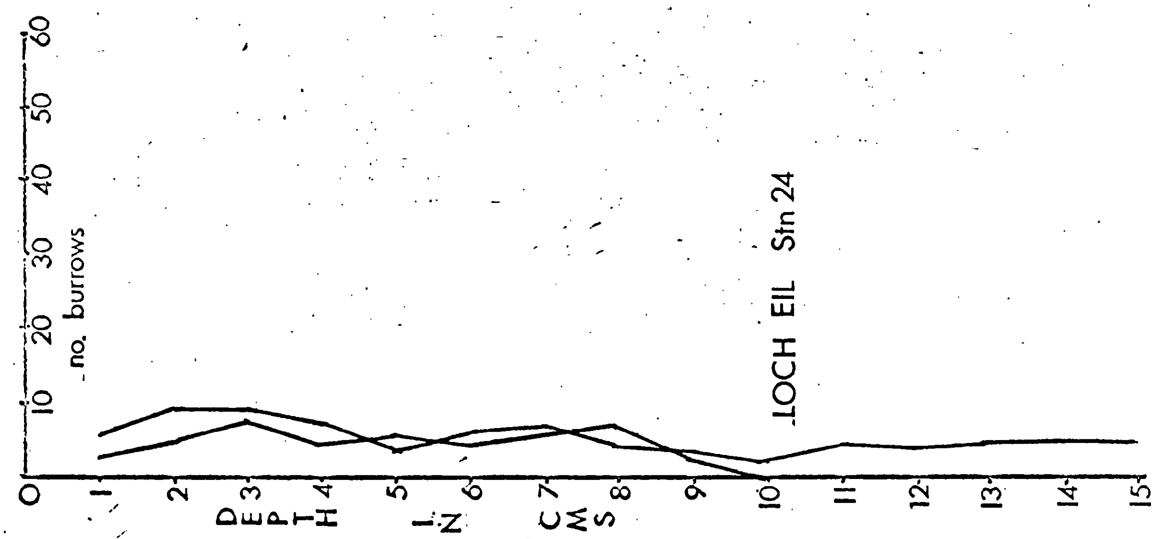


fig 4.5 (con) Depth distribution of burrows in Ardmucknish Bay, the Sound of Mull and Lochs Linnhe, Eil and Etive.

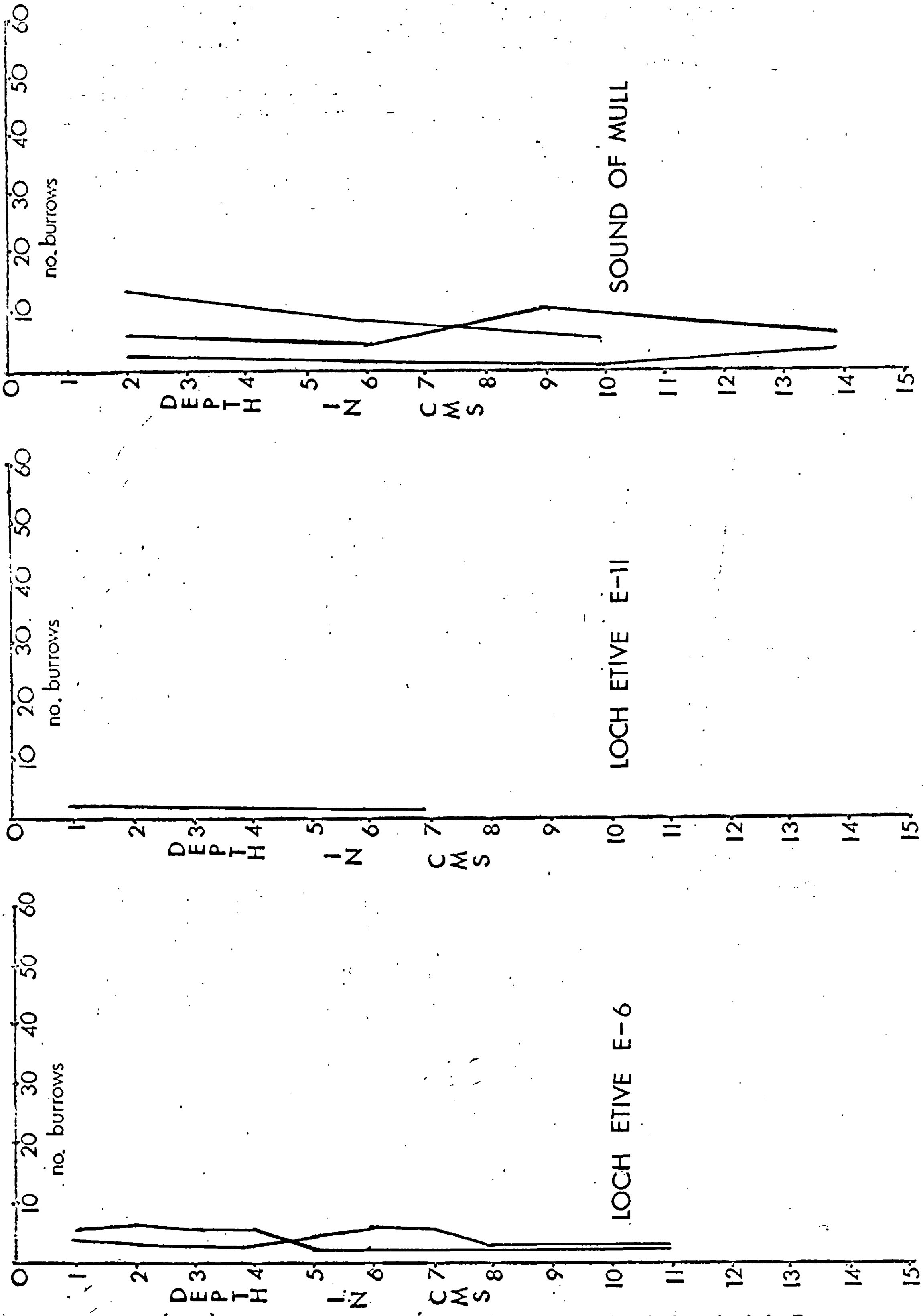


fig 4.5 (con) Depth distribution of burrows in Ardmucknish Bay, the Sound of Mull and Lochs Linnhe, Eil and Etive.

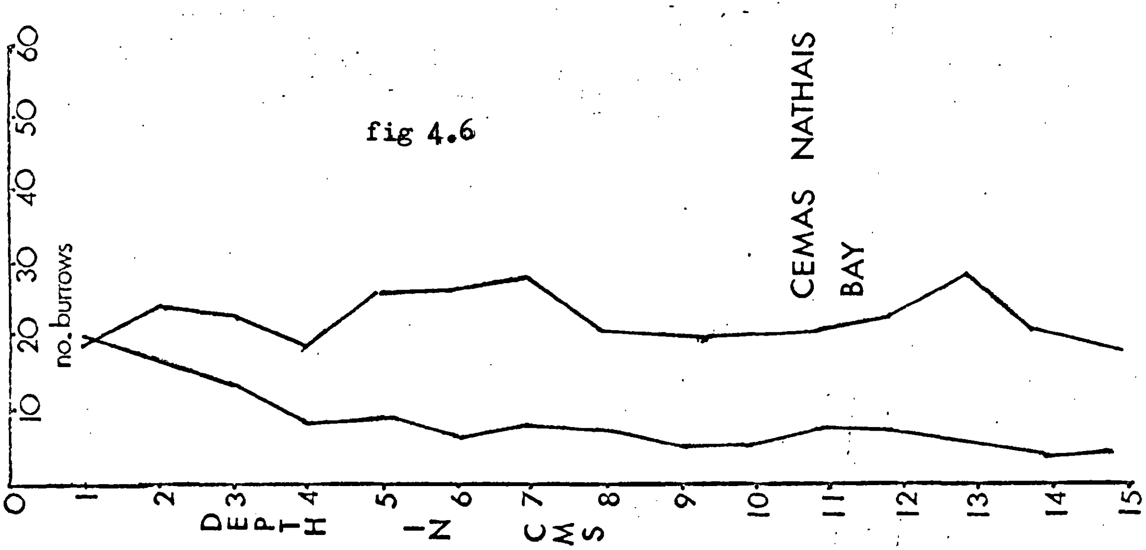


fig 4.6

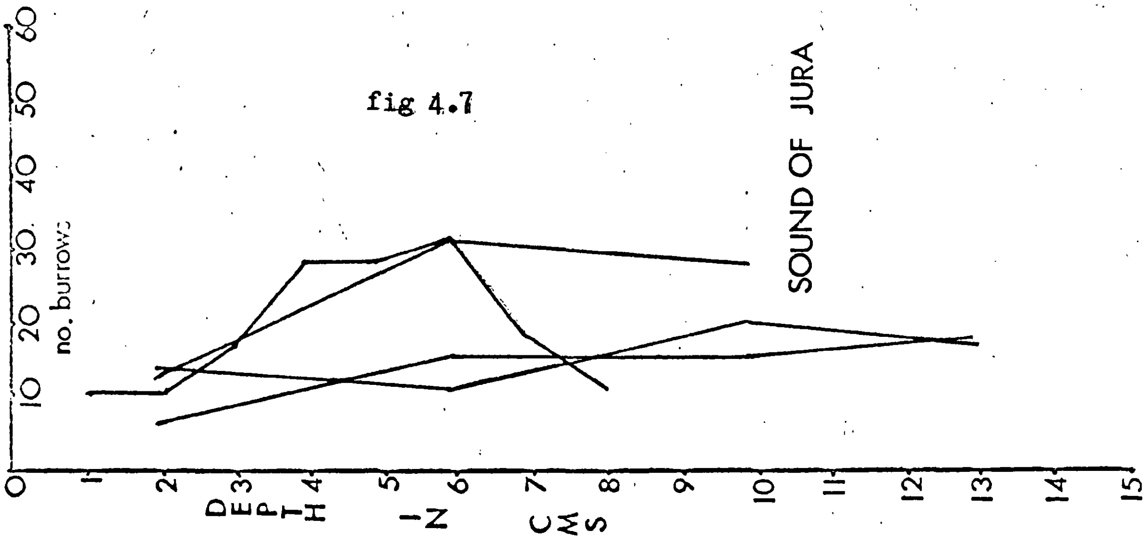


fig 4.7

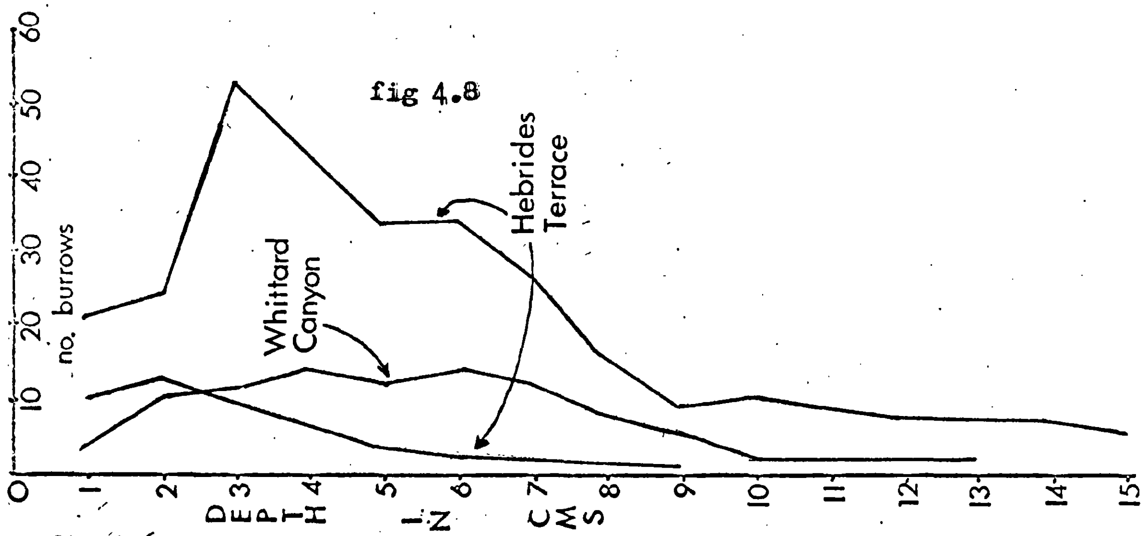


fig 4.8

fig 4.6 Depth distribution of burrows in Cemas Nathais Bay.
fig 4.7 Depth distribution of burrows in the Sound of Jura.
fig 4.8 Depth distribution of burrows on the Hebrides Terrace and Whittard Canyon.

of those from Cemas Nathais Bay with around 10 burrows in the top 2 cm rising to a maximum of around 30 at a depth of 6 cm. The other two more closely resembled the profiles described above from Ardmucknish Bay and other sites (fig 4.7).

4.3.4 Continental Slope Sites (fig 4.8)

At both sites the maximum number of burrows did not occur at the surface. In the Whittard Canyon boxcore and one of the Hebrides Terrace boxcores the maximum number of burrows at any depth did not exceed 15. In the other Hebrides Terrace boxcore large numbers of 1 mm diameter branching burrows between 3 and 5 cm in the sediment gave a maximum of 53 burrows at 3 cm depth.

4.4 Length of burrows/boxcore

The total number of intersections between a grid of lines 1 cm apart, placed parallel to the sediment surface and burrows recorded on an X-ray radiograph gives an estimate of the length of burrows contained in the sediment. This would be the true length if all burrows ran vertically from the surface but as burrows can have any orientation, it underestimates the true length by probably up to 30%. The length of burrows in a boxcore was obtained by adding the number of intersections recorded from each boxcore subsample.

4.5 Results (fig 1.9 in back pocket)

4.5.1 Firth of Clyde

The shallow marine sites average around 100 cm of burrows/boxcore; the deep marine and sea-loch sites between 200 and 300 cm of burrows/ boxcore. The greatest length of burrows (394 cm) was recorded from the Cumbrae Deep. Polluted sites around the Garroch Head Sludge Dumping Ground fall within the range recorded from the other shallow marine sites.

4.5.2 Argyll Sea Lochs and Inshore Sounds

Boxcores from Lochs Etive, Eil and Linnhe, Ardmucknish Bay and the Sound of Mull all contained around 50 cm of burrows. Site C-12 at the head of Loch Creran averaged 100 cm/boxcore and Cemas Nathais Bay and the deep Sound of Jura site both had around 250 cm/boxcore.

4.5.3 Continental Slope Sites

The boxcore from the Whittard Canyon had 100 cms of burrows and the two boxcores from the Hebrides Terrace had widely divergent totals, 49 and 303 cms respectively.

4.6 Discussion and Conclusions

The numbers of burrows in the top few centimetres was around 30 in boxcores from both the Firth of Clyde and Loch Creran and was due to the large numbers of tube dwelling polychaetes found at these sites. They were present in smaller numbers at the other sites.

The deeper burrows were constructed by capitellid polychaetes. The similar depth distribution of burrows in the deeper Firth of Clyde sites was produced by Dasybranchus caducus, a species restricted to this area. The spiral burrows of Notomastus latericeus were occasionally concentrated at a particular depth in the sediment, which produced a peak in the profile as at 4-6 cm in the Sound of Jura boxcores. The sharp decline in the numbers of burrows with depth at station C-12, Loch Creran was due to the absence of capitellids. At polluted sites the proximity of the redox potential discontinuity to the surface restricted burrowers to the top layers of the sediment (Pearson & Rosenberg 1978).

When the samples were arranged in order of increasing water depth (fig 1.9 in back pocket) the length of burrows/boxcore showed a maximum at the shallowest and deepest sites. In the Firth of Clyde this distribution appeared to be inversely related to the numbers of the burrowing echinoid Brissopsis lyrifera. It may be that these less sheltered sites are better exploited by a subsurface deposit feeder or that the subsurface burrowing of the echinoids prevents settlement by tube building polychaetes, a form of trophic group amensalism (Rhoads & Young 1970). The low numbers of burrows at station E-11, Loch Etive and in Loch Linnhe and Loch Eil was probably caused by low oxygen levels in the bottom waters. At the latter sites this was due to the high biological oxygen demand of the microfauna involved in the breakdown of pulpmill waste (Pearson & Stanley 1979).

At station C-12, Loch Creran, the average length of burrows/boxcore was 100 cm. Taking the average diameter of a burrow to be 2 mm, this gives a total volume of burrows of about 3 cm^3 and a total surface area of burrows of around 60 cm^2.

Burrows occupy 0.1% by volume of the top 5 cm of the sediment but represent an increase in surface area of 10%.

Chapter 5 : Spatial dispersion of burrow entrances

5.1 Introduction

Data are required on the spatial dispersion of species in marine level bottom communities in order to provide information on biological interaction and to devise meaningful sampling programmes that take patchiness into account.

Spatial dispersion has been investigated experimentally (Holme 1950, Levinton 1972), using random multiple samples (Clark & Milne 1955) and using a systematic pattern of samples (Gage & Geekie 1973b). However, studies of plant distribution have shown that the spatial pattern is dependent on the scale investigated, so a method has been devised of investigating the distribution at various scales by combining adjacent quadrats (Greig-Smith 1964, p. 85). This has been applied to marine benthic communities by combining diver-obtained samples taken along a transect (Angel & Angel 1967, Gage & Coghill 1977) and by combining boxcore subsamples (Rosenberg 1974). On a larger scale the spatial distribution of the large burrowing crustaceans which inhabit muddy sediments has been investigated by SCUBA divers using rope grids divided into metre squares (Atkinson 1974a,b)

In this study the distribution of burrow entrances was analysed since these are a measure of the species ambit*, an important diversity regulating mechanism on the scale of the individual animal (Jumars 1975b, 1976).

