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PhD thesis

# TAPHONOMIC PROCESSES IN A DEEP WATER <u>MODIOLUS</u>-BRACHIOPOD ASSEMBLAGE FROM THE WEST COAST OF SCOTLAND

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"(We) did steal one happy day .. to probe the sea–bottom and endevour to decipher more of its story...and all were lucky enough to tumble on board .. as the strong-winded launch puffed across to the deepest water to be had inside the Atlantic. (.. some of the very few deeper spots .. are in our neighbouring Linne Loch.)

Well! well ! and what have we got? Did you ever see such clumps of *Sertularia*, those beautiful plant like zoophytes, as we have here; and the masses of *Terebratulae* of the most splendid proportions will force us to talk of these shells in future with regal indifference. Here are two beauties, almost white, with their serpent heads (*Caput–serpentis*), seated on living shells of *Modiolae* or horse–mussels. Set them in water and you will observe that, although fixed to the shell of the mussel by a strong muscular attachment, beyond the power of voluntary removal, yet they revolve upon it in the most curious fashion, half forcing one to look for eyes, so serpent like do they appear as they revolve. They are really finely–grown specimens, far beyond anything we have in our own loch, (L. Creran) yet they are affixed to and have reached maturity upon living *Modiolae* of very moderate size compared with those found at a fathom or so in the laminarian zone. This is surely proof enough that the large mussel is better suited for shallow water, while the *Terebratulae* are clearly better grown in the depths. This is evidently the case with various other species, and we go on passing the material through our hands, now tumbling two varieties of *Holothuriae* into water, now chucking little bits of sticks, with remote resemblance to crustaceans, into receptacles, until what with hermit crabs with beautiful green eyes and jackets like boiled partans and large *Porcellani* crabs, *Mundia rugosa*, mixed up with fragments of mutilated Norwegian lobsters, *Nephrops norvegicus*, our receptacles are getting filled with a motley collection."

(From W. Anderson Smith, Notes from the Western Highlands, 1897)

## SUMMARY

Taphonomy "the study of processes of preservation and how they affect information in the fossil record" (Behrensmeyer and Kidwell, 1985) is an important geological discipline. This study, by incorporating experiments on carbonate transplanted to shallow water with benthic sampling, explored the relationship between the calcimass of living and dead (sub-fossil) constituents of a deep water brachiopod-bivalve community in the Firth of Lorn (site 1. of Curry, 1982). The community, which occurs on a gently sloping sea floor at depths between 160 and 200m, was investigated by dredging, grab sampling, coring and video transects. Biomass and calcimass of the community were determined indirectly from regressions of shell length against weight on animals collected from 10 grab samples.

The large endobyssate bivalve *M. modiolus*, which forms large stable clumps modifies the sediment by introducing "secondary hardbottom" (*sensu* Surlyk, 1972) into an otherwise soft sediment. The valves of living *M. modiolus* serve as substrate for a diverse epifauna, the most distinctive member of which is the articulate brachiopod *Terebratulina retusa*.

The standing calcimass (2370.5 $g/m^2/yr$) and carbonate production (excluding polychaetes, bryozoans and barnacles) of the community is very high (330 $g/m^2/yr$) which in the absence of carbonate destruction would result in a rate of autochthonous carbonate accumulation in excess of 1 mm/yr. *M. modiolus* contribute 93.5% of the standing calcimass, but accounts for only 37.8% of estimated production (mainly due to a lifespan estimated at 40 years). Three other species, the ophiuroid *Ophiothrix fragilis*, the bivalve *Astarte sulcata* and the articulate brachiopod *Terebratulina retusa* together contribute an additional 58.5% of carbonate production.

Length-frequency histograms of 0-year class *T. retusa* from seasonal samples suggest that growth rate is initially slow (an increase in length from 0.212 mm to 0.539 mm over the first 260 days). Similar rates have been published from laboratory studies (Rickwood, 1977; Stricker and Reed, 1985) but growth rate is well below that estimated from conventional length-frequency histograms (eg.

Curry, 1982) or field studies (Thayer, 1977; Doherty, 1979).

Autecological implications of a strongly sigmoidal growth curve were investigated by examining substrate related mortality. Larval *T. retusa* appear non-selective in their choice of substrate and although virtually all adult *T. retusa* are attached to mature *M. modiolus*, 35 alternative substrates were recorded. Patterns of substrate utilization suggest that from a length of approximately 2 mm to maturity there is an increase in the proportion of *T. retusa* attached to the surface of *M. modiolus*, indicating that alternative substrates (eg. hydroid thecae, ascidian tests and calcareous worm tubes) are more liable to fail as the *Terebratulina* mature. At lengths below 2 mm the surface of *M. modiolus* appears to be sub-optimal, the proportion of *Terebratulina* utilizing this substrate falling from approximately 80% of settlement to 40% at lengths of between 1.7 & 2.8 mm. It is postulated that grazing pressures, believed to be restricted to this substrate (Akpan, 1981) may account for this inflection at lengths of approximately 2.3 mm grazers being unable to dislodge brachiopods above this critical size.

Estimates of carbonate production were compared with the composition of biogenic carbonate from > 4 mm, > 2 mm, and > 1 mm sediment fractions of grab and box core samples. *Ophiothrix fragilis* and *Amphiura chaijei* which together were estimated to contribute 31.6% of total carbonate production accounted for only 0.5% of authochthonus carbonate in these fractions. Even accounting for the concentration of ophiuroid debris in the finer fractions, the absence of ophiuroid debris is remarkable.

Excluding ophiuroid debris and the two most minor authochthonous carbonate contributors, reveals an apparent trend in the remaining autochthonous carbonate towards selective preservation bias of smaller items. These trends were not seen in field experiments of relative rates of abrasion and laboratory studies of relative dissolution rates of the major carbonate components. Furthermore, estimated rates of destruction by abrasion were very low and S.E.M. examination of grains recovered from the death assemblage did not show evidence of

dissolution. This size related bias may therefore provide evidence of the consequence of selective bioerosion of non-agitated grains first proposed by Boekschoten (1968).

*Terebratulina retusa* is an outlier to this trend, being less common than estimates of production and preservation would predict, corresponding with the semi-quantitative evidence for under-representation of articulate brachiopods in death assemblages from the Algerian shelf (Caulet, 1967) and Canadian sub-littoral (Nobel *et al.* 1976). *T. retusa* shells recovered from the sediment were extremely friable. Initially this was thought to be a localized dissolution phenomenon, however S.E.M. preparations subsequently demonstrated that the observed strength loss was a consequence of a skeletal architecture which is common to the majority of articulate brachiopods. The rate of 'softening' was determined experimentally and proved to be remarkably rapid (93% strength loss 200 days after death, as measured by point loading; Collins, 1986). The friable carbonate liberates large numbers of distinctive calcite fibres into the sediment which should be recognizable as microfossils.

Similar observations of structurally weakened brachiopod carbonate have subsequently been reported from the Norwegian coast, the Mediterranean, western USA and New Zealand. The reduced strength of brachiopod shells will increase the potential for mechanical and bio-mechanical fragmentation and therefore under-representation. It is probable that the magnitude of 'softening' is inversely related to size and is liable to bias against smaller shells (Collins, 1986).

A significant deviation from the expected 1:1 ratio of pedicle to brachial valves of *T. retusa* (bv/pv = 1.6) was similar to the figure for *Terebratulina* septentrionalis from a shallow subtidal rocky coastline on the east coast of Canada (bv/pv = 1.5; Noble & Logan 1981). The preferential preservation of brachial valves of *T. retusa* compares with a strongly biased preservation of pedicle valves for *Macandrevia cranium* from the Scottish shelf and *Gryphus vitreus* from Corsica. It is suggested that biased valve ratios of these four

Recent examples are the consequence of selective destruction, selective transport need not be invoked.

Transport was also investigated experimentally, by laying a representative sample of shells on a moderately exposed sediment surface, at a depth of 9 m. Positions were recorded in a series of photographic mosaics and final recovery included suction sampling to a depth of approximately 30 cm. The large *Moidolus* valves moved the greatest distances, an unusual result thought to be due to reworking of larger items by crabs with a biologically bound and bioturbated sediment and entrapping the smaller shells and valves. It is suggested that the significance of current-mediated transport has been overstated, due to over concentration on the swash zone and flume tank and the failure to recognize the potential for biologically mediated transport and sediment binding.

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# INTRODUCTION

Taphonomy: "all the processes operating on the post-mortem remains of the living biota between the time of their death and the subsequent collection by the investigator of that portion of the biota surviving destruction." (Powell *et al.*, 1984)

# 1 INTRODUCTION

The discipline of taphonomy broadly encompasses the concept of 'fossilization' (the transition of animal remains from the biosphere to the lithosphere) and is sub-divided into two topics *biostratinomy* and *fossil diagenesis*. Biostratinomy involves those processes leading to the incorporation of skeletal hardparts into the sediment (the particle typically behaving as a discrete unit). The processes which characterize fossil diagenesis act upon the sediment as a whole (eg. recrystallisation, permineralisation and replacement).

Little work has been conducted on preservation bias attributed to fossil diagenesis, although the significance of mineralogy is well recognized (eg. Lawrence 1968, Koch and Sohl 1983).

Biostratinomy can be divided historically into three stages. The earliest work was published in the latter half of the ninteenth century (Swinchatt, 1966). These early descriptive studies recognized the roles of molluscs, sponges, algae, holothurians and worms as active in breaking up shells and reworking of sediments (eg. Walther, 1893). Semi-quantitative studies are still important sources of information concerning bioerosion (Boekschoten, 1966, 67; Akpan *et al.*, 1982; Akpan & Farrow, 1985), biomechanical fragmentation (Swinchatt 1965), and such features as valve sorting (Lever 1958, 1961; Lever and Thijssen, 1968; Trewin and Welsh, 1972; Myers, 1977) and orientation (Emery,1968; Clifton 1971).

The foundations of the experimental approach were laid by Pratje (1929) and Klahn (1932) in Germany who invoked physical processes to explain preservational biasing. A number of experiments (Hallam, 1967; Driscoll, 1967; Driscoll and Weltin, 1973; Elsma, 1968; Lefort, 1970; Trewin and Welsh, 1976) attempted to determine the taphonomic significance of the abrasion and mechanical fragmentation recognized by the earlier German work.

Attempts have also been made to refine our understanding of physical and chemical processes, including the recognition of the significance of microstructure and shell chemistry to skeletal durability (an index of the resistance to physical destruction, Chave, 1964; Hallam, 1965), rates of shell softening (Purdy 1963; Collins 1986), and dissolution (eg. Peterson, 1976; Flessa & Bray, 1983). Taphonomic features such as the degree of dis-articulation, fragmentation and current drifting (e.g. Menard & Boucot, 1951; Boucot *et al.*, 1958; Clifton, 1971; Fuetterer 1978a, 78b, 78c) have been explained in terms of physical processes. Physical forces are more constant and therefore palaeontologically more satisfactory than biological equivalents because of the profound changes undergone by the biota during the Phrenozoic (*e.g.* Thayer, 1982).

The third approach, direct observation of preservation bias by comparison of the living community with the death assemblage, is a later developement. The approach is closely allied to benthic ecology and the techniques are an extension of those used to survey benthic communities. Historically, it was probably Birkett (quoted in Hallam, 1967) who first recognized the significance of dead shell material to the ecologist. Comparisons of live and dead faunas (the latter further sub-divided into short term and long term death assemblages) have since been made from a variety of shallow marine environments, including rocky coastline (Noble *et al.*, 1976), shallow coastal lagoons (Johnson, 1965; Warme, 1969; Petersen, 1976), an estuary (Cadée, 1968) and shallow offshore environments (Warme *et al.*, 1976; Bosence, 1978; Carthew & Bosence 1986, Stanton 1976; Powell *et al.*, 1982; Powell *et al.*, 1984). Significant attempts have recently been made to place such comparisons into a more ecological framework (Stanton *et al.*, 1981; Powell & Stanton, 1985; Staff *et al.*, 1985).

Although there is now a considerable amount of work published on Recent biostratinomy, few fossil papers are concerned primarily with taphonomy. The cause of this is perhaps the lack of cohesion in the Recent studies (no textbook has yet attempted to draw all the disparate threads together since Schaefer in 1972) and as a result fossil biostratinomy is very conjectural, although rigorous analysis of well preserved horizons can produce "a surprisingly complex history of an inconspicous... bed" (Boyd & Newell, 1972). Of the studies dealing with taphonomy of fossil sequences, many are from Tertiary and Quaternary deposits, where comparison with Recent sediments is less complex (eg. Boekschoten, 1967; Kern 1971; Frey & Basan, 1981).

Behrensmeyer & Kidwell (1985) have argued that the more process-orientated and experimental approach, undergoing a resurgence in the USA, coupled with the potential role of taphonomy in the evaluation of temporal resolution in the fossil record gives modern taphonomic studies an increasingly significant role. They propose a new working definition "*the study of process of preservation and how they affect information in the fossil record*" to reflect the elevated status of the subject. However, the successes they quote demonstrate a poor benefit to cost ratio, reflecting a concentration on relatively obscure problems.

This study aims to determine the bias arising from biostratinomic processes operating upon skeletal hardparts in a deep-water epifaunal community. The community is characterized by ophiuroids, brachiopods and the endo-byssate bivalve *Modiolus modiolus* (L.), believed to be an important source of temperate water carbonate (eg. Allen *et al.*, 1979; Farrow *et al.*, 1984).

Temperate carbonate sediments are all biogenic or skeletal in origin, and the majority are derived from epifaunal or semi infaunal organisms, because they tend to be richer than infaunal communities both in numbers of species and in total biomass and calcimass (Craig & Jones, 1966; Kay & Knights, 1975; Farrow *et al.*, 1984). ***M. modiolus*** (the largest Mytilid in British waters) forms extensive beds in high energy areas (e.g Isle of Man, Tebble, 1966, Strangford Lough, Roberts, 1975; N.E. Orkneys, Farrow *et. al*, 1984) and has been shown to achieve rates of carbonate accumulation locally equivalent to those observed from the tropics (Farrow *et al.*, 1984).

The *Modiolus* community has been described by a number of authors, from a wide variety of depths across much of the northern hemisphere (Appendix I). Thorson (1971) states "in the cold-temperature N.E. Atlantic we meet the *Modiola* (*Modiola* = *Modiolus*) epifauna, which as far as species are concerned, is the most luxuriant society these seas can offer". In the Firth of Lorn and Sound of Mull the *Modiolus* community has been recognized at a number of isolated sites (Comely, 1978; Curry, 1982) and has been studied in detail from Port Appin (Comely, 1978) where it occurs in shallow water.

Brachiopod – bivalve associations

Palaeocommunity reconstructions often have pedunculate brachiopods emerging mysteriously out of the sediment (eg. Cocks and McKerrow 1978), although a survey of the literature of Recent articulate brachiopods suggests that rooting pedicles (Rudwick, 1961; Richardson & Watson 1975; Curry, 1981, 83) are atypical. The ability of the pedicle to digest into carbonate is common to three superfamilies (the Rhynchonellidae, Terebratulacea and Terebratellaea; Eckman, 1896) and attachment appears to be a larval requirement in all species (Rudwick, 1970).

Evidence of long lifespans of articulate brachiopods (eg. Thayer, 1977; Doherty, 1979; Curry, 1981; Peck, pers comm; this study) suggest that epifaunal species require stable substrates. The endobyssate bivalve *Modiolus modiolus* supplies this requirement and associations of *Modiolus* and articulate brachiopods also occur at a number of widely dispersed sites (Fig. 1). Off Point Caution (San Juan Island) at a depth of 120 m *Terebratalia transversa* and *Terebratulina* sp. have been dredged up attached to *M. modiolus*. Both *Terebratalia transversa* and *Hemithyris psittacea* have been recorded in shallow water *Modiolus* communities off the Alaskan shelf (Lees & Driskell, 1981). In the Bay of Funday, *Terebratulina septentrionalis* is only infrequently recovered with *M. modiolus* (Caddy, 1970; Peer *et al.*, 1981), but is often recovered "on the upper shell valves of scallops" (Caddy 1970: 6). E. Thomsen (*pers comm.*, 1986) records a shallow water *Modiolus modiolus*, *M. phaseolinus*, *Terebratulina* sp. off the coast of northern Norway. A parallel association occurs off southwest Africa at a depth of 3,413 m where two species of brachiopod, a pedunculate species of the genus *Waldheimia* and the cemented inarticulate *Pelagodiscus*

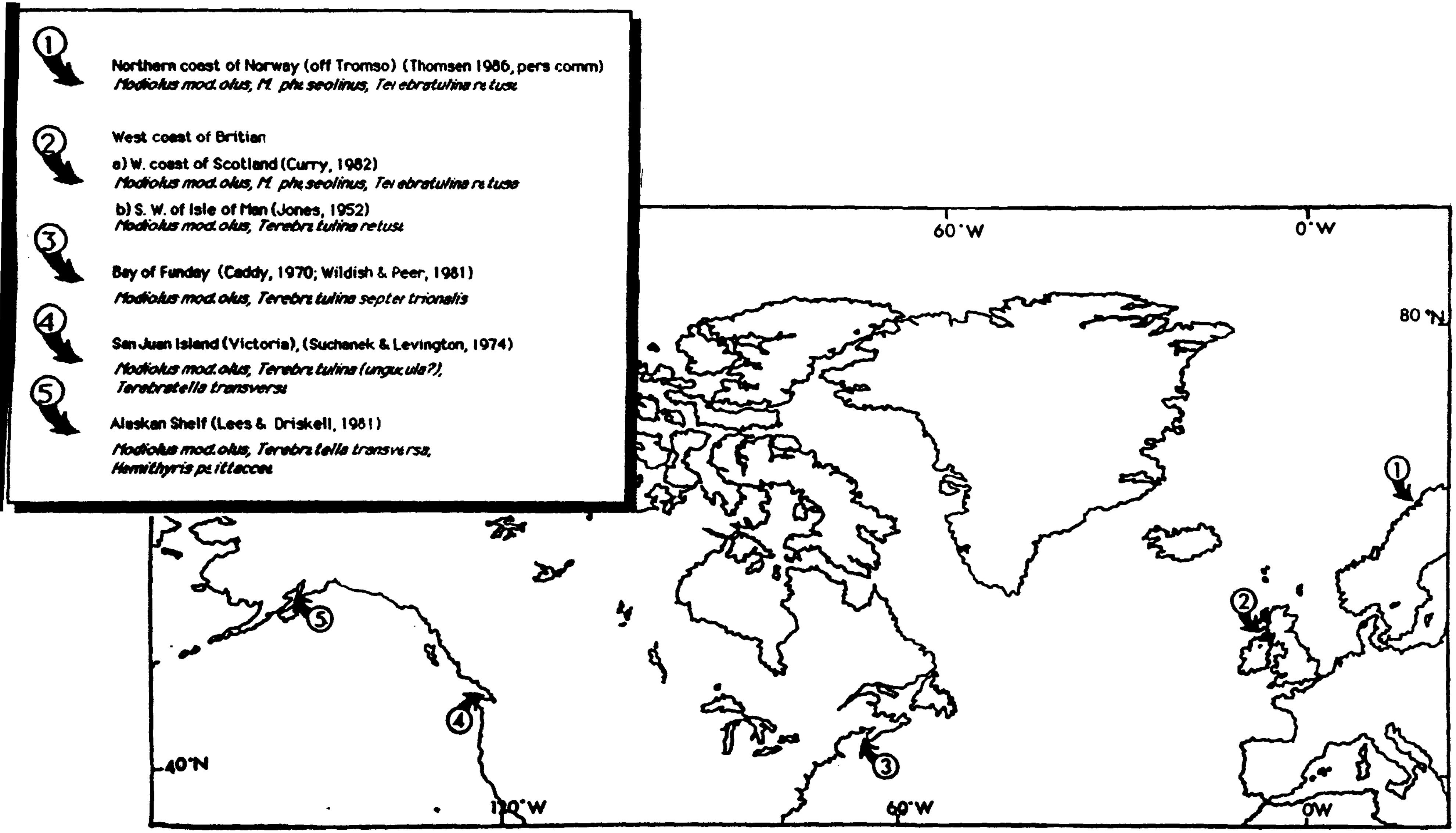


**Figure 1**

Distribution of Modiolus - brachiopod associations *atlanticus* were recovered attached to a large (maximum length 35 mm) free lying abyssal bivalve *Limopsis tenella* (Oliver & Allen, 1980).

In many horizons in the Paleozoic, pedunculate brachiopods are found in the same beds as free-lying and free-living bachiopods and associations with epifaunal and endobyssate bivalves in the Mesozoic. McKerrow *et al.* (1969) describe communities from the Great Oolite of Kirtlington, Oxfordshire in which the terebratulid *Epithyris* occurs with a species of oyster, Hudson & Morton (1969) report an association of *Modiolus* and a rhynchonellid from the Jurassic of Skye. Bernard and Almeras (1981) record a community in an estimated 200 meters of water, in which terebratulid brachiopods are associated with colonial bryozoans and the bivalve *Lopha*. Fursich (1984) describes a series of Upper Jurassic associations from Greenland, the terebratulid *Taimyrothyris spp.* occurs in association with two large byssate bivalves *Grammatodon* and *Isognomon*. The fossil record of associations between epifaunal brachiopods and large long-lived endobyssate bivalves is equivocal, because aragonitic bivalves are often preserved as interior moulds and therefore do not exhibit pedicle boring traces.

# PART I

# LIVING COMMUNITY

# I 1 PROCEDURES

## I 1.1 Collection

Collections of *Modiolus* communities were made from three sites on the west coast of Scotland (Fig. I 1.1), detailed analysis was restricted to the community in a deep water channel in the Firth of Lorn. No attempt was made to survey the pattern of benthic diversity in the Firth of Lorn, such studies have been conducted already by both Comely (unpublished data) and Gage (1972a, b, 74). A video survey highlighted slight changes in the community composition from the base of the steep slope, with a reduction in diversity towards the highly bioturbated, *Mellinia* dominated, central depression (see section I 2.2).

Level bottom populations of *Terebratulina retusa* from the Firth of Lorn are established on mini-reefs, formed of living clumps of the endo-byssate bivalve *Modiolus modiolus* (Fig. I 1.2) which were readily collected by dredging and grab sampling (Curry, 1982). The main aim of the study was an analysis of the comparison between the dominant members of the living community and death assemblage. Because of the stunted and/or slow growing nature of many of the component species of the community an attempt was made to estimate production of carbonate rather than to make a direct comparison between the standing calcimass and the percentage of autochthonous carbonate in the death assemblage.

### I 1.1.1 Quantitative methods

Two methods were used to obtain quantitative samples of the community and the underlying sediment, grab sampling and coring (the latter detailed in section II 1.2.1). For both techniques it was necessary to obtain an accurate position of the vessel during collection, achieved using the Decca Chain Navigation system, supplemented by triangulation and echo sounder, the latter proving useful because of the distinctive bottom topography (Fig. I 2.1).

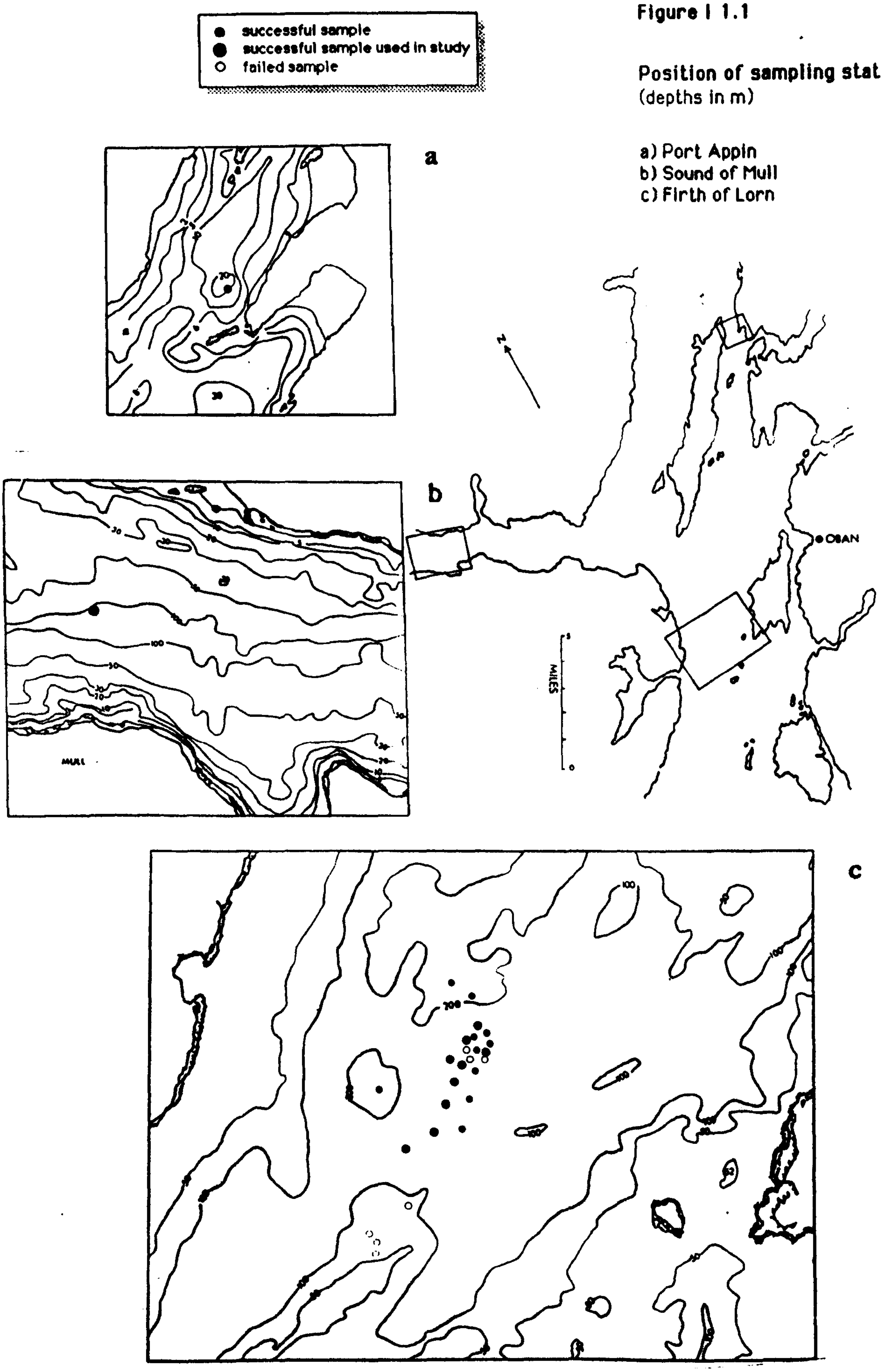
### Grab sampling

Grab sampling was the most practical method of collecting a representative

Figure I 1.1

Position of sampling stations
(depths in m)

a) Port Appin
b) Sound of Mull
c) Firth of Lorn



sample of the macrofauna and substrates with sessile fauna, although the gravel inclusions in the sediment restricted penetration to 5–7 cm.

Circumstance dictated that over the course of the sampling program it was necessary to use two different types of benthic grab, both designed for work on this type of coarse sediment. The grabs used (the Hunter–Simpson grab, and the Day Grab; Table I 2.1) have been compared directly on a variety of coarse sediment types with no significant differences in the composition of the samples (Hunter & Simpson, 1976).

The temperature and volume of samples were measured directly following collection. Sediment for sieve analysis was scooped from the measuring bin in a plastic collecting beaker, prior to on–deck sieving, the sediment being washed through a disperser and over a 1 mm mesh sieve. The residue was fixed by the addition of approximatly 50 mls of 40% neutralized seawater formalin stained with rose bengal, and stored in 2 l plastic buckets fitted with airtight lids. The buckets were turned a number of times during the day of collection to ensure adequate dispersion of the formalin.

Collections of sediment for SEM were made by hand picking samples off the undisturbed suface of the grab, immediately rinsing in one change of tap water and two rapid changes of double distilled water to remove salts before air drying on board and packing in cotton wool for storage and transport.

### I 1.1.2 Qualitative methods

#### Dredging

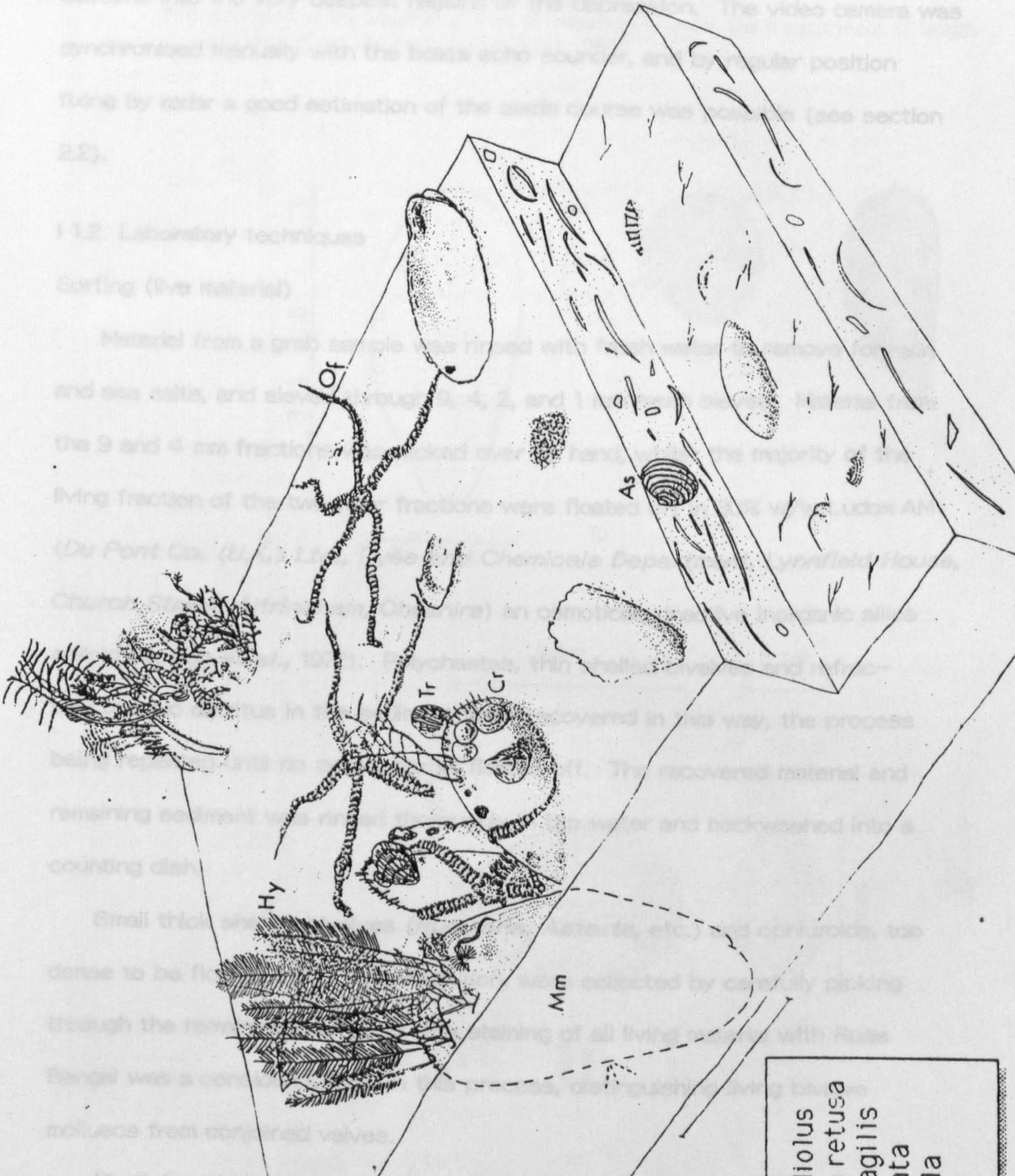
A scallop dredge, with a 75 mm external mesh of steel rings and a 15 mm internal nylon mesh was used for bulk sampling. Because of the semi–infaunal position of the *M. modiolus* and the nature of the sediment, a single upslope dredge collected hauls too big to be adequately dealt with.

#### Video Survey

The Institute of Offshore Engineering (Edinburgh) provided access to a sled mounted unit with underwater video and stills cameras. Over a period of

Figure I 1.2

Generalized block diagram of M. modiolus community



three days it was possible to undertake a limited survey of the population in the Firth of Lorn, although the umbilical was too short to allow the sled to descend into the very deepest regions of the depression. The video camera was synchronised manually with the boats echo sounder, and by regular position fixing by radar a good estimation of the sleds course was possible (see section 2.2).

### I 1.2 Laboratory techniques

Sorting (live material)

Material from a grab sample was rinsed with fresh water to remove formalin and sea salts, and sieved through 9, 4, 2, and 1 mm mesh sieves. Material from the 9 and 4 mm fractions was picked over by hand, whilst the majority of the living fraction of the two finer fractions were floated off in 30% w/w Ludox AM (*Du Pont Co. (U.K.) Ltd., Dyes and Chemicals Department, Lynnfield House, Church Street, Altrincham, Cheshire*) an osmotically inactive inorganic silica colloid (Bowen *et al.*, 1972). Polychaetes, thin shelled bivalves and refractory organic detritus in the sediment were recovered in this way, the process being repeated until no more material floated off. The recovered material and remaining sediment was rinsed thoroughly in tap water and backwashed into a counting dish.

Small thick shelled bivalves (*Nuculana, Astarte,* etc.) and ophiuroids, too dense to be floated off in Ludox solution, were collected by carefully picking through the remaining sediment. The staining of all living material with Rose Bengal was a considerable aid in this process, distinguishing living bivalve molluscs from conjoined valves.

*Modiolus* shells and other potential substrates collected by grab sample from the Firth of Lorn, were rinsed gently in cold water and air-dried overnight to remove the fix and colloidal silica.

Details of the position of the *M. modiolus* epi-fauna (fitted by eye on a 9x5 grid pattern, superimposed on the surface of the *M. modiolus*; Fig. I 1.3c)

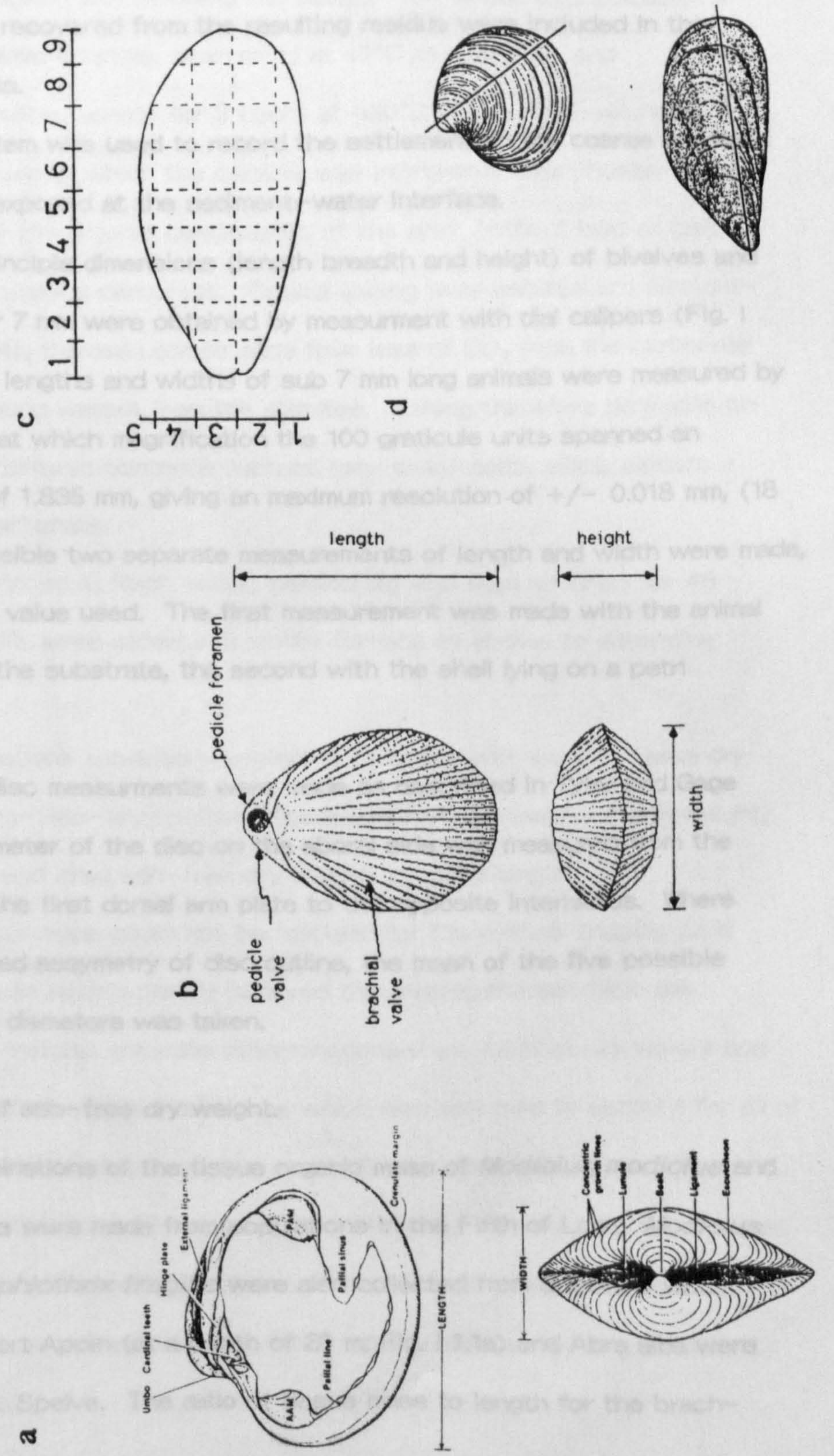
Figure I 1.3

a) Generalised bivalve illustrating terminology and major dimensions used in study (from Seed, 1980)

b) Generalised brachiopod illustrasting terminology and major dimensions used in study

c) Grid positions of M. modiolus used in distributional study.

d) Illustration of the position of axis of maximum growth, the measurment of length used throughout the study (from Seed 1980).



the substrate to which the epifauna were attached and the probability of overgrowth were recorded for 101 *M. modiolus*. Once all visible animals had been recovered and measured, all cryptic substrates (eg. the undersurfaces of tabular bryozoa, periostracal hairs) were removed and examined. Ascidians posed a particular problem because of their complex morphology; following removal of visible epifauna the ascidians were digested in sodium hypochlorate solution. *T. retusa* shells recovered from the resulting residue were included in the population analysis.

A similar system was used to record the settlement on the coarse fractions of the sediment exposed at the sediment-water interface.

The three principle dimensions (length breadth and height) of bivalves and brachiopods over 7 mm were obtained by measurment with dial calipers (Fig. I 1.3b & d). Shell lengths and widths of sub 7 mm long animals were measured by graticule at 50x, at which magnification the 100 graticule units spanned an actual distance of 1.835 mm, giving an maximum resolution of +/- 0.018 mm, (18 $\mu$m). Where possible two separate measurements of length and width were made, and the greatest value used. The first measurement was made with the animal still attached to the substrate, the second with the shell lying on a petri dish.

Brittle star disc measurments were made as described in Tyler and Gage (1980). The diameter of the disc on the aboral side was measured from the distal margin of the first dorsal arm plate to the opposite interradius. Where specimens showed assymetry of disc outline, the mean of the five possible radial-interradial diameters was taken.

## Determinations of ash-free dry weight.

Initial determinations of the tissue organic mass of *Modiolus modiolus* and *Astarte sulcata* were made from populations in the Firth of Lorn. *Modiolus modiolus* and *Ophiothrix fragilis* were also collected from a shallow water population off Port Appin (at a depth of 20 m; Fig. I 1.1a) and Abra alba were collected from L. Spelve. The ratio of tissue mass to length for the brachiopods *Terebratulina retusa* and *Crania anomala* from the Firth of Lorn has already been determined by Curry & Ansell (1986).

*Modiolus* and *Astarte* collected by dredge sample were lightly cleaned with a stiff brush to remove epizooites. Tissue wet weight was measured in bivalve molluscs by opening the valves following cutting of the muscles, draining the mantle cavity, removing and weighing the tissue. The tissue was placed in a pre-weighed ceramic crucible, oven dried at 85°C re-weighed, and incinerated in a muffle furnace for 5 hours at 480°C before a final weighing.

The temperature at which the material was incinerated was chosen to allow full combustion of the organic components of the shell, without loss of carbon dioxide from the skeletal carbonate. Critical ashing temperatures are discussed by Paine (1964), the main errors arise from loss of $CO_2$ from the carbonate and chemically bound waters from the silicates. Ashing therefore produces an estimate of the inorganic contents such as sea-water salts, silica, calcium phosphate and carbonate.

Shells were rinsed in fresh water, blotted dry and then air dried for 48 hours. Some shells were ashed in a muffle furnace as above, to determine organic content.

The determinations provided regressions of tissue wet weight, tissue dry weight, tissue ash-free-dry-weight (tissue AFDW = dry weight - ash weight), shell dry weight, and shell ash-free dry weight, on shell length.

The above technique could not be followed for *Ophiothrix fragilis* as it was not possible to satisfactorally removed the organic fraction from the skeletal fraction, instead seperate determinations were made of dry weight and AFDW of the arms and discs. Carbonate, which was assumed to account for all of the ash weight, was therefore slightly overestimated, failing to account for both seawater salts and sediment within the stomach. For each animal, the disc and the longest arm (seperated from the disc at the third ossicle form the base of the disc) were ashed and then the latter value multiplied by five and added to the disc weight.

Estimates of carbonate biomass and production were produced by multiplication of the AFDW estimate by a standard multiplication factor (4.46 n = 15, SD 0.28) derived from the above analysis.

### I 1.3 Data Analysis

All data analysis was preformed by the S numerical analysis package. This is a data analysis package running under the UNIX operating system consisting of a powerful data-base with numerous data structures and simple enquiry and procedural languages, enabling the building of complex routines for both interrogation of the data base, and by involving the extensive pre-programmed statistical and graphical functions, complex data analysis.

## 2 COMMUNITY STRUCTURE

### I 2.1 INTRODUCTION

Section I 2 is a qualitative analysis of all those species found in either the living community or as skeletal carbonate in the death assemblage, recovered either by UWTV, dredge sampling, grab sampling or coring. This section also makes use of unpublished data supplied by Mr. Clive Comely from a survey conducted in the Firth of Lorn. A complete species list is given in Appendix II).

#### I 2.1.1 Study Area

The Firth of Lorn is situated on the Scottish west coast bounded by the islands of Mull and Lismore on the north west side and the mainland of Argyll to the south east (Fig. I 1.1).

The sediments on the floor of the Firth of Lorn are products of an intense Pleistocene glaciation which gouged deep valleys up to 275 m deep (Binns *et al.*, 1974) in the sea bed, some of which follow the NE-SW strike of the Dalradian metamorphic basement rocks, others have a trend NNE-SSW, parallel to faults cutting the Lower Old Red Sandstone sediments and which Hall & Rashid (1977) interpret as sinstral strik-slip splays of the Great Glen Fault. The ruggedness of the sea floor is apparently cut by an erosion surface at 30-40 m in depth, which is believed to be an early glacial wave cut platform (Hall & Rashid, 1977).

The distribution of Recent sediment types in the Firth of Lorn is predominately related to bathymetry. Muddy and fine-grained sediments predominate in deep water, throughout the inshore and extend to about 30m offshore before graduating rapidly into beach gravels (Binns *et al.*, 1974). The Firth of Lorn was an important shipping lane and consequently the bottom is also rich in coal and clinker. At some sites in Kerrera Sound, *Chlamys islandica*, a Pleistocene relict shell is dredged from the sea bottom (Akpan, 1981). The *M. modiolus* community is found in a elongated channel lying between the islands of Mull and Kerrera, which reaches depths slightly in excess of 200 m, the community occurs on a slightly gravelly muddy sand, with coarse biogenic inclusions, at the foot of a steep NE facing rock wall opposing a bioturbated depression at 206 m (Fig. I 1.1c, 2.1, and 2.4).

### Hydrography

The Firth of Lorn has a fjordic circulation pattern which is superimposed on the main oceanic current system, affecting the west coast of Scotland, the North Atlantic current, a continuity of the north-easterly flowing Gulf Stream. Presumably the balance of inflows into the Firth of Lorn is affected by meteorological conditions. The strength of surface currents associated with the tidal ebb and flow are typically in the region of 0.5–2 knots, although tidal streams of over 4 knots have been recorded (Admiralty Charts numbers 2387 and 2378).

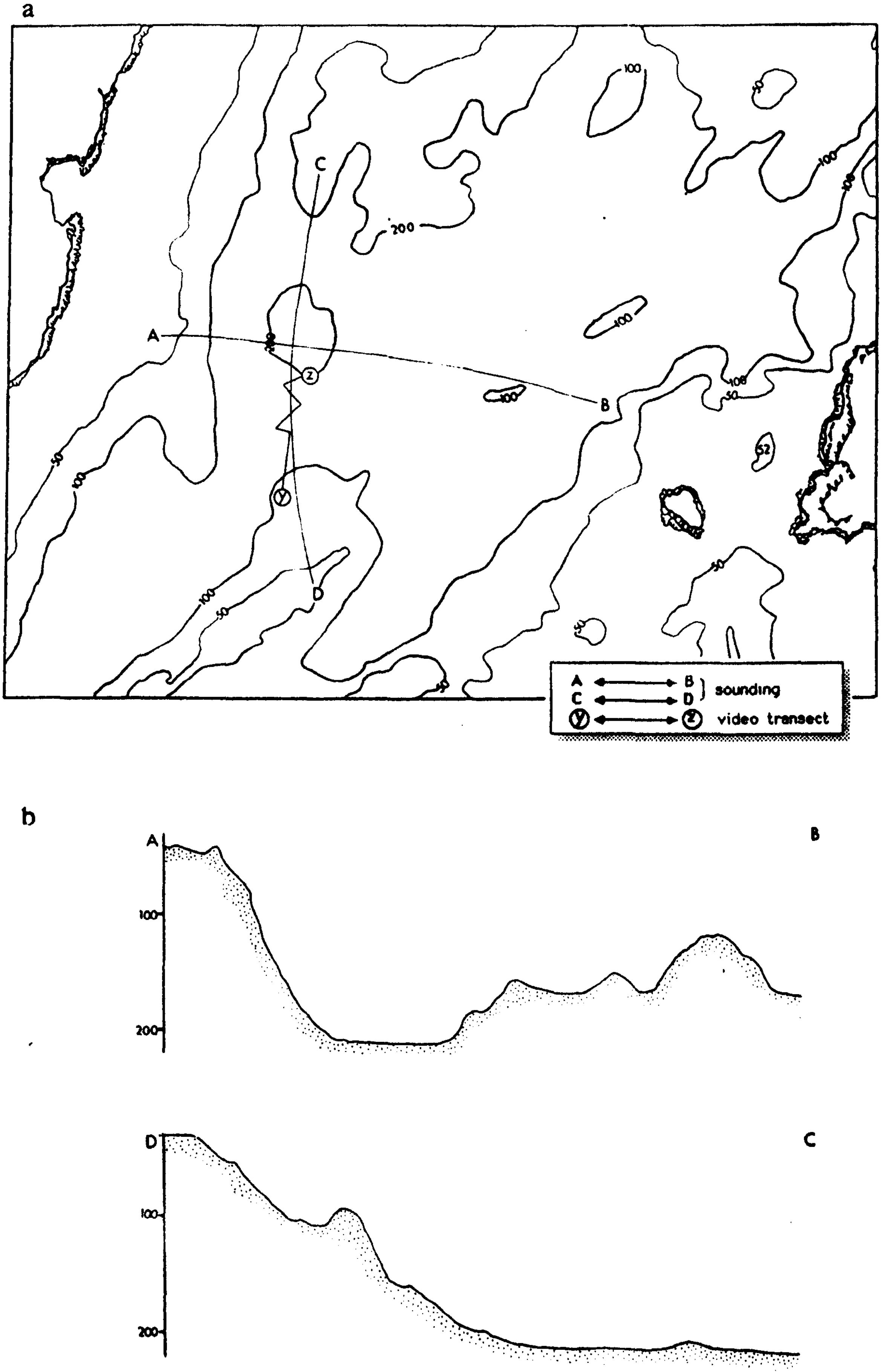
Deep water is drawn in from the coastal shelf and the North Channel by the compensation current, increasing the distribution of the nutrients regenerated in the deep basins. This water, flowing between Northern Ireland and the Mull of Kintyre might also be expected to contain some proportion of high nutrient Clyde water, this being reflected in the high phosphate concentrations recorded by Grantham *et al.* (1983) in the winter. The water mass experiences extremely rapid rates of turnover and the waters of the Firth are thought to be completely exchanged in a period of less than 2 months (Grantham *pers comm.* 1985).

In winter the water is very well mixed, the temperature, salinity and nutrient concentrations all show little variation with depth. By contrast in the sea lochs that form the upper reaches of the Firth of Lorn (beyond the entrance to the Sound of Mull) the water is strongly stratified for much of the year, with pockets of deeper, warmer water recorded in February as a result of the large volume of fresh water input (Grantham *et al.* 1983). Thermal stratification occurs in the lower reaches in the summer and the bottom waters fluctuate between a recorded minimum of 6.5°C in February and a maximum of 13°C in August (Curry, 1982). The temperature within the sediment fluctuates less,

Figure I 2.1

**Bathymetry of the Firth of Lorn**
(depths in m)

a) General bathymetry & position of transect lines
b) N - S & E - W profiles



from a recorded minimum of 7.25°C in February to a maximum of 12.25°C in August (Fig. I 2.2). Comely (*pers comm.*) recorded temperature and salinity profiles in the water column to a depth of 90 m off the southern tip of Lismore in the period 1962 – 1963, both the range and the maximum temperatures are lower, the temperature at 90 m is almost static (Fig. I 2.2).

### I 2.1.2 The *Modiolus* community

*Modiolus modiolus* forms the basis of a climax community which is recognizable from a wide variety of substrates and can form large beds covering areas of anything up to ten square miles (Jones, 1951). Typically *M. modiolus* are found epifaunally, living by byssal attachment to hardgrounds (Wiborg, 1946; Earll, 1974; J. Witman, *pers comm.*), stony, shelly or sandy gravels. The extent of recession has been discussed by Comely (1978), the greatest degree of recession being associated with current–swept bottoms.

On soft substrates the adults usually occur as semi–infaunal clumps of up to 30 individuals (Roberts, 1975) oriented at a steep angle, anterior down with only a small area of the posterior margin exposed. Gravel components (which in mature communities are predominantely *Modiolus* shells), provide a stable platform for byssal attachment, semi–infaunal *Modiolus* cannot stabilize on pure mud or sand. The accumulation of gravel components alters the sediment texture and restricts infaunal habitat space, thereby precluding the existance of deposit feeders and other infaunal bio–turbators which would destabilize the epifaunal community. The clumping behaviour provides semi–stable semi–permanent 'mini reefs', permitting the introduction of a diverse epifauna and is also likely to enhance the settlement and survival of both young and adult *Modiolus* and other byssate bivalves (Roberts, 1975, Lees & Driskell, 1981). The ecological consequences of such feedback have been reviewed by Kidwell & Jablonski (1983).