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* A species ambit is an imaginary circle around an animal defining the area over which it ranges (Lloyd 1967, p. 2).

5.2 Method

Boxcores which had been subsampled into either 4, 5, 6 or 7 vertical slices were analysed. The sediment surface revealed on the X-ray radiograph was divided into five equal sections which, in the case of the majority of the boxcores, gave a 5 cm square quadrat of sediment surface. The number of burrow entrances in each section was recorded on a grid, representing the surface of the boxcore divided into the requisite number of quadrats. At station C-12, Loch Creran, a separate count was made of the abundant tubes of Melinna palmata. A coefficient of dispersion* was calculated for each boxcore. The coefficient of dispersion is given by the ratio $S^2/\bar{x}$ where S^2 is the variance $\sum_{i=1}^{n} \frac{(x_i-\bar{x})^2}{n-1}$ and $\bar{x}$ is the mean $\sum_{i=1}^{n} \frac{x_i}{n}$. If the distribution follows a Poisson distribution, i.e. if the burrow entrances are randomly distributed, the coefficient of dispersion will be one. Values greater than unity show an aggregated distribution and values less, an even distribution. The upper and lower limits of the Poisson distribution in each case are given by the formula $1 \pm 2\sqrt{\frac{2n}{(n-1)^2}}$.

A block of sixteen quadrats was taken from each boxcore to be analysed at scales corresponding to multiples of the quadrat size by combining adjacent quadrats in the method described by Greig-Smith (1964, p. 85).

Coefficients of dispersion and their limits were calculated for blocks of 1 quadrat, 2 quadrats, 4 quadrats, 8 quadrats and 16 quadrats and the results plotted as a graph of the value of the coefficient against block size.

* of the number of burrow entrances

At station C-12, Loch Creran, and at Ardmucknish Bay sufficient boxcores were taken to permit study of the distribution of burrow entrances between boxcores. Coefficients of dispersion and their limits were calculated for each site on a scale of 600 cm^2, the total surface area of a boxcore.

5.3 Results

5.3.1 Complete boxcores divided into quadrats (table 5.1)

Only two boxcores, one from Ardmucknish Bay (25 cm^2 quadrats) and one from the Arran Deep (15 cm^2 quadrats) showed aggregation; burrow entrances in the other boxcores were randomly distributed.

5.3.2 Blocks of 16 quadrats analysed by Greig-Smith's method of pattern analysis (Table 5.2, fig 5.1-5.7)

Boxcores from four sites showed aggregation at various scales. Burrow entrances at station C-12 and Ardmucknish Bay were distributed in patches around 400 cm^2 in areal extent (figs 5.1, 5.5). Ardmucknish Bay also contained patches of around 200 cm^2 (fig 5.5). A single boxcore from the Sludge Dumping Ground in the Firth of Clyde contained a 50 cm^2 patch of burrows (fig 5.3). Burrows in two boxcores from the Arran Deep displayed aggregation at every scale investigated; 16 cm^2, 32 cm^2, 64 cm^2 and 128 cm^2 (fig 5.7).

5.3.3 Distribution between boxcores (Table 5.3)

Both station C-12, Loch Creran, and Ardmucknish Bay were aggregated at a scale of 600 cm^2 when all burrows were considered. However, when only the tubes of *Melinna palmata* at station C-12 were considered, a random distribution was found.

Table 5.1 Values which show significant aggregation are underlined.

Table 5.1a Complete boxcores divided into 25 cm^2 quadrats (4 x 5 grid)

Limits: 0.33-1.67

Site			$s^2/\bar{x}$
C-12	Box 1		1.18
	Box 2		1.53
	Box 3		0.94
	Box 4		1.03
	Box 5		1.01
C-12	*Melinna palmata* tubes	1	0.99
		2	0.87
		3	0.99
		4	1.01
		5	0.7
Firth of Clyde	Site 1		0.66
	Site P1		1.11
	Site P2		0.45
	Site P3		0.97
Loch Eil	Station 24	Box 1	1.15
		Box 2	0.45
	Station I	Box 1	0.5
			0.52
Loch Linnhe	Station II	Box 1	0.54
		Box 2	0.64

/Continued

Table 5.1a continued

Site		$s^2/\bar{x}$
Ardmucknish Bay	Box 1	0.9
	Box 2	0.71
	Box 3	1.0
	Box 4	0.79
	Box 5	0.5
	Box 6	0.81
	Box 7	1.67
	Box 8	0.91

Table 5.1b Complete boxcores divided into 20 cm^2 quadrats (5 x 5 grid)

Limits: 0.41-1.59

Site	$s^2/\bar{x}$
Sound of Jura	0.72

Table 5.1c Complete boxcores divided into 16 cm^2 quadrats (6 x 5 grid)

Limits: 0.47-1.53

Site		$s^2/\bar{x}$
Kilbrannan Sound		1.1
Loch Riddon	Box 1	0.46
	Box 2	0.66
Cemas Nathais	Box 2	0.73

Table 5.1d Complete boxcores divided into 15 cm^2 quadrats (7 x 5 grid)

Limits: 0.51-1.49

Site		$s^2/\bar{x}$
Arran Deep	Box 1	0.7
	Box 2	1.7
Cemas Nathais	Box 1	0.85

Table 5.2 $s^2/\bar{x}$

Values which show significant aggregation are underlined.

Site	25cm^2	50cm^2	100cm^2	200cm^2	400cm^2
5.2.A					
Loch Creran C-12 (5)	1.06	1.31	1.52	1.51	2.77
Loch Creran C-12 Melinna tubes (5)	0.93	o.99	1.17	0.96	1.68
Firth of Clyde Site 1 (1)	0.59	0.83	0.94	-	-
Site P2 (1)	0.5	0.7	1.3	-	-
Site P3 (1)	0.87	1.26	1.45	-	-
Site P1 (1)	1.3	2.33	0.81	-	-
Loch Eil Station 24 (2)	0.7	0.85	0.93	1.1	-
Station 1 (2)	0.36	0.67	0.3	0.12	-
Loch Linnhe Station 11 (2)	0.59	0.56	1.06	0.81	-
Ardmucknish Bay (8)	p.91	0.99	1.2	1.9	2.54
5.2.B Site	20cm^2	40cm^2	80cm^2	160cm^2	-
Sound of Jura (1)	o.72	0.56	0.63	0.94	-
5.2.C Site	16cm^2	32cm^2	64cm^2	128cm^2	
Kilbrannan Sound (2)	1.1	0.8	0.97	0.55	-
Loch Riddon (2)	0.4	0.4	0.3	0.5	-
Cemas Nathais	0.4	0.7	0.5	-	-
5.2.D Site	15cm^2	30cm^2	60cm^2	120cm^2	-
Arran Deep (2)	2.46	3.2	4.0	7.7	-
Cemas Nathais	0.67	1.2	2.2	-	-

Table 5.3 Between boxcore distribution (quadrats: 600 cm^2)

Values which show significant aggregation are underlined.

	Number of boxes	$s^2/\bar{x}$	Upper Limit
Loch Creran C-12	5	3.07	2.58
Loch Creran C-12 Melinna tubes	5	1.46	2.58
Ardmucknish Bay	8	2.65	2.14

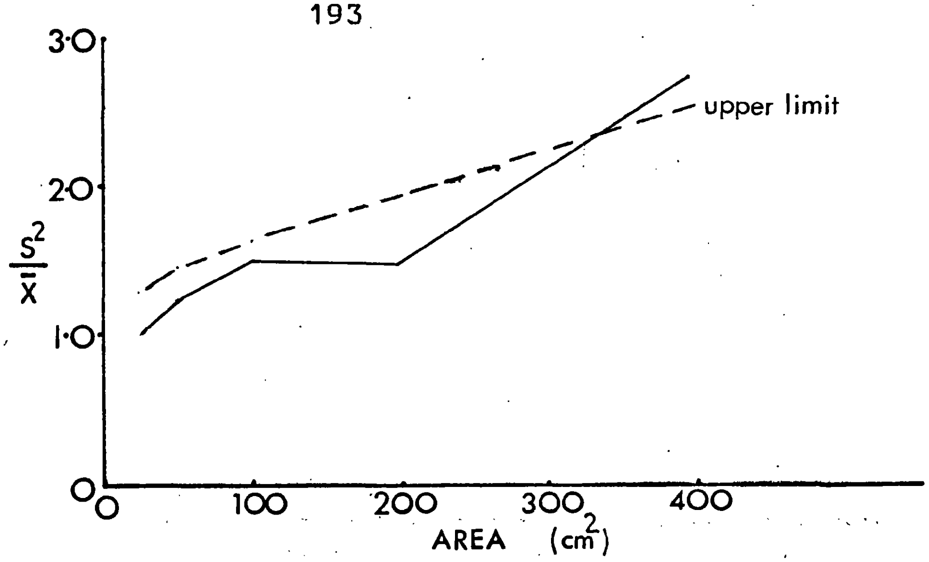


fig 5.I Coefficient of dispersion against block size for station C-I2, Loch Creran.

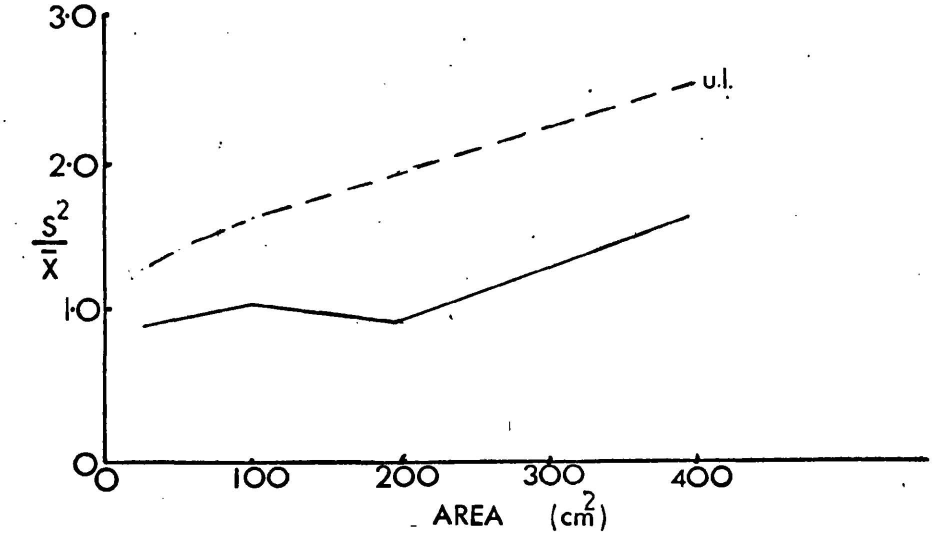


fig 5.2 Coefficient of dispersion against block size for Melinna tubes at station C-I2, Loch Creran

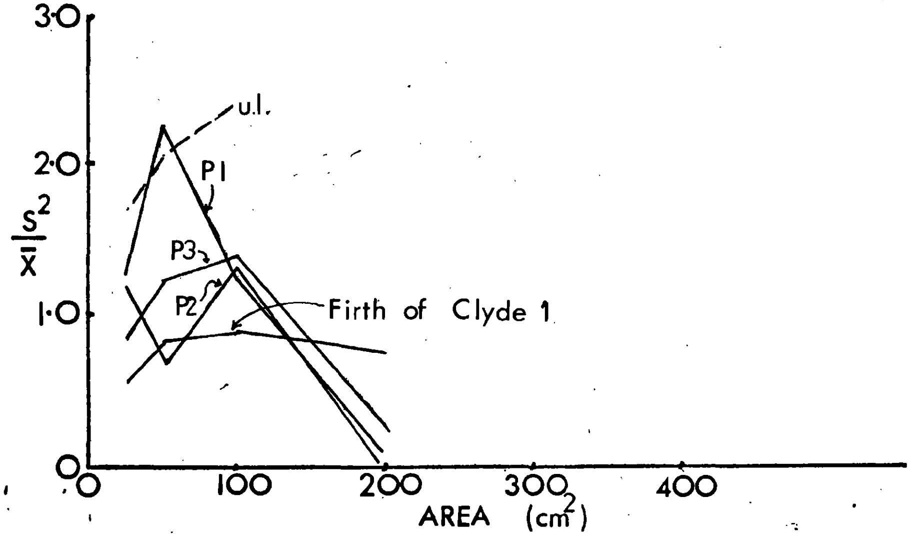


fig 5.3 Coefficient of dispersion against block size for polluted sites in the Firth of Clyde.

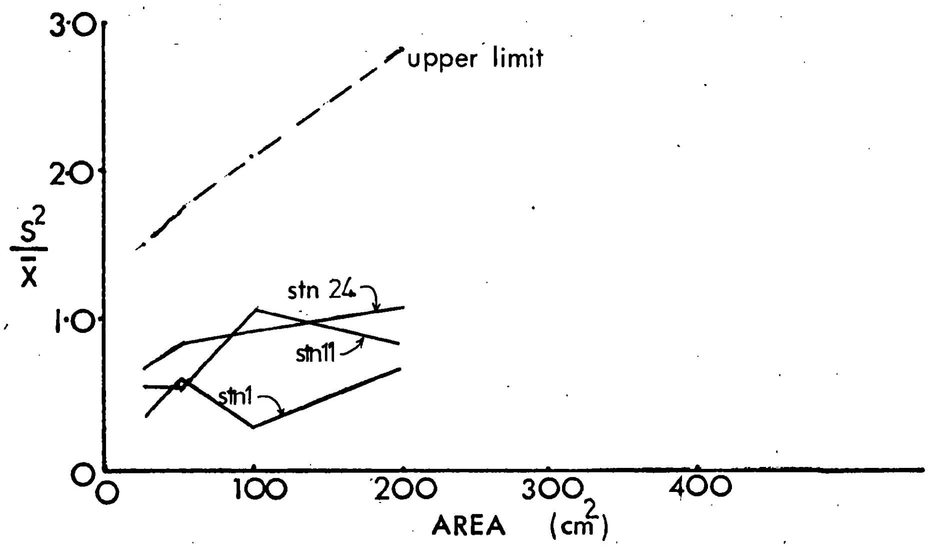


fig 5.4 Coefficient of dispersion against block size for stations in Loch Linnhe and Loch Eil.

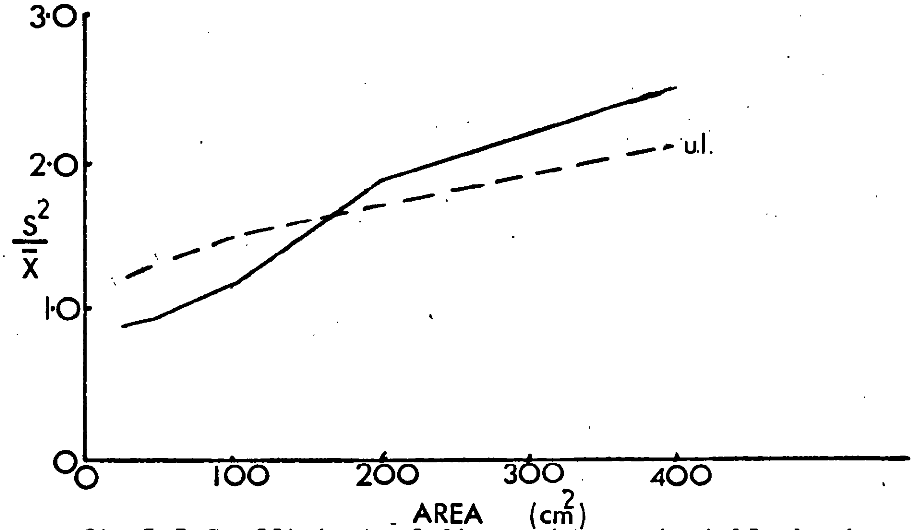


fig 5.5 Coefficient of dispersion against block size for Ardmucknish Bay.

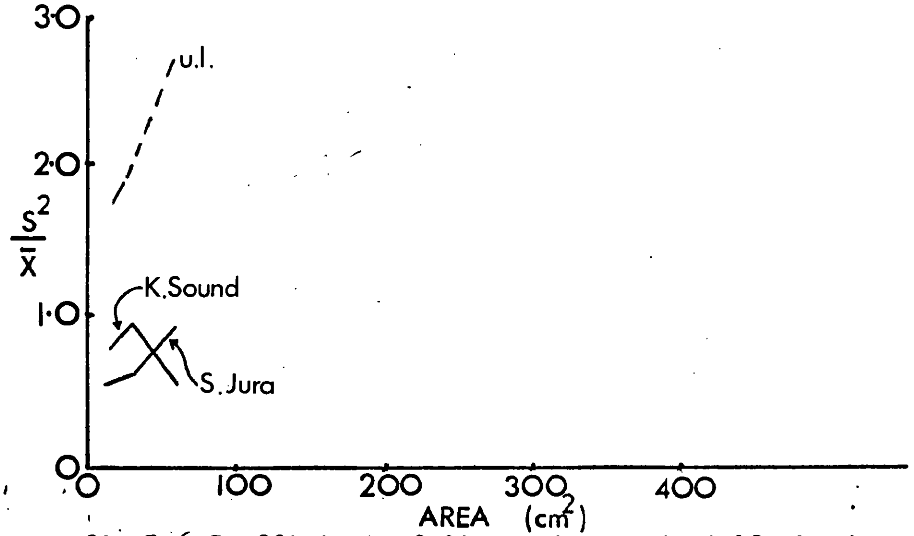


fig 5.6 Coefficient of dispersion against block size for Kilbrannan Sound and the Sound of Jura.