### I 2.1.3 Previous Work in the Area

In the latter part of the ninteenth century this area was surveyed by Victorian conchologists and naturalists mentioned by such authors as Forbes,

Figure I 2.2

Annual temperature fluctuations for the surface and base of the water column

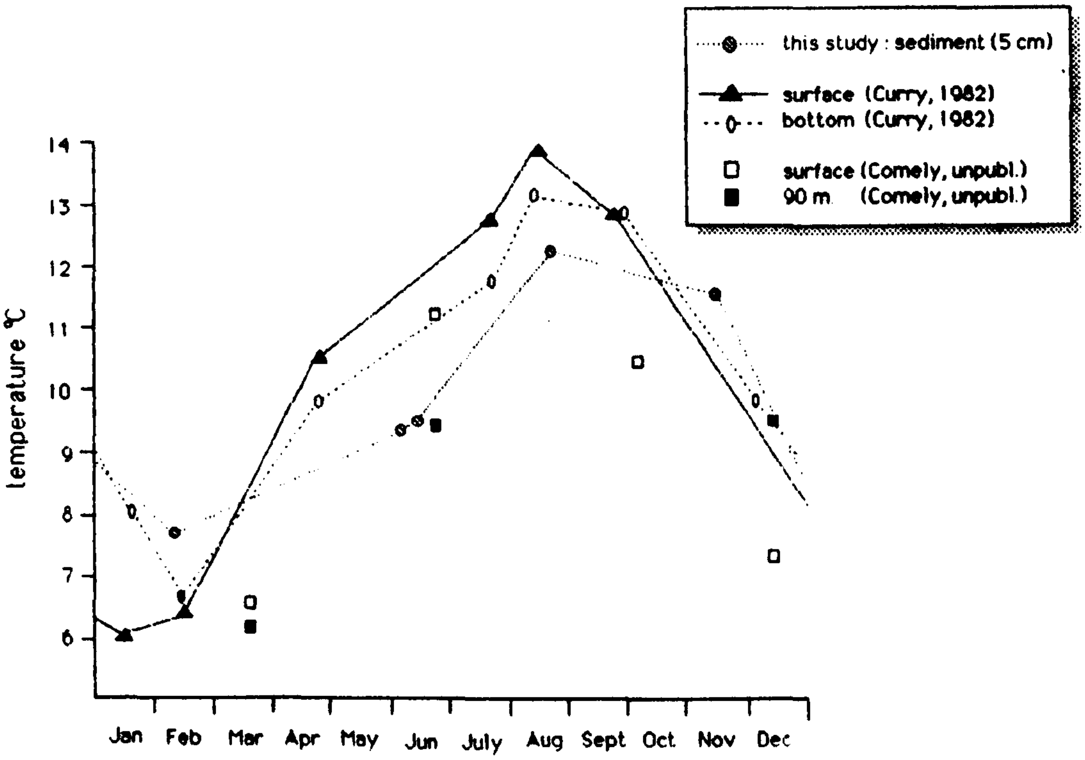
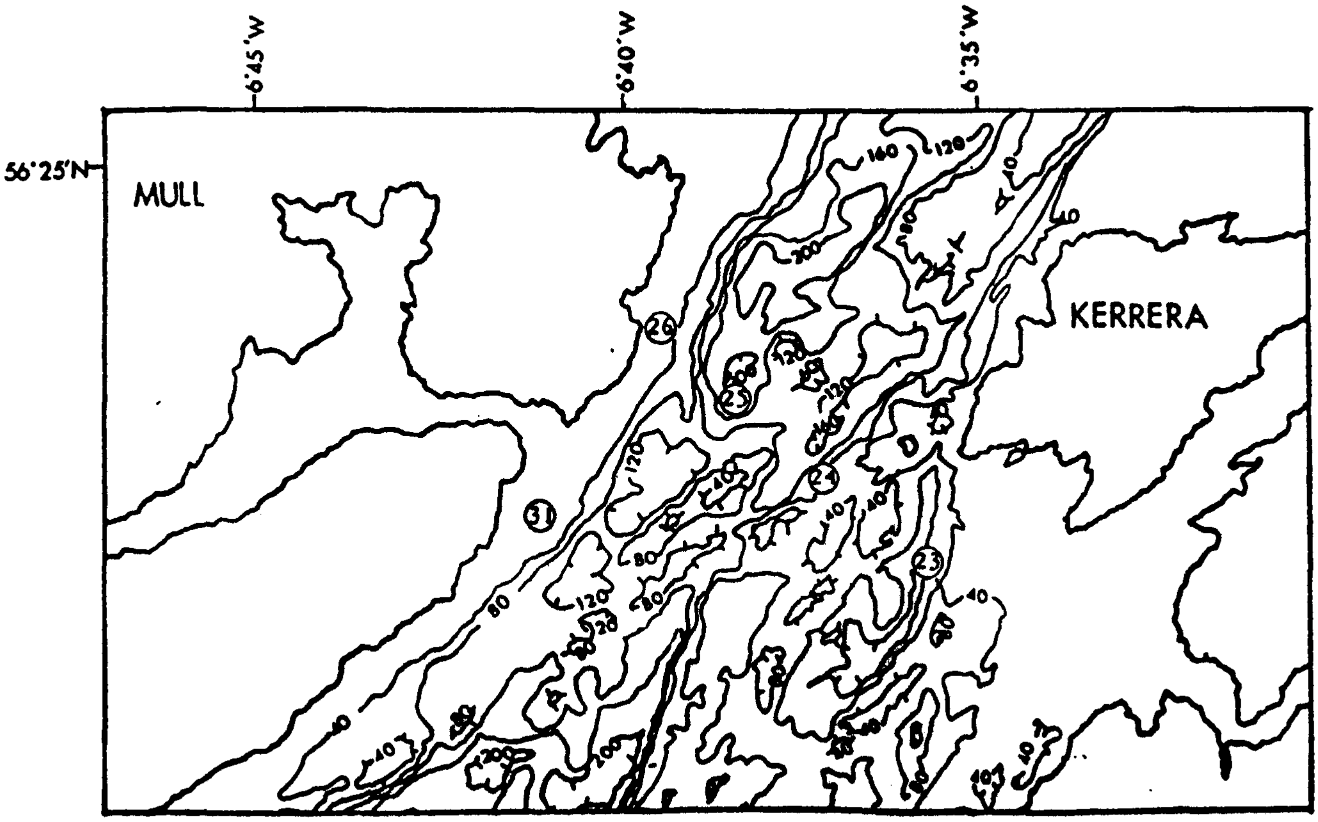


Figure I 2.3

Position of Comely's stations
(for details see Appendix III)



Hanley and Johnston and the reports of Goode & Marshall (1882) and Marshall & Marshall (1882) working from Oban.

During the period 1959 – 1963 Mr T. B. Bagenal and Mr. Clive Comely (SMBA, P.O. Box 3, Oban, Argyll) conducted an extensive survey of the Firth of Lorn and Loch Creran because of the potential use of the latter as a nursery for young plaice. Three Van Veen Grab samples were collected at each of 30 stations at every mile along NW–SE transect lines approximately 2 miles apart. This work (which was not published) includes five stations around the study area (Fig. I 2.3). Details of the stations and fauna are included in Appendix III.

Further benthic surveys were conducted from inside a number of sea lochs associated with the same hydrographic system (Gage, 1972a & b, 74) including a region of the north eastern Firth (Lochnell Bay).

Curry (1979, 82, 83a) investigated the population structure and micro-borings within the shell of *Terebratulina retusa* from the Firth of Lorn. Other work in the area has included the type and extent of bio–erosion of biogenic particles (Akpan, 1981; Akpan & Farrow, 1985), and in the Sound of Jura, transport of biogenic carbonate (Brown, 1979). Comely (1978) briefly reported on the population structure and growth rate of the stunted *M. modious* recovered by Curry (1979; 82).

### I 2.2 Distribution of the community within the study area

In conjunction with Dr. Paul Kingston (Herriot–Watt University, Edinburgh) an underwater television (UWTV) survey was undertaken of the brachiopod populations in the Firth of Lorn, using a colour video and 35 mm stills camera, attached to a light aluminium sled.

Traditional methods (dredging and grab sampling) only provide limited information of the vagile fauna and no information at all of animals living attached to hardgrounds such as underwater outcrops and large boulders. The television survey can provide some of this information, as well as clarifying other aspects of the community which are difficult to interpret by more trad–

itional sampling methods (c.f. Brown, 1979). Of a total of three runs, the run from south to north, beginning on a shelf at 80 m, dropping off a steep slope at 100 m and finally travelling across the *Modiolus* grounds at the base of the slope between 150 m and 206 m provided the most information about changes of sedimentary facies (Fig. I 2.1, 2.4)

Although adult *Modiolus modiolus* are extremely common in the area because the animals are clumped and support a diverse epifauna their presence was less dramatic than would be suggested by densities estimated from grab samples. Occasionally a prominent clump was observed on the film and attached *Terebratulina retusa* discernable as yellow 'blobs'. When the *Modiolus* were almost fully buried, it appeared as though the *T. retusa* were living on the surface of the fine tilth which overlaid the sediment. Large numbers of small un-identified fish and sand eels were observed during filming, darting away from the approaching camera. Occasionally Bib, (a small gadoid), and other larger fish were evident and the filter feeding brittle star *Ophiothrix fragilis* is ubiquitous.

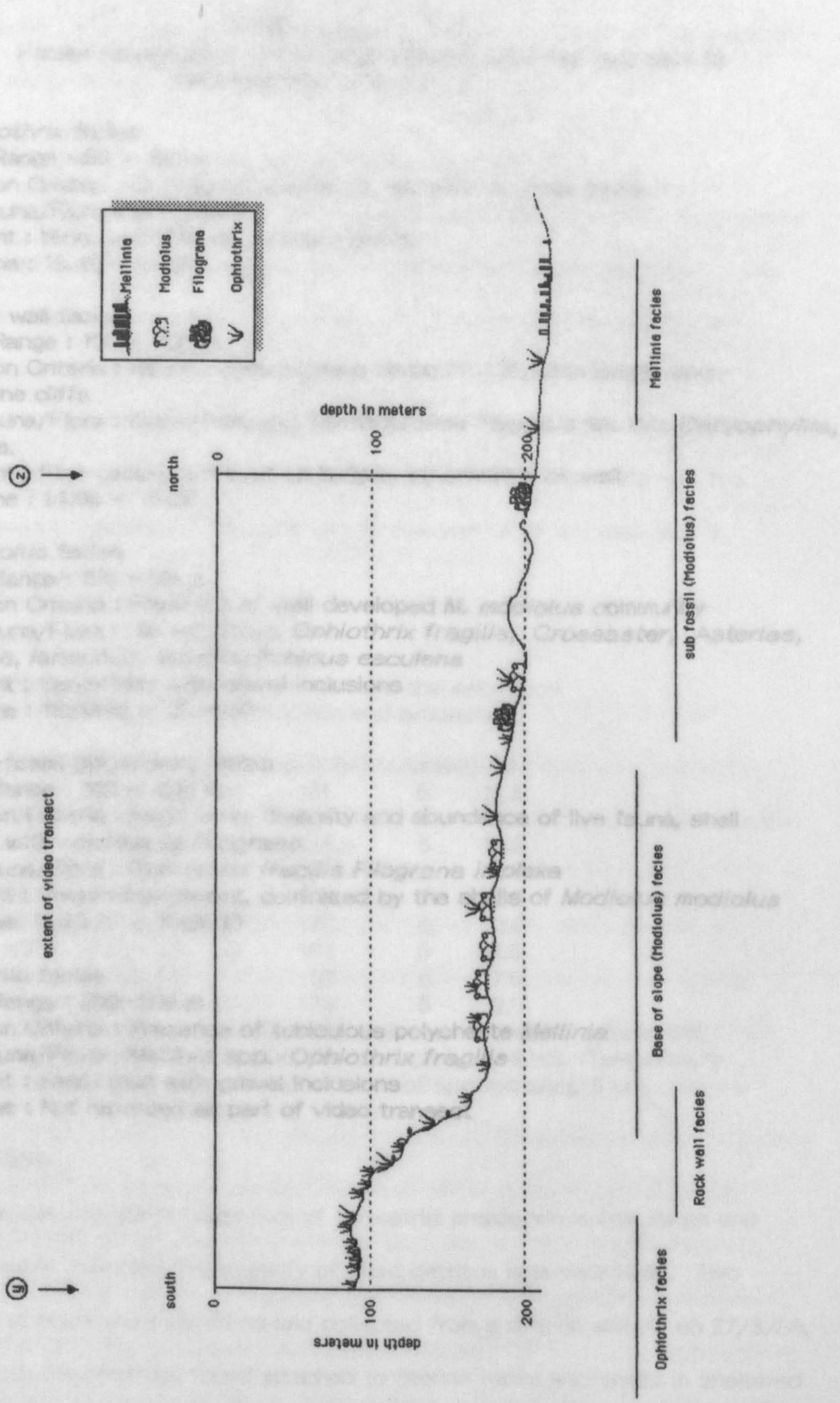
The five facies fall into natural categories on the basis of combined faunal and sediment associations (Table I 2.1; Fig. I 2.4). The shallow water *Ophiothrix* facies appears more sandy than the *Modiolus* facies, which would seem logical in view of the reduced potential for winnowing of fines at the greater depth.

The exposed rock of the slope provides attachment sites for large numbers of *Terebratulina retusa, Carophyllium smithii* and hydroids, which upon death will presumably accumulate at the base of the slope. The sand drapes on the ledges are populated by large numbers of ophiuroids (Fig. I 2.4).

The base of the slope is populated by large numbers of *Modiolus modiolus* forming large clumps (Fig. I 2.4; see also Fig. I 1.2) acting as mini reefs upon which a diverse epifauna is established. During the latter part of the run, the densities of colonial *Filograna* increased and the numbers of ophiuroids and *M. modilus* clumps diminished.

**Figure I 2.4**

Video transect of the Firth of Lorn with major facies and communities



## TABLE I 2.2
Facies recognized in Underwater Television Survey (transect 3)
(See also Fig. I 2.4.)

1. *Ophiothrix* facies
Depth Range : 80 – 100 m
Definition Criteria : O. *fragilis* ubiquitous, absence of other fauna
Live Fauna/Flora : O. *fragilis*
Sediment : Winnowed shell coquina and gravel
Film Time : 13.40 – 14.06

2. Rock wall facies
Depth Range : 100 – 160 m
Definition Criteria : Steeply shelving rock slope (1: 1.3), with ledges and submarine cliffs
Live Fauna/Flora : *Ophiothrix* and *Terebratulina Pagurus* sp. Bib, *Caryophyllia*, Hydroids.
Sediment : Fine sediment drapes on ledges, otherwise rock wall
Film Time : 14.06 – 15.09

3. *Modiolus* facies
Depth Range : 160 –195 m
Definition Criteria : Presence of well developed *M. modiolus* community
Live Fauna/Flora : *M. modiolus*, *Ophiothrix fragilis*, *Crossaster*, *Asterias*, *Pagurus*, *Ianachus*, *Mundia*, *Echinus esculens*
Sediment : Sandy Mud with gravel inclusions
Film Time : 15:09:10 – 15:14:50

4. sub–fossil (*Modiolus*) facies
Depth Range : 180 – 200 m
Definition Criteria : Much lower diversity and abundance of live fauna, shell coquina with colonies of *Filograna*.
Live Fauna/Flora : *Ophiothrix fragilis Filograna implexa*
Sediment : Coquinid pavement, dominated by the shells of *Modiolus modiolus*
Film Time: 15:25:27 – 15:26:10

5. *Mellinia* facies
Depth Range : 200–206 m
Definition Criteria : Presence of tubiculous polychaete *Mellinia*
Live Fauna/Flora : *Mellinia* spp. *Ophiothrix fragilis*
Sediment : sandy mud with gravel inclusions
Film Time : Not recorded as part of video transect

A zone of shell accumulation surrounds the final marked zone, which was not observed, but which on the basis of grab sampling and coring is thought to consist mainly of the tubicolous polychaete *Mellinia* sp.

## I 2.3 Composition of the community within the Firth of Lorn

The following section summarises the grab and dredge sampling programmes. Two dredge samples were semi-quantitatively analysed over the period of the study in an effort to estimate the density of the sedentary and motile epifauna. More detailed analysis of the total population was established from a series of six grab samples collected on 23/08/83, and additional collections over the following nine months (Table I 2.1; Fig. I 1.1). A complete species list is given in Appendix II and data on the compostion of the sediment is included in section II 1.3.1.

TABLE I 2.1
Details of the grab samples used in the estimation of community composition and production.

| Sample | date | grab | depth(m) | volume(l) | °C |
|---|---|---|---|---|---|
| c202 | 23/08/83 | H | 151 | 6 | 12.5 |
| c204 | 23/08/83 | H | 165 | 5 | 12.5 |
| c206 | 23/08/83 | H | 155.5 | 6 | 12.5 |
| c207 | 23/08/83 | H | 163 | 5 | 12.0 |
| c208 | 23/08/83 | H | 168 | 7 | 12.0 |
| c209 | 23/08/83 | H | 172 | 5 | 12.0 |
| c306 | 29/11/83 | D | 181 | 6 | 11.5 |
| c408 | 10/02/84 | D | 152 | 8 | 7.5 |
| c506 | 24/05/84 | D | 174 | 6 | 9.0 |

Hunter-Simpson (H) and Day (D) grabs were used to sample the sediment (both 0.1 m$^2$.). Depths corrected to MLWS. Temperature of sediment was measured at a depth of approximately 5 cm.

### I 2.3.1 Algae

Although occasional fragments of terrestrial angiosperms (eg. twigs and leaves) were collected, the majority of plant detritus was macroalgal. Two species of algae were identified and collected from a dregde sample on 27/3/86, *Laminaria saccharina*, found attached to stones rocks and shells in sheltered positions from the extreme lower shore to about 20 m, and the intertidal species *Ascophyllum nodosum*. The respective wet weights of 50.35g and 51.21g respectively collected from a dredge sample containing an estimated 400 adult *M. modiolus* indicate that such allochthonous inputs may be very significant. *Ascophyllum* along with a number of other intertidal macroalgae has flotation devices, which will increase the potential for dispersal prior to sinking.

### I 2.3.2 Phylum – Cnidaria (Subclass – Zoantharia, Order Madreporaria)

*Carophyllia smithii* (Devonshire Cup Coral) was one of the species under-sampled by both dredge and grab sample, forming a common constituent of the unsampled rock wall facies (facies 2. of the UWTV survey) although also found within other areas attached to living and dead shells of *M. modiolus*. The broad based form which occurs in areas exposed to currents in excess of 100 cm/sec (Wilson, 1975) was not recovered from the Firth of Lorn, but were recorded by Brown (1979) from the Sound of Jura.

### I 2.3.3 Phylum Echinodermata

#### Class Ophiuroidea

In the Firth of Lorn *Ophiothrix fragilis* is the most cosmopolitan of the four species considered, occuring over a wide variety of substrates and depths and in all but the *Mellinia* facies.

Distribution is apparently related to feeding strategy, although *Ophiothrix fragilis* is omnivorous and will feed on worms, crustaceans, bivalves, compound ascidians, echinoderms, formainifera (Mortensen, 1927; Eales, 1967) and carrion (Vevers, 1956; Nagabhushanan & Colman, 1959), it is basically a suspension feeder (Roushdy & Hansen, 1960; Brun, 1969; Warner, 1971). *Ophiothrix fragilis* is therefore restricted to areas of moderate to high current speeds (Reese, 1966; Brun, 1969; Warner, 1971; Broom, 1975; Holm & Barret, 1977; Brown, 1979; George & Warwick, 1985) which carry suspended material across the vertically extended feeding arms (Warner, 1971). Dense aggregations are formed in areas of moderate to high current activity, although aggregations are not known to form in shallow water, probably because wave surge effects render them unstable, Warner (1971) has observed tumbling masses of dislodged ophiuroids in very strong currents. Brun (1969) estimated current speeds of between 0.7 and 1.2 m/sec crossing *Ophiothrix* beds formed on gravel bottoms with rocky outcrops off the Isle of Man.

Reese (1969) suggested that the dense aggregations of O. *fragilis* form as a result of the passive responses to physical environmental factors. Dense aggregations would serve for mutual protection from predation, increase stability and improve the efficiency of filter feeding in currents and aid cross-fertilisation (Brown, 1979). The smothering effect of dense aggregations must be detrimental to sessile filter feeding epifauna underneath the dense beds, both by interfering with feeding patterns and also possibly from browsing by O. *fragilis*. Vevers (1956) recorded that O. *fragilis* in brittle-star beds occurred almost to the exclusion of other epifaunal invertebrates.

The feeding and growth of *Amphiura chiajei* have been investigated by Buchanan (1964). The animal is a deposit feeder, unlike the related species *A. filiformis* which is a filter feeder (buried in fine mud with only the tips of its arms exposed). It lives quasi-epifaunally, the disc partially buried, the arms stretched across the sediment surface; detritus collected by the tube feet is transported to the mouth. The life orientation of *A. chiajei* makes identification from video surveys difficult.

Although both C. Comely (*pers comm.*) and C. Smith (*pers comm.*) have found both *A. filiformis* and *A. chiajei* occuring together at sites in the Firth of Lorn, *A. chiajei* is the only species found in the deep water *M. modiolus* community, probably due to the presence of gravel inclusions (Comely *pers comm.*, this survey). Comely found that *A. chiajei* was present at 40% of all stations in his survey. In this study *A. chiajei* occurred at an estimated density of 77/m², a higher density than Comely (*pers comm.*) estimates for his nearest stations of 3-37/m² (Appendix III). *A. chiajei* was a significant component of the Creran fauna surveyed by Gage (1972a, b) and also occurs at densities of 20/m² in the the Sound of Jura (Brown, 1979).

The population structure observed by Buchanan (1964) was reminiscent of a single normal distribution curve, the entire population consisted of fairly large animals with an average disc diameter greater than 7.5 mm. The histogram produced from this sample (Fig. I 2.5) is slightly right skewed (sensu Curry, 1982) with animals disc diameters ranging from 4 to 9.5 mm. It is possible that small fragile animals were lost during the sieving process.

*Ophiocomina nigra* was a common constituent of dredge hauls although, being an atypical orange colour, they were initially mis-identified, grab sampling recovered only one mature animal (disk diameter 14.2 mm) which was included with *Ophothrix fragilis* in estimates of production. Earll (1974) states that Shetland *Modiolus* beds in exposed sites are dominated by O. *fragilis* and O. *nigra*, whereas those in sheltered sites are populated by ascidians. O. *nigra* has previously been reported as the minor partner (1 - 9%) in mixed associations with O. *fragilis* (Jones, 1951; Vevers, 1956; Rowell, 1960; Brun, 1969; Earll, 1974), although Jones (1951) believed that *Ophiohtrix fragilis* was commoner in deeper, and more current swept areas. Warner (1971) observed a strict seperation of the two species in an area where population densities were relatively low. In the Firth of Lorn, Rowell (1960) recorded O. *nigra* associated with the ophiuroids *Ophiothrix fragilis*, *Ophiopholis aculeata* and *Ophiura textura* at a depth of between 20 and 35 m west of Crinan.

O. *nigra* is unusual in that it employs a wide variety of feeding strategies (Fontaine 1965), the growth rate of O. *nigra* from the Firth of Clyde has been investigated by Gorzula (1977).

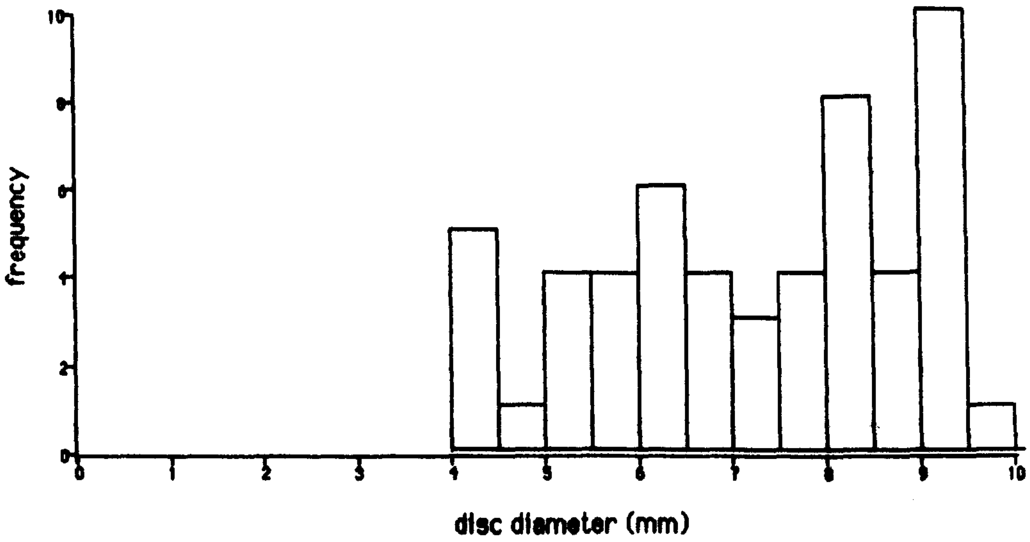
## Class Asteroidea

A great diversity of asteroids were recovered from dredge samples including *Luidia ciliaris*, *Anseropoda placenta*, *Crassoaster papposus*, *Solaster endeca*, *Asterias rubens* and the filter feeding *Henricia sanguinolenta*.

*Asterias* and *Crassoaster* are believed to be the most abundant predatory asteroids in the Firth of Lorn. A dredge sample containing 214 *M. modiolus* collected on 10/11/84 contained a single *Asterias rubens* with a radius of 60.8

**Figure I 2.5**

Size frequency distribution of *Amphiura chaijei* (coll 23/8/83)



mm, a small *Crassoaster* was the only asteroid recovered by grab sample. Experiments demonstrated that the stunted *M. modiolus* do not have a size refuge from moderately sized *Asterias* (section I 3.3.1). Brown (1979) suggests that the distribution of *C. papposus* may be linked to that of epifaunal molluscs such as *M. modiolus* found in moderately high energy environments which form part of the diet. It is perhaps significant that *C. papposus* is also a constituent of the Alaskan *Modiolus* fauna (Lees & Driskell, 1981). The apparent ability to induce bivalves to gape (Feder & Christensen, 1966) may prevent *M. modiolus* from reaching a size refuge from *Crassoaster*.

### Echinoidea

The two regular echinoderms, *Echinus esculentus* and *Psammechinus miliaris* recovered in dredge samples were probably feeding on allochthonous macro-algae, although both are believed to be omnivorous.

The clypeasteroid, *Echinocyamus pusillus* is a small (< 15 mm) gravel dwelling species which was present in the grab samples at an estimated density of $6/m^2$ similar to the figure of $7/m^2$ estimated by Comely, (*pers comm.*) for station 25 (Appendix III). Unusually all the animals recovered were in the size range 9.5 – 11.0 mm and it is therefore possible that smaller animals were overlooked. In a subsample of a dredge containing 214 adult *M. modiolus* (collected 10/11/84), eight *Echinocyamus pusillius* were present, the minimum length was 9.3 mm and the maximum length 11.4 mm (mean 10.1, SD 0.77), the dry weight of these animals was not recorded.

## I 2.3.4 Phylum Mollusca

### Polyplacophora

*Lepidopleurus asellus* is the most widespread of the four British lepidopleuran chitons. It is a marine grazer occuring offshore to 200 m, the estimated density in the Firth of Lorn ($36/m^2$) is approximately half the estimated density in the Sound of Mull ($60/m^2$), possibly reflecting a depth control. *L. asellus* recovered from the Firth of Lorn ranges from 2–12 mm in length. Akpan (1981: 98) observes that "Worm tubes and calcareous algae were amongst the substrates which often carried chiton grazing traces. In contrast to limpet marks, they were never found on live shells. The chiton seems to prefer grazing on the muscle scar. At the deeper sites (76–96m) of the Orkney sea, the grazing traces occurred only on the muscle scars of *Glycymeris glycymeris* shells. As with *Acmaea*, the chiton tends to avoid grazing near complicated worm encrustations and was not observed to graze across bryozoan encrustations."

Class Gastropoda

Subclass Prosobranchia

Most of the few gastropods recovered alive from the Firth of Lorn, were species grazing upon the epifauna, both *Didora apertura* and *Emarginula reticulata* are believed to be sponge raspers which also ingest detritus (Fretter & Graham, 1976). In the Sound of Jura, Brown (1979) records *E. reticulata* from only one station and at this site vase shaped sponges were also found, in the aquarium they have been observed feeding exclusively on sponges (M. James. *pers comm.*). The cowrie *Trivia* feeds on ascidians, of the two species found in the U.K, only *T. monacha* was identified from the Firth of Lorn, but the gross means of identification are not infallible (Brown, 1979) and all have subsequently been designated *Trivia* sp.

*Capulus ungaricus* is an unusual gastropod which is a common member of the *Modiolus* epifauna (Jones, 1951). It is typically found commensal on the posterior margin of living *M. modiolus*, the long unretractable proboscis collecting mucus and fine particles from within the mantle cavity of the host (Yonge, 1938). On older *M. modiolus* shells it can form a distinctive abraded scar area.

Many of the gastropod species only recovered as dead shells are typically believed to be macro-algal grazers, including *Patina pellucida*, *Littorina* sp. *Gibbula* sp, *Calliostoma zizyphinum*, and a number of detritivores including the Rissoacids *Alvania* sp. *Onobia semicostata* and *Hydrobia ulvae* and the patellid

*Propalium ancyloidea.*

Two predatory gastropods, *Ocenebra erinacea* and *Natica* sp. were both only recovered from the death assemblage. The sediment of the Firth of Lorn would appear unsuitable for Naticids which are adapted to feed on infaunal bivalves, moving rapidly beneath the surface of sand. *Ocenebra erinacae* is an epifaunal predator, which has been observed to bore anomiid bivalves in the littoral (Fretter & Graham, 1962), their long proboscis can also be inserted between bivalve or barnacle valves, causing death without leaving a trace. The shells of *Nuculana minuta, Venus ovata, Anomia* sp. and *Parvicardium ovale* with distinctive countersunk boreholes may be allochthonous.

Class Bivalve

Nuculidae & Nuculanidae

Distributional details are given in Ansell *et al.* (1978), on the West Coast of Scotland the species has been recorded in the Firth of Lorn (Comely, *pers comm.*), Loch Creran (Gage, 1972a), Loch Etive (Gage, 1972b; as dead shells only) and the Clyde Sea Area. Jones (1951) does not record *Nuculana minuta* from the Isle of Man *Modiolus* or *Terebratulina* faunas. Distribution is patchy in the Clyde Sea Area, being found in deep or moderately deep water to a maximum depth of 210 m (Allen, 1962), with greatest densities in lower Loch Fyne, with a mean density of 61/m$^2$ and a maximum density of 210/m$^2$ (Ansell *et al.* 1978). Chumley (1918) recorded *Nuculana minuta* (as *Leda minuta*) on muddy and sandy bottoms, and Allen (1962) in sandy mud, mud and gravel, while Ansell *et al.* (1978) collected *Nuculana minuta* mostly from muddy bottoms.

In the Firth of Lorn, *Nuculana minuta* occurs around the deep central depressions, and densities do not exceed 13/m$^2$ (Comely *pers comm.*). The estimated density of *Nuculana minuta* (6/m$^2$) is similar to the estimate made by Comely (*pers comm.*, Appendix III, station 25) of 7/m$^2$. The largest valve recovered (9.6 mm) was much smaller than maximum length estimates provided by Ansell *et al.* (1978; Fig. 6) of between 13 and 16.5 mm. On the basis of growth rings, Ansell *et al.* (1978) estimate that the lifespan of *Nuculana minuta* is between 7 and 8 years.

One living example of *N. nucleus* was collected by the grab sampling programme. Shells of another *Nucula* species, probably *N. sulcata* where recovered from the sediment but because of the difficulty of identification particularly with the periostracum missing (Cadée, 1968) all *Nucula* collected in the sediment were assigned to *Nucula* sp. Comely (*pers comm.*, 1986) states "*N. sulcata* is widely distributed on the muddy, sandy grounds at all depths to 220 m in the Firth of Lorn. *N. nucleus* occurs where there is a high percentage of gravel and stones, associated with the *M. modiolus* communities. This distribution is similar to that found by Allen (1954) in the Clyde."

### Arcidae

The nesting bivavle *Arca tetragona* is relatively common in the clean shell gravels between Loch Don and the Lady Rock at a depth of approximately 50 m, although it was rare in dredge samples from the *Modiolus* community. The robust shells were infrequently recovered from the sediment in the Firth of Lorn.

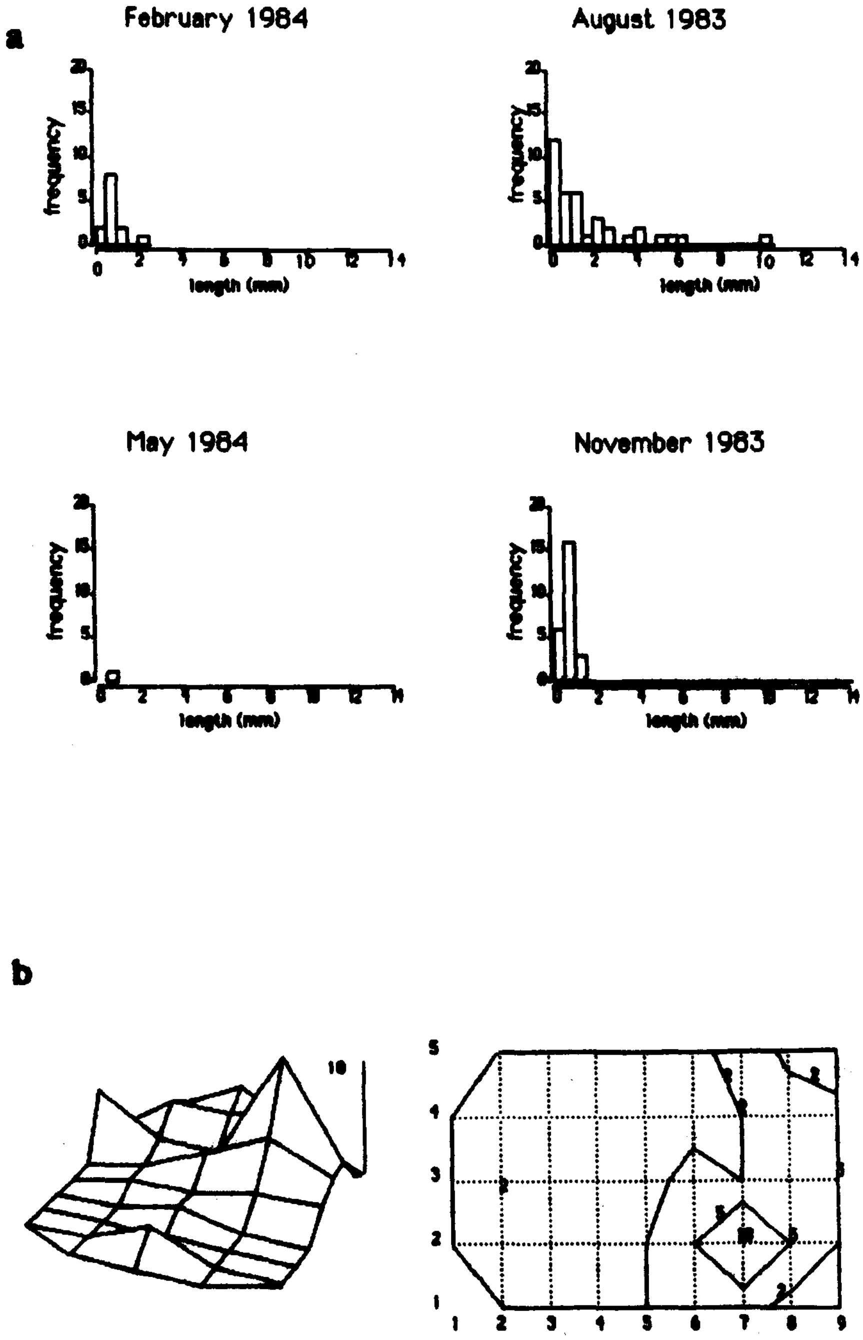
### Anomiidae

Anomiidae are principally identified by the number, shape and extent of the muscle scars of the upper (left) valve. In small animals, which made up the bulk of the living material and shell material recovered from the sediment, it is virtually impossible to distinguish individuals by this criterion. *Anomia epihippum* and *Monia squamata* and *Monia patelliformis* were identified as large dead shells from the sediment, although only *Monia squamata* was definitely living in the community. Two types of Anomiidae were recovered from the sediment, a smooth shelled form and a ribbed form, variably spined, these were designated *Anomia* smooth and *Anomia* ribbed respectively in the sediment analysis.

Although the estimated density of *Anomia* sp. was relatively high, the live population was strongly left skewed (Fig. I 2.6a), the largest living individ–

Figure I 2.6

a) Seasonal length frequency histograms *Anomia* sp.
b) Contour and density plots of *Anomia* sp. on *Modiolus* (pooled samples).



ual collected (length 10.3 mm) was below the maximum length of even the smallest Anomiidae (Tebble 1966). Juveniles were most abundant in the August sample (Fig. I 2.6a), but there was little seasonal variation in the density of *Anomia* on *M. modiolus* (Table I 2.3), although greatest in November.

TABLE I 2.3
Density of *Anomia* sp. on *M. modiolus*

| | SAMPLE DATE | | | |
|---|---|---|---|---|
| | 23 Aug. 1983 | 29 Nov. 1983 | 10 Feb. 1983 | 24 May 1984 |
| No. of *M. modiolus* | 45 | 18 | 18 | 20 |
| No. of *Anomia sp.* | 38 | 26 | 13 | 1 |
| *Anomia* sp./*M.modiolus* | 0.8 | 1.4 | 0.7 | 0.05 |

Mytilidae

*Modiolus modiolus* the 'horse mussle' is a long lived slow growing mussle, which can reach lengths of 20 cm, it is a common constituent of the Scottish fauna and is occasionally fished commercially. Zenkevitch (1963) defined *Modiolus modiolus* as a north boreal species, in the Atlantic it ranges from the White Sea to the Bay of Biscay, off Iceland and the Faroes down the east coast of N. America to N. Carolina. In the Pacific it ranges from the Bering Sea to Japan and California. (Roberts, 1975). Around Europe, it is especially abundant in the Barent and White Seas, Norway, Iceland and the northern coasts of Britain, but is apparently absent from much of the Baltic, (Brown and Seed, 1977). Being a large suspension feeder it is restricted to areas of considerable water exchange.

*M. modiolus* has been recorded from a wide range of depths and sediment types, from 225m (Shelford, 1935) to an erratic presence in the intertidal (Read & Cuming, 1967; Davenport & Kjoersvik 1982), the presence of a permanent aperture (the byssal notch) limiting the littoral extension.

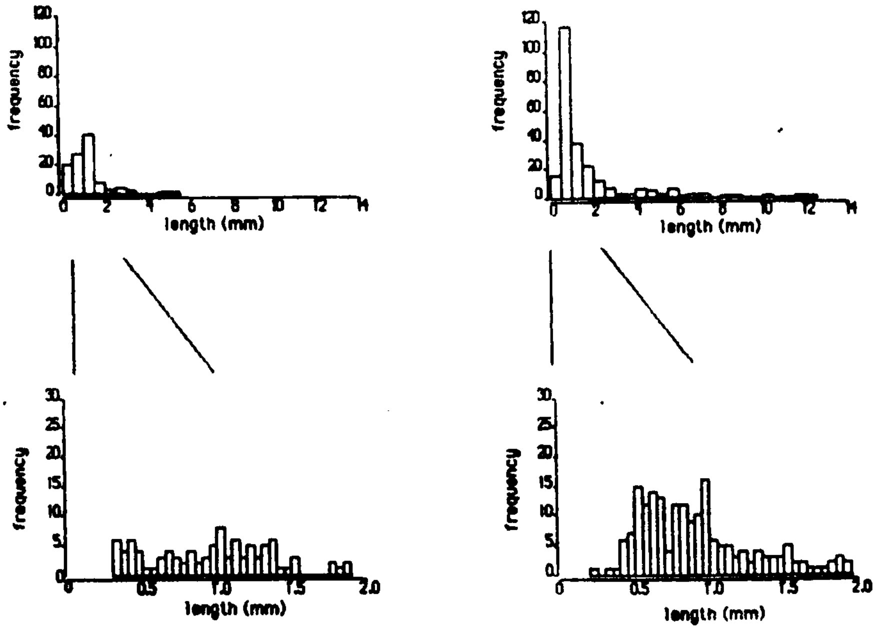
*Modiolus phaseolinus* is considerably smaller than the closely related *M. modiolus* (reaching a maximum length of only 19.0 mm; Tebble, 1966). It was extremely common in the Firth of Lorn, numerically the second most abundant species after *T. retusa* and because of this abundance, where identification proved difficult (typically because the dentition was destroyed when attempts

Figure I 2.7

Length frequency histograms for Modiolus phaseolinus collected by grab sample (for details of samples see Table I 2.1)

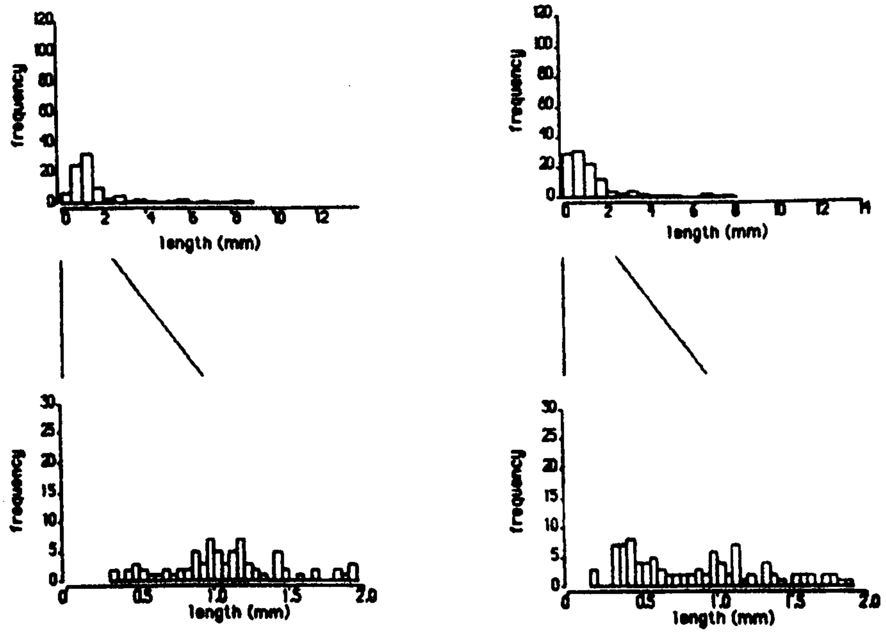
February 1984

August 1983



May 1984

November 1983



were made to seperate the valves) small living modioliform mussels were attributed to *M. phaseolinus*. Conversely in the sediment, while complete valves were easily distinguished, all unidentified Mytilidae fragments were attributed to *M. modiolus*. Separation of *M. modiolus* and *M. phaseolinus* by the purple nacre of the latter (Tebble, 1966) proved not to be reliable.

Comely (*pers comm.*) recognized that the ability of *M. phaseolinus* to settle and develop in such numbers in competition with established specimens of *M. modiolus* posed an interesting problem. Comely (1978) observed that spat-fall in *M. modiolus* was sparse and continuous. The low densities of settled *M. modiolus* postlarvae, probably attest both to a reduced mortality of newly settled spat and longevity of adult animals.

TABLE I 2.4
Density of *M. phaseolinus* on *M. modiolus*

| | SAMPLE DATE | | | |
|---|---|---|---|---|
| | 23 Aug. 1983 | 29 Nov. 1983 | 10 Feb. 1983 | 24 May 1984 |
| No. of *M. modiolus* | 45 | 18 | 18 | 20 |
| No. of *M. phaseolinus* | 246 | 115 | 109 | 94 |
| *M. phaseolinus/M.modiolus* | 5.5 | 6.4 | 6.1 | 4.7 |

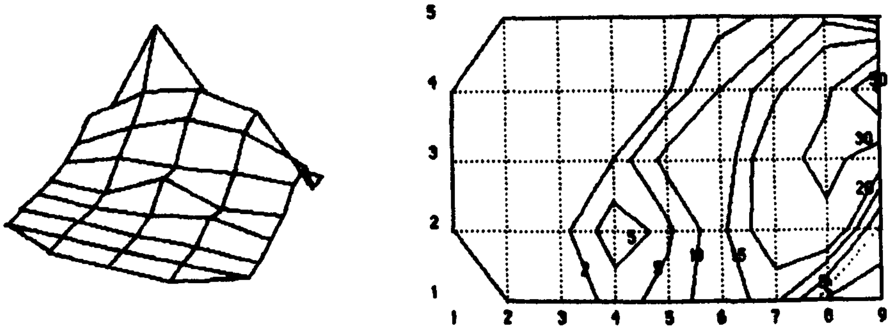
There have been no studies conducted into the reproductive cycle of *M. phaseolinus* but the relatively large numbers of animals collected allow for reasonable histograms to be produced. Although there is little change in settlement density (Table I 2.4), the strongly left skewed size-frequency histograms suggest that very small ( $< 0.5$ mm) animals reach a maximum density in the November sample (Fig. I 2.7). Predation and settlement in this species is discussed in section I 3.3.1).

There appears to be little substrate selectivity in this species (Table I 4.5), and like *T. retusa*, the numbers of animals attached directly to the surface of *M. modiolus* increase with size, although the change is not so striking. The highest densities occur near the posterior of the shell (Fig. I 2.8). Like *T. retusa* the most common substrate is *M. modiolus* which accounts for 44% of the population, with solitary ascidians second (13.7%; Table I 4.4).

Although *Musculus discors* is typically associated with the simple asc-

**Figure I 2.8**

Contour and density plots of M. phaseolinus on Modiolus (pooled samples).



idians *Ascidia mentula*, *Ascidella aspera* and *Ciona intestinalis* it is occasionally found in other nestling sites. In the Firth of Lorn *M. musculus* was relatively common (78/m$^2$) being found in all but one case, embedded within ascidian tests.

Pectinidae

*Chlamys opercularis* is bysally attached as a juvenile, but in adult life is a free and active swimmer and is found on firm sandy gravel, sandy mud or shelly ground down to 183 m (Tebble, 1966). As a juvenile, this species is associated with *Modiolus modiolus* (Tebble, 1966; Roberts, 1975). Underwater television transects frequently 'put this species to flight' it was a moderately common constituent but is not dominant in dredge hauls and was once collected in a grab sample.

A diverse pectinidae fauna was found in the death assemblge, including *Chlamys striata*, *C. tigerina*, *C. varia*, *C. nivea* and *Similipecten similis*. Although not found alive, a large right valve of *Chlamys distorta* was found attached to the concave inner surface of a stunted *M. modiolus*, and may therefore have been a member of the living community.

Astartidae

Only two of the five British Astartidaes, *A. sulcata* and *A. elliptica* were recovered from the Firth of Lorn. *Astarte sulcata* is distinguished from *A. elliptica* by differences in the periostracum and the presence of a crenulate margin in the former. However, as the periostracum had been lost from many of the sub-fossil animals, some *A. sulcata* have smooth margins (Tebble, 1966) and the juveniles are very difficult to distinguish, it is possible that some of the material has been mis-identified.

*Astarte sulcata* is found in a variety of substrates from mud, muddy gravel, to shingle or sandy gravel from 6-210 m (Allen, 1962; Tebble, 1966); it is a dominant bivalve in the Sound of Jura (Brown, 1979) and is present at a number of Comely's stations in the Firth of Lorn (Appendix III). In large dredge hauls it is possible to collect large numbers of *A. sulcata,* associated with them are a smaller number of *A. elliptica,* in one collection accounting for eleven of 80 *Astarte* identified (ie 14%). This ratio is paralleled in fossil samples, in one grab sample (c3f5) of the 27 astarte valves recovered, 4 (ie 15%) were *A. elliptica*. Of the 28 living *Astarte* collected in grab samples, all were *A. sulcata*. *Astarte sulcata* is a more temperate water species than *A. elliptica, A. sulcata* occuring from S. E. Greenland sea, into the Mediterranean and off N. W. coast of Africa, while *A. elliptica* is only known from northern waters, Labrador and Massachusetts, to the Greenland sea, the White sea and the British Isles (Tebble, 1966).

Both the shell and dentition are robust and these are presumably related to their shallow burrowing mode of life (Yonge, in Yonge & Thompson, 1976). The biometry of three species collected in Keil Bay has been investigated by Schaefer *et al.* (1985).

Cardiidae

Four species of *Parvicardium* occur off the west coast of Scotland (Brown, 1979), but it is probable that only *P. ovale* is present in the *Modiolus* community. All four live animals were identified as *P. ovale,* and it was the only species recorded in surveys of Loch Etive and Loch Creran by Gage (1972a & b, 74). The maximum size of *P. ovale* is 12.7 mm (Tebble, 1966), but the largest shell recovered from the sediment had a length of only 9.3 mm and the great majority where much smaller than this (section II 1.3.3.1).

Hiatellidae

*Hiatella arctica,* is a bysally attached nestler or rock borer which may be confused with the smoother shelled *Lutraria lutraria*. The shells of British *Hiatella* are morphologically very variable, reflecting their mode of life and Tebble (1966) includes them all within *H. arctica*. The Firth of Lorn *M. modiolus* community represents an extension of the depth range of this species.

*H. arctica* was estimated to be the sixth most abundant species in the community (58/m$^2$). The population appeared to be stunted, the largest animal was a mere 6.2 mm long, compared to a maximum length of 38 mm (Tebble, 1966). Many *Hiatella* were found free-lying in the sorted sediment (possibly indicating a life position amongst the byssus), the majority of those epifaunal on *M. modiolus* were found bysally attached to the surface, although some were located in the groove running along the dorsal side of the shell posterior to the ligament. Hunter (1949) considers the most common habitat of *H. arctica* to be the byssus of *M. edulis* and *M. modiolus.*

A number of bivalves were only recovered from the death assemblage, either because they were not sampled or they were transported in as dead shells. Failure to sample a species living within the community may arise either because the species is deep burrowing as are *Mya arenaria, Dosinia exoleta, Sphenia binghami* and *Thracia phaseolinus* or because they are relatively rare. Species unlikely to be living in such a coarse sediment area include *Chlamys septemradiata* and *Corbula gibba,* both well adapted to life in silty habitats (Yonge, 1946) and *Mytilus edulis* which is a predominately shallow water species.

### I 2.3.5 Phylum Annelida

### Class Polychaeta

Little attention was paid to non calcareous-tube dwelling polychaetes, although the scale worm *Lepidonotus squamata* was a common member of the *M. modiolus* community and has also been recorded from *M. modiolus* communities by Jones (1960).

### Serpulids

No attempt was made to distinguish between the various serpulids in the Firth of Lorn because the fragments of calcareous tube are virtually indistinguishable in the sediment. The serpulids from the Firth of Lorn included *Pomatocerous triqueter* and possibly also *Protula tubularis.*

Serpulids were present in all grab samples, typically attached to the living and dead shells of *M. modiolus* and occasionally living *T. retusa*. Conversely 2.8% (43) of the *T. retusa* were found attached to the tubes of living serpulids with a further 1.1% attached to dead tubes and 0.7% at the junction made between the worm tubes and the surface of *M. modiolus*. The maximum size of *T. retusa* attached to a living serpulid (4.96 mm) suggests that the lifespan of the worm was in excess of two years.

*Filograna implexa* is a very distinctive serpulid which occurs in two forms, either attached for the whole of its length on a hard substrate, or intertwined in small fragile clumps. The latter form, although more common in the Firth of Lorn, is probably undersampled by dredge because of its great fragility.

Requiring hardgrounds to become established, *Filograna* is restricted to areas with gravel components; distribution is further limited by the unusual habit of protecting the young within the adult tube (Nelson-Smith, 1967). The UWTV survey suggests that the density of *Filograna* colonies increases with depth (Fig. I 2.4) which bears out the survey by Caddy (1970) in the Bay of Funday where *F. implexa* was found in deeper water than both *Terebratulina septentrionalis* and *M. modiolus*.

### I 2.3.6 Phylum Arthropoda - Class Crustacea

#### Subclass Cirripeda

Only two species of barnacles were found alive in the Firth of Lorn, the assymetric *Verruca stroemia* and the large deep water species *Balanus hameri*. *Verruca stromia* was ubiquitous in the *M. modiolus* community, with a distribution similar to *Pomatocerous triqueter*.

#### Subclass Malacostra Anomura

Hermit crabs are probably biostratinomically important in the reworking of sediment. In the *Modiolus* community they were mostly housed in exotic gastropod shells including *Gibbula*. spp and *Calliostoma* spp.

No living hermit crabs were recovered in grab samples, although *Eupagurus bernhardus*, *Pagurus pubescens* and *Eupagurus prideauxi* (with the associated anemonae *Adamsia palliata*) were commonly collected in grab samples. A sub-sample of crabs collected from a large dredge haul on 10/11/84 yielded a single specimen of *Euagurus prideauxi* with a carapace length of 8.0 mm. The largest claw from a living *Eupagurus bernhardus* collected in any dredge sample had a longest dimension of 31.9 mm, a width of 18.2 mm and a maximum aperature of 9.9 mm.

Roberts (1975) observed that *Eupagurus bernhardus* (carapace width (CW), 47–93 mm) fed on *M. modiolus* in the size range 15–25 mm at a rate of 0.15–0.3 *M. modiolus* per day, higher rates were found by other crustaceans, not recovered from the Firth of Lorn. Warner (1971) recovered *Ophiothrix fragilis* from 10 of 24 stomachs of *Eupagurus bernhardus* examined, and during this study an unidentified Pagurid was observed feeding on the severed arm of an *O. fragilis* in the holding tanks.

The squat lobster *Mundia rugosa* was a common member of the fauna, recorded from UWTV and dredge samples. A single specimen (carapace length (CL) including anterior spine, 20.9 mm, weight 882 mg) was collected in an August grab sample.

### Brachyura

Attempts were made to estimate the density of crustaceans from a dredge sample collected on 10/11/85. A subsample of the total collection containing 214 living *Modiolus* contained four *Hyas coractatus* (CL, 36.7, 29.5, 25.7, 24.0 mm), four *Inachus leptochirus* (CL, 22.0, 17.9, 21.8, 21.5 mm), and one each of *Inachus dorsettiensis* (CL, 20.7 mm), *Macropodia egyptia* (CL, 17.2 mm), *Ebalia tuberosa* (CL, 14.1 mm) and *Medaeus couchi* (CL 17.0 mm, CW 24.5). The largest claw recovered for the latter species over the period of the study was 25.4 mm long.

### I 2.3.7 Phylum Brachiopoda

### *Terebratulina retusa*

*Terebratulina retusa* is the most abundant of the 21 species of Recent brachiopods found around the British Isles (Brunton and Curry, 1979). Jeffreys (1863) writes "I have repeatedly taken *Terebratulina caput-serpentis* (= *T. retusa*) and *Crania anomala* in such profusion on the Western Coasts of Scotland, as to be compelled by sheer '*embarras des richesses*' to throw many hundreds overboard in the course of a days's dredging." The naturalist W. Anderson Smith (1897) in a description of a dredging trip from "the deepest water to be had inside the Atlantic" (possibly off the south of Lismore, see Preface) "the masses of Terebratulae of the most splendid proportions will force us to talk of these shells in future with regal indifference." *T. retusa* is also common off the coast of Norway (Dall, 1920) and has been recorded as far west as the east coast of Greenland (Wesenberg-Lund, 1940), and as far south as the Mediterranean (Davidson, 1886-188; Dall, 1920). Curry (1979) observes that the precise geographic limits of *T. retusa* are unknown, as the two N. Atlantic species of *Terebratulina* are morphologically similar and have often been confused. Available data on brachiopod distribution of *T. retusa* on the west Coast of Scotland has been summarised by Brown (1979) and Curry (1979, 82).

The life cycle of *Terebratulina* is poorly understood, *T. septentrionalis* collected from the east coast of Canada have been observed to brood young within the mantle cavity, but brooding has not been observed in *T. retusa* from the Firth of Lorn, although this may be symptomatic of stressful of sampling. From analysis of population structures, growth lines and gonad quality Curry, (1982) interpreted bi-annual spawning of *T. retusa* from this population. Locally, distribution of *T. retusa* appears patchy, supporting the view that larval dispersal is restricted (Noble *et al.*, 1976; Thayer, 1977). However, the colonisation by at least three generations of *T. retusa* on a hardground in an otherwise totally unsuitable shallow muddy bay at Camus Nathas (N. E. Firth of Lorn; C. Smith, *pers comm.*) suggests that some larvae are capable of more extensive dispersal. Substrate selection is discussed in section I 4.3.