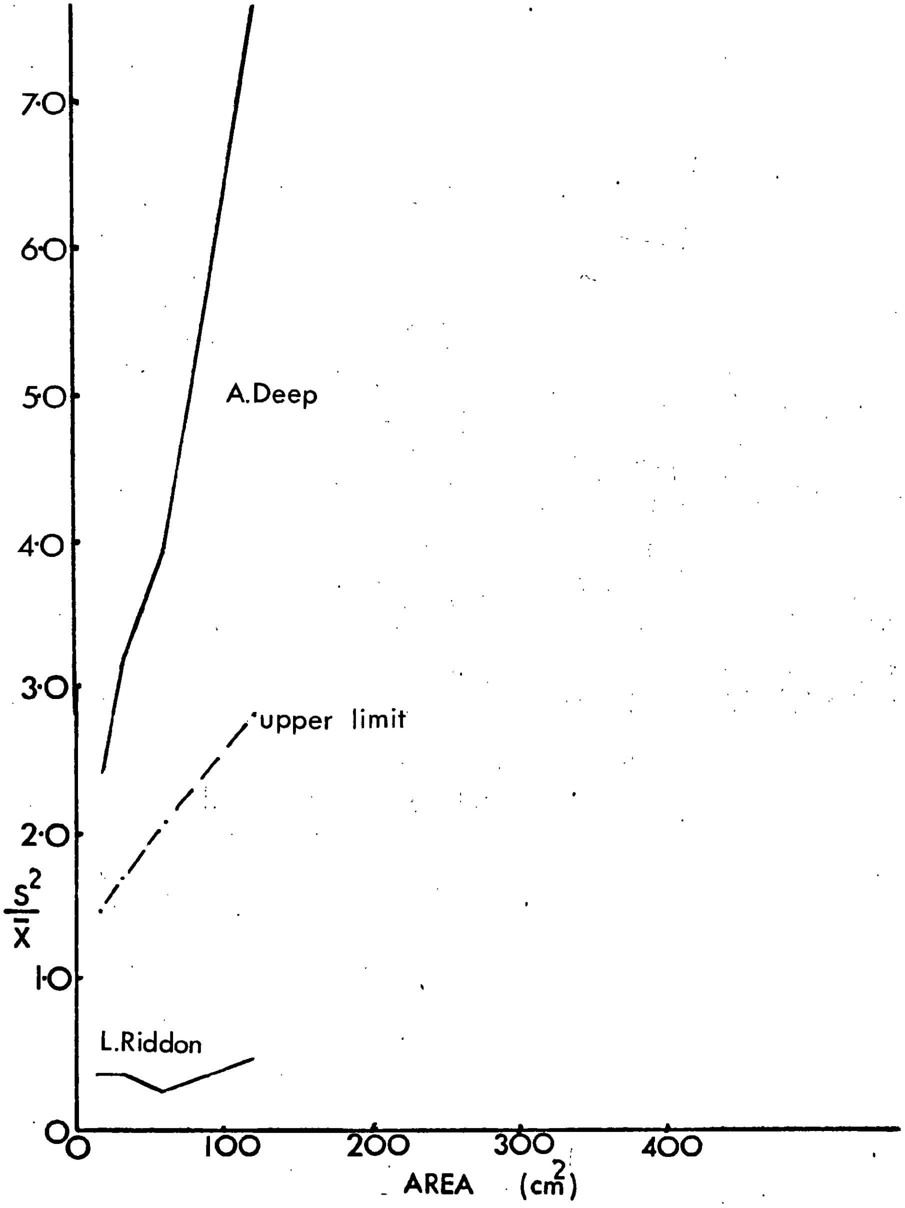


fig 5.7 Coefficient of dispersion against block size for the Arran Deep and Loch Riddon.

5.4 Discussion and Conclusions

5.4.1 Areas of 10-20 cm^2

This is the ambit of the individual sessile surface deposit feeder. *Melinna palmata* was observed in aquaria to 'rake' the sediment up to 3 cm away from its tube entrance and spionids use their palps to forage up to several centimetres from the tube. Jumars and Fauchald (1977, p. 16) have hypothesised that the length of prostomial appendages may be related to food availability. Foraging area is undoutably related to food availability since *Melinna palmata* has been recorded at densities of $5{,}000/m^2$ (= one tube per 2 cm^2) off Northumberland (Buchanan 1963b). The foraging area of each individual will tend to act as a spacing mechanism which will be maintained, since planktonic larvae settling in the foraging area will be consumed (Thorson 1966).

5.4.2 Areas of 20-100 cm^2

The areal extent of the branching burrow systems constructed by the errant polychaetes *Nephtys* and *Glycera* lie within this range. The many surface openings included in these burrow systems might have been expected to produce aggregation at this level in the analysis; however, aggregation was not found, presumably because their distribution was masked by the occurrence of other burrows around them.

5.4.3 Areas larger than 100 cm^2

Patches of these dimensions could be caused in at least four different ways:-

5.4.3.1 Gregarious Settlement: The presence of other individuals of the species is a factor in the settlement of the larvae of some species (Gray 1974). This would tend to produce an aggregated distribution.

5.4.3.2 Environmental heterogeneity: Eddies in the water mass may be reflected in the distribution of the benthos by controlling spatfall (Orton 1937) or by their effect on the sedimentation of the plankton on which the benthos feeds. Patches of decaying plant material or the carcasses of animals will produce an organically enriched area which will be reflected in benthos distribution (Gage & Geekie 1973b, Pearson & Rosenberg 1978).

5.4.3.3 Predation: Predation by shoals of bottom feeding fish can deplete the fauna of a patch of bottom sediment producing in a benthic community a mosaic of patches each at a different stage of ecological succession (Dayton & Hessler 1972).

5.4.3.4 Distribution of large burrows: The presence of one of the large burrow systems built by crustaceans such as *Nephrops* and *Goneplax* or fish such as *Lesuerigobius* and *Cepola* will effect the area around it. Some of the smaller benthic species are known to 'plug into' these larger burrow systems and their burrows have been recorded from resin casts of the large burrows (Atkinson et al. 1977). Pearson and Rosenberg (1978, p. 288) consider *Nephrops* to be "the dominant component in the physical structure of the whole community" as it is predominantly their burrowing activities which oxygenate the top 10 cm of the sediment. The magnitude of the effect of these large burrows on the distribution of the smaller benthic species is dependent on the longevity of a particular burrow system. No observations made from burrows in the natural environment have yet been published but casual observations (P. Morgan pers. comm. 1980) suggest that in Loch Riddon these burrows only last for a few months. A longer existence might be expected at other sites with a different sediment consistency as would seem to be necessary for the formation of nodules around them (Brown & Farrow 1978). Preliminary results from suction samples taken by divers around burrows revealed a sparser fauna in their immediate vicinity, perhaps due to crustacean predation (Nash & Pye unpublished observations 1979).

Chapter 6 : Conclusions

6.1 Comparison of principal sites

6.1.1 Method

Nine principal sites from which more than one boxcore had been obtained were selected to represent the complete range of environments sampled and the distribution of burrow types amongst them was compared by means of a similarity index.

The Jaccard coefficient was used as this ignores negative matches which could be the result of insufficient sampling. Analysis was carried out in both the Q and R modes, clustering sites and burrow types respectively. Rare burrow types, those occurring at only one of the principal sites (types 3, 5 and 11), were omitted (Table 6.1, Table 6.2).

The relationships between sites and between burrow types have been presented in the form of constellation diagrams as these show not only the greatest similarity between pairs of sites or burrow types but also lesser connections not readily apparent from a dendrogram, the alternative method of presentation (figs 6.1, 6.2).

6.1.2 Results

The most similar sites were the adjacent shallow marine sites in Ardmucknish and Cemas Nathais Bays. These, in turn, were closely linked to both the sea-loch sites of Loch Creran and Loch Riddon and to the deeper marine site in the Sound of Jura.

The Sound of Jura site was most closely connected to the shallower Sound of Mull site, The deep Firth of Clyde site in Kilbrannan Sound

Table 6.1 : Summary Table of Burrow Types from principal sites

Rare burrow types - 3, 5 and 11 - omitted

	TUBES		U-BURROWS		SPIRALS			BRANCHING BURROWS		
Principal Sites	1	2	4	6	7	8	9	10	12	Total
Kilbrannan Sound	X				X		X	X	X	5
Arran Deep	X		X		X		X	X		5
Loch Riddon	X	X	X	X	X			X		6
Ardmucknish Bay	X	X	X		X	X		X		6
Cemas Nathais Bay	X	X	X		X	X		X		6
Sound of Mull	X				X	X		X	X	5
Sound of Jura	X	X			X	X		X	X	6
Loch Creran C-12	X	X	X	X	X	X		X		7
Loch Etive E-6	X		X	X				X		4
Total	9	5	6	3	8	5	2	9	3	

Table 6.2

Burrow Types

	1	2	4	6	7	8	9	10	12	
		0.56	0.67	0.33	0.89	0.55	0.22	1.0	0.33	1
			0.57	0.33	0.63	0.67	0.0	0.56	0.14	2
				0.5	0.55	0.38	0.29	0.67	0.0	4
					0.22	0.13	0.17	0.33	0.0	6
						0.62	0.25	0.89	0.38	7
							0.0	0.55	0.33	8
								0.22	0.17	9
									0.33	10
										12

BURROW TYPES

PRINCIPAL SITES

	K.S	A.D	L.R	A.B	C.N	S.M	S.J	C-12	E-6
Kilbrannan Sound									
Arran Deep	0.67								
L. Riddon	0.38	0.57							
Ardmucknish Bay	0.38	0.57	0.71						
Cemas Nathais Bay	0.38	0.57	0.71	1.0					
Sound of Mull	0.67	0.43	0.38	0.57	0.57				
Sound of Jura	0.57	0.38	0.5	0.71	0.71	0.83			
L. Creran C-12	0.33	0.5	0.86	0.86	0.86	0.5	0.63		
L. Etive E-6	0.29	0.5	0.67	0.43	0.43	0.29	0.25	0.57	

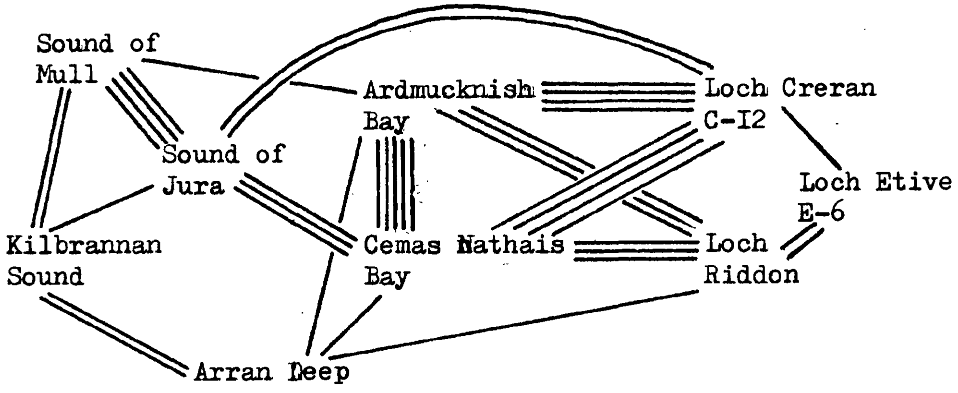
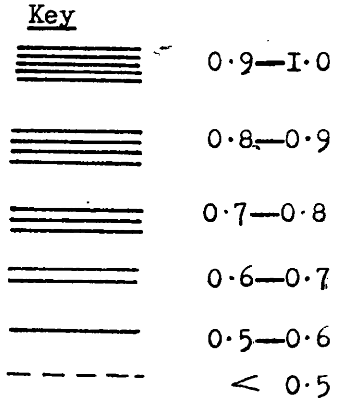


fig 6.1 Constellation diagram showing the relationships between principal sites.



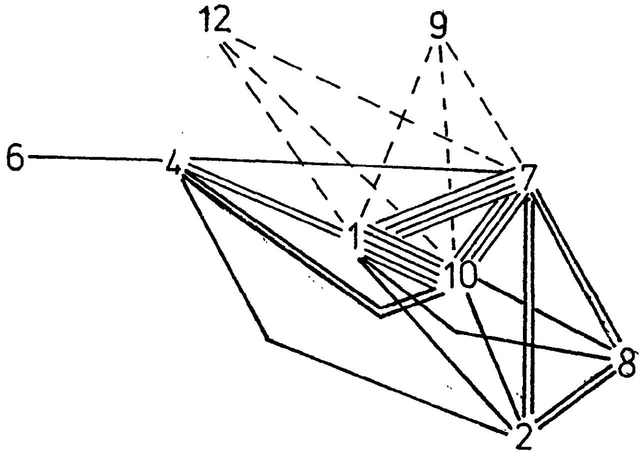


fig 6.2 Constellation diagram showing the relationships between burrow types (key to burrow types table 3.I)

had some affinity with the nearby Arran Deep site and with the Sound of Mull. The Loch Etive site clustered with the other sea-lochs.

The ubiquitous burrow types, 2 mm diameter tubes and burrows and *Amphiura* burrows (types 1, 10 and 7 respectively) clustered together. The less common burrow types mainly displayed affinities to this grouping. However, the larger tubes (type 2) were linked with the occurrence of both spiral *Notomastus* burrows (type 8) and shallow U-burrows (type 4) which, in turn, were linked to the deep U-burrows found in sea-lochs (type 6).

6.2 Distribution of Burrow Types: Summary (fig 1.9 in back pocket)

6.2.1 Tubes less than 2 mm diameter

This type of burrow was encountered at all the depths sampled but the species constructing the tubes differed. In the shallow sea-lochs, Loch Creran and Loch Riddon, tubes were produced by the ampharetid polychaetes *Melinna palmata* and *Amage adspersa* respectively. In the Firth of Clyde and Argyll inshore sounds the tubes were those of spionid polychaetes, chiefly *Spiophanes bombyx* with subordinate numbers produced by maldanid polychaetes.

6.2.2 Tubes greater than 2 mm diameter

These tubes were constructed by terebellid polychaetes, chiefly *Terebellides stroemi*, the eunicid polychaete *Onuphis conchylega* and by cerianthid anemones. This burrow type was most common in shallow marine and sea-loch sites where both terebellids and cerianthid anemones are most abundant. Occasional tubes were found at deeper sites in the Firth of Clyde where *Terebellides stroemi* is a widespread but rare species (Clark 1960). At 216 m in the Sound of Jura tubes ornamented with shell debris were found extending across the sediment surface; these were probably produced by *Onuphis conchylega*.

6.2.3 Pectinaria Tubes

The conical tubes of cemented sand grains constructed chiefly by *Pectinaria belgica* were found at two deep sea-loch sites, Loch Linnhe station II (95 m) and Loch Etive station II (115 m) and in Kilbrannan Sound (126 m). Rhoads (1974, p. 286) has suggested that such "conveyor belt" species, by introducing nutrients to the sediment surface from depths below the redox potential discontinuity, should increase benthic productivity. However, the two sea-loch sites at which this species was recorded were characterised by a rather sparse fauna, so the hypothesis appears untenable.

6.2.4 Shallow U-burrows

Shallow U-burrows are constructed by holothurians, the scalibregmid polychaetes *Scalibregma inflatum* and *Lipobranchius jeffreysii* and by amphipods. This burrow type was recorded from all depths but at low densities, so no significance should be attached to its absence at sites where only one boxcore was obtained. In shallow sea-lochs these burrows are produced by the holothurian *Cucumaria elongata*, in shallow marine sites by *Scalibregma inflatum* and the holothurian *Leptosynapta inhaerens* and in deep sites in the Firth of Clyde by *Lipobranchius jeffreysii*.

U-burrows with parallel, vertical limbs found at depths of 1200 m on the Hebrides Terrace have been tentatively attributed to amphipods.

6.2.5 Deep U-burrows, 1 cm diameter

This type of burrow was produced by the bivalve *Thracia convexa* and by the large polychaete *Chaetopterus variopedatus*. It is characteristic of shallow sea-lochs, where *Thracia* was found to be especially abundant.

6.2.6 *Amphiura burrows*

These burrows were produced by both *Amphiura filiformis* and *A. chiajei* and were found throughout the area. Their absence at some sites (e.g. the Arran Deep) was due to the collapse of the burrow as the animal emerged in response to the sampling.

6.2.7 2 mm diameter spiral burrows

These burrows are produced by the capitellid polychaete *Notomastus latericeus*. They are rare in sea-lochs but are common at all depths in the Argyll sounds; large numbers were recorded from the deep site in the Sound of Jura. In the Firth of Clyde spiral burrows were absent from the deeper parts and appeared to be restricted to depths of less than 100 m.

6.2.8 2 mm diameter wavy burrows

This type of burrow is produced by the capitellid polychaete *Dasybranchus caducus*. It is found only in deep sites in the Firth of Clyde where it occurs in a wide range of sediment types from the sandy muds of Kilbrannan Sound to the fine muds of the Arran Deep.

6.2.9 2 mm diameter branching burrows

These burrow systems were produced by the errant polychaetes *Nephtys*, *Glycera* and *Goniada* and the priapulid *Priapulus caudatus*. *Nephtys hombergi* is common at all depths in the Firth of Clyde and *N. hystricis* at all depths in the Argyll sounds. *Glycera*, *Goniada* and *Priapulus* are less abundant but are similarly widespread. This burrow type was recorded at every site where more than one boxcore was taken except the sparsely populated deep station in Loch Etive (E-II).

6.2.10 1 cm diameter branching burrows

These are produced by the crustacean Calocaris macandreae and were most common at the deep sites in the Firth of Clyde and Sound of Jura. Calocaris does occur at shallower depths and part of its burrow system was found in a boxcore from the Sound of Mull (depth 66 m).