*Crania anomala*

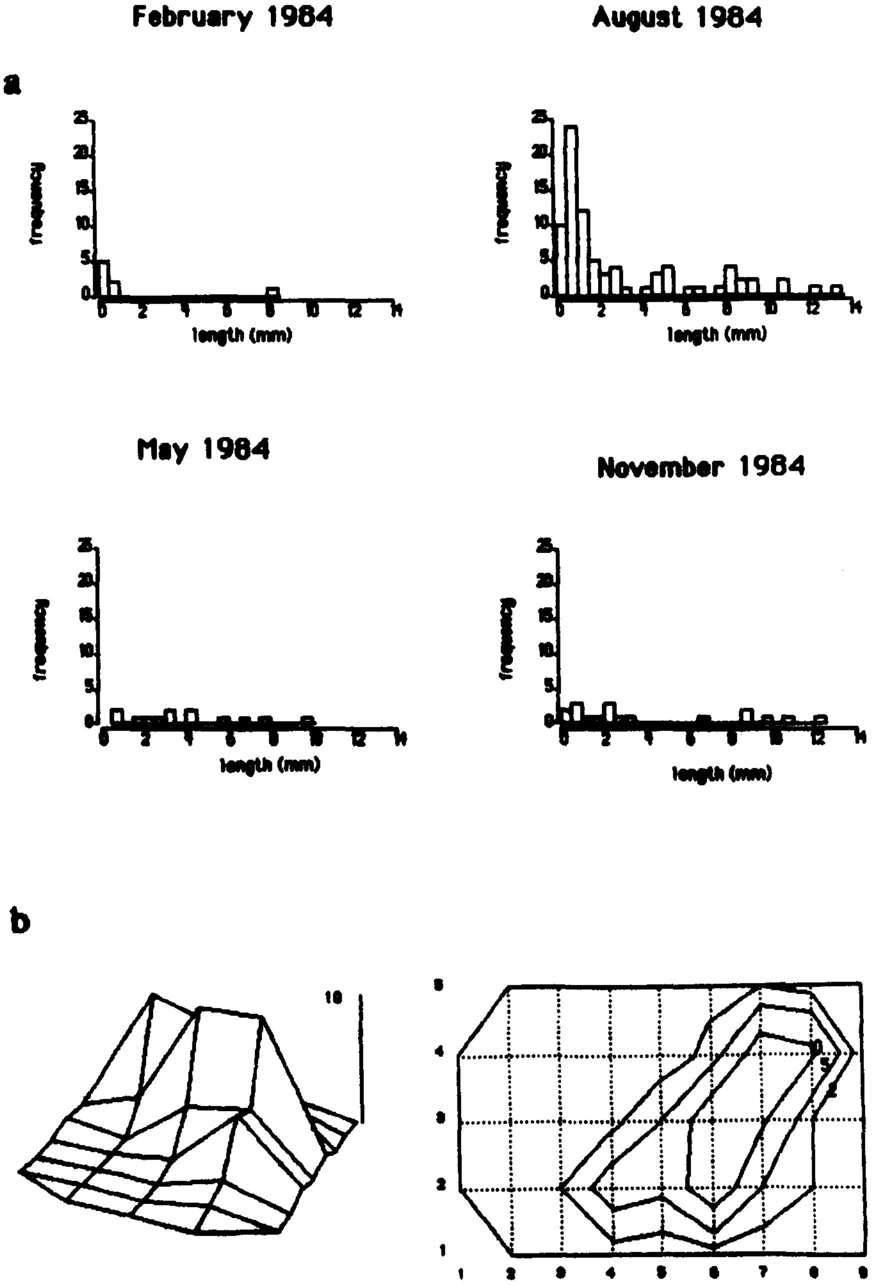
*Crania anomala* is a spirolophous inarticulate brachiopod, cemented by its pedical valve to exposed hard substrate. The attached (pedicle/ventral) valve varies in thickness and the thickened valves of Mediterranean forms may be a specific feature (Logan, 1979). Work on the ontogeny of early stages and population structure (Rowell, 1960) was conducted on material collected off the island of Garbh Reisa not far from this study area.

*Crania* is the only inarticulate brachiopod found around the British coastline, and it occurs in great abundance off the West Coast of Scotland. It has also been recorded from the Shetlands, Hebrides, off the north west and south of Ireland, the south coast of England and in the English Channel (Brunton & Curry, 1979). Farrow *et al.* (1984) consider it an important constituent of rocky areas (c. 80 m) on the Orkney shelf, and it constitutes a significant fraction of the sediment at a site of Barra Head (Wilson, 1979). It is noticeably absent in the Irish Sea and off the east coast of England. Elsewhere it has been found off the Canary Islands, the Faroes, Norway, Iceland and Spitzbergen (Brunton and Curry, 1979). *C. anomala* occupies similar habitats to *T. retusa*, but generally extends into shallower water.

Being cemented it is found attached to clean hard substrates. Densities of *C. anomala* on living *M. modiolus* are low, but boulders collected in the clam dredge, and not sampled by grab sampling are extensively settled. Many *C. anomala* appear to settle in small irregularities in the substrate and distribution of animals on *M. modiolus* is in many cases related to major growth checks, which form grooves running across the surface of the shell. The majority of animals were located on the ventral half of the *M. modiolus* shell (Fig. I 2.9b) and unlike most other species appeared to occupy fairly extensive areas of the posterior of the shell, indicating either that settlement occurs earlier in the lifetime of *M. modiolus* or that the *Crania* are able to settle and

Figure I 2.9

a) Seasonal length frequency histograms Crania anomala
b) Contour and density plots of C. anomala on M. modiolus (pooled samples).



survive in more cryptic habitats in the deeper recesses of the clump.

The settlement densities of *C. anomala* do not indicate any seasonality in the spawning, although there is a peak in juveniles in the August sample, which corresponds with the elevated density of 2.3 *Crania* per *M. modiolus* (Fig. I 2.9a). The population structure of the August sample is strongly right skewed (Fig. I 2.9a) and similar to the size-frequency distributions of Rowell (1960) from shallow water (20–35 m) off Crinan, all other histograms contain too few individuals to show any meaningful pattern.

Rowell (1960) who investigated the development in *Crania*, collected animals in the months of April, May, October and November. Breeding was believed to extend from April to November, spawning occuring in April and November. The elevated density in August (Table I 2.5) would therefore appear to be anomalous.

TABLE I 2.5
Density of *Crania anomala* on *M. modiolus*

| | SAMPLE DATE | | | |
|---|---|---|---|---|
| | 23 Aug. 1983 | 29 Nov. 1983 | 10 Feb. 1983 | 24 May 1984 |
| No. of *M. modiolus* | 45 | 18 | 18 | 20 |
| No. of *C. anomala* | 82 | 18 | 8 | 13 |
| *C. anomala/M.modiolus* | 1.8 | 1 | 0.4 | 0.6 |

Unlike *T. retusa* which shows considerable variation in substrate, *C. anomala* appears to be highly selective, all but one animal being attached to the surface of *M. modiolus*, either living or dead (Table I 4.5).

### I 2.3.8 Phylum Porifera

Attention is commonly drawn to associations of sponges and brachiopods, particularly in relation to the paucity of epifauna on some shells, which is attributed to a thin layer of sponge (Surylk, 1974).

Three species of sponge, found associated with *T. septentrionalis* from the east coast of the USA were also identified by Dr. J. Witman, from the Firth of Lorn. *Iophon nigricans* and *I. patterson*, (characteristically buff coloured when living and black when preserved in alcohol) have also been observed as small mounds on the surface of rock walls on the east coast of Canada (J.

Witman *pers comm.*). *Placamionida ambigua* also recorded from Iceland may only be associated with brachiopods (J. Witman *pers comm.*).

In addition, a striking blue siliceous sponge *Hymedesmia* sp. (identified by R. Harvey.) is very common on the surface of *M. modiolus*.

### I 2.3.9 Phylum Chordata – Class Osteichthyes

Attempts to obtain a representative sample of benthic feeding species for analysis of gut contents by long line fishing, (baiting the hooks with *M. modiolus*), was unsuccessful, collecting only two lesser spotted dogfish. The dredge sampled four additional species, two benthic feeders, an unidentified flatfish, *Gaidropsarus mediterraneus*, and the piscivores *Lophius piscatorius* and *Lepidorhombus whiffiagonis*. A single *Trisopterus luscus* was observed to repeatedly cross the path of the sled on the final UWTV transect. Occasionally large numbers of very small creatures took flight from the path of the sled, these may have been the lesser sand eel *Ammodytes tobionus* or possibly small crustaceans.

## I 2.4 DISCUSSION

### I 2.4.1 The *Modiolus* community

A review of the literature furnishes a number of descripitve studies of *Modiolus* communities, which are listed in Appendix I. An attempt was made to estimate the significance of the association of various species. Cluster analysis based on the presence of key genera seperates the communities out, apparently at random, the greatest similarity with the Firth of Lorn, being the *Modiolus* community from the Isle of Man described by Jones (1951). Any attempt to define key genera is limited by the widspread distribution of *M. modilus*. If such attempts were made, two types of species would be included, those associated with *M. modiolus* itself (eg the gastropod *Capulus* and the polychaete *Lepidonotus squamata*) and epifaunal guild equivalents (eg. filter feeding ophiuroids, articulate brachiopods, barnacles etc) introduced by the presence of the localised hardground into an otherwise unsuitable environment.

### I 2.4.2 Occurrence of the community in the Firth of Lorn

Although *M. modiolus* are widely distributed, the presence of a community in such deep water is unusual (Appendix I and section I 3.4). Comely (1978: 190) remarks "The *Modiolus* population..(found in the)...Firth of Lorne consists of small adults together with large numbers of very small (0–2 year) animals. It is possible that spat derived throughout the Firth of Lorne area are concentrated at this area, which is at the confluence of three major current systems, and hence the maintenance of a numerically flourishing population in what would not otherwise appear to be a truly congenital location for a *Modiolus* community." Current speed, appears to be critical to the establishment of the *M. modiolus* community, a current speed which was too low would favour deposit feeders whose presence would then prevent the successful establishment of suspension feeders (c.f. Rhoads & Young, 1970). In areas of extreme current speeds, especially where tidal dynamics cause the sediment to undergo erosion–deposition cycles, suspension feeders are rapidly buried and only a few hard deposit feeders can survive (c.f. Wildish & Peer, 1983).

Distribution of brachiopods in relation to current speed has been noted by a variety of authors. Eshleman & Wilkens (1979) investigating the distribution of *Terebratalia transversa* found that brachiopods were absent from areas where the current velocity exceeds about 3 knots (4.8 km/hr). LaBarbera (1977) found that larval *T. transversa* avoided areas with current speeds in excess of 0.2 cm/s. (0.72 km/hr). Brachiopods were also absent from areas with little or no current, suggesting that active pumping alone may not be capable of maintaining the animals in still water. (N.B. the current velocities cited by these authors are "open water" currents recorded from navigational charts, and the boundary layer effect would greatly decrease the current speeds experienced by the animal, see section III 1.3.1).

Scoffin *et al.* (1980) investigating carbonate sedimentation on the Rockall Bank to the west of the study area, recorded a number of species also obtained in the Firth of Lorn. *Echinus esculentus* was recorded to 106 m at densities of

1 per 20 m of drift. The small echinoid *Echinocyamus pusillus* was common in the gravelly sediment in shallow water, but no dense ophiuroid populations were observed. Small *Venus* sp., *Glycymeris glycymeris* and fragments of *M. modiolus* were recorded from depths less than 100 m but were not important as sediment contributors. The smaller rock epifauna recorded by these authors *Anomia* sp. terebratulid brachiopods, *Chlamys* spp., cup corals, serpulids, encrusting bryozoa, ophiuroids (especially *Ophiactis balli*) asterozoans and sponges, is possibly the deeper form of the community observed in the Firth of Lorn.

### *Modiolus* – brachiopod association

*Modiolus* is the longest surviving genus in the sub-family Modiolinae, having been first recorded in the late Silurian or early Devonian. The simple modioliform shell, with its subterminal umbos, lack of sculpture and absence of hinge teeth is almost certainly convergent.

Bivalves assigned to the Family Astartinae are present in Devonian rocks, although the genus *Astarte* is confined to rocks younger than Jurassic, indeed throughout the Jurassic the Astartidae, represented by *Astarte* and other genera, was the commonest heterodont bivalve and *Modiolus* the commonest representative of the sub-family Modiolinae (Kaufmann, 1967). At present *Astarte* dominates only in the arctic and sub-arctic and forms a common constituent in Tertiary deposits in Great Britian and elsewhere. Astarte was the most common species in the Tielrode deposits (Pliocene) studied by Boekschoten (1967). Formerly *Astarte* was common in tropical waters (Woodring, 1960).

Ophiuroids have a long geological history, ophiuroids with fully developed vertebrae first appeared at the beginning of the Devonian, the earliest examples of the genus *Ophiothrix* are from the Sequanian (Lower Jurassic) of France.

The genus *Terebratulina* (d'Orbigny, 1847) first evolved in the Upper Jurassic of Europe and India, colonising the margins of the Tethys Ocean. During the Jurassic, *Terebratulina* migrated through the recently opened Straits of Gibraltar to the margins of the Atlantic Ocean and representatives have been found in the Cretaceous of England and North America (Curry, 1979). Subsequently the genus underwent tremendous radiation and had a cosmopolitan distribution throughout the Tertiary. *Terebratulina* survives as one of the most common and geographically widespread of the Recent brachiopod genera (Curry, 1979). Cemented inarticulates have an extended geological history, the genus *Crania* extends back into the Mesozoic.

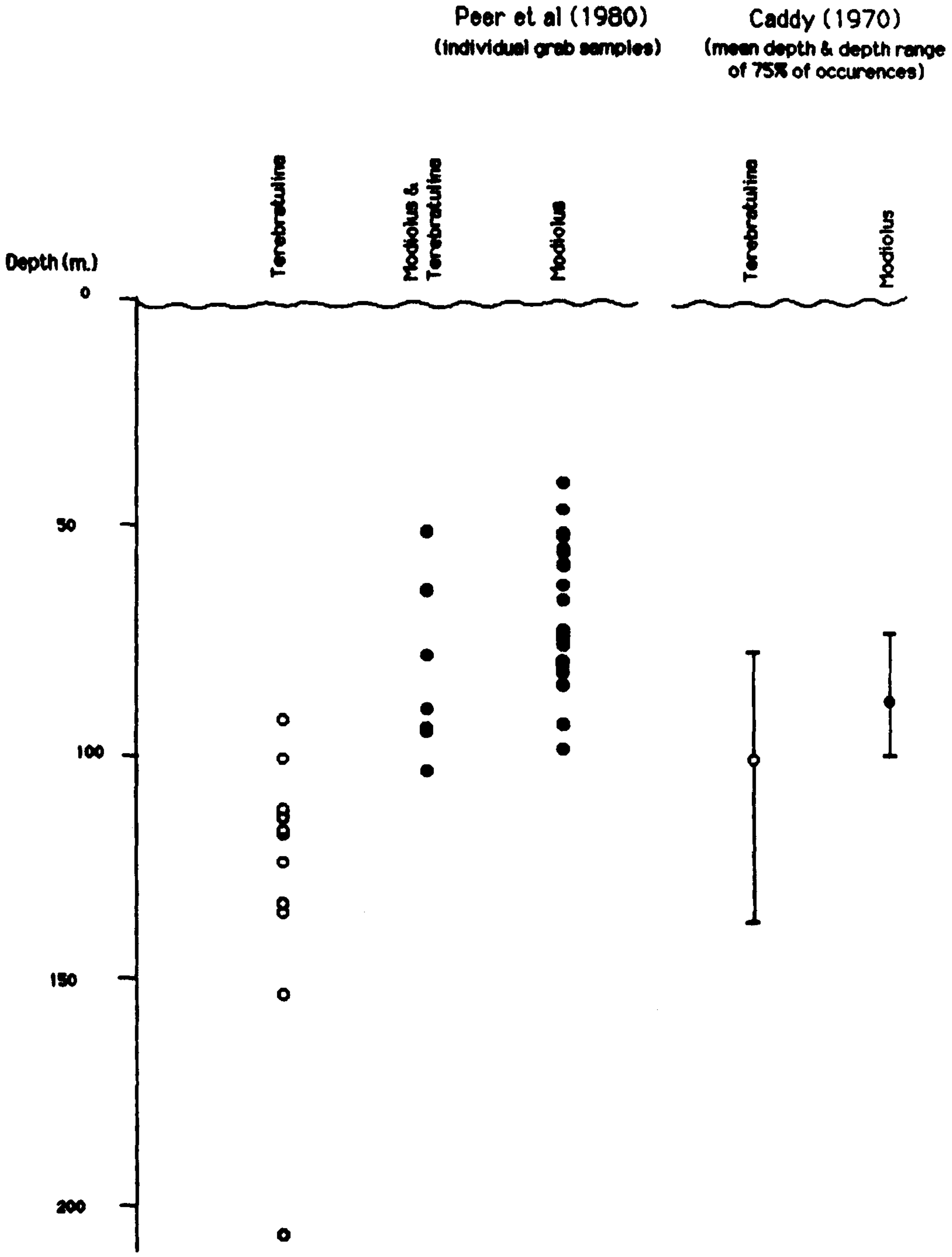
Associations of *Terebratulina*, *Crania* and *Modiolus modiolus* have only been mentioned previously by Rowell (1960) and Curry (1982), both occurrences from the Firth of Lorn. Jones (1951) collected all three species from the ground within a fifteen mile radius of the Isle of Man. *Terebratulina retusa* was collected in eight and *Crania anomala* in seven of 17 grab samples of mixed coarse gravel, sand and shells in an area where the sea floor is predominately a coquinoid pavement, chiefly of *Glycimeris glycimeris*. Jones (1951: p.137) observes that in this area, "the brachiopods *Terebratula* (= *Terebratulina*) retusa and *Crania anomola* are locally common", as are the solitary coral *Paracyathus taxilianus*, the ophiuroids *Ophiothrix fragilis* and *Ophiocomina nigra* and the bivalve *Lima loscombi*. Most of the shells are bored by the sponge *Cliona celata*. Jones (1951) does not mention an association with *M. modiolus*, but it is plain that *T.retusa* and *M. modiolus* must overlap in at least one grab sample. *T. retusa* is also found in one sample of muddy sand with some gravel and broken shells, although *C.anomala* is absent.

Rowell (1960) collected both *Crania anomala* and *T. retusa* west of Crinan at depths between 20 and 35 m attached to the concave inner surface of scallop valves and a number of ophiuroids, several of which Rowell (1960: p. 36) notes "are common in the so called *Modiolus* epifauna".

Neither *Crania anomala* nor *T. retusa* occur in the western Atlantic, but associations between articulate brachiopods and *M. modiolus* are widespread although uncommon (see Introduction and Fig. 1). Caddy (1970) conducted 196 dredge hauls in the Lower Bay of Funday in depths from 55 - 146 m, listing the mean depth of all species. *M. modiolus* occurred in 88 hauls, with 75% of the samples occuring in hauls made between 73 and 110 m, with a mean depth of 82.0 m. *T. septentrionalis* occurred in 91 samples, the bulk of the collections (92%) being from hauls between 73 and 146 m with a mean depth of 100.7 m (Fig. I 2.10). Peer *et al.* (1980) provide a more detailed breakdown of a survey of a similar region by grab sample. *M. modiolus* occurred in 30 of 96 samples at a mean depth of 71.0 m and *T. septentrionalis* in 19 of 96 samples with a mean depth of 110.8 m (Fig I 2.10). The distribution appears to be partly depth related, the absence of *T. septentrionalis* associated with the shallow water *M. modiolus* (which cannot be substrate limited) and conversely the failure of *M. modiolus* to penetrate into deep water is an interesting phenomenon worthy of further investigation.

Figure I 2.10

Comparative depth range of M. modiolus and T septentrionalis in the Bay of Funday; data from Caddy (1970) and Peer et al. (1980).



# I 3 PRODUCTION ESTIMATES

## I 3.1 INTRODUCTION

In most palaeocommunity reconstructions, data on numerical abundance of the fossil assemblages is used to describe the original community or preserved component thereof (Stanton & Dodd, 1976; Hoffman *et al.*, 1978; Stanton & Nelson 1980, etc.). The inherent difficulty in reconstructing even the preservable component of the original community makes utilization of all useful data desirable (eg. Parker, 1976; Stanton, 1976; Adamczak, 1981). Stanton *et al.*, (1981) Staff *et al.* (1985) and Powell & Stanton, (1985).

This section describes the secondary production of the major carbonate producing species in the Firth of Lorn. No attempts have yet been made to estimate the production of carbonate in a *Modiolus* community, although George & Warwick (1985) have described the production in a community, which although the *Modiolus* itself is inconspicous because of its small size, might be classically defined such (*sensu* Thorson 1957). Wildish & Peer (1983) have estimated production of the benthic macrofauna in the lower reaches of the Bay of Funday, where *Modiolus modiolus* dominates the production and the genera *Astarte* and *Terebratulina* make a significant contribution to the total estimated production.

## I 3.2 METHODS

### I 3.2.1 Biomass Estimates

Regression analysis furnished inverse logarithmic relationships of length (as an index of size) against tissue ash free dry weight (tAFDW) and shell dry weight (sDW) of fresh material (Table I 3.1). These relationships were used to derive estimates of tissue AFDW and shell weight of formalin preserved material of known length. Although these estimates are crude in comparison with individual weight determinations, they circumvent the problems associated with unpredictable variations in weight of ethanol or formalin preserved material, resulting from tissue leakage and sequestering of salts (Mills *et al.*, 1981). The failure to account for erratic seasonal variations in tissue AFDW, (*M. modious* from the west coast of Scotland vary by more than 50%; Comely 1978) alters production estimates, but allows direct comparisons of samples collected at different times.

Tissue AFDW is used as a measure of production for the molluscan bivalves (c.f. Moore, 1972; George & Warwick, 1985), the organic material present in the shell (mainly in the form of inter crystalline conchiolin and the external periostracum) is ignored, although it may account for a substantial proportion of AFDW, because it cannot be metabolized. Crude conversion factors are supplied in Table I 3.2.

### I 3.2.2 Production Estimates

Growth production of marine benthic invertebrates requires knowledge of standing biomass (typically measured per $m^2$), growth rate, recruitment and mortality. Production estimates are relatively straightforward, assuming that age classes are easily seperable, however this is not true of any of the four major carbonate producers in the *Modiolus* community, and the methods used to distinguish the cohorts for each species are discussed in the relevant sections. The standing biomass of individual year classes of *M. modiolus* and *T. retusa* are estimated as seasonal averages, those of *O. fragilis* and *A. sulcata* as the densities from the August 1983 samples.

Growth production was calculated as follows;

The mean annual weight increments where calculated from the weight change from one cohort limit to the next :-

(I 3.i) $$\text{Increment} = (w2 - w1)$$

Production was estimated by multiplying the mean number in each cohort by the mean weight increment.

(I 3.ii) $$\text{Production} = N(\text{mean in cohort}) \times \text{Increment}$$

A more precise production estimate (method 1 of Crisp, 1961) was applicable only to the 0-year class of *T. retusa*.

Robertson (1979) obtained crude inverse logarithmic relationships between lifespan and the ratio of production to biomass (P/B ratio) for benthic marine

## TABLE I 3.1 a

Linear regression data of members of the *Modiolus* brachiopod association relating weights (W, mg) to shell length (L. mm); n = number of determinations; r = coefficient of correlation; Data fitted to the equation log W = b.log L − a

| | a | b | n | r | SE a | SE b |
|---|---|---|---|---|---|---|
| *Astarte sulcata* | 1.482 | 2.455 | 42 | 0.926 | 0.854 | 0.630 |
| *Abra alba* | 2.241 | 3.127 | 43 | 0.948 | 0.641 | 0.212 |
| *Modiolus modiolus* | 3.122 | 3.335 | 39 | 0.896 | 0.518 | 0.271 |
| *Ophiothrix fragilis* | 0.14 | 2.659 | 6 | 0.993 | 0.168 | 0.143 |
| Curry & Ansell (1986) | | | | | | |
| *Terebratulina retusa* | 1.596 | 2.504 | 9 | 0.981 | | |
| *Crania anomala* | 1.288 | 2.355 | 9 | 0.907 | | |
| George & Warwick (1985) | | | | | | |
| *Parvicardium ovale* | 2.272 | 0.863 | | 0.90 | | |
| *Modiolus modiolus* | 0.986 | 1.632 | | 0.96 | | |
| *Hiatella arctica* | 1.246 | 1.630 | | 0.91 | | |
| *Ophiothrix fragilis* | 0.66 | 2.847 | | 0.99 | | |
| Schafer *et al.* (1985) | | | | | | |
| *Astarte elliptica* | 2.563 | 3.126 | 36 | 0.995 | | |

## TABLE I 3.1 b

Linear regression relating weights (SW, mg) to shell length:(as above)

| | a | b | n | r | SE a | SE b |
|---|---|---|---|---|---|---|
| *Terebratulina retusa* | 0.869 | 2.750 | 271 | 0.959 | 0.054 | 0.049 |
| *Abra alba* | 2.077 | 3.464 | 43 | 0.983 | 0.101 | 0.042 |
| *Modiolus modiolus* | 1.039 | 2.780 | 252 | 0.977 | 0.065 | 0.037 |
| *Astarte sulcata* | 0.605 | 2.964 | 47 | 0.987 | 0.093 | 0.070 |
| Schafer *et al.* (1985) | | | | | | |
| *Astarte elliptica* | 0.799 | 2.974 | 49 | 0.998 | | |

## TABLE I.3.2

Comparative contributions of organic and inorganic fractions, with the smaller value (B) as a percentage of the larger (upper) value (A).
Inclusion of data from the Firth of Lorn to data provided by Moore (1972,^), Schaefer *et. al.* (1985,+) and (Curry & Ansell (1986,*).

| A | sDW | sAFDW | sAFDW | WW | WW | A |
|---|---|---|---|---|---|---|
| B | tAFDW | sDW | aAFDW | sDW | tAFDW | B |
| BRACHIOPODA | | | | | | |
| *Terebratulina retusa** | 3.4 | 3.1 | 48.1 | – | 3.5 | |
| *Crania anomala** | 6.3 | 4.4 | 41.0 | – | – | |
| ECHINODERMATA | | | | | | |
| *Ophionepthys limicola^* | 7.7 | – | – | – | – | |
| *Amphipholis coniortdes^* | 8.0 | – | – | – | – | |
| *Moria atropos^* | 4.5 | – | – | – | – | |
| MOLLUSCA | | | | | | |
| *Tagelus divisus^* | 16.8 | – | – | – | – | |
| *Donax vittatus** | 14.8 | 2.8 | 16.0 | – | – | |
| *Mytilus edulis** | 11.7 | NA | 30.1 | – | – | |
| *Modiolus modiolus* | 9.2 | 4.9 | 33.3 | 49.8 | 5.0 | |
| *Tellina martinicensis^* | 4.7 | – | – | – | – | |
| *Chione cancellata^* | 7.2 | – | – | – | – | |
| *Astarte elliptica+* | 2.6 | 2.9 | 52.5 | – | – | |
| *Astarte sulcata* | 1.4 | 2.1 | 53.9 | 81.0 | 1.0 | |

*sDW* = shell dry weight; *tAFDW* = tissue ash free dry weigh; *sAFDW = shell ash free dry weight; aAFDW* = total ash free dry weight; *WW* = total formalin preserved wet weight.

invertebrates. In those instances where no published P/B ratios exist and where it was not possible to identify year classes, production was estimated using the equations of Robertson (1979);

(I 3.iii) $\log P/B = 0.062065 + -0.78261.\log Ls$ (bivalves)

(I 3.iv) $\log P/B = 0.069732 + -0.70860.\log Ls$ (others)

where *Ls* is lifespan (in years).

## I 3.3 RESULTS and DISCUSSION

### I 3.3.1 *Modiolus modiolus*

Growth Rate

Use was made of the annual growth lines on the outside of the shells to age the animals. Although early growth checks are easy to visualize, growth lines become more difficult to determine as a result of interference rings and crowding towards the anterior of the shell. Removal of the periostracum (by soaking in 4% sodium hypochlorite for seven days) and the use of transmitted light aided in the visualization and measurement of annual growth lines. The distance of growth checks from the umbo was estimated using dividers and the seperation of the dividers was measured with dial calipers.

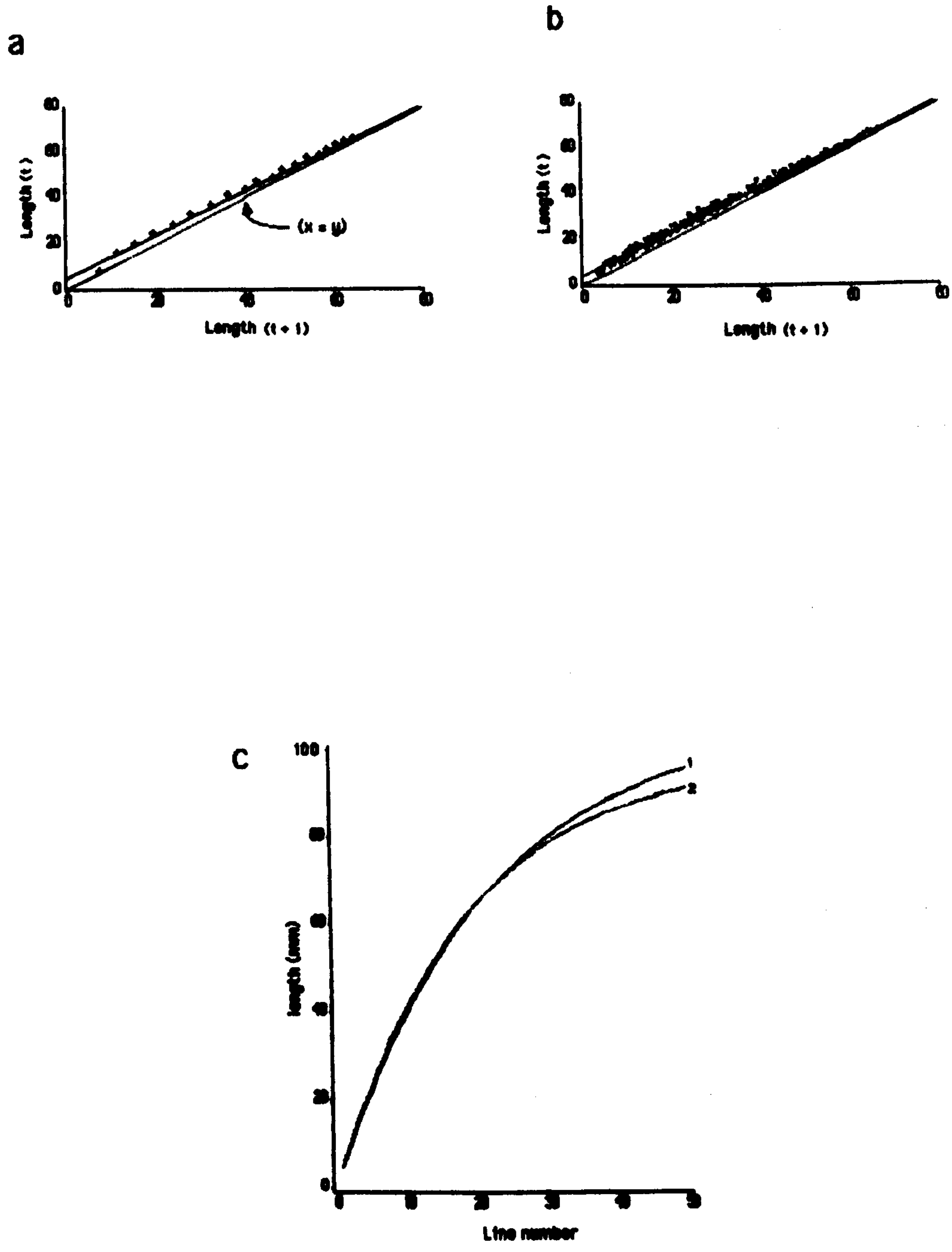
Checks were made on the completeness of the data sets by plotting both 'growth curves' and Ford-Walford plots for all 29 animals (Fig. I 3.1a & b). Oversteep portions of a growth curve and inflexions in otherwise straight lined Ford-Walford plots were believed to indicate missed growth lines. Eight such instances were noted and in each case an additional, Not Available (NA) data value was inserted between the relevant data points, removing them from the data analysis.

A Ford-Walford plot was obtained for the whole data set (Fig. I 3.1b), by plotting the length (in mm) at a particular age *Lt* against length a year later *L(t + 1)* on the ordinate. The plot provides a straight line for the decaying part of the growth curve, for the 29 *M. modiolus* from the Firth of Lorn, fitting the equation;

(I 3.v) $L(t+1) = 4.79(+/- 0.197) + 0.955Lt (+/- 0.006)$ $r = 0.996$

Figure I 3.1

Growth rate estimates for M. modiolus from the Firth of Lorn
a) Ford Walford plot derived from growth curve of Comley (1978; Fig. 7)
b) Ford Walford plot derived from growth ring analysis (29 animals)
c) Growth curves fiting functions derived from (a) & (b)
1 $L_{(t+1)} = 4.79 + 0.955\,L_{(t)}$
2 $L_{(t+1)} = 5.10 + 0.948\,L_{(t)}$



A Ford–Walford plot of the disassembled growth curve provided by Comely (1978; Fig. 7) for *M. modiolus* from the Firth of Lorn (Fig. I 3.1a) yielded a similar relationship;

(I 3.vi) $L(t+1) = 5.10(+/- 0.320) + 0.948Lt (+/- 0.007)$ $r = 0.996$

Yearly growth increments were calculated using the growth model outlined as equation I 3.v (Fig. I 3.1c). The early rate of growth of this model is slower than I 3.vi, partly because of the recognition in this study of an additional growth line, before the first ring identified by Comely (1978: Fig. 7) which improves the fit of the early part of the Ford Walford plot (c.f. Fig. I 3.1 a & b). This line which was successfully observed in 25 of the 29 animals examined is less obvious than the '7 mm.' line, as the line itself is correspondingly small and because the umbo region is typically abraded and eroded.

The two Ford Walford plots provide crude estimations of the age of the largest *M. modiolus* collected from the Firth of Lorn, an animal 93.1 mm long being aged 43 or 50 years from the respective equations. Although differences in the estimated rates of growth are very small (Fig. I 3.1c) and are within the range expected from natural populations, the mean size of the adults in the Firth of Lorn population published by Comely (1978; Fig. 5) appears to be correspondingly smaller.

The more conservative (ie younger) estimates of age derived from equation I 3.v, were used to describe the population, giving a estimated lifespan for most animals of 40 years. Although the growth rate is similar to the caged *M. modiolus* of Seed & Brown (1978), the lifespan estimate is much longer than those of Comely (1978; Cregan 20 years, Ardyne 35 years) and Seed & Brown (1978, 30 years), also derived from growth ring analysis. The maximum size (length 93.1 mm, grab samples, 97.1 mm largest of all) of *M. modiolus* are smaller than the shallow water animals recovered by Wiborg (1946), Comely (1978), Seed & Brown (1978) and Lees & Driskell (1981). Stunting in deep water populations has also been noted by Caddy (1970: 5) from the Bay of Funday (mean depth of populations 90 m), "most (*M. modiolus*) were stunted specimens (less than 3" in length)". Similar stunting has been observed in one of two populations collected by Lees & Driskell (1981) from the shallow sub-tidal of Knoll Head, (Alaskan Shelf). Comely (1978) in a comparison of the Firth of Lorn *M. modiolus* with shallow water populations, notes that in deep water the shells are well shaped, without any evidence of boring organisms and that relative shell volumes were 15–20% smaller, the latter observation being supported by the separation of points of *Modiolus* from Porth Appin, from those from the Firth of Lorn and Sound of Mull, in a log/log plot of tissue AFDW aganist length (Fig. I 3.2b). Variation in growth rate is apparent within the Firth of Lorn population, eg. an animal 62.3 cm long was observed to be extensively bio-eroded by *Cliona* sp. and to have the same squared off posterior margin with deep lip observed from intertidal *Modiolus* collected from Port Appin by Comely (1978).

Population structure

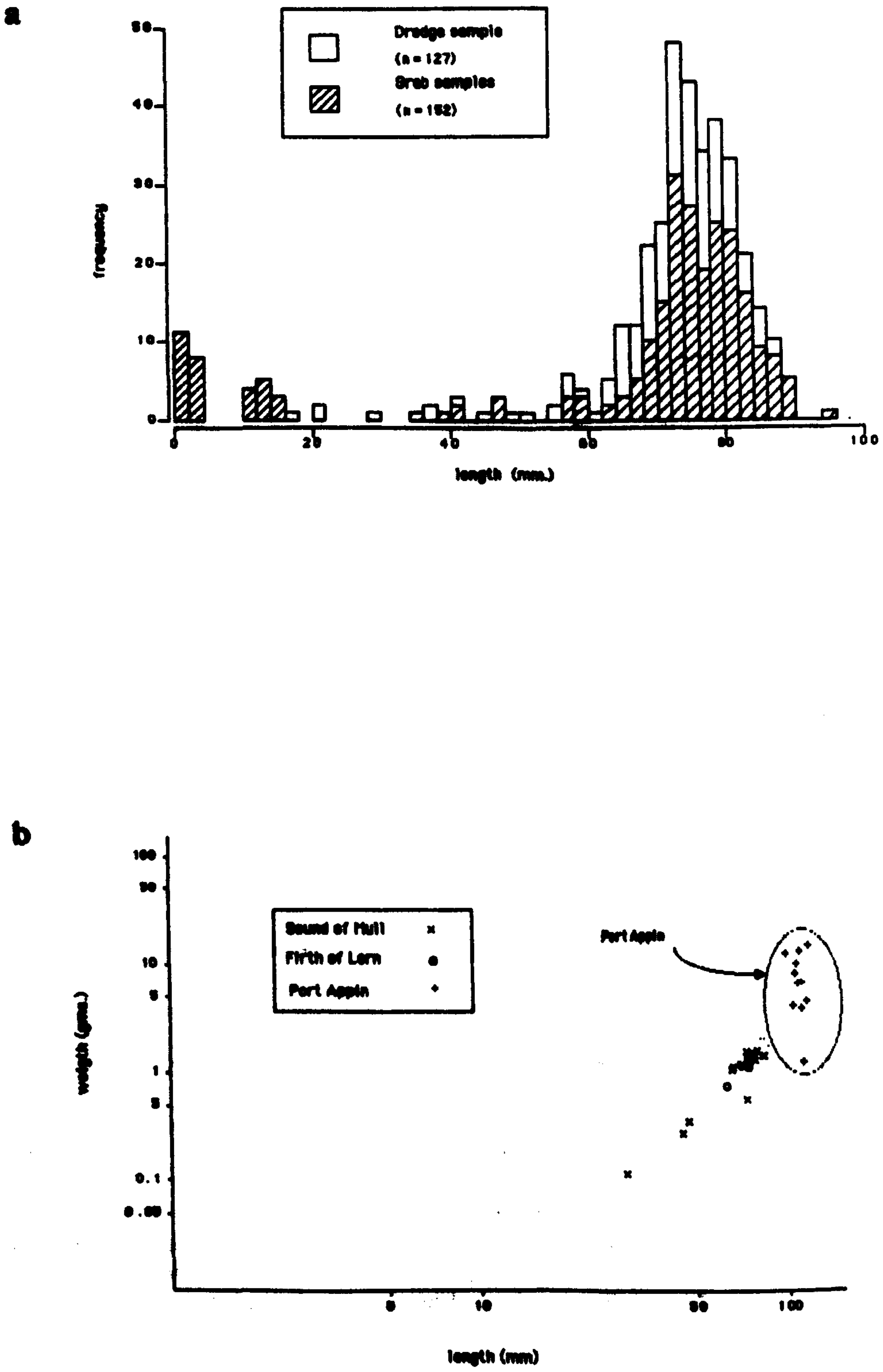
The population structure of *M. modiolus* from the Firth of Lorn has previously been described by Comely (1978; Fig. 5). Population structures were obtained during this study both from a single dredge sample and as a composite of all the grab samples (for details see Table I 2.1). The maximum observed lengths of *M. modiolus* from the two studies were 86.0 and 93.1 mm respectively, with estimated ages from equation 3.v of 36 and 46 years. These two length-frequency distributions are in close agreement with each other (Fig. I 3.2a), but lack the juvenile peak and hence the marked bimodality of the distribution published by Comely (1978). The absence of a major juvenile peak may be partly the result of attributing *Modiolus* to *M. phaseolinus* when the dentition, (the most reliable taxonomic character, Tebble, 1966) was damaged.

Within the Firth of Lorn, *M. phaseolinus* is widely distributed and at other stations as well as in this deep water community, *M. phaseolinus* is typically more numerous (Table I 3.3). Unusually it is only at station 25 (the

Figure I 3.2

(a) Composite size frequency histogram of M. modiolus from Firth of Lorn single dredge sample (10/1/84), and all grab samples (for details see Table I 2.1).

(b) Comparison of relative tissue AFDW in M. modiolus collected from from the Firth of Lorn (180 m.), Sound of Mull (105 m.) & Port Appin (10 m).



station closest to this survey) that Comely observes *M. modiolus* to be more numerous.

TABLE I 3.3
Associations of *M. modiolus* and *M. phaseolinus*
(* = Data supplied by C. Comely)

| | | *M. modiolus* | | *M. phaseolinus* | | |
|---|---|---|---|---|---|---|
| Station | Depth(m) | No. | Wet Wt. | No. | Wet Wt. | Ratio |
| | | | Firth of Lorn | | | |
| 1962(1)* | 56 | 7 | 80.2 | 247 | 5.5 | 1:35 |
| 1962(20)* | 80 | 37 | 512.35 | 466 | ND | 1:12.6 |
| 1962(25)* | 160 | 27 | 476.6 | 11 | 0.6 | 2.4:1 |
| 1983 | 180 | 200 | 2475.0 | 575 | 2.3 | 1:2.9 |
| | | | Creran | | | |
| 1962(1)* | – | 137 | 3.15 | 1325 | 17.7 | 1:9.7 |
| 1961(2)* | – | 48 | 28.0 | 184 | 6.7 | 1:3.8 |
| 1962(2)* | – | 44 | 27.5 | 487 | 12.9 | 1:11 |
| 1962(3)* | – | 9 | 2.0 | 83 | 2.8 | 1:9.2 |

Similar unimodal and bimodal population structures have been observed in *M. modiolus* from a wide range of habitats (Wiborg, 1946; Rowell, 1967; Comely, 1978; Brown & Seed, 1977; Seed & Brown, 1978; Lees & Driskell, 1981). The absence of clear modal peaks of juveniles is believed to be a result of contínous spawning and intense predation of juveniles (Seed & Brown, 1977). An absence of seasonal breeding in *M. modiolus* has been observed by Seed & Brown (1975) in subtidal *M. modiolus* from Strangford Lough (N. Ireland), and Comely (1978) from the west coast of Scotland. A similar explanation was forwarded for the bimodal population structure of *Modiolus demissus* Dillwyn from a Georgia Salt Marsh (Kuenzler, 1961), where mussels less than 200 mg. contributed 27% of the total population but only 1.8% of the biomass. The only strikingly different population structure is from a *Sabellaria* reef in the Bristol Channel (George & Warwick, 1985), where *M. modiolus* reach a maximum size of 12.3 mm (density 245/$m^2$). The authors do not discuss the reasons why this should be so, but a large number of potential asteroid and crustacean predators are present.

A simple predation experiment was conducted to determine if the stunted *M. modiolus* were able to achieve a size refuge in the Firth of Lorn.

The experiments were conducted in three large, lidded tanks with freshly circulating seawater. A coarse (50 mm mesh) plastic netting was laid on top of pebbles in the base of each tank which was then filled to a depth of approximately 30 mm with a mixture of sand from the low shore in Dunstaffnage Bay and a commercial quartz gravel. *M. modiolus* collected by dredge sample were crudely scrubbed to remove epifauna, measured and labelled with a water insoluble marker pen, at all times attempting to minimise stress to the animals. Twenty *M. modiolus* were placed in each of two tanks and a control group of 10 were placed in the third. The *M. modiolus* were embedded in the sediment, to a depth of approximately 25 mm at a low angle and allowed to establish themselves. After 15 days all the animals were checked to ensure that they were alive and firmly attached by the byssus to a solid substrate, either the stones in the base of the tank, the tank itself or the embedded plastic mesh. A single *Asterias* was then placed in each of the two experimental tanks, which were checked at 54 days and 121 days after the initiation of the experiment, but otherwise left undisturbed. No replacement of consumed individuals was made because the experiment was designed to test if *M. modiolus* in the Firth of Lorn had a size refuge from such predators, rather than any size preference exerted by *Asterias rubens*.

After 54 days seven of the twenty *M. modiolus* had been consumed in tank A, and 9 in tank B, and after a further 67 days all the *M. modiolus* had been consumed, giving a maximum predation rate of 0.19 and a minimum of 0.13 *Modiolus /Asterias/*day (Table I 3.4). These rates are in line with the estimates of Lees & Driskell (1981) for a variety of Canadian asteroids (0.025 *Modiolus/Pycnopodia/*day, 0.205 *Modiolus/ Evasterias/*day and 0.046 *Modiolus/Orthasterias/*day). The significance of the result lies in the observation that *M. modiolus* (under these conditions) have no size refuge from predation by moderately large *Asterias*.

Field observations by Lees & Driskell (1981) reached a similar conclusion, asteroids consumed approximately 20% of the *M. modiolus* population per year, and although 70% of the prey items were below the mean size of the population, asteroids were capable of taking all sizes of *Modiolus*.

TABLE I 3.4
Size selection by *Asterias rubens* preying on *M. modiolus*

| | | | size range of consumed *M. modiolus* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| tank | *Asterias* | | initial | | | | consumed over 54 days | | | |
| | R (mm) | N | Min | Max | Mean | SD | Min | Max | Mean | SD |
| A | 140 | 20 | 60.8 | 97.1 | 75.9 | 7.68 | 66.8 | 84.9 | 73.8 | 6.48 |
| B | 140 | 20 | 58.9 | 91.8 | 77.0 | 7.42 | 66.3 | 83.1 | 73.7 | 5.58 |
| C | - | 10 | 70.5 | 89.8 | 74.3 | 4.86 | All survived | | | |

Roberts (1975) conducted choice experiments with *Modiolus modiolus* and *Mytilus* edulis on both *Asterias rubens* and *Crassoaster (Solaster) papposus*, however the large specimens of both species died before showing any feeding behaviour. Small *Asterias* (R approximately 115 mm) preferred *M. modiolus*, feeding on animals in the range 15–49 mm at a rate of between 0.15 and 0.55 *M. modiolus* per day per animal. Comely (1978) however, observes that at one strong current Scottish site (where the size of predators is limited by the hydrodynamic regime and the largest *Asterias* were approximately R 70 mm) none of the heavy settlement of *M. edulis* survived beyond 35 mm. Comely therefore suggests that *Modiolus* are at a selective advantage at this site. Wright & Francis (1984) has demonstrated experimentally that the periostracal spines (retained by *M. modiolus* throughout life, albeit sparsely) have survival value in inhibiting attachment by the pedatory whelk *Thais lapillus*.

In an experimental manipulation Lees & Driskell (1981) observed that *M. modiolus* with reduced epifauna and shell debris were consumed over the period of a year by asteroids, and it is reasonable to suggest that a diverse epifauna must serve a similar function to the periostracal hairs. In this context it is interesting to speculate on the survival value of the sediment particles which adhere to the periostracum of *M. modiolus*, particularily of juveniles (Tebble, 1966). Nielsen (1975) and Lees & Driskell (1981) have suggested that the recessed habitat also has considerable survival value.

In the light of these considerations the predation experiments, although they included a degree of burial and attachment to solid substrates could not mimic the close apposition, diverse living epifauna and deep burial of living *M. modiolus* clumps in the Firth of Lorn and therefore may overstate the potential of asteroids to feed on large *M. modiolus*.

It is also instructive to compare the population structures of *M. modiolus* and *M. phaseolinus*; although the latter species is twice as abundant in the Firth of Lorn, the population structure is strongly right-skewed. *M. phaseolinus* do not show the bimodality of *M. modiolus* possibly because the maximum size of the latter species (19 mm) is too small to achieve a size refuge (Fig. I 2.8).

## Biomass

The estimated density of *M. modiolus* in the Firth of Lorn (125/m$^2$), although much higher than the figures published by Comely (1978) for Scottish shallow water populations, is similar to Comely's unpublished data from the area (90/m$^2$; Appendix III), and estimated densities in Strangford Lough (170/m$^2$; Roberts, 1975), Faxe Bay (max 90/m$^2$; Spark, 1935) and the Bay of Funday (Peer *et al.*, 1980). However, the standing biomass in shallow water communities is probably much greater because the *Modiolus* are not stunted. Some of the maximum density estimates (eg. Spark, 1935, Faroes, 330/m$^2$; Peer *et al.* 1980, station 61, 500/m$^2$; Lees & Driskell 1981, Jakolof Bay, 672/m$^2$) would require almost total cover of the sea floor by *M. modiolus*.

The size range over which regressions for tissue AFDW was based was unavoidably biased towards larger animals, and therefore the biomass of smaller *M. modiolus* (length < 13.73 mm) was recalculated using the regression for small *M. modiolus* provided by George & Warwick (1985). The total for both estimated biomass and production were increased, the former by 0.01% and the latter by 0.1%, reflecting the insignificant contribution which these animals make to standing biomass in the study area.

TABLE I 3.5
Summary of production for *Modiolus modiolus*
(as this table combines cohorts, mean annual increment figures are not supplied)

Tissue Ash Free Dry Weight

| Year Classes | No. in cohorts | Initial wt.(mg) | Final wt.(mg) | mean increment | P (g/m$^2$) | B (g/m$^2$) |
|---|---|---|---|---|---|---|
| 0–9+ | 14 | 0.0 | 156.5 | – | 0.25 | 0.84 |
| 10–19+ | 25.3 | 156.5 | 882.5 | – | 1.75 | 14.02 |
| 20–29+ | 99.1 | 882.5 | 1657.2 | – | 9.55 | 116.93 |
| 30–39+ | 17.9 | 1657.2 | 2446.0 | – | 1.45 | 45.30 |
| 40–49+ | 2.5 | 2446.0 | 3006.9 | – | 0.16 | 6.96 |
|  |  |  |  |  | 13.143 | 200.10 |

Carbonate

| Year Classes | No. in cohorts | Initial wt.(mg) | Final wt.(mg) | mean increment | P (g/m$^2$) | B (g/m$^2$) |
|---|---|---|---|---|---|---|
| 0–9+ | 14 | 0.0 | 2476.2 | – | 3.43 | 14.50 |
| 10–19+ | 25.3 | 2476.2 | 9872.9 | – | 18.49 | 178.10 |
| 20–29+ | 99.1 | 9872.9 | 17703.3 | – | 70.62 | 1486.46 |
| 30–39+ | 17.9 | 17703.3 | 23887.9 | – | 12.36 | 471.80 |
| 40–49+ | 2.5 | 23887.9 | 29090.5 | – | 1.27 | 68.17 |
|  |  |  |  |  | 126.66 | 2219.06 |

*M. modiolus* dominates the community, the estimated standing biomass of 200 g/m$^2$ accounts for 87.8% of the total biomass and the standing calcimass 2219 g/m$^2$ 93.5% of the living carbonate in the community (Table I 3.5). Productivity is relatively low because the population contains few juveniles and the bulk of the animals are within an estimated age range of 20 to 26 years. The estimated P/B ratio (0.05) is the lowest published P/B ratio for a marine bivalve, indeed the only equivalent ratio, is the recalculated figure of Banse & Mosher (1980) for the African elephant (*Loxodonta africanus*) and consequently *M. modiolus* accounts for only 28% of the tissue AFDW production and 37.8% of the carbonate production. Production is much lower than the estimated wet tissue weight turnover of 2.0 kg/m$^2$/yr proposed by Lees & Driskall (1981), for *M. modiolus* in Katemak Bay on the basis of cropping rates of approximately 20%/yr. The predicted P/B ratio of *Modiolus desmissus* from a Georgia Salt Marsh (0.28) is, however, relatively low even though estimated growth rate was greater and the lifespan shorter (Kuenzler, 1961).

The production estimates, based on tissue ash free dry weight ignore contributions from the shell and byssus. Organic material within the shell accounted for 10.6% of the shell dry weight of *Modiolus desmissus* and two-thirds of the total AFDW (Kuenzler, 1961). A determination of the organic fraction within the shells of *M. modiolus* was conducted on 10 formalin pre-served animals. A smaller proportion of the shell dry weight (4.87%; SD = 1.31) was lost on ignition, accouning for only 33.3% of the total AFDW (see Table I 3.2 for comparative figures). This additional organic fraction was not included in these biomass and production figures for *M. modiolus*, as it is usually ignored in productivity estimates. The disparity in the shell organic fraction between the two *Modiolus* species is probably associated with absence of periostracum from much of the shell of *M. modiolus*. Byssus which was also ignored in this study accounted for between 30 and 60% of total weight in the study conducted by Comely (1978), the value being highest in current swept areas, in the study by Kuenzler (1961) byssus was equivalent to approximately 42% of AFDW.

*Ophiothrix fragilis*

Growth rate

Gorzula (1977) using a modification of the technique proposed by Jensen (1969), who observed rings from the vertebral ossicles of *Ophiocomina nigra* and produced an estimated growth rate of the disc to be 2.1 mm/year for brittle stars between the fourth and tenth years. Wintzell (1918) and Thomsen & Vorren (1986) illustrate what appeared to be similar growth rings in ophiuroid arm vertebrae, *Ophiothrix fragilis* being illustrated by Wintzell (1918) with eight such rings. The application of the technique used by Gorzula (1977) failed to furnish definable growth lines and in the absence of seasonal samples for this animal, estimates of growth rate for this species are based on published work.

Taylor (1958) demonstrated that O. *fragilis* from the Irish Sea reached a

Figure I 3.3

(a) Composite size frequency histogram of Ophiothrix fragilis from Firth of Lorn (coll. 23/8/83).
(b) Comparison of (1) regression derived from George & Warwick (1985) & (2) relationship derived from O. fragilis collected from Port Appin (+).