6.2.11 Conclusion

2 mm diameter tubes and branching burrows and the burrows of the ophiuroid Amphiura occur at all the depths sampled. Shallow U-burrows, larger diameter tubes and the burrow systems of the crustacean Calocaris macandreae also occur at all depths but at lower densities. Deep U-burrows produced by the bivalve Thracia convexa are characteristic of shallow sea-lochs and Pectinaria tubes of the coarser deep sites. The deep burrowing niche is occupied by capitellid polychaetes; the spiral burrows of Notomastus latericeus are found at all depths except the deeper parts of the Firth of Clyde where Dasybranchus caducus produces a distinctive wavy burrow.

6.3 A model relating burrow types to water depth (fig 6.3)

By combining information from sites in similar environments, a model relating burrow types to water depth is presented.

Shallow sea-loch sediments are deposited in a very sheltered environment and have a high organic content (about 5% org. C.) derived from terrestrial sources. They are characterised by the deep U-burrows of the bivalve *Thracia convexa*. The tubes of ampharetid polychaetes are common and run predominantly obliquely through the sediment. *Amphiura* burrows and the branching burrows of errant polychaetes are also found.

Shallow marine sites are more exposed and burrows are less abundant than at both shallow sea-loch and deep marine sites. Spionid tubes with a predominantly vertical orientation and the branching burrows of errant polychaetes are the most common burrow types. The shallow U-burrows produced by the polychaete *Scalibregma* and the holothurian *Leptosynapta* and the 4 mm diameter tubes of *Terebellides stroemi* are commonest in this environment. *Amphiura* burrows and the spiral *Notomastus* burrows are also found, and in the Firth of Clyde at these depths the burrowing echinoid *Brissopsis* and the infaunal gastropod *Turritella communis* are at their most abundant.

Deep sea-loch sites are subject, periodically, to low oxygen concentrations and the fauna is sparse. Tubes of *Spiochaetopterus* and the conical tubes of cemented sand grains built by *Pectinaria* are the only burrow types found.

Two alternative deep marine burrow assemblages are presented.

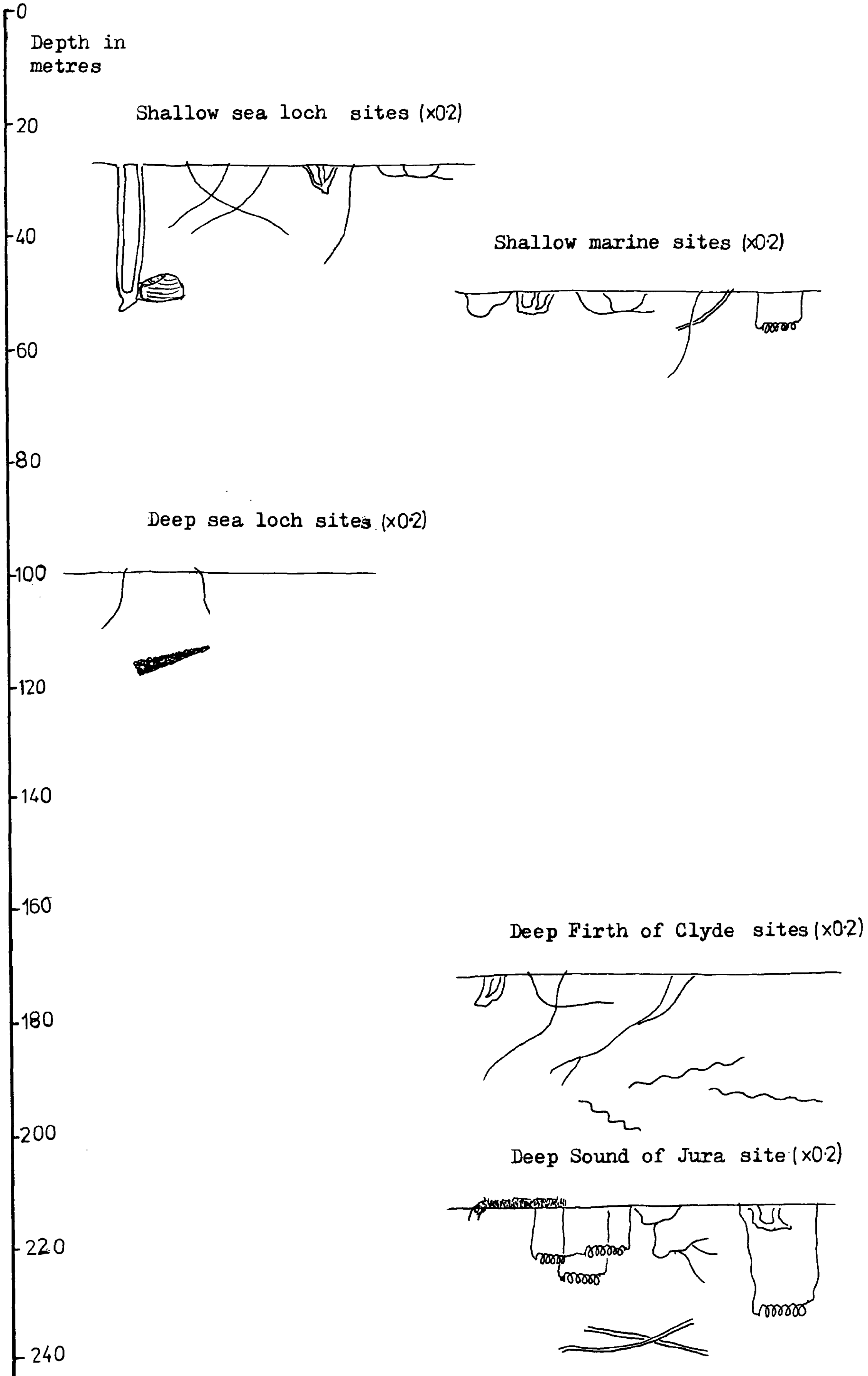


fig 6.3 Model relating burrow types to water depth.

In the Firth of Clyde these sites are characterised by the wavy burrows of the capitellid polychaete Dasybranchus caducus; spionid tubes are the commonest burrow type. In the Sound of Jura the spiral burrows of the capitellid polychaete Notomastus latericeus are common at depth in the sediment; narrow tubes are less common than the shell ornamented tubes of the eunicid polychaete Onuphis which run along the sediment surface.

6.4 A model relating burrow types to organic enrichment of the sediment (fig 6.4)

Pearson and Rosenberg (1976) have produced a summary diagram (fig 6.5) of the changes in the fauna under increased organic loading, based on aquarium observations of animals obtained from surveys of polluted sites. X-ray radiographs of boxcore subsamples reveal the burrows actually found at these sites and provide a test of this diagram. Information from boxcores obtained from sites designated as normal, transitory or polluted (Pearson & Rosenberg 1976) by intensive benthic surveys (Pearson & Stanley 1979, Pearson 1980 in prep.) is presented as a model relating burrow types to organic enrichment of the sediment.

Sites in the normal zone at shallow marine sites contain a diverse but sparse assemblage of burrows consisting of 2 mm diameter branching burrows and tubes, shallow U-burrows, Amphiura and spiral burrows. (The burrow of Nephrops was too large to be sampled with a boxcore). The transitory zone contains an enriched fauna with more species and a higher biomass than in the normal zone (Pearson & Rosenberg 1978) and this is reflected in boxcores by an increased number of burrows. Large numbers of spionid tubes and shallow U-burrows built by Scalibregma inflatum are found and the larger diameter tubes of Terebellides stroemi are also more common.

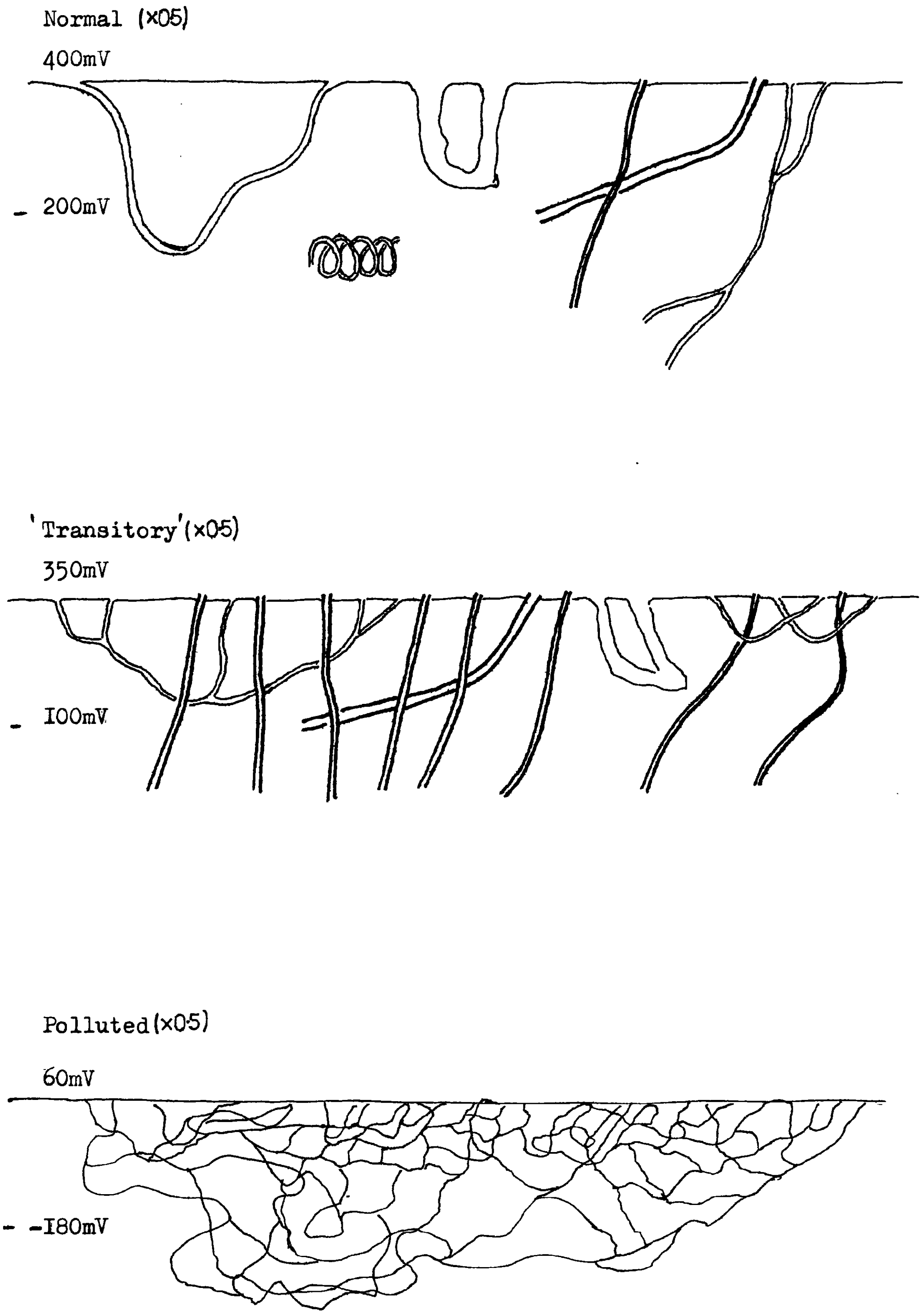


fig 6.4 Model relating burrow types to organic enrichment of the sediment. Eh values, given for the surface and depth 40mm, are taken from Pearson & Stanley (I979).

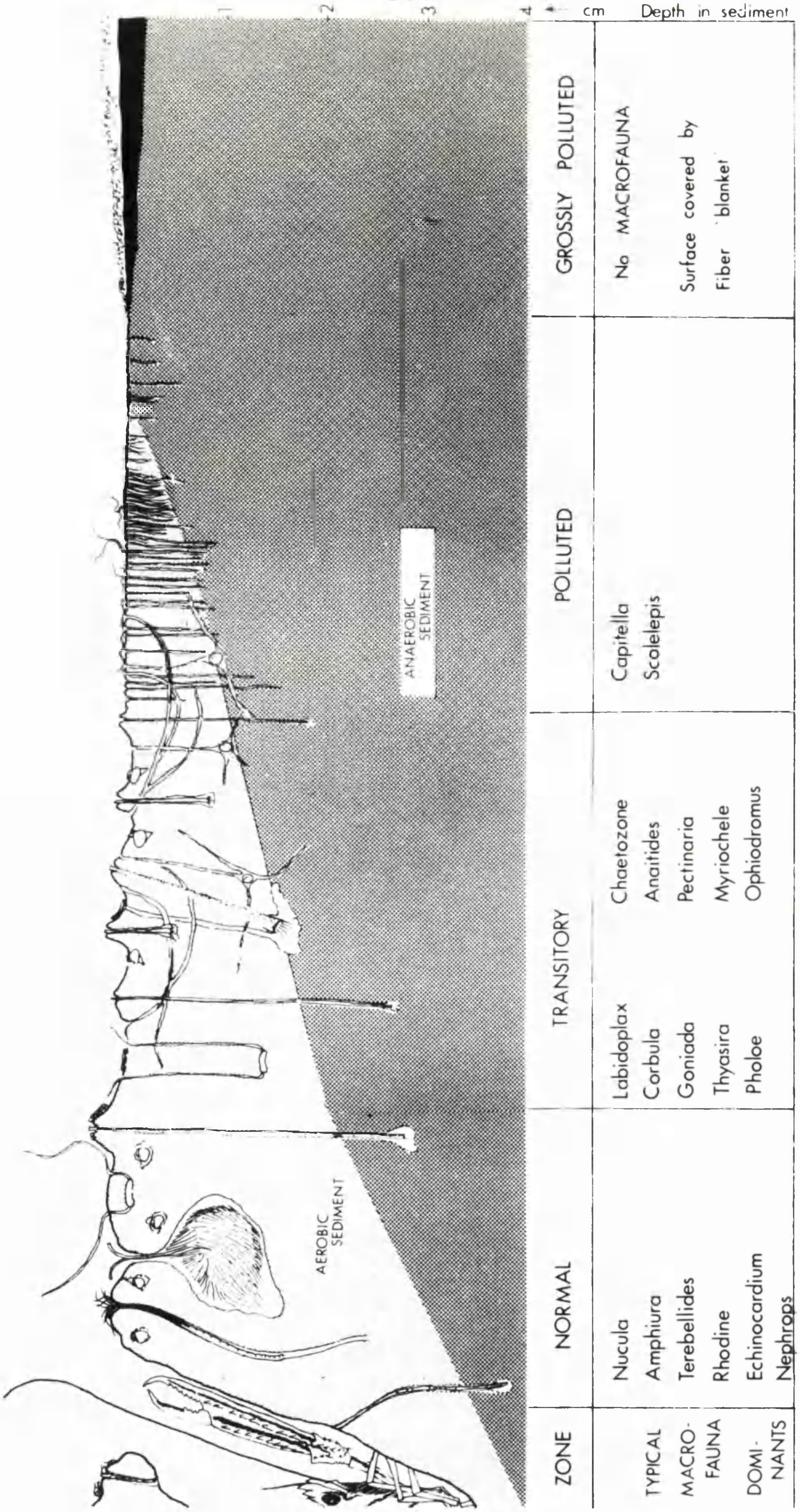


fig 6.5 Changes in the fauna and sediment under increased organic loading.
(from Pearson & Rosenberg 1976)

The polluted zone contains large numbers of a few opportunistic species (Pearson & Rosenberg 1978). The capitellid polychaete *Capitella capitata*, a common indicator of pollution, constructs a dense network of burrows in the top 4 cm of the sediment.

6.5 Comparison with other Recent ichnocoenoses (fig 6.6)

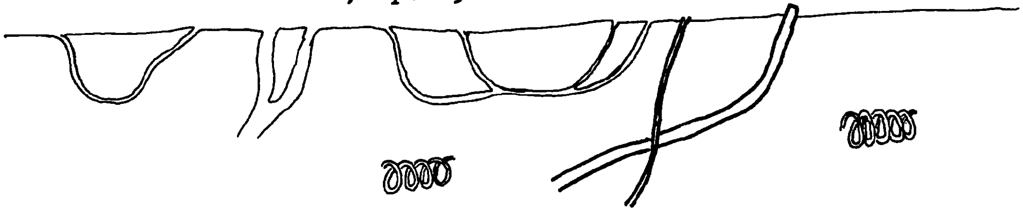
The fauna of this area belongs to the Amphiura community of Thorson (1957). This is one of a group of brittle star communities that are found worldwide in sublittoral fine sediments (Thorson 1957). Ichnocoenoses have been described from some of these (Dörjes & Hertweck 1975): in the North Sea (Reineck et al 1967, 1968, Hertweck 1970), in the Gulf of Gaeta (Hertweck 1973) and off Sapelo Island, Georgia (Hertweck 1972, Dörjes & Howard 1975).

In the North Sea off the north German coast in muds and sands 15-30 m deep the commonest burrow was the U-burrow constructed by a fluctuating population of the echiurian Echiurus echiurus (Hertweck 1970). Burrows of the polychaetes Scalibregma inflatum, Notomastus latericeus and Nephtys hombergi and the tubes of Cerianthus and Pectinaria were also found.

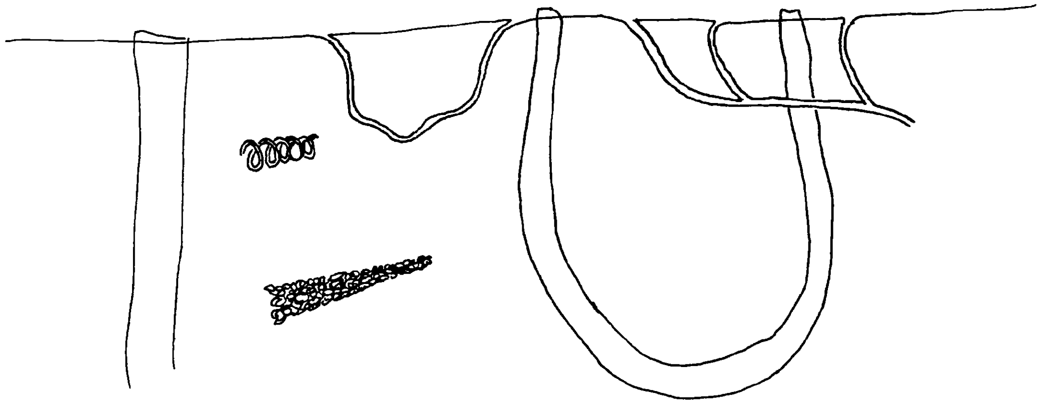
In the Gulf of Gaeta off the coast of southern Italy in muds at depths below 15 m the commonest burrow was that of the polychaete Nephtys hombergi. The fauna, described as an Amphiura chiajei community (Dörjes 1971) included the tube-building species Amage adspersa, Melinna palmata, Spiophanes bombyx and Terebellides stroemi, the burrowing genera Glycera, Notomastus and Cucumaria, the bivalves Abra alba, Nucula nucleus and Corbula gibba and the gastropod Turritella communis. The burrows of the echinoid Echinocardium cordatum were recorded from these sediments as well as from shallower depths.

Off Sapelo Island, Georgia in silty sand between 5 and 10 m deep a community named after the burrowing ophiuroid Hemipholis elongata has been described (Dörjes 1972). The commonest burrow was that of the crustacean Callianassa biformis. Branching burrow produced by the capitellid polychaete Capitomastus aciculatus and Glycera americana

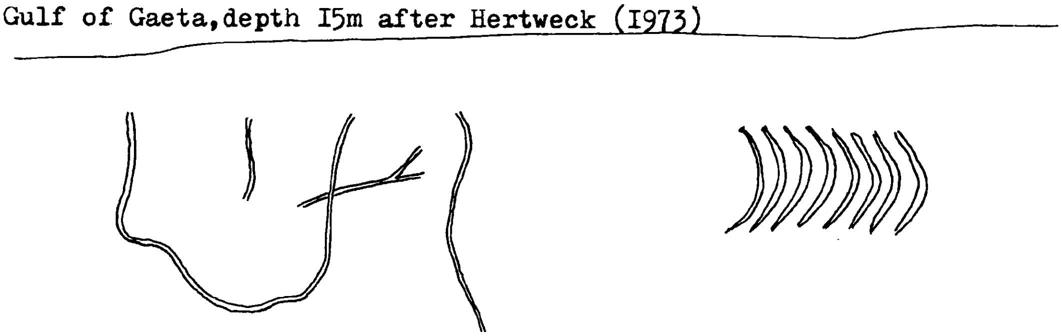
West Coast of Scotland,depth 50m



North Sea,depth 30m after Reineck et al.(1967)



Gulf of Gaeta,depth 15m after Hertweck (1973)



Sapelo Island,Georgia,depth 5-10m.Redrawn from Dörjes & Howard (1975)

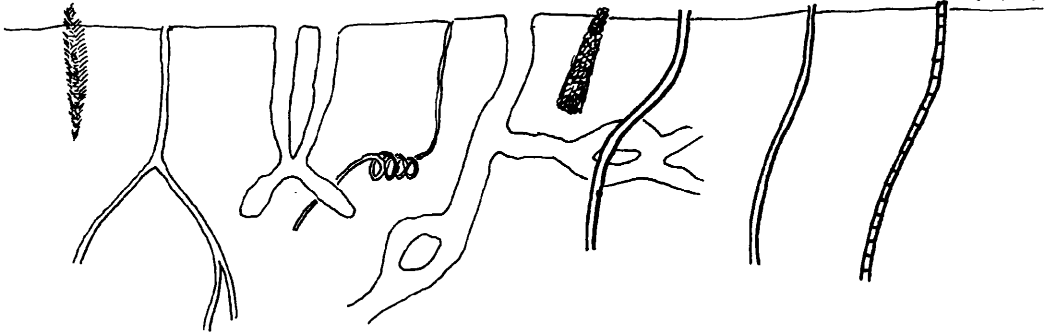
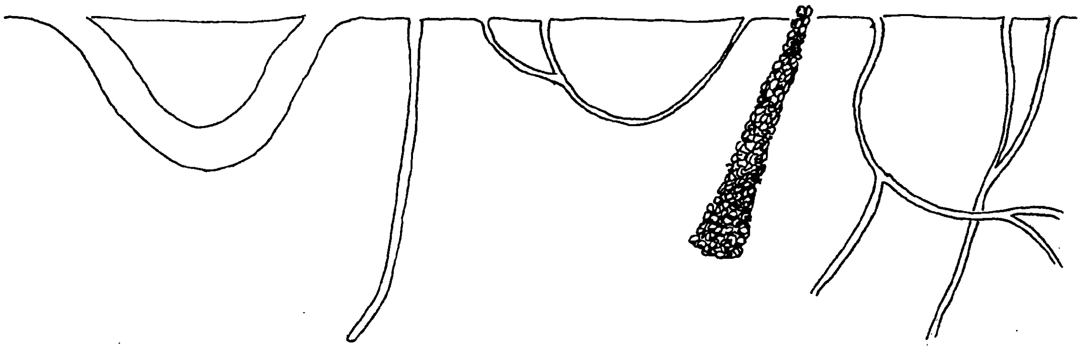


fig 6.6 Ichnocoenoses described from brittle star communities. (All burrows drawn x½.)

and the spiral burrow of Notomastus latericeus were found in addition to the tubes of chaetopterids, spionids including Spiophanes bombyx, pectinarids and Owenia fusiformis. Further offshore a coarse relict sediment was inhabited by a burrowing echinoid Moira atropos and tube dwelling polychaetes. All these communities occur below wave base where bottom currents are weak, hence physical disturbance is unlikely and burrowing and tube building amongst surface feeding animals is a protection against predation. Organic matter is settling out of the water mass so surface deposit feeding is as successful as suspension feeding and the sediment contains sufficient organic matter to justify exploitation by burrowing forms: a greater diversity of niches is available than in shallower high energy environments where suspension feeding from the bottom traction current is the only method of feeding possible for microphagous species. Food is not as scarce as in abyssal environments where programmed grazing is necessary to exploit a patchily distributed resource (Kitchell 1979). Jumars and Fauchald (1977) found that the number of sessile species increased with depth until 400 m and then decreased in bathyal and abyssal environments. They attributed the increase to increasing sediment stability and the decrease to decreased food availability which made it necessary for deposit feeding species to be mobile in order to collect sufficient food.

However,this diversity of burrow types is not confined to marine habitats below wave base, both Myers (1977a,b) and Ronan (1977) have demonstrated a diverse suite of burrow types in sheltered intertidal sandflats where suspension feeding, surface and subsurface deposit feeding are all practised (fig 6.7). In these shallow environments where sediment is deposited by bottom currents, burrowing will be concentrated along specific food rich layers and a programmed feeding strategy may be required to exploit it (Risk & Tunnicliffe 1978).

Bodega Bay,California adapted from Ronan (1977)



Charlestown Pond,Rhode Island adapted from Myers (1977a,b)

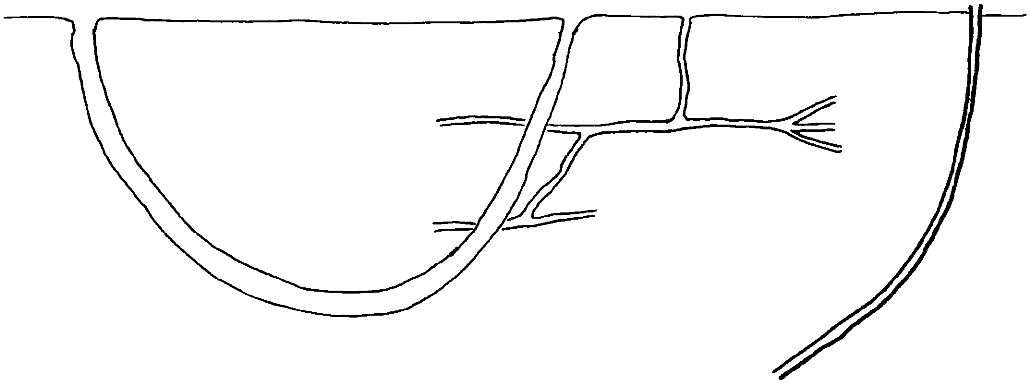


fig 6.7 Ichnocoenoses from sheltered intertidal sandflats.
(All burrows drawn x½.)

In deeper waters where material is settling from suspension such layers do not occur and burrowing is random through the sediment.

Trophic group amensalism (Rhoads & Young 1970), the exclusion of suspension feeders by the feeding activities of deposit feeders, has been reported from the shallow muds off Massachusetts, U.S.A. (Rhoads & Young 1970), tropical lagoons (Aller & Dodge 1974) and shallow sand deposits (Myers 1977a). It does not occur in the muds off the west coast of Scotland. Suspension feeding bivalves such as *Thracia convexa*, *Artica islandica* and *Mya truncata* all live in the muddy sediment in spite of its high water content caused by the feeding activities of deposit feeding bivalves such as *Nucula*. However, these muds do not undergo the tidal resuspension that produces the dense mud suspensions in Buzzards Bay, Massachusetts, which clog the gills of any suspension feeding bivalve attempting to live there.

6.6 Implications for Trace Fossils

6.6.1 Preservability

The implications for the study of trace fossils of any study of Recent burrows are dependent upon the preservability of the Recent burrow types. Hertweck (1972) found that 15% of the total living species in the Sapelo Island transect produced lebensspuren and only half of these were found preserved. Burrows may be preserved by being infilled by a different type of sediment or by nodules forming around them during diagenesis as a result of the chemical changes which occur in the sediment surrounding the burrow. Animals crawling through the sediment may produce distinctive sedimentary structures (Howard et al 1974).

In boxcores no unoccupied burrows were found at depth and they were assumed to have collapsed upon the death of the producing animal. Faecal pellet infilled burrows, attributed to the capitellid polychaete <u>Dasybranchus caducus</u> were recorded and they may be preserved if the faecal pellets retain their distinctive morphology. Diagenesis of the sediments may render visible burrows and tubes not observed at present, as has been demonstrated by staining Quaternary sediments from the north east Irish Sea (Pantin 1978). Nodules have been formed around crustacean burrows from muds in Loch Sunart and the Firth of Clyde (Brown & Farrow 1978). The distinctive biogenic structures produced by burrowing echinoids were not found in the sediments studied. This may be because they are shallow burrowers and any traces produced would be destroyed by deeper burrowing species (Bromley & Asgaard 1975) or because sedimentary structures produced by oriented grains cannot be distinguished in fine grained sediments.

6.6.2 Analogous Trace Fossil Assemblages

Trace fossils have been described from shales and other fine sediments from a wide range of ages and areas. Burrows in Miocene sediments in Denmark have been named after their possible producers by analogy with burrows found in the North Sea (Radwański 1977). Burrows built by sea anemones, echiuroids, holothurians and echinoids were found. Howard (1972) has described an assemblage of trace fossils from thin-bedded grey siltstones from the Upper Cretaceous Blackhawk Formation of Utah, U.S.A. consisting of *Asterosoma*, *Arthrophycus*, *Teichichnus* and *Scolicia* as well as unnamed chevron trails and smooth tubes. The lower Jurassic Lias clays of Dorset, South Wales and Yorkshire contain the trace fossils *Chondrites*, *Thalassinoides* and *Rhizocorallium* (Hallam 1960b, Sellwood 1970). The ichnofaunas of Palaeozoic fine sediments are dominated by the trilobite traces *Cruziana* and *Rusophycus* (Crimes 1970). Other traces such as *Planolites* and *Scolicia* do occur and first appear in late PreCambrian sediments (Alpert 1977), coincident with the major radiation of the Metazoa. Unlike the flysch ichnocoenose, the ichnofauna of shelf seas has maintained the same high level of diversity throughout the Phanerozoic (Seilacher 1977).

In the bathymetric zonation of trace fossils proposed by Seilacher (1967) sediments of shelf seas are characterised by ichnofaunas of the *Cruziana* and *Zoophycos* facies. These consist of trails such as *Cruziana* and *Scolicia*, burrows such as *Thalassinoides*, *Chondrites* and *Planolites* and spreiten burrows such as *Rhizocorallium*, *Teichichnus* and *Zoophycos*.

As illustrated by Frey (1975, fig 2.9) modern burrows may represent only the current open burrow of a more complex structure eventually revealed by diagenetic enhancement. A modern equivalent of the spreite burrow *Rhizocorallium* has yet to be found. The burrows built by the rag-worm *Nereis* in North Sea tidal flats closely resemble *Teichichnus* (Schäfer 1972). *Zoophycos* has been recorded from DSDP cores (Ekdale 1977) but the producing animal is unknown; several hypotheses have been advanced to explain its formation (Plička 1970, Bradley 1972, Simpson 1977).

The bilobed trail *Scolicia* is probably formed by a large scavenging gastropod. Present day decapod crustaceans have fewer legs than trilobites and do not walk with the pronounced sideways swing to their legs which produced the trace fossil *Cruziana* (Seilacher 1970).

The unbranched or rarely branched burrow *Planolites* may be produced by errant polychaetes or since the former mud tube would be difficult to distinguish from the surrounding sediment it might be produced by sedentary polychaetes such as ampharetids and spionids. *Chondrites* is probably the burrow of an errant polychaete (few examples resemble the regular probing model of Simpson (1957)). *Thalassinoides* is generally accepted to be a crustacean burrow (Häntzschel 1975).

Appendix I

A.1.1 The Reineck Box Corer (fig I.2)

The boxcorer consists of a gimbaled supporting frame, central column with box holder, triggering mechanism, closing mechanism and sample box. The column stands vertically in the frame and can move freely within the gimbals; thus the sample box, fixed in place at the base of the column, penetrates the sediment when the corer reaches the bottom. The closing mechanism is triggered by the slackening of tension in the cable, it consists of a plate mounted on a pivoted arm which swings in to close off the base of the sample box.

A.1.1.1 The frame

The frame, by means of its gimbals, ensures a vertical penetration of sediment by the box and supports the central column both on the bottom and on deck. Made of tubular aluminium it comprises of a base 2.65 m x 1.37 m with legs (1.3 m long) running up from each of the corners to the gimbal mounting (41 cm x 37 cm), 1.15 m above the base.

For use in depths of thousands of metres the tubular frame should be drilled so that the pressures encountered are equalised inside and outside the tubing.

A.1.1.2 The central column

The central column is 2.3 m long with a square cross-section (10 cm x 10 cm). Two thickened sections 0.6 m apart restrict its movement through the inner gimbal and a metal pin inserted through the column just above the gimbals holds it off the deck while the sample box is replaced.

The column is filled with lead and additional lead weights can be bolted to the column just above the box holder for increased penetration of firmer substrates (hard sands).

The box fits inside a metal rim at the base of the column and is held in place by two metal rods which slot through the holes in the top of the box and in the metal rim. Two downward pointing prongs also help to hold the box in position.

The top of the box holder is partially covered to lessen washing of the sample on the way up but also to allow water to pass out of the box during penetration and to reduce the bow wave in front of the descending corer.

A.1.1.3 Triggering mechanism

The winch cable is attached by a shackle to a metal ring which fits into a slot cut in the top of the column. A lever hooks into the ring and is held in position by the tension in the cable. On impact with the bottom the tension in the cable slackens and the lever drops out of the ring triggering the closing mechanism.

A.1.1.4 The closing mechanism

The closing mechanism consists of a yoke-shaped arm pivoted about the top of the boxholder. At the end of the arm a slightly curved metal plate is welded between the two branches of the yoke. This plate fits snugly under the bottom of the box during recovery of the core and its leading edge is sharpened to facilitate its passage through the sediment.

The other end of the arm houses a pulley around which a rope runs. One end of the rope passes through a pulley at the top of the column and is attached to the lowering cable via the metal ring of the triggering mechanism; the other is attached to the top of the column. Thus when the triggering mechanism is activated, renewed tension in the cable as the corer is hauled in pulls the pivoted arm from a horizontal to a vertical position, bringing the plate into position under the bottom of the sample box.

A.1.1.5 Removal of the sample box

The holes in the yoke-shaped arm through which the axle passes are oval and when the tension in the cable is reduced a small gap develops between the box and the closing plate. Into this gap a stainless steel base plate is pushed and the rods holding the box in place are removed. While the arm is swung back to a horizontal position, the box is lowered gently on to the deck and two springs used to clip the base plate to the sides of the box. The box is now ready for transport back to laboratory for examination.

Appendix 2 Sample Sites : Depth, Particle Size and Position

Table A.1

Sample Site	Depth	Particle Size			Position Radar/Decca/Lat. Long.	
		Sand	Silt	Clay	Decca Red*	Decca Purple*
Firth of Clyde 1	74m	-	40	60	D18.0	J50.0
Firth of Clyde 2	43m	35	35	30	D 5.4	I67.4
Firth of Clyde 3	47m	15	42	43	D 8.0	I58.3
Firth of Clyde 4	76m	-	32	68	D16.7	H78.1
Firth of Clyde 5	47m	30	36	34	E 0.5	H69.8
Firth of Clyde 6	56m	-	54	46	D18.9	G56.5
Firth of Clyde 7	54m	5	48	47	E 5.2	G51.8
Firth of Clyde 8	50m	8	50	42	E15.9	G52.2
Firth of Clyde 9	47m	30	42	28	F 2.5	G51.7
Kilbrannan Sound	124m	53	15	31	E20.7	J52.3
Cumbrae Deep	105m	60	16	24	D23.0	J74.0
Arran Deep	170m	-	30	70	E10.0	J60.5
Loch Riddon	30m	35	35	30	see fig 3.I	
Loch Goil	77m	8	70	22	see fig 3.I	
Firth of Clyde P1	79m	-	-	-	E 0.0	J53.0
Firth of Clyde P2	74m	-	-	-	E 0.0	J58.0
Firth of Clyde P3	72m	-	-	-	D21.0	J53.0
Firth of Clyde P4	83m	-	-	-	E 0.0	J63.0

* Decca: CHAIN 3B/MP (N.British) corrected.