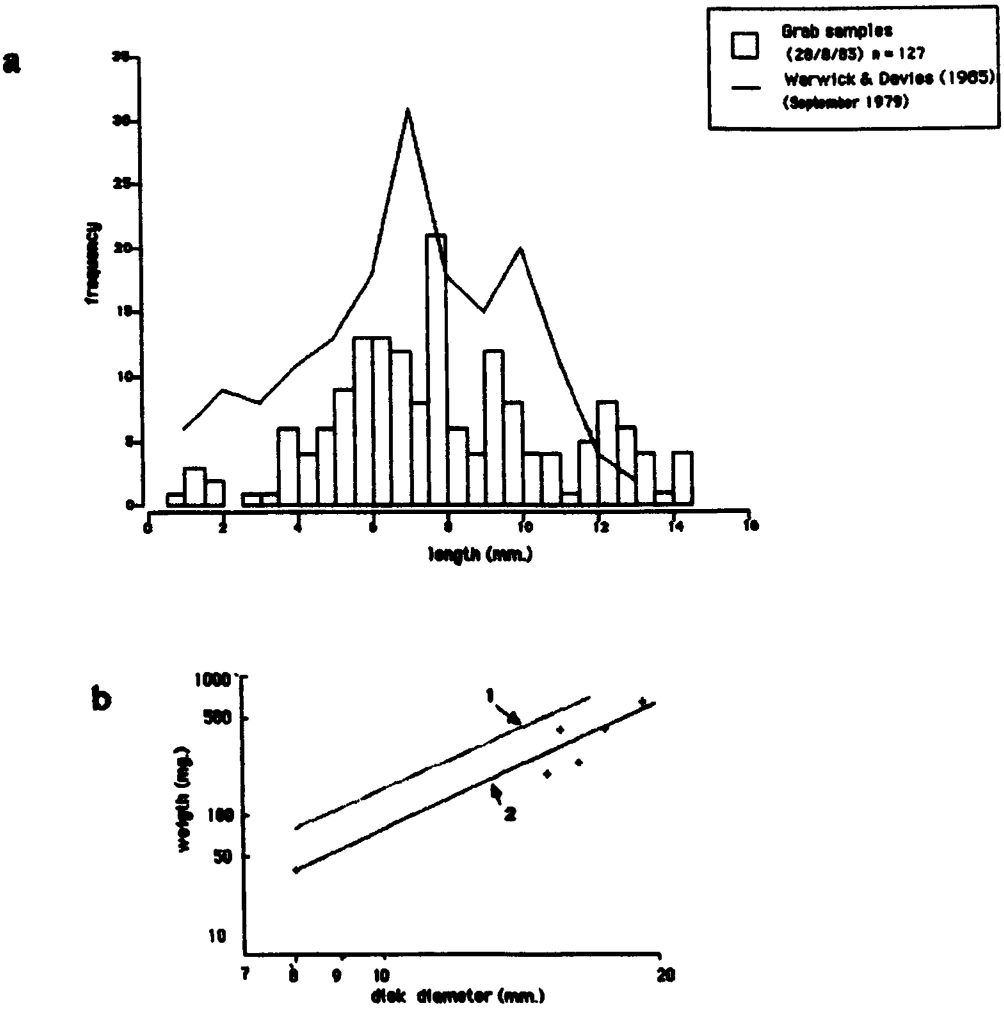
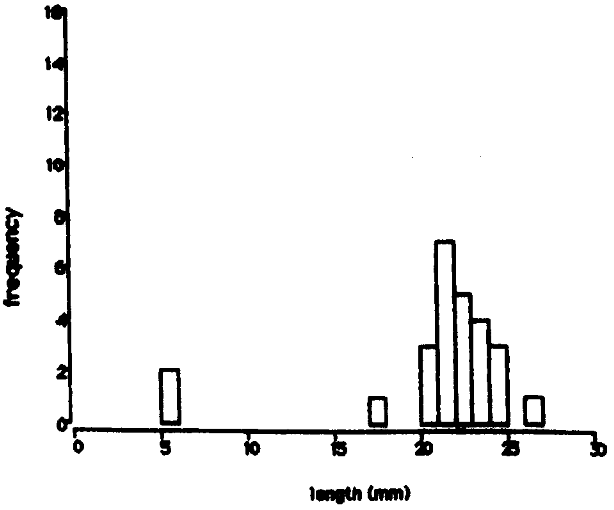


**Figure I 3.4**

Size frequency distribution of Astarte sulcata in the Firth of Lorn



disc diameter of approximately 14 mm within two years, most of the two year olds dying off after spawning (cited in Gorzula, 1977). Allain (1974) deduced that the 8–10 mm group was the 2+ year class and his work is in close agreement with the size of the 2+ year class estimated by George & Warwick (1985) from a shallow water population in the Bristol Channel (5–10 mm and 7–10 mm).

### Population structure

The length frequency histogram obtained for the August 28th 1983 collection (Fig. I 3.3a) is in reasonably close agreement with the September collection of George & Warwick (1985; Fig. 1), with juveniles poorly represented. Similar agreement is seen in the May size frequency distributions of George & Warwick (1985; Fig. 1) and of Brun (1969; Fig. 6), although Warner (1971; Fig. 2) illustrates the dangers of attaching too much to such similarities. The presence of some juveniles (< 2 mm disc diameter) was a characteristic feature of all collections made by George & Warwick (1985). Adult *O. fragilis* in the Bristol Channel were heavy with gonads in May and July but juvenile *Ophiothrix* (> 2mm disc diameter) were found in samples throughout the year, peaking in November (George & Warwick, 1985). Allain (1974) reported recruitment off the Norman–Breton coast at any time between August and October.

### Biomass and production

*Ophiothrix* was present in large numbers in all dredge and grab samples in the Firth of Lorn, the estimated densities of 238/$m^2$ are similar to those of Comely (unpublished data) for station 25 (120/$m^2$) and Vevers (1956; 380/$m^2$) but well below the maximum densities estimated from the dense beds observed in shallow water (eg. Brun, 1969, 1904/$m^2$; Warner, 1971, 1864/$m^2$; George & Warwick, 1985, 838/$m^2$).

The lower densities reported from the Firth of Lorn, although partly accounted for by an absence of juveniles, may be an indication of reduced detrital input and/or reduced current speeds. It was noted that many of the *O. fragilis* in the *M. modiolus* facies were sitting on surfaces projecting up from the sediment water interface (to such an extent that they obscured *M. modolus* clumps in the video survey). Their positioning would enable the filtering arms to protrude further above the viscous sublayer (see section III 1.2.2 for description of current profiles).

Biomass was estimated from the relationship between disc diameter and AFDW of *O. fragilis* provided by George & Warwick (1985). The limits of the size classes of the September collection given by the same authors (0+ = 0–3 mm; 1+ = 3–8 mm; 2+ = 8–14 mm) were used to estimate production (Table I 3.6). The size ranges of the cohorts compare favourably with the May estimates provided by Brun (1969; 0+ = 0–3 mm; 1+ = 3–7 mm; 2+ = 7–16 mm). Tissue AFDW, plotted against disc diameter for six undamaged animals from Port Appin, fitted a regression line below, but parallel to, the function produced by George & Warwick (1985) (Fig. I 3.3b).

TABLE I 3.6
Summary of production for *Ophiothrix fragilis*

| Year Class | No. in cohorts | Total Ash Free Dry Weight<br>Initial wt.(mg) | Final wt.(mg) | mean increment | P (g/m²) | B (g/m²) |
|---|---|---|---|---|---|---|
| 0+ | 10 | 0.0 | 5.0 | 4.99 | .03 | 0.06 |
| 1+ | 131 | 5.0 | 81.5 | 76.5 | 7.04 | 3.91 |
| 2+ | 93 | 81.5 | 434.4 | 352.9 | 22.94 | 13.09 |

Annual production was estimated at 30 g/m² with a mean annual biomass of 17 g/m² giving the highest estimated P/B ratio of any organism in the community (1.8), a figure identical to the more credible P/B estimate derived by George & Warwick (1985) from seasonal samples. No wet weight conversion was made for this species.

A summary table of carbonate production is not given, as estimates of carbonate biomass and production were produced by multiplication of the AFDW estimate by a standard conversion figure (3.46 n = 15, SD 0.28), derived from a collection of undamaged shallow water ophiuroids from Port Appin (Fig. I 2.3c, site given in Fig. 1.1). This conversion figure is lower than the equivalent multiplication factor derived by Moore (1972) for two amphiuroids from a sub–littoral habitat in Florida bay (Table I 3.2).

The estimate was checked by dividing the weight of all recovered O. *fragilis* material (air-dried overnight) on a simple proportion basis (1 part AFDW : 3.46 parts carbonate) to provide an estimated biomass and calcimass. The total dry weight values are consistent, (standard deviation for seven samples, only 17% of the mean) in what, from the UWTV survey appears to be a somewhat heterogeneous community. The values estimated from this crude summation and division are, total AFDW 22.2 g/m², carbonate 77.6 g/m², (1.3 times the figures estimated from regessions on disc weights in each case.)

The estimated biomass is much lower than the estimates from the dense *Ophiothrix* beds (eg Brun 1969, wet wt 2800 g/m²; Warner 1971, 651 g/m²) but similar to the figure of 31.3 g/m²/yr obtained by George & Warwick (1985) for an epifaunal community in the Bristol Channel.

### I 3.3.3 *Terebratulina retusa*

#### Growth rate

Initially it was intended to use the growth curve of Curry (1982; Fig. 7d), however this had to be re-interpreted in the light of data obtained from population structures collected from seasonal grab samples, both are discussed in section 4.3.

#### Population structure

The population structure was very strongly left skewed (*sensu* Raup & Stanley, 1978) (Fig. I 4.2), which in association with a slow initial growth rate means that although *T. retusa* occurs in greater densities than any other carbonate producer in the Firth of Lorn, adults account for only 7% of the population but 90% of production and 88.5% of the biomass.

#### Biomass and Production

Biomass of the *T. retusa* was estimated from the size weight regression provided by Curry & Ansell (1986) produced for animals collected from the same locality. Cohorts were defined from the limits of each year group in the growth curve derived in section 4.4.

Production could only be accurately assessed for the first cohort, and variable growth rate makes even this difficult. Estimated production for 1+ animals is variable, because there is no readily distinguished cohort (Table I 3.7; Fig. I 4.2).

TABLE I 3.7

Summary of seasonal production of *Terebratulina retusa*

| Age (months) | No. of grabs | Density ($m^2$) | Mean wt (mg.) | Biomass (mg/$m^2$) | Growth increment | Elimination loss (mg/$m^2$) | P (mg2) |
|---|---|---|---|---|---|---|---|
| 0+ | 1 | 1260 | 0.0009 | 1.17 | 1.17 | – | 1.17 |
| 3+ | 1 | 3360 | 0.0015 | 4.92 | 2.02 | –2.52 | –0.5 |
| 6+ | 1 | 1710 | 0.0018 | 3.22 | 0.51 | 2.72 | 3.2 |
| 9+ | 7 | 341 | 0.0030 | 0.96 | 0.41 | 3.29 | 3.7 |
| Mean 0+ | | 1668 | 0.0015 | 2.56 | | | 7.6 |
| 12+ | 1 | 670 | 0.104 | 69.4 | 67.4 | –33.2 | 34.2 |
| 15+ | 1 | 760 | 0.094 | 71.4 | –7.6 | –8.9 | –16.5 |
| 18+ | 1 | 560 | 0.116 | 65.0 | 12.3 | 21.0 | 33.3 |
| 21+ | 7 | 350 | 0.09 | 31.6 | –9.1 | 21.63 | 12.5 |
| Mean 1+ | | 585 | 0.113 | 59.3 | | | 434.4 |

Total AFDW for individual *T. retusa* was estimated using the equation of Curry & Ansell (1986), giving a standing biomass of 2.1 g/$m^2$/yr, a mean annual production of 1.93 g/$m^2$/yr, and a P/B ratio of 0.81 (Table I 3.8), very similar to the estimated P/B ratio of 0.82 derived for an eight year old bivalve from the inverse logarithmic relationship of Robertson (1979; equation I 3.iii). The low P/B ratio reflects both the relatively slow growth rate and the poor ratio of AFDW to shell weight (Curry & Ansell, 1986) for this species. Carbonate biomass was estimated to be 21.4 g/$m^2$/yr. and carbonate production 8.1 g/$m^2$/yr giving a marginally higher P/B ratio of 0.38.

The 0.005 mg. estimate of shell weight for post-settlement animals (of length 0.318 mm) from the length/shell weight regression is relatively close to the empirical value of Stricker & Reed (1985) for *Terebratalia transversa* (Sowerby) 0.0017 mg. Such small differences in weight will make little difference to the overall biomass and production figures as animals less than 0.7 mm account for only 0.2% of the estimated calcimass and 0.4% of the production.

TABLE I 3.8
Summary of production for *Terebratulina retusa*

Ash free dry weight

| Year Class | No. in cohort | Initial wt.(mg) | Final wt.(mg) | annual increment | P (g/$m^2$) | B (g/$m^2$) |
|---|---|---|---|---|---|---|
| 0+ | 1668 | 0.0 | 0.0056 | 0.056 | 9.34 | 2.56 |
| 1+ | 585 | 0.056 | 0.748 | 0.743 | 434.0 | 59.35 |
| 2+ | 89.3 | 0.748 | 3.9 | 3.2 | 285.7 | 163.7 |
| 3+ | 45.0 | 3.9 | 8.7 | 4.8 | 213.7 | 259.9 |
| 4+ | 32.5 | 8.7 | 16.0 | 7.25 | 235.6 | 389.6 |
| 5+ | 26.8 | 16.0 | 26.1 | 10.1 | 270.5 | 531.9 |
| 6+ | 17.1 | 26.1 | 38.2 | 12.1 | 207.4 | 566.7 |
| 7+ | 2.5 | 38.2 | 53.2 | 15.0 | 37.5 | 103.8 |
| Total | | | | | 2077.6 | 1264.2 |
| | | | | | P/B | 0.81 |

Carbonate

| Year Class | No. in cohort | Initial wt.(mg) | Final wt.(mg) | annual increment | P (g/$m^2$) | B (g/$m^2$) |
|---|---|---|---|---|---|---|
| 0+ | 1668 | 0.0 | 0.051 | 0.051 | 0.085 | 0.021 |
| 1+ | 585 | 0.051 | 8.44 | 8.39 | 4.908 | 0.633 |
| 2+ | 89.3 | 8.4 | 48.5 | 40.1 | 3.580 | 1.945 |
| 3+ | 45.0 | 48.5 | 111.4 | 62.9 | 2.830 | 3.261 |
| 4+ | 32.5 | 111.4 | 210.7 | 99.3 | 3.227 | 5.073 |
| 5+ | 26.8 | 210.7 | 353.4 | 142.7 | 3.838 | 7.108 |
| 6+ | 17.1 | 353.4 | 528.0 | 174.5 | 2.983 | 7.773 |
| 7+ | 2.5 | 528.0 | 761.3 | 233.3 | 0.583 | 1.439 |
| Total | | | | | 22.03 | 27.2 |
| | | | | | P/B | 0.81 |

### I 3.3.4 *Astarte sulcata*

#### Growth Rate

There are no growth lines on the external shell of *Astarte sulcata*, which is heavily ornamented with concentric ribs. Attempts were made to age the shell from acetate peels of 20 embedded and etched valves. Features of the sectioned shell appeared to be related to ornamentation, and neither verified or countered the five year lifespan estimated by Wildish & Peer (1983) for this genus in the Bay of Funday. No studies on the growth rate or longevity of *Astarte* species have been reported in the literature. Arntz *et. al.* (1976) class *Astarte* as a 'long lived' bivalve and Jaeckel (1952) assumed a maximum age of more than two years. A P/B ratio was derived from equation I 3.iii using the estimated five year lifespan of Wildish and Peer (1983) for this genus.

Population structure

The population structure of living *Astarte sulcata* was strongly right skewed (Fig. I 3.4) unlike the sub-fossil material where the population was dominated by juveniles (Fig. II 2.4). This may indicate some degree of under-sampling of juveniles in the living community, perhaps because the very thick shells obscure the Rose Bengal stained living tissues.

Biomass and production

The estimated standing biomass of Astarte was only 1.6 g, but the tissue AFDW as a percentage of dry shell weight is one of the lowest reported, (1.4%; *cf.* 2.6% for *A. elliptica*, Schaefer *et al.*,1985; Table I 3.2) and consequently *A. sulcata* contributes 2.1% of the calcimass and 20.9% of the carbonate production (Table I 3.9).

No estimates of production by *Astarte* have been published, although three *Astarte* species (*A. elliptica*, *A. borealis* and *A. montagui*) comprise approximately 15% of the total biomass in Kiel Bay (Western Baltic) (Arntz, 1980; Weigelt, 1985).

I 3.3.5 Other Species

*Amphiura chiajei*

Standing biomass of this species was estimated by dividing the total dry weight of this species (2.35 g) into a tissue fraction and a carbonate fraction, using the ratios established for *Ophiothrix fragilis*. Tissue standing biomass was estimated to be 0.76 g/m$^2$ and carbonate 2.6 g/m$^2$. This ratio of tissue to carbonate (1:3.46) is slightly lower than estimates of Moore (1972) for two amphiuroids from the sublittoral of Florida Bay (1 : 5.0; see Table I 3.2).

Growth rate for the disc of *Amphiura chiajei* was estimated by Buchanan (1964) as not more than 0.25 mm per year (1.3 mm over five years). Even allowing for a more rapid growth in earlier years, maximum age must be between 10 and 15 years, unlike *A. filiforms* which Buchanan also investigated and which was thought to live no longer than four years. A P/B ratio of 0.8 was derived from the equation I 3.iv assuming a mean lifespan of 12.5 years. This gives an estimate for carbonate production of 2.2 g/m² (Table I 3.9).

*Echinocyamus pusillus*

Tissue AFDW and carbonate were estimated by splitting the bench-dried dry weight figure into tissue and carbonate fractions using the ratios of Moore (1971) for the echinoderm *Moria atropos* (see Table I 3.2). Standing tissue biomass and carbonate were estimated to be 0.04 and 1.2 g/m² respectively (Table I 3.9). No attempt was made to estimate production, because there is no published information on the lifespan of this animal.

*Muscusus discors*

The biomass of *Muscusus discors* 0.14 g/m² was estimated using the regression of George & Warwick (1985) for small *Modiolus modiolus* (Table I 3.1a), using the estimated P/B ratio of 1.75 obtained for *Musculus senhausius* from Tomoe Cove (Japan) (Tanaka & Kikuchi 1971 quoted from Robertson, 1979) gave an estimated production figure of 0.245 g/m². Carbonate was estimated using the AFDW/tissue ratio for *M. modiolus* (Table I 3.2).

*Parvicardium ovale*

Estimated density for *P. ovale* was only 5/m² and biomass estimates obtained from the equation of *George & Warwick (1985) for M. modiolus* were thus very crude (Table I 3.9).

*Abra alba*

Density of *Abra alba* in the Firth of Lorn was estimated to be 14/m², biomass and calcimass were estimated using relationships derived from animals collected from the southern limb of L. Spelve (Table I 3.1a & b). The P/B ratio used to estimate production was that obtained by Buchanan & Warwick (1974) for a deep water (80 m) population of *Abra nitida* off the coast of Northumberland. This P/B ratio (1.11) is lower than the estimate of Warwick &

## TABLE I 3.9a

AFDW biomass and production estimates (gm/$m^2$/yr)

| | N($m^2$) | B | % | P | % | P/B | Ls |
|---|---|---|---|---|---|---|---|
| *Modiolus modiolus* | 171 | 200 | 87.8 | 13.4 | 28.2 | 0.07 | 40–45 |
| *Ophiothrix fragilis* | 238 | 17 | 7.4 | 30 | 63.2 | 1.76(b) | 3–4(b) |
| *Astarte sulcata* | 37 | 1.6 | 0.7 | 1.9 | 4.0 | 1.18(e) | 5(c) |
| *Terebratulina retusa* | 2466 | 2.1 | 0.9 | 1.26 | 2.7 | 0.81 | 9 |
| *Amphiura chiajei* | 77 | 0.76 | 0.3 | 0.63 | 1.32 | 0.8(a&e) | 10–15(f) |
| *Crania anomala* | 115 | 0.30 | – | 0.35 | 0.7 | 1.18(e) | 5(d) |
| *Modiolus phaseolinus* | 479 | 0.19 | – | 0.224 | 0.5 | 1.18(e) | ND |
| *Musculus discors* | 58 | 0.14 | – | 0.245 | 0.5 | 1.75(a) | 2?(a) |
| *Hiatella arctica* | 51 | 0.08 | – | 0.04 | – | 0.5(b) | ND |
| *Ecinocyamus pusillius* | 6 | 0.04 | – | ND | – | ND | ND |
| *Anomia* sp. | 71 | 0.02 | – | 0.024 | – | 1.18(e) | ND |
| *Abra alba* | 14 | 0.02 | – | 0.022 | – | 1.11(a) | 2+(a) |
| *Thyasira gouldi* | 2 | 0.002 | – | 0.002 | – | 1.18(e) | 5?? |
| *Emarginella* | 20 | 0.002(i) | – | ND | – | ND | ND |
| *Nucluana minuta* | 6 | 0.004 | – | 0.002 | – | 0.7(e) | 7–8(g) |
| *Parvicardium ovale* | 5 | 0.003 | – | ND | – | 1.18(e) | ND |
| *Pomatoceros triquiter* | ND | ND | – | ND | – | ND | ND |
| *Bryozoa* | ND | ND | – | ND | – | ND | ND |
| *Lepidopleurus asellus* | 35 | 0.03 | – | ND | – | ND | ND |
| Hydroids | 2.58 | 1.13 | – | – | – | – | |
| *Mellinia* | 2.7 | 1.18 | – | – | – | – | |
| TOTAL | 227.4 | | | 47.47 (ignoring 2.5% of biomass) | | | |

(a) Lifespan & P/B from same genera in Table 1 of Robertson (1979); (b) P/B from Appendix 3 in George & Warwick (1985); (c) Lifespan from Wildish & Peer (1983) Table 1; (d) Lifespan from estimate of Rowell (1961); (e) P/B ratio derived from relevant equation of Robertson (1979); (f) Lifespan estimated from Buchanan (1964); (g) from Ansell *et.al.* (1978); (h) P/B from Tanaka & Kikuchi (1971) estimate for *Musculus senhausius*; (i) Biomass estimate from gastropod equation of Powell & Stanton (1985). ND (Not determined); NR (Not relevant).

## TABLE I 3.9b

Carbonate biomass and production estimates (gm/$m^2$/yr)

| | N($m^2$) | B | % | P | % | P/B |
|---|---|---|---|---|---|---|
| *Modiolus modiolus* | 171 | 2219 | 93.5 | 126.6 | 37.8 | 0.057 |
| *Ophiothrix fragilis* | 238 | 58.8 | 2.48 | 103.8 | 31.0 | NR |
| *Astarte sulcata* | 37 | 59.5 | 2.51 | 70.2 | 20.9 | NR |
| *Terebratulina retusa* | 2466 | 27.2 | 1.14 | 22.0 | 6.6 | 0.81 |
| *Crania anomala* | 115 | 4.4 | 0.19 | 5.2 | 1.5 | NR |
| *Amphiura chiajei* | 77 | 2.6(2) | 0.11 | 2.18 | 0.65 | NR |
| *Modiolus phaseolina* | 479 | 1.9 | 0.07 | 2.19 | 0.65 | NR |
| *Musculus discors* | 58 | 1.4 | 0.05 | 2.45 | 0.73 | NR |
| *Hiatella arctica* | 51 | 0.58(1) | 0.024 | 0.68 | 0.20 | NR |
| *Anomia* sp. | 71 | 0.10 | 0.004 | 0.12 | 0.03 | NR |
| *Ecinocyamus pusillius* | 10 | 1.2(3) | – | ND | – | NR |
| *Abra alba* | 14 | 0.06 | – | 0.066 | 0.02 | NR |
| *Thyasira gouldi* | 2 | 0.009(1) | – | 0.01 | – | NR |
| *Emarginella* | 20 | 0.01 | – | ND | – | NR |
| *Nucluana* | 6 | 0.046(g) | – | 0.032 | 0.01 | NR |
| *Parvicardium ovale* | 5 | 0.03 | – | 0.033 | 0.01 | NR |
| *Pomatoceros triquiter* | ND | ND | – | ND | – | NR |
| *Bryozoa* | ND | ND | – | ND | – | NR |
| *Lepidopleurus asellus* | 35 | ND | – | ND | – | NR |
| TOTAL | 2370.5 | | | 330 | | |

Based on AFDW CaCO conversion factor for (1) *Tellina martinicensis* (Moore, 1972), (2) *O. fragilis*, (3) *Moria atropos* (Moore, 1972). (Carbonate Production calculated from P/B ratios given in Table I 3.9a, unless stated).

George, (1980) for a shallow water (10 m) *Abra alba* population from Swansea Bay (P/B 1.35).

### *Hiatella arctica*

Tissue AFDW biomass was estimated from the equation of George & Warick (1985), (see Table I 3.1) to be 0.08 g/m²/yr. The P/B ratio supplied by the same authors for this species gave an annual production estimate of 0.04 g/m²/yr (Table I 3.9).

### *Crania anomala*

Tissue weight was estimated from the equation supplied by Curry & Ansell (1986) and the P/B ratio from the bivalve equation of Robertson (1979) using the four year lifespan estimate of Rowell (1960). Cadée (1968) estimates lifespan to be 13 years on the basis of growth lines and the P/B ratio estimated from this lifespan is also considered in section II 2.5

## I 3.4 CONCLUSIONS

### I 3.4.1 Inaccuracies

Estimates of benthic macrofauna production are equivocal because of likely systematic sampling errors which arise from less frequent and more haphazard sampling and the compromise nature of available sampling techniques. Grab and core samples often lack the sampling depth and surface area to quantitatively estimate some species (c.f. Wildish, 1983), whereas dredge samples underestimate fragile and small species and ignore the infauna. In addition, the selective retention of grab samples (rejecting those with small volume samples) and grab failures (which may indicate hardgounds with different production estimates, cf. Fig. 1.1) may over-emphasize the homogeneity of the community, and the density of the carbonate producers. (eg. a grab sample would fail repeatedly to penetrate a barren coquinoid pavement, but these failures would be ignored in the subsequent estimation of productivity).

The assessment of secondary production of benthic organisms lacks the counterbalance of independant estimates of aspects of productivity, such as growth rate and weight changes (using mark and recapture techniques or laboratory studies (c.f. Keunzler, 1961), applicable to intertidal and shallow subtidal community estimates.

The ability to accurately estimate the age of organisms that comprise the community, is a pre-requisit of an accurate assesment of benthic secondary production. This is well illustrated with reference to *M. modiolus* which dominates the standing biomass of the community. Growth is believed to be slow, which (in conjunction with an absence of juveniles) lead to a very low P/B estimate for this species, and the surprising conclusion that although the standing calcimass of *Ophiothrix fragilis* is only 3% of *Modiolus*, total carbonate production is almost equivalent.