Appendix 2 Continued   Sample Sites : Depth, Particle Size and Position

Table A.1 (con)

Sample Site	Depth	Particle Size			Position Radar/Decca/Lat. Long.
		Sand	Silt	Clay	
Cemas Nathais Bay	25m	27	56	17	see fig 3.21
Ardmucknish Bay	50m	10	30	60	see fig 3.21
Sound of Mull	66m	17	47	36	Glas Eilean 349° 1·15nm Ardmore Pt. 238° 1·5nm
Sound of Jura	216m	33	47	20	N.end Gigha 283° 6·1nm Ardmore Pt. 064° 12·2nm
Loch Creran C-12	22m	35	44	21	see fig 3.21
Loch Etive E-6	40m	18	51	31	see fig 3.21
Loch Etive E-11	115m	17	51	32	see fig 3.21
Loch Eil Stn 24	31m	2	94	4	see fig 3.29
Loch Eil Stn 1	42m	11	71	18	see fig 3.29
Loch Linnhe Stn 10	90m	30	67	3	see fig 3.29
Loch Linnhe Stn 11	95m	12	83	5	see fig 3.29
Whittard Canyon	1330m	24	48	28	48° 28'N 10° 21'W
Hebrides Terrace	1200m	17	50	33	56° 46.7'N 9° 13'W

Appendix 3 Faunal lists obtained from grab samples

All samples obtained with a Van Veen Grab ($0\cdot 1m^2$).
Extracted with 2mm sieve.

Sample: Irvine Bay A
Position: Decca D6·8 I69·5
Depth: 55m
Fauna: Polychaeta
I Pectinaria belgica
Mud tubes
Bivalvia
I Nucula turgida
I Nucula tenuis
3 Mysella bidentata
5 Abra alba
Echinodermata
I Amphiura filiformis
Dead shells
I Saxicavella jeffreysi
I Turritella communis
I Abra prismatica

Sample: Irvine Bay B
Position: Decca D7·95 I70·5
Depth: 55m
Fauna: Polychaeta
I Nephtys hombergi
I Notomastus latericeus
2 Ammotrypane aulogaster
I Terebellides stroemi
Bivalvia
5 Nucula tenuis
II Nucula turgida
2 Abra alba
2 Montacuta sp.
Echinodermata
3 Brissopsis lyrifera
2 Amphiura filiformis

Sample: Irvine Bay C
Position: Decca D8·4 I70·9
Depth: 55m
Fauna: Polychaeta
I Nephtys hombergi
I Orbinia latreilli
2 Notomastus latericeus
2 Scalibregma inflatum
Bivalvia
7 Nucula turgida
2 Nucula tenuis
5 Abra alba
I Corbula gibba
I Venus casina
Gastropoda
I Neptunea antiqua
Echinodermata
3 Brissopsis lyrifera
2 Amphiura filiformis

Sample: Irvine Bay D
Position: Decca D6·5 I66·9
Depth:50m
Fauna: Polychaeta
- 4 Nephtys hombergi
- I Lumbrinereis hibernica
- 2 Mediomastus fragilis

Bivalvia
- 4 Nucula turgida
- 7 Abra alba

Echinodermata
- I Brissopsis lyrifera
- 2 Amphiura filiformis

Sample: Irvine Bay E
Position: Decca D7·7 I68·2
Depth: 55m
Fauna: Polychaeta
- 2 Nephtys hombergi
- I Harmothoë lunulata
- I Spiochaetopterus typicus

Coelenterata
- I Cerianthus LIoydi

Bivalvia
- 8 Nucula turgida
- 2 Nucula tenuis

Echinodermata
- 2 Brissopsis lyrifera
- 5 Amphiura filiformis

Sample: Irvine Bay F
Position: Decca D8·65 I68·4
Depth: 40m
Fauna: Polychaeta
- 6 Nephtys hombergi
- 2 Notomastus latericeus
- 3 Goniada maculata
- 2 Amaea trilobata
- I Clymene sp.
- 2 Lumbrinereis hibernica
- I Phyllodoce sp.
- I Polynoë kinbergi
- 3 Spiophanes bombyx

Bivalvia
- 2 Nucula turgida
- I Abra alba

Gastropoda
- II Turritella communis

Echinodermata
- 3 Leptosynapta inhaerens

Amphipoda
- I Ampelisca sp.

Sample: Irvine Bay G
Position: Decca D7·6 I64·I
Depth: 60m
Fauna: Polychaeta
I Nephtys hombergi
3 Spiophanes bombyx
3 Pectinaria belgica
Bivalvia
I Nucula sulcata
I Nucula turgida
Dead shells
I Donax vittatus
I Corbula gibba
Echinodermata
3 Brissopsis lyrifera
3 Amphiura filiformis

Sample: Irvine Bay H
Position: Decca D8·I I 64·5
Depth: 60m
Fauna: Polychaeta
I Harmothoë lunulata
I Lipobranchius jeffreysii
I Terebellides stroemi
I Pectinaria belgica
Bivalvia
2 Nucula sulcata
I Abra alba
I Chlamys septemradiata
Echinodermata
2 Leptosynapta inhaerens

Sample: Irvine Bay I
Position: Decca D8·8 I65·5
Depth: 60m
Fauna: Polychaeta
I Nephtys hombergi
I Glycera rouxi
I Glycera alba
I Goniada maculata
I Harmothoë lunulata
I Terebellides stroemi
I Pectinaria belgica
Bivalvia
7 Abra alba
3 Nucula sulcata
I Nucula turgida
I Corbula gibba
Echinodermata
I Amphiura chiajei
Crustacea
I Crangon crangon
I Macropipus sp.
Gastropoda
I Natica alderi

Sample: Kilbrannan Sound A
Position: Decca E2I·2 J5I·8
Depth: I24m
Fauna: Polychaeta
I Harmothoë lunulata
2 Nephtys hombergi
I Glycera rouxi
I Onuphis conchylega
I Scalibregma inflatum
I Lipobranchius jeffreysii
40 Owenia fusiformis
40 Spiophanes bombyx
I Amphicteis gunneri
I Pista cristata
I Thelepus setosus
Bivalvia
6 Nuculana minuta
I Chlamys septemradiata
Scaphopoda
I Dentalium entalis
Echinodermata
3 Amphiura chiajei
Crustacea
I Crangon crangon

Sample:Arran Deep A
Position: Decca EI0·0 J59·5
Depth: I80m
Fauna: Polychaeta
I Glycera rouxi
20 Spiophanes bombyx
Bivalvia
3 Nucula sulcata
Echinodermata
I0 Amphiura chiajei

Sample: Cumbrae Deep A
Position: Decca D23·0 J74·0
Depth: I05m
Fauna: Polychaeta
2 Nephtys hombergi
3 Scalibregma inflatum
I Lipobranchius jeffreysii
I0 Ammotrypane aulogaster
I0 Owenia fusiformis
I Terebellides stroemi
Bivalvia
I Chlamys opercularis
I Chlamys septemradiata
I Arctica islandica
2 Venus ovata
I Corbula gibba
2 Thyasira flexuosa
I Mysia undata
Gastropoda
I0 Turritella communis
I Aporrhais pes pelicani
Dead shells
2 Littorina littorea

Sample: Loch Riddon A
Position: South end of loch
Depth: 25m
Fauna: Polychaeta
6 Nephtys hombergi
4 Notomastus latericeus
2 Diplocirrus glauca
I Spiophanes bombyx
I Amage adspersa
I Terebellides stroemi
Bivalvia
2 Nucula turgida
Dead shells
2 Nucula sulcata
I Arctica islandica
I Venerupis rhomboides
I Saxicavella jeffreysi
I Corbula gibba
Turritella communis fragments
Echinodermata
I Echinocardium flavescens
2 Amphiura chiajei

Sample: Loch Riddon B
Position: Mid-loch
Depth: 25m
Fauna: Polychaeta
3 Nephtys hombergi
2 Terebellides stroemi
I0 Amage adspersa
3 Spiophanes bombyx
2 Clymene oerstedii
Echinodermata
3 Echinocardium flavescens
60 Amphiura chiajei
2 Cucumaria elongata
Priapuloidea
I Priapulus caudatus

Sample: Loch Goil A
Position: Lochgoilhead
Depth: 20m
Fauna: Polychaeta
6 Sabella pavonina
Bivalvia
I Abra alba
I Corbula gibba
2 Thyasira flexuosa
Dead shells
I Mytilus edulis

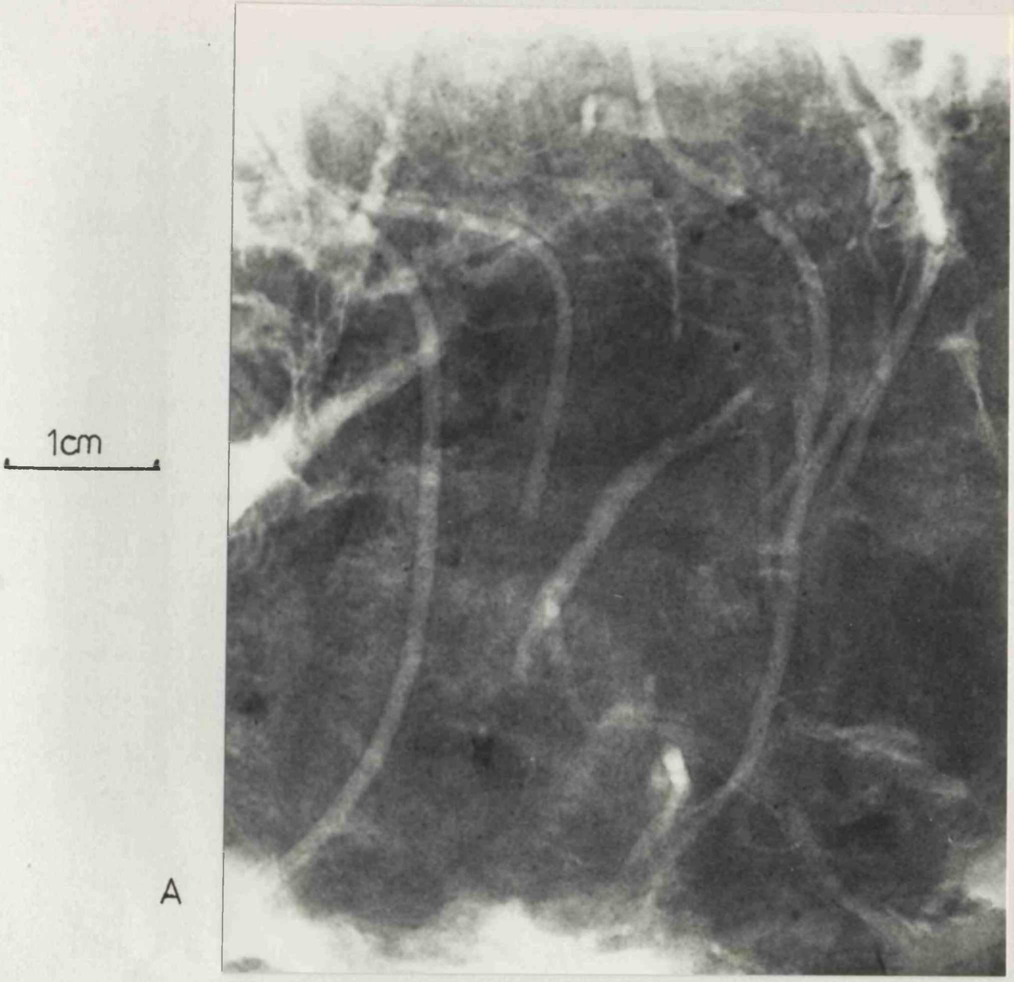
Sample: Fairlie Channel A
Position: Decca DI8·0 I76·I
Depth: 30m
Fauna: <u>Polychaeta</u>
3 Aphrodite aculeata
I Halosydna gelatinosa
2 Stylarioides flabellata
5 Terebellides stroemi
I Thelepus cincinnatus
I Nicolea venustula
<u>Bivalvia</u>
I Astarte sulcata
2 Dosinia lupinus
<u>Echinodermata</u>
IO Amphiura filiformis

Appendix 4 Photographs of burrows taken from X-ray radiographs of boxcore subsamples.

PLATE 1

A. Vertical section,4cm thick, showing the tubes built by *Spiophanes bombyx* extending subvertically from the sediment surface in Kilbrannan Sound (depth 124m).

B. Horizontal section of the top 4cm of sediment from the Arran Deep (depth 180m) showing the tubes built by *Spiophanes bombyx*, branching burrows built by *Nephtys hombergi* and horizontal movement by the bivalve *Nucula sulcata*. Scale bar 1cm.



A

B

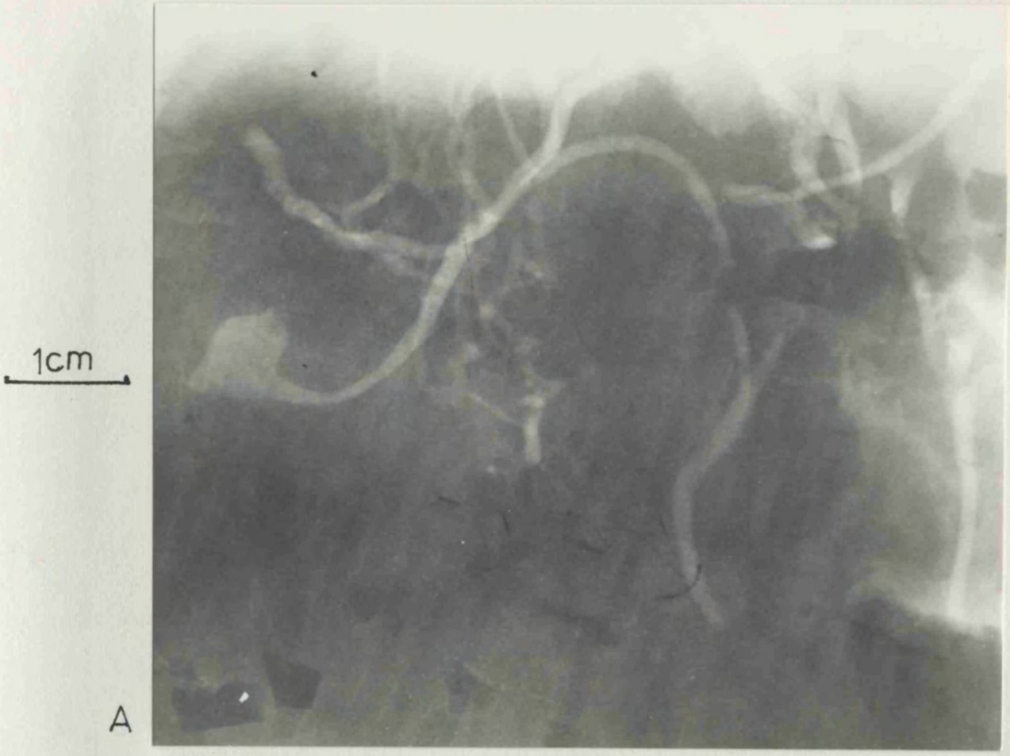
PLATE 2

The branching burrow system built by *Nephtys hombergi*.

A. Vertical section,4cm thick from site 2, Firth of Clyde (depth 43m).

B. Vertical section,4cm thick, from the Arran Deep (depth 180m).

B includes tubes built by *Spiophanes bombyx*.



A

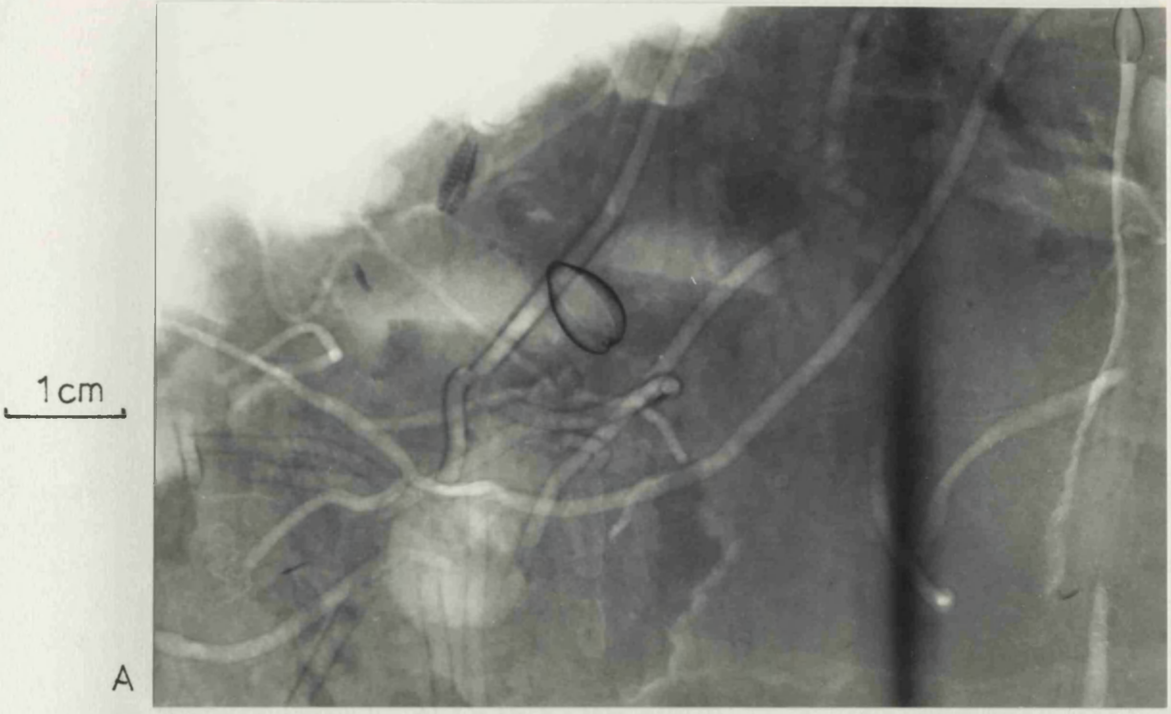
B

PLATE 3

U-burrows from the Arran Deep (depth 180m)

A. Vertical section,4cm thick, showing a U-burrow constructed by Scalibregma inflatum. Nucula sulcata,spionid tubes and a possible bivalve escape trace (on the right hand side) are also revealed.

B. Vertical section,4cm thick, showing part of a burrow probably constructed by Lipobranchius jeffreysii.



A

B

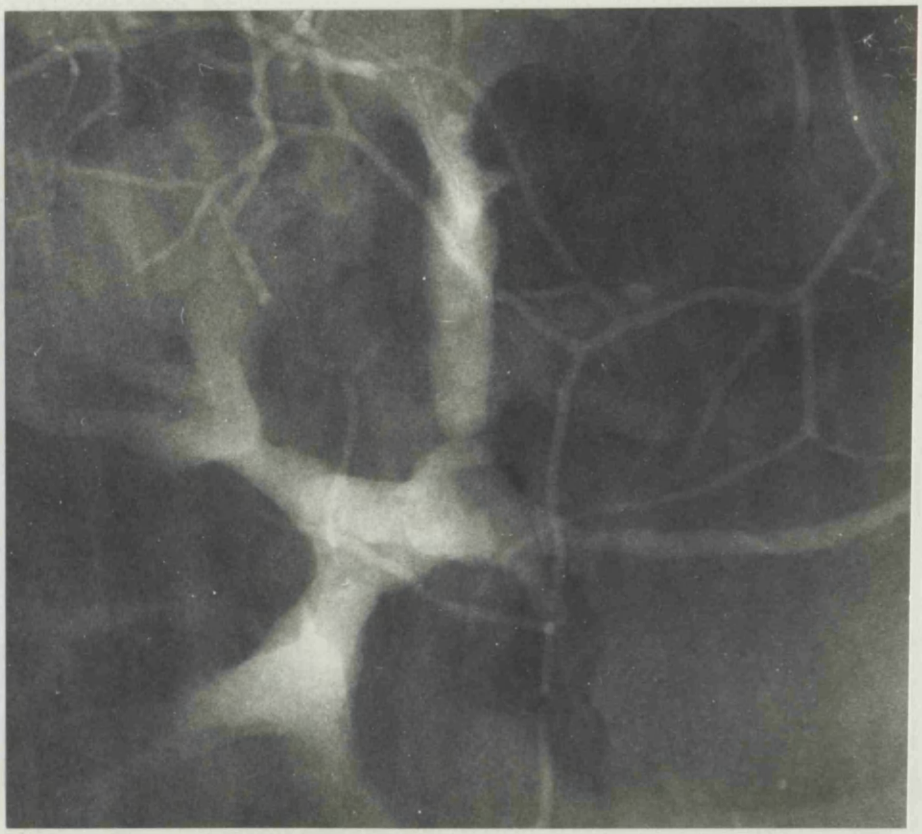
PLATE 4

Burrows of the ophiuroid Amphiura.

A. Vertical section, 4cm thick, from Loch Riddon (depth 30m).

B. Horizontal section, 4cm thick, from Cemas Nathais Bay (depth 25m). Branching burrows probably constructed by the hesionid polychaete Ancistrosyllis groenlandica .

A

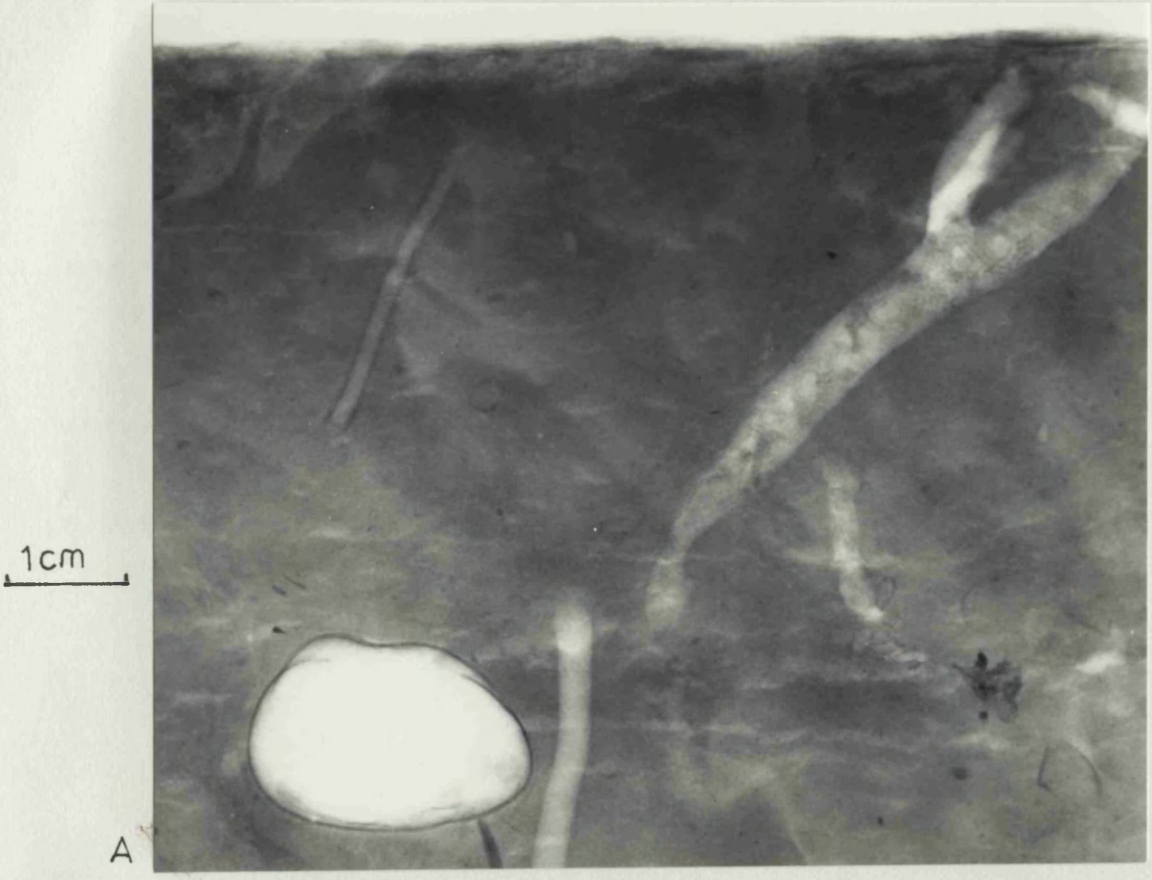


B

PLATE 5

A. Vertical section, 5cm thick, from Loch Riddon (depth 30m) showing part of an *Amphiura* burrow and the test of the echinoid *Echinocardium flavescens*.

B. Vertical section, 6cm thick, from station C-12 Loch Creran (depth 22m) showing tubes built by *Melinna palmata* and a J-burrow constructed by the sipunculid *Golfingia vulgaris*.


1cm
A


1cm
B

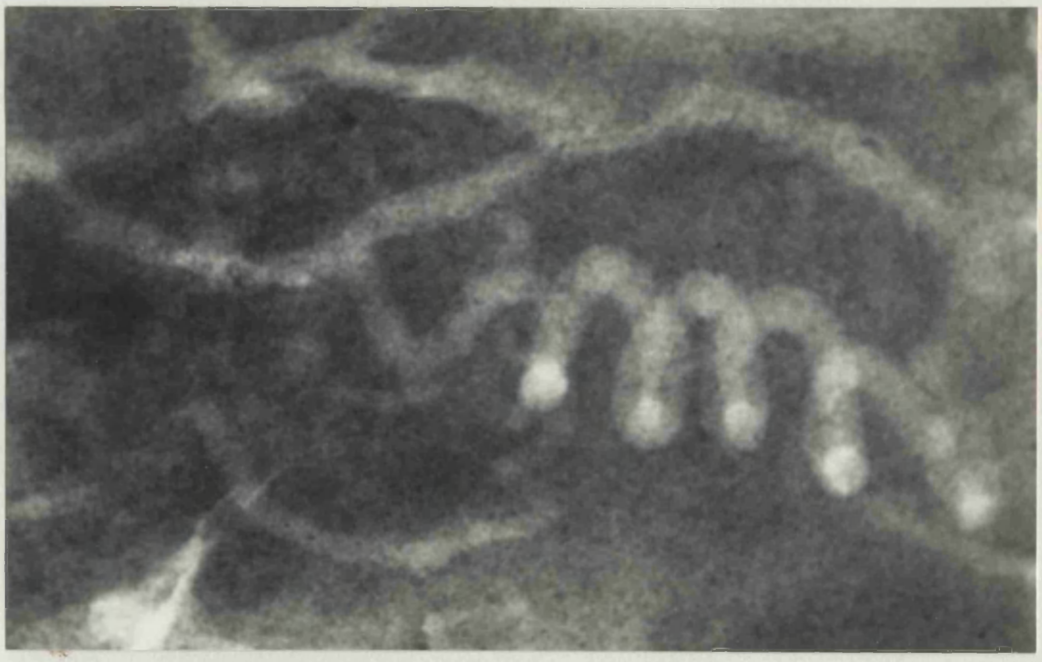
PLATE 6

Capitellid polychaete burrows

A. Vertical section,4cm thick, from the Sound of Jura (depth 216m) showing a spiral burrow constructed by *Notomastus latericeus*, 5cm below the sediment surface.

B. Vertical section,5cm thick, from Kilbrannan Sound (depth 120m) showing a wavy burrow constructed by *Dasybranchus caducus* extending from 7 to 13cm below the sediment surface.

A



B

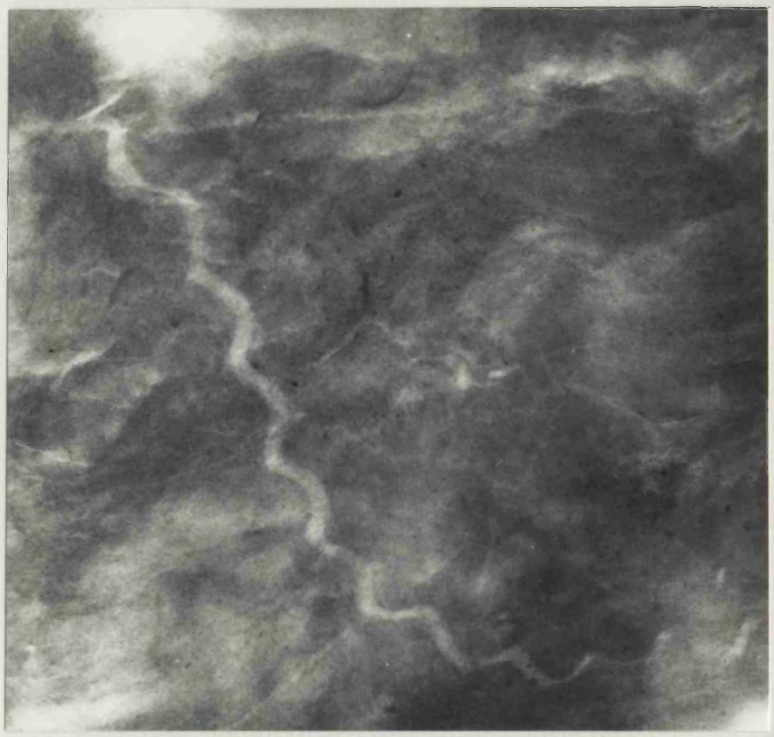
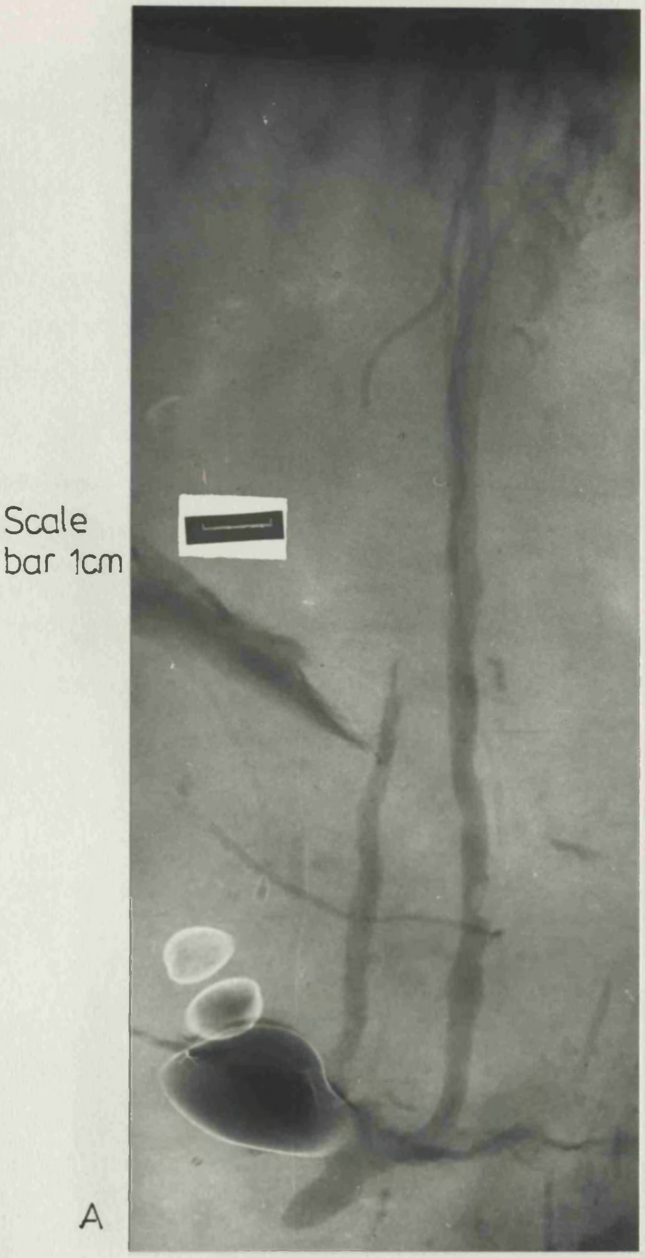


PLATE 7

A. Vertical section,4cm thick,from Loch Riddon Firth of Clyde (depth 30m) showing a U-burrow 15cm deep, constructed by the bivalve Thracia convexa. Two Nucula shells are also revealed.

B. Vertical section,4cm thick, from site 9, Firth of Clyde (depth 47m) showing a concentration of dead shells of the gastropod Turritella communis randomly orientated in the sediment 15cm below the surface.


Scale
bar 1cm
A

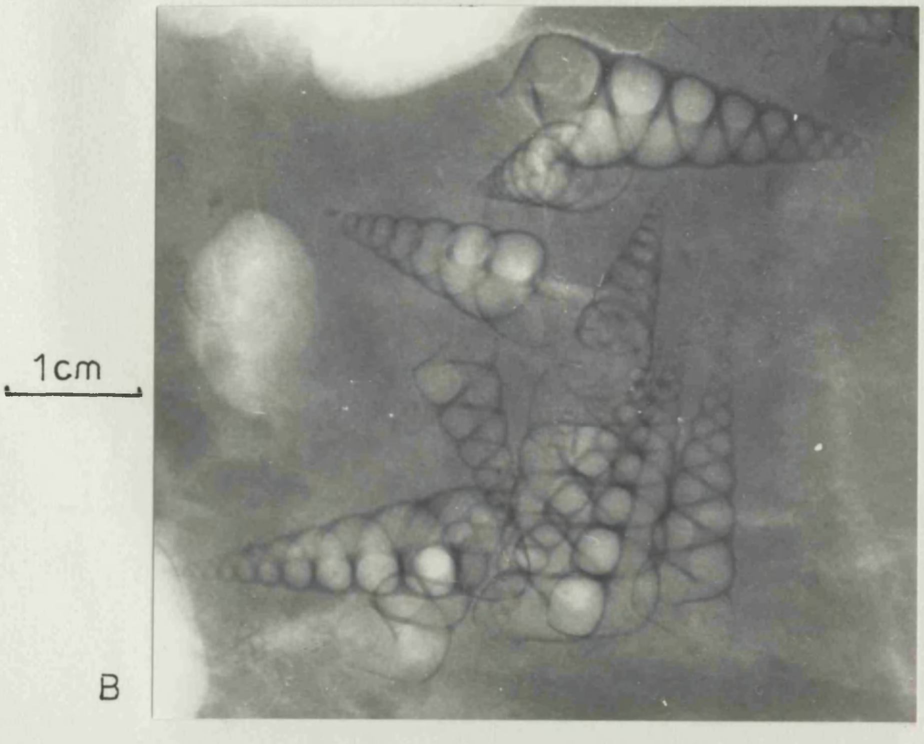

1cm
B

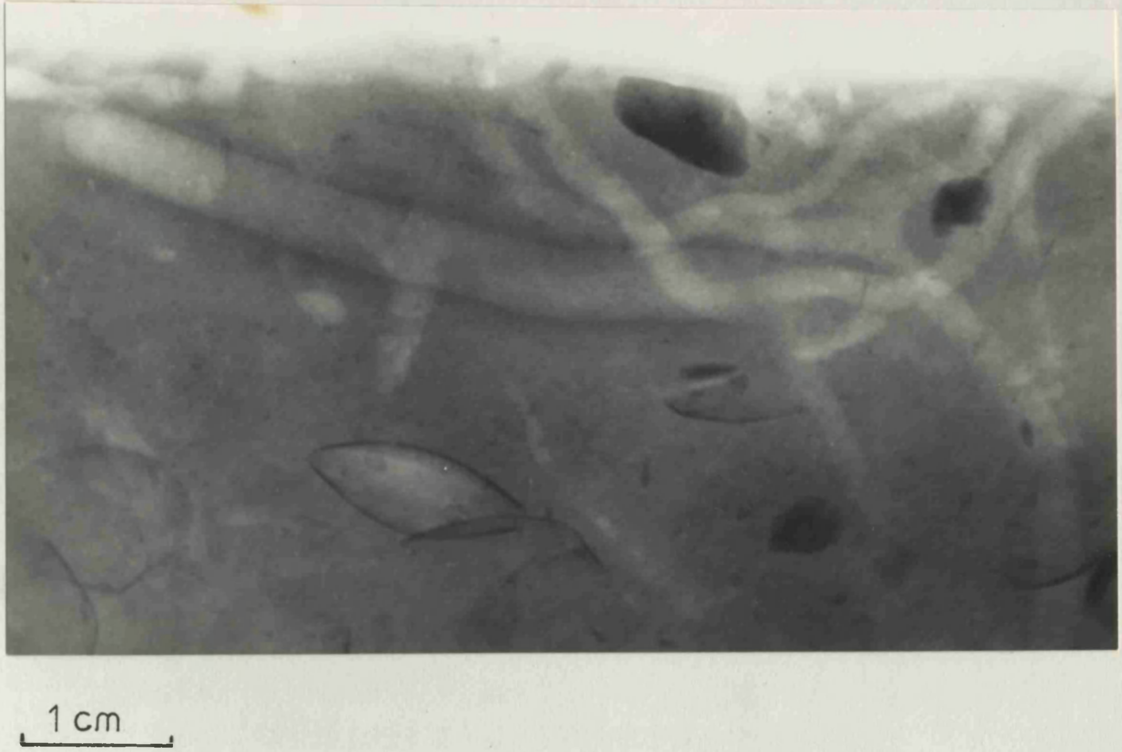
PLATE 8

Polluted sites around the Garroch Head Sludge Dumping Ground, Firth of Clyde.

A. Vertical section, 5cm thick, from the 'transitory' zone (site P3, depth 72m) showing a tube built by *Terebellides stroemi* and a U-burrow constructed by *Scalibregma inflatum*. A dead *Abra* shell is also revealed.

B. Vertical section, 5cm thick, from the polluted zone (site P1, depth 83m) showing the burrows built by *Capitella capitata*.

A



B

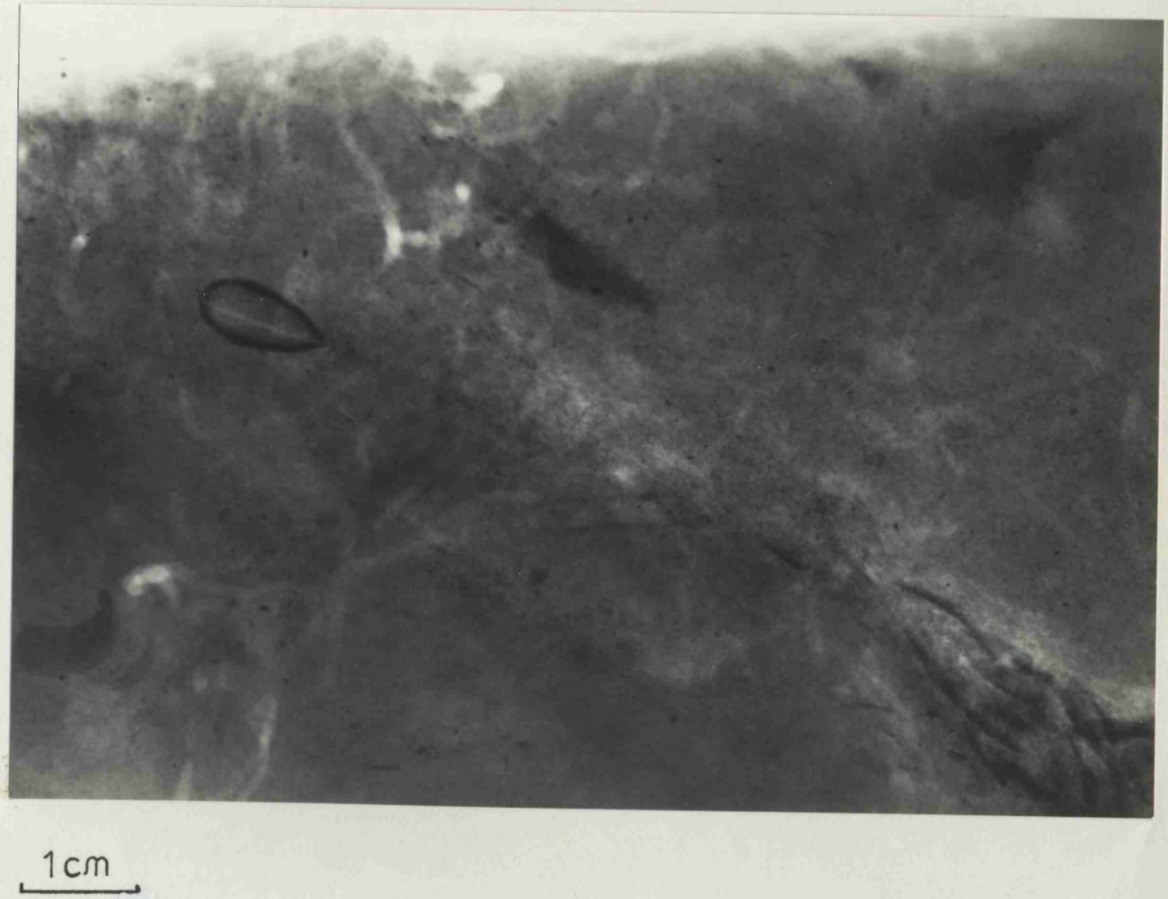
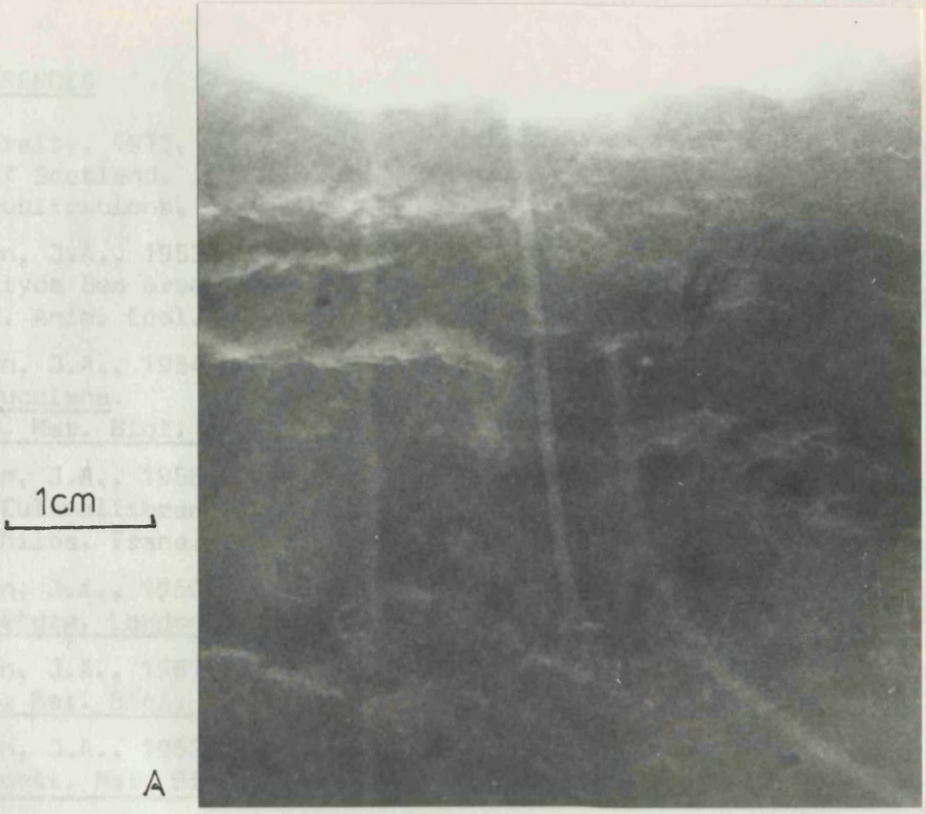


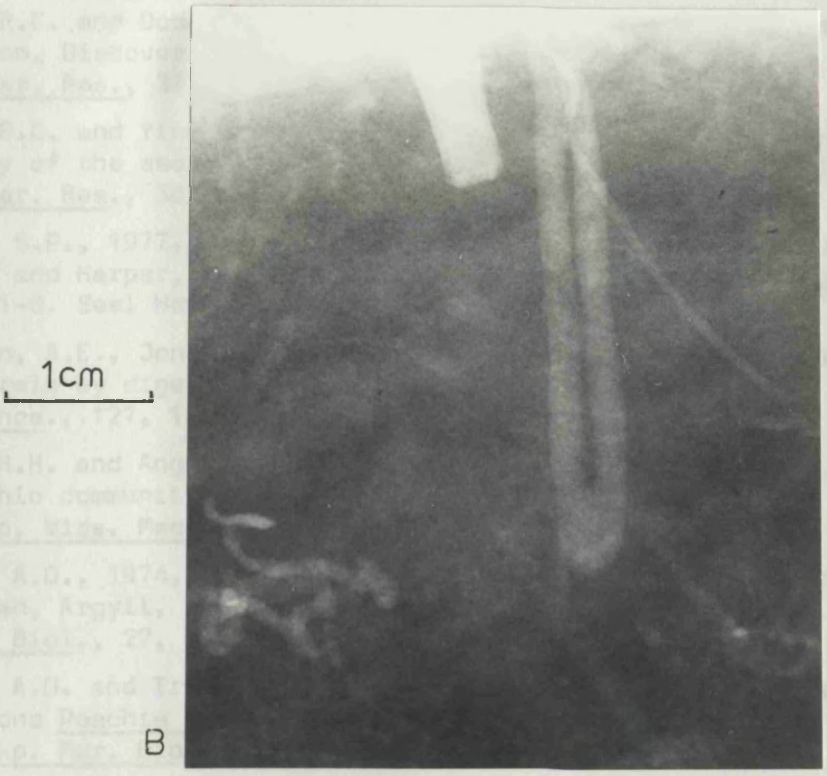
PLATE 9

Continental slope sites

A. Vertical section,5cm thick, from the Whittard Canyon, S.W. Approaches (depth 1330m) showing the tubes of pogonophores.

B. Vertical section,5cm thick, from the Hebrides Terrace (depth 1200m) showing a U-burrow probably constructed by an amphipod.


1cm
A


1cm
B

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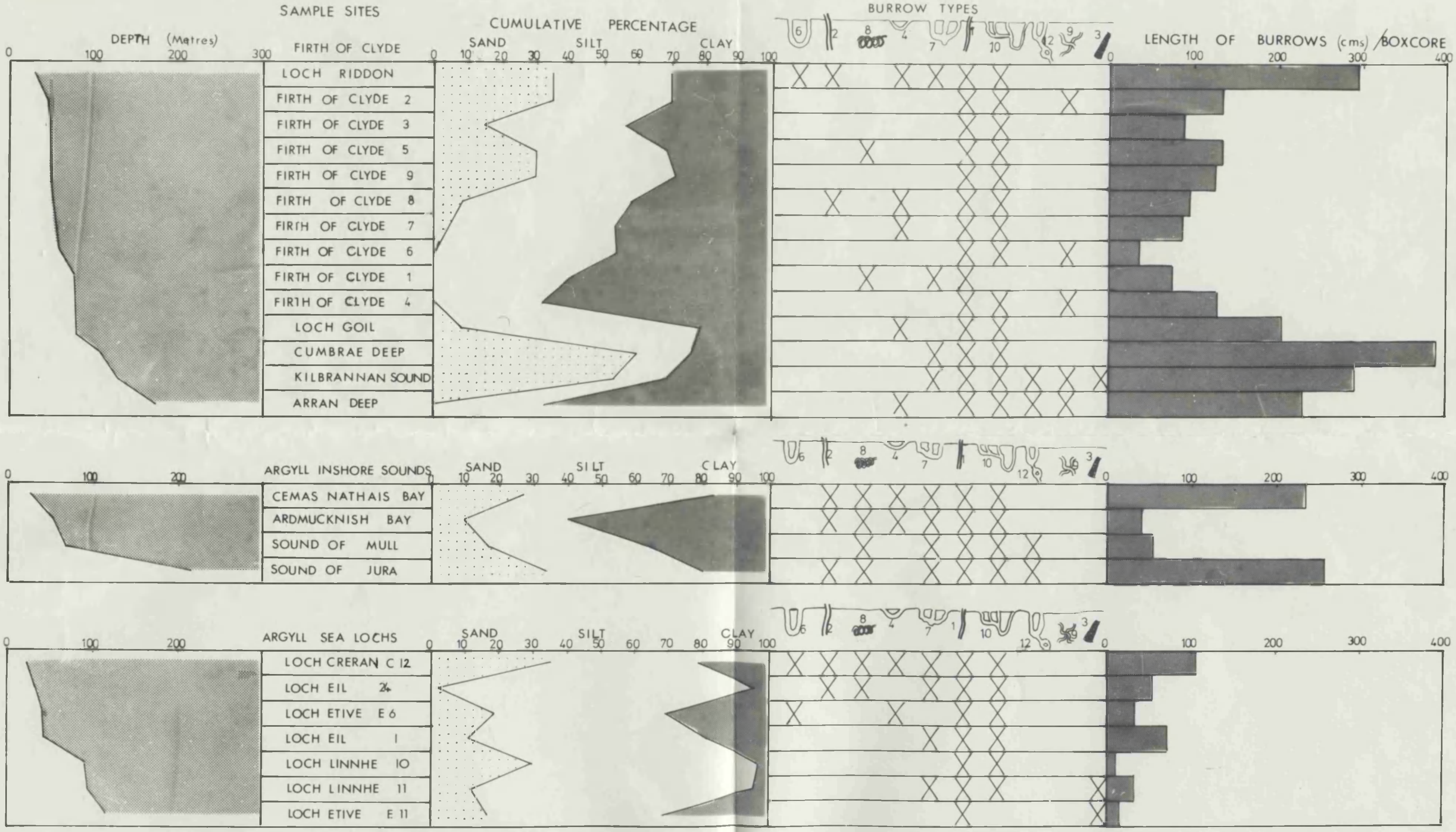

fig 1.9 Summary diagram showing the relationship between depth, particle size, burrow type and length of burrow/boxcore in the study area.

Table 3.9 Distribution of organisms with a high fossilation potential	L. Creran C-12	Cemas Nathais Bay	L. Riddon	L. Eil Stn 24	L. Etive E-6	L. Eil Stn 1	Firth of Clyde 2	Firth of Clyde 3	Firth of Clyde 5	Firth of Clyde 4	Ardmucknish Bay	Firth of Clyde 8	Firth of Clyde 7	Firth of Clyde 6	Sound of Mull	Firth of Clyde 1	Firth of Clyde 4	L. Goil	L. Linnhe 10	L. Linnhe 11	Cumbrae Deep	L. Etive E-11	Kilbrannan Sound	Arran Deep	Sound of Jura
<u>Bivalves</u>																									
Nucula sulcata	X		X		X		X	X								X	X			X	X	X		X	X
Nucula Turgida			X							X															
Nucula tenuis				X	X			X									X					X		X	
Nucula minuta			X																				X	X	X
Chlamys opercularis	X																X				X		X		X
Chlamys septemradiata					X												X				X	X	X	X	
Myrtea spinifera					X															X		X			
Lucinoma borealis				X	X															X		X			
Thyasira flexuosa	X			X	X	X														X	X	X			
Mysella bidentata	X			X																					
Artica islandica		X	X		X				X												X		X		
Acanthocardium echinatum	X		X																						
Dosinia lupinus	X	X			X	X	X																		
Venus ovata	X				X				X												X				X
Venus striatula					X					X															
Mysia undata	X	X				X	X																		
Abra alba	X	X	X		X		X	X		X	X		X		X	X	X			X	X			X	X
Cultellus pellucidus	X																								
Mya truncata	X	X								X															
Corbula gibba	X	X	X	X	X	X						X									X			X	X
Thracia convexa	X	X	X		X											X									
Glossus humanus		X														X									
Solecurtis chamasola									X																
<u>Gastropods</u>																									
Gibbula cineraria		X																							
Littorina littorea	X	X																			X				
Turritella communis	X	X					X	X	X	X											X				
Buccinum undatum		X																					X		
Lora turricula																					X				
Cylichna cylindricea	X																								
Natica montagui	X	X							X	X														X	
Acteon tomatilis									X																
Aporrhais pespelicanni		X																			X				
<u>Scaphopods</u>																									
Dentalium entalis									X														X		X
<u>Echinoids</u>																									
Brissopsis lyrifera							X	X	X		X	X	X	X			X							X	X
Echinocardium flavescens			X																						

<u>Table 3.9</u> <u>Distribution of organisms with a high fossilisation potential</u>