### I 3.4.2 Total Community Production

In the estimate of community production, a number of species collected by dredging and recognised to be important to the dynamics of the community were ignored, because they were absent or virtually absent from the grab samples (eg. echinoderms including *Asterias*, *Ophiocomina*, crustaceans). Other species were ignored because they were not carbonate producers (polychaetes, hydroids) or because carbonate production was difficult to assess (bryozoans, barnacles and calcareous polychaetes), estimates on the significane of production in the latter group are available from sediment analysis (section II 1.3).

Within the limitations outlined above, which will overestimate the importance of the four species above, on virtually all ranking criteria these four (all suspension feeders) dominate the community (Table I 3.10). Warwick (1982) has previously noted that the production of epifaunal communities was dominated by a few suspension feeders, and this is also true of other studies (eg. Wildish & Peer, 1983; George & Warwick, 1985).

A distance matrix based on rank positions demonstrates that numerical abundance, the usual palaeontological descriptor of an assemblage is the least similar of the five ranking measures (Fig. I 3.5). Although the distortion is introduced by large numbers of sub-2 mm *T. retusa* and *M. phaseolinus* which would not typically form a significant part of the recovered death assemblage (see section II).

TABLE I 3.10
Percent contribution of the four selected species to the overall community estimates

| | Abundance | Biomass | AFDW P | Calcimass | $CaCO_3$ P |
|---|---|---|---|---|---|
| *M. modiolus* | 4.4 | 87.8 | 28.2 | 93.5 | 37.8 |
| *Ophiothrix* | 6.1 | 7.4 | 63.2 | 2.48 | 20.9 |
| *Terebratulina* | 64.1 | 0.9 | 4.0 | 2.51 | 31.0 |
| *Astarte* | 0.96 | 0.7 | 2.7 | 1.14 | 6.6 |
| TOTAL | 75.6 | 96.6 | 98.1 | 99.63 | 96.3 |

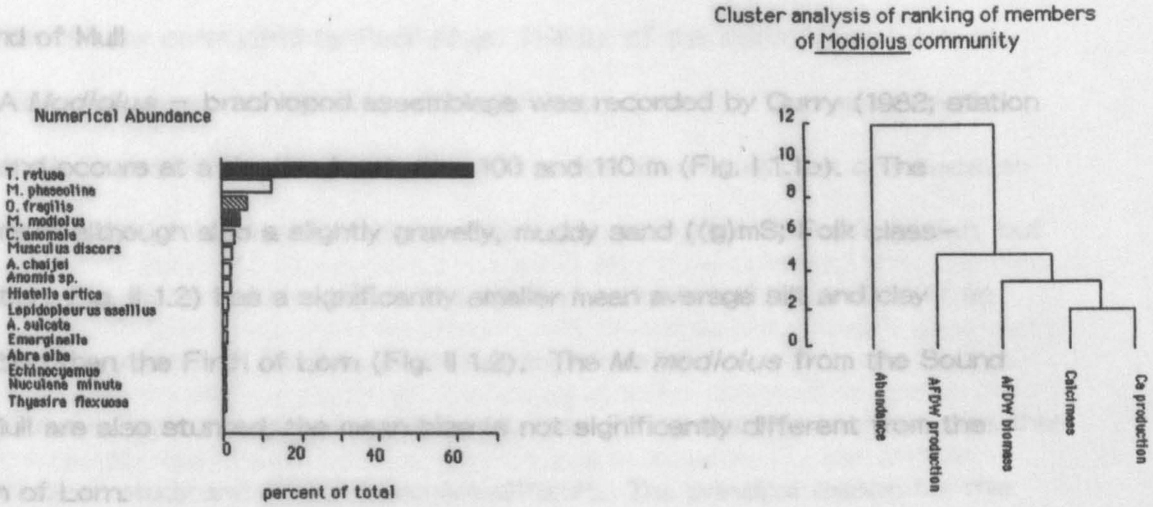
Overall community productivity (47.7 $g/m^2/yr$) is relatively low when compared with very large standing biomass, (227.7 $g/m^2/yr$) and it therefore follows that the community P/B of 0.21 is also low, swamped by the dominance of *M. modiolus*. In general the overall decrease in biomass away from the shoreline and into deeper water (Rowe, 1971) is well known, and this community must be considered atypical.

Observations of angiosperm and macroalgal remains washed into the community demonstrate at a macroscopic level the significance of allochthonous sources of organic detritus to this community, both from the productive and extensive shorelines lining the Firth and also possibly from nutrient rich Clyde water drawn into the community by the compensation current (Grantham *et al.*, 1983).

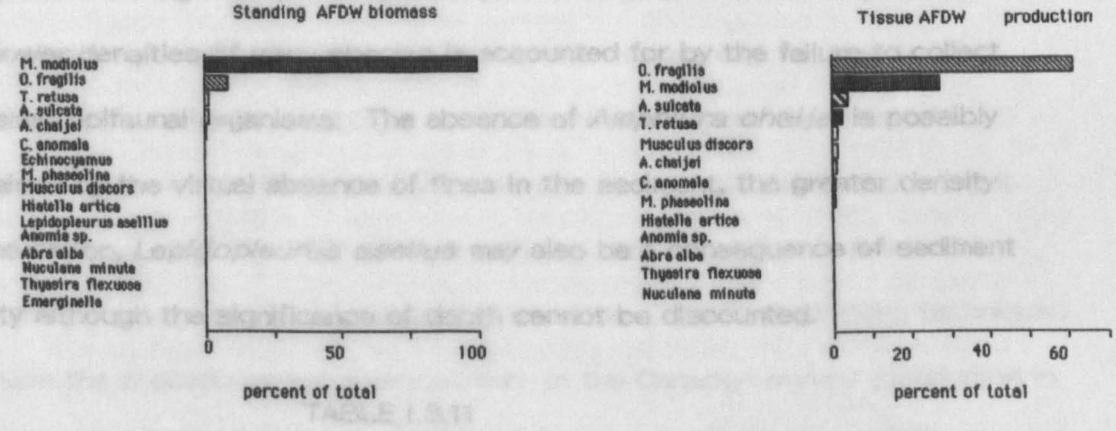
Comely (1978) argues that the community itself arises in an otherwise unsuitable position as a consequence of the confluence of three current systems, concentrating spat derived from throughout the Firth of Lorn. Although only conjectural, and not required to explain the occurrence of *M. modiolus* for which an adequate breeding population occurs in the community, this argument is a compelling explanation of the presence of *M. phaseolinus*. *M. phaseolinus* which is widespread in the Firth of Lorn (Comely, unpublished data) numerically dominates in all the deep water *Modiolus* communities (Comely unpublished data; Table I 3.3). In this study only six of the 527 *M. phaseolinus* collected had

Figure I 3.5

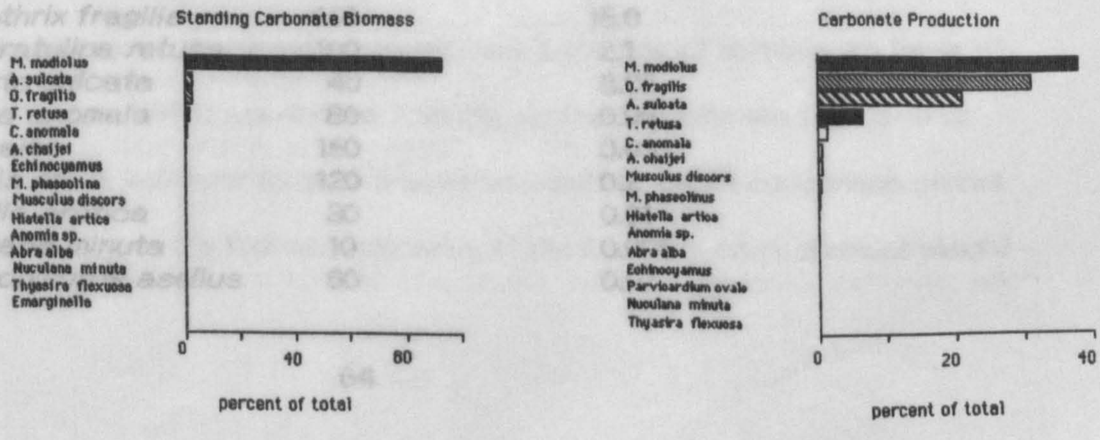
Abundance, biomass and production rankings in the Firth of Lorn <u>M. modiolus</u> community



Tissue Weight



Carbonate



lengths in excess of 8 mm (Fig. I 2.7) although the maximum length of this animal is 19 mm (Tebble, 1966), strongly suggesting that there is an inadequate *in situ* breeding population and recruitment is therefore allochthonous.

### I 3.5.3 Comparison with other *Modiolus* communities

#### Sound of Mull

A *Modiolus* – brachiopod assemblage was recorded by Curry (1982; station 25) and occurs at a depth of between 100 and 110 m (Fig. I 1.1b). The sediment although also a slightly gravelly, muddy sand ((g)mS; Folk classification, Fig. II 1.2) has a significantly smaller mean average silt and clay fraction than the Firth of Lorn (Fig. II 1.2). The *M. modiolus* from the Sound of Mull are also stunted, the mean size is not significantly different from the Firth of Lorn.

A single grab sample from this population collected on 7/6/83 was analysed for comparative purposes. The overall distribution of fauna and estimated total biomass was in remarkable agreement with the Firth of Lorn study, (within the limits of a single sample comparison). The total absence of *M. phaseolinus* and lower densities of many species is accounted for by the failure to collect the small epifaunal organisms. The absence of *Amphiura chaijei* is possibly explained by the virtual absence of fines in the sediment, the greater density of the chiton, *Lepidopleurus asellus* may also be a consequence of sediment quality although the significance of depth cannot be discounted.

TABLE I 3.11
Tissuw–AFDW standing biomass of large macrofauna Sound of Mull
(estimated from single grab sample, collected 7/6/83)

| | Numbers/$m^2$ | AFDW Biomass |
|---|---|---|
| *Modiolus modiolus* | 100 | 157 |
| *Ophiothrix fragilis* | 150 | 15.0 |
| *Terebratulina retusa* | 100 | 2.1 |
| *Astarte sulcata* | 40 | 8.05 |
| *Crania anomala* | 80 | 0.05 |
| *Abra alba* | 150 | 0.03 |
| *Anomia* sp. | 120 | 0.2 |
| *Hiatella arctica* | 30 | 0.01 |
| *Nuculana minuta* | 10 | 0.006 |
| *Lepidopleurus asellus* | 60 | 0.07 |

Estimates of production which have included the bivalve *Modiolus* have been published for animal communities in the Bay of Funday, Canada and for a reduced epifaunal community in the Bristol Channel.

Bay of Funday

The survey conducted by Peer *et al.* (1980), of the macrofaunal benthos across a wide sweep of the lower Bay of Funday (see Fig. 1), summarised by Wildish & Peer (1983) is the most obvious comparative study, not only because of the dominant role played by *M. modiolus* in overall secondary production, but because the study included the only published estimates of production of an articulate brachiopod (*Terebratulina septentrionalis*).

The synthesis presented by Wildish & Peer (1983) was broader in scope than the present study and comparisons are difficult. The principal reason for this was the authors failure to estimate production from discrete communities, production figures are only supplied for the whole of the lower reaches of the Bay of Funday, although the source data (Peer *et al.*, 1980) and an earlier dredge survey by Caddy (1970) make it clear that the *M. modiolus* and *Terebratulina septentrionalis* occur in different (albeit overlapping) regions (c.f. Figure I 2.10), controlled principally by tidal currents. Therefore, although *M. modiolus* accounts for 75% of the total secondary production of the Bay it was present at only 30 of 98 samping stations. Little variation in production estimates between the two areas should occur as a result of sampling techniques because the procedures were very similar. In the Canadian survey (conducted in the summer of 1978) the material was collected by Hunter-Simpson grab, although the material was subsequently sieved to a marginally smaller size (> 0.8 mm) than this study.

Problems arise in attempting to compare estimates of biomass, as those of Wildish & Peer (1983) are derived from the wet weight biomass (inclusive of shells) of 10% seawater formalin preserved material. Direct comparison cannot be made between the biomass estimates of the Canadian study and wet weight corrections of the AFDW material from the present work because of variations in wet weight caused by formalin preservation (Mills *et al.*, 1981).

No data is provided by the authors on the time interval between collection and the determination of wet weight, but it is probable that it was relatively rapid "Ashore the samples were washed again through a 0.8 mm² sieve to remove formalin." (Peer *et al.*, 1980: 1). To establish a relationship it was therefore first necessary to determine the rate of weight loss of material in 10% formalin seawater.

A simple experiment established a crude conversion factor for the community dominant, *M. modiolus*. Sixteen *Modiolus* collected from the Firth of Lorn and held in tanks with exchanging seawater for 10 days following collection. The shells were scrubbed clean of epifauna and length measured to the nearest 0.1 mm. Wet weight was determined by allowing the shell to drain until the resulting drainage water begun to be replaced by mucus. (c.f. Comely, 1978). Live wet weight was remeasured fifteen minutes later. The animals were then placed for 10 minutes in a plastic bucket with an airtight lid containing two litres of 10% sea-water formalin neutralised with 2.4 gm of borax per litre. The animals were then rinsed in tap water before soaking for 30 minutes in distilled water. The shells were held on the bench for 30 minutes before their day 0 weight was read. Weights were measured at intervals of 1,4,8,15, and 987 days, the formalin not being changed, as this is unlikely to occur to material on which production estimates are based.

The greatest variation in weights (a drop of 10%) was observed over the first 10 days. The subsequent fall over the succeeding 985 days showed less variation than that obtained by varying the draining time by thirty minutes. Although the formalin was buffered and the animals held in a small volume there is a possibility of some acid digestion of the carbonate, which was not checked for.

To obtain comparisons for the study with Wildish and Peer (1983), material was held in formalin for a period of two months. Comparisons were made between formalin preserved wet weight (inclusive of shell), tissue-AFDW and shell weight for 10 *M. modiolus modiolus*, 6 *T. retusa* and 6 *Astarte sulcata*. Tissue AFDW was chosen as the baseline for comparison because it experiences the minimum variation (Mills *et al.*, 1981).

Comparisons between the two data sets which are presented in Table I 3.12 were calculated as follows :-

Conversion of *Modiolus modiolus* from Firth of Lorn data to Wildish and Peer (1983).

AFDW Biomass of *M. modiolus* = 238
AFDW of *M. modiolus* as a percentage of total
formalin preserved wet weight (from Table II 3.2) = 5%
Formalin preserved wet weight biomass = 4760
Estimated Lifespan 'eLs' = 40
P/B ratio derived from equation of Robertson (1979)
using eLs from Wildish & Peer (1983) = 0.52
Production (using estimated P/B ratio) = 4760 x 0.52 = 2475

*Astarte undata* and *A. subaequilatera* were recorded together in only five out of 27 stations at which the genus *Astarte* was recorded and a mean value is used.

TABLE I 3.12

Comparison of productivity estimates (g/m$^2$/yr) from (1) Wildish and Peer (1983) and (2) this study for the following species (A) *Modiolus modiolus* (B) *Terebratulina septentrionalis* (Bay of Funday) & *T. retusa* (Firth of Lorn) (C) mean of *Astarte subaequilatera* and *A. undata* (Bay of Funday) and *Astarte sulcata* (Firth of Lorn).

| | A | B | C |
|---|---|---|---|
| Lifespan (Ls) | 40 | 8 | ND |
| Estimated Lifespan (eLs) | 20 | 7 | 5 |
| P/B ratio (2) | 0.07 | 0.81 | ND |
| Est P/B ratio (eLs) | 0.52 | 1.11 | 1.42 |
| Est P/B ratio (Ls) | 0.29 | 0.82 | ND |
| Production (1) | 485.3 | 42.5 | 38.35 |
| Maximum Production (1) | 1769.3 | 180.8 | ND |
| Production(2) from (1) | 2475 | 60.2 | 227.2 |
| Production(2) | 11.0 | 1.9 | 1.7 |
| Production(1) from (2) | 3.2 | 0.71 | ND |

Lifespan (Ls), lifespan estimates from this study; Estimated Lifespan (eLs) lifespan estimates from Wildish & Peer (1983); P/B ratio (2) Calculated P/B ratios, this study; Est P/B ratio, P/B/ ratios estimated from the inverse logarithmic relationship of Robertson (1979) used by Wildish & Peer (1983). Production estimates for (1) taken from Wildish & peer (1983: Table 1).

The highest biomass of *M. modiolus* found in the Bay of Funday was at site 65 (Peer *et al.* 1980; Appendix II p.55) the two grab samples (0.2 m$^2$) containing a combined total of 100 *M. modiolus*, with a wet weight biomass of 2023 g (Site 65). However, the maximum published production value, 1769.23 (g/m$^2$/yr) (Wildish & Peer, 1983: Table 1) is considerably lower than that derived using the appropriate P/B ratio from equation (i) of Robertson (1979) (5259.8 g/m$^2$/yr).

Comparative figures suggest that although the production values from the Bay of Funday are high, the combined recalculated tissue-AFDW figures for *M. modiolus* and *T. septentrionalis* (3.9 g/m$^2$/yr), believed to account for 79% of production in the Bay of Funday, (an overestimation due to the high P/B ratio for *M. modiolus*) are lower than other estimates of production in intertidal and offshore environments. The greatest published estimate of standing biomass of *M. modiolus* is the figure of 14,569.4 g/m$^2$/yr estimated by Lees & Driskell (1981) from a shallow water site on the Alaskan Shelf. This wet weight figure can be crudely translated into a tissue–AFDW of 728 g/m$^2$/yr. Using the P/B ratio from this study, which is liable to be too low (as the population is not deep water) gives a production estimate of 50.96 g/m$^2$/yr, a figure greater than many estimates of total community production.

### Bristol Channel

George & Warwick (1985) have estimated annual production in a hard bottom epifaunal community from the Bristol Channel which they describe as being classically defined as a *Modiolus* community, but in which *Modiolus* is inconspicuous due to its small size.

Production in this community is dominated by *Ophiothrix fragilis*, with densities and production similar to the estimate for the Firth of Lorn. In the July 1976 sample, the estimated density of *O. fragilis* was 262/m$^2$, with a standing biomass of 15.50 g (compared with an estimated 238/m$^2$, with a standing biomass of 17 g/m$^2$/yr from the August sample in the Firth of Lorn).

### I 3.5.4 Comparison with productivity in other communities

Total community production of the carbonate producing organisms within the *Modiolus* community in the Firth of Lorn is of a similar order of magnitude to most other published estimates from the total production in many intertidal and shallow subtidal sites, although standing biomass is typically much higher. Although no other estimates of communities from such deep waters have been published, productivity must be considered unusually high. The deepest water community for which productivity was estimated is the study by Buchanan & Warwick (1974) of a *Brissopsis lyrifera/Amphiura chiajei* community at 80 m depth off the coast of Northumberland, U.K. where P = 1.74, B = 3.9 and P/B = 0.4.

In general, productivity is believed to be higher in epifaunal communities than in infaunal ones (e.g. Kay & Knights 1975), the productivity of epifaunal mussels in temperate waters can be very high indeed, productivity in an intertidal population of the epifaunal bivalve *Mytilus edulis* from the Ythan

Estuary, Scotland was estimated to be 298 g/$m^2$ (dry weight) even though lifespan was estimated to be ten years (Milne & Dunnert, 1972). The proportion of epifauna with calcareous hard parts is higher in epifaunal communities than infaunal communities (Craig & Jones, 1966), as is the relative thickness and the durabilitly of the hardparts themselves (Stanley, 1970). Coupled with a higher overall productivity and trophic simplicity (Warwick, 1982), epifaunal communities become palaeontologically significant in a hitherto unrecognised way (c.f Bosence, 1979b).

Recent carbonate sediments in temperate waters (defined as 30° North and South of the equator and where water temperatures are less than 20°C) have been reported from many parts of the world (eg. Chave, 1967; Lees, 1975; Nelson, 1978; Alexandersson, 1978a,b, 79; Scoffin *et al.*, 1980; Nelson & Bornhold, 1983; Farrow & Scoffin, 1979; Farrow *et al.*, 1984). In all these instances the carbonates are biogenic or skeletal in origin, presumably due to the low air or water temperatures which inhibit any inorganic precipitation. It is now apparent that if the supply of terrigenous clastics at the seabed is sufficiently low, then the potential exists for carbonate dominated shelves to develop at any latitude (Chave, 1967).

TABLE I 3.13
Carbonate production (g/$m^2$/yr)

| | Molluscan | | | | Total | | |
|---|---|---|---|---|---|---|---|
| | Mean | Min | Max | SD | Mean | Min | Max |
| (1) Bank | 20 | 8 | 40 | 9.6 | 188 | 37 | 462 |
| (1) Muddy algal gravel | 17 | 4 | 42 | 14.5 | 30 | 4 | 144 |
| (2) Artificial substrates | – | 25 | 30 | – | – | – | – |
| (3) Sublittoral | – | 33–45 | 400 | – | – | – | – |
| (3) Shallow Rocky Macrobenthos | – | – | – | – | 400 | 70 | 4400 |
| (3) Shelf Macrobenthos ( < 100mm) | – | – | – | – | 5 | 6 | – |
| (4) Shelf, > 50% Ca(CO) | – | – | – | – | 24 | 4 | 135 |
| (4) Orkney Islands, > 75% Ca(CO) | – | – | – | – | 77 | 14 | 312 |
| (4) North Ronaldsay, North Bank | – | – | – | – | 130 | 940 | 540 |
| (4) East Orkney, Platform Edge | – | – | – | – | 248 | 114 | 646 |
| (4) Stronsay, Firth Banks | – | – | – | – | 400 | 250 | 400 |
| (5) New Zealand Cenozoic | – | – | – | – | 16 | 8 | 40 |

(1) Bosence (1980), Mannin Bay (2) Samtheim (1973) Baltic, (3) Moore 1972 (Florida Bay) (4) Smith (1971) California Borderland (4) Allen (1983), Scottish Shelf; Nelson (1978), New Zealand shelf.

Carbonate production in the Firth of Lorn was estimated to be 330 g $Ca(CO)_3$ /$m^2$/yr. Only two sets of figures for carbonate production in temperate waters have been published previously. Crude estimates of calcium carbonate production have been made over large areas of the Californian borderland between 31°30' and 34°30' N. (Smith, 1971). Figures of 70 to 440 g $Ca(CO)_3/m^2/yr$ are given for intertidal rocky substrates and 5 to 6 $g/m^2$ for the benthos. Molluscs dominate carbonate production in the intertidal, subtidally the main carbonate producers are bryozoans, red algae and echinoderms. Estimates are thought to have low accuracy because the sampling of the benthic populations are limited and the growth rates are mainly estimates.

Bosence (1980) has published carbonate production rates for coralline algal gravels form Mannin Bay (Ireland). The figures, which are a combination of estimates of molluscan and algal carbonate production range from a minimum of 4 to a maximum of 462 g $Ca(CO)_3/m^2/yr$ (Table I 3.13). Bosence (1980) ignores the contribution of foraminifera, barnacles and serpulids because they comprise only a small fraction of the sediment.

Sarntheim (1973) estimates carbonate production of molluscs from artificial substrates in the Baltic to be 25–50 g $Ca(CO)_3/m^2/yr$, these figures are slightly higher than the mollusc estimates of Bosence (1980) (4–42 g $Ca(CO)_3/m^2/yr$). The estimates of molluscan carbonate production by Moore (1972) from sublitoral areas of Florida Bay are very variable, the mean value is 33–45 g $Ca(CO)_3/m^2/yr$, but the maximum estimate of 400 g $Ca(CO)_3/m^2/yr$) is considerably higher than the equivalent from the Firth of Lorn (196.8 g $Ca(CO)_3/m^2/yr$).

Allen (1983) estimated the rate of carbonate accumulation on the Orkneys shelf, from estimates of depth and possible time of accumulation. The average rate of accumulation for the entire shelf is 77/g/$m^2$/yr (Farrow *et al.*, 1984), but as a result of the local concentrating effects of wave and tidal transport, rates almost an order of magnitude higher were possible (540 g/$m^2$/yr; Table I 3.13).

Using the specific gravity of calcite (2.7), Boucot (1981) recalculates available production data, this crude conversion will yield an accumulation rate of 1 mm/yr for a production rate of 270 g/m$^2$/yr. The rate of accumulation for the Firth of Lorn (ignoring allocthanous inputs) would be 1.2 mm/yr, which, in the absence of destructive processes, would completely fill the depression in the Firth of Lorn in under 200,000 years!

## I 4 GROWTH RATE & SETTLEMENT OF *TEREBRATULINA RETUSA*

### I 4.1 INTRODUCTION

It is important to establish the rate at which an animal grows because of the many areas that require or benefit from the application of this information, (e.g. production, population dynamics, ecology). For peduncally attached brachiopods, growth rate in the period following settlement is notable both for the paucity of information and for its potential evolutionary significance. Selection operates to its greatest effect at points of greatest vunerability in the life history. As sessile epifauna, articulate brachiopods are most vulnerable in the period immediately following settlement (Doherty, 1979; Witman & Cooper, 1983), being exposed to the dual stresses of disturbance and overgrowth which intuitavely confer selective advantage on those animals pre-adapted to avoid them (which brachiopods are not) or able to achieve a size refuge rapidly.

Although Elliott recognised as much in 1951 (p. 20) "the basic factor affecting (the distribution of) terebratelloid brachiopods is fixation to one spot for all but the earliest portion of life-history", the theme has not been developed. The picture of growth rates in articulate brachiopods that has emerged is broadly consistent in its support of the logarithmic growth model of Levington & Bambach (1969) (Richards & Bambach, 1975; Thayer, 1977). This crude model derived from early studies (1923-1959) of bivalve growth rate, has the unfortunate property of being self re-enforcing, because an assumtion of rapid early growth has underplayed the need to adequately sample the very small post-larvae (Muss, 1973). The broad support that this model commands to describe articulate brachiopod growth, originates from a very distorted sample; many more growth curves have been produced for fossil species than the five published studies of living animals, three of which were from intertidal sites and only one for a population deeper than 15 m. There is in addititon virtually no reliable data on growth or survival in the crucial early period following settlement.

Three methods have been employed to study the growth rate of articulate brachiopods, 1) identification of annual rings 2) monitoring growth of marked animals and 3) dissembling of size frequency distributions. A fourth method, employing radiometric dating techniques has been applied to bivalves but not to brachiopods.

### Identification of annual rings

Paine (1969) cautions against the use of growth lines to age shells "*Terebratella transversa* shells exhibit a bewildering array of growth lines...(many) have a number of major growth lines considerably in excess of their maximum potential age. For instance, the single Edmonds specimen, at most five years old, has eight or nine such lines." Both Doherty (1979) and Curry (1982) have however successfully incorporated the analysis of growth lines in studies with independant checks from the modal positions in length-frequency histograms and in the former study measurement of *in situ* rates of growth.

Growth line analysis is an unsatisfactory method of establishing growth rate before the first period of growth cessation, because the identification of first 'major' growth line is rarely axiomatic and is complicated by erosion and re-deposition (Fig. I 4.1). Another drawback to the method is that it will over estimate growth rate of a population if growth rate is variable and selection operates in favour of animals achieving a rapid initial growth rate (e.g. sessile organisms), because analysis is usually conducted on large specimens.

### Monitoring growth of marked individuals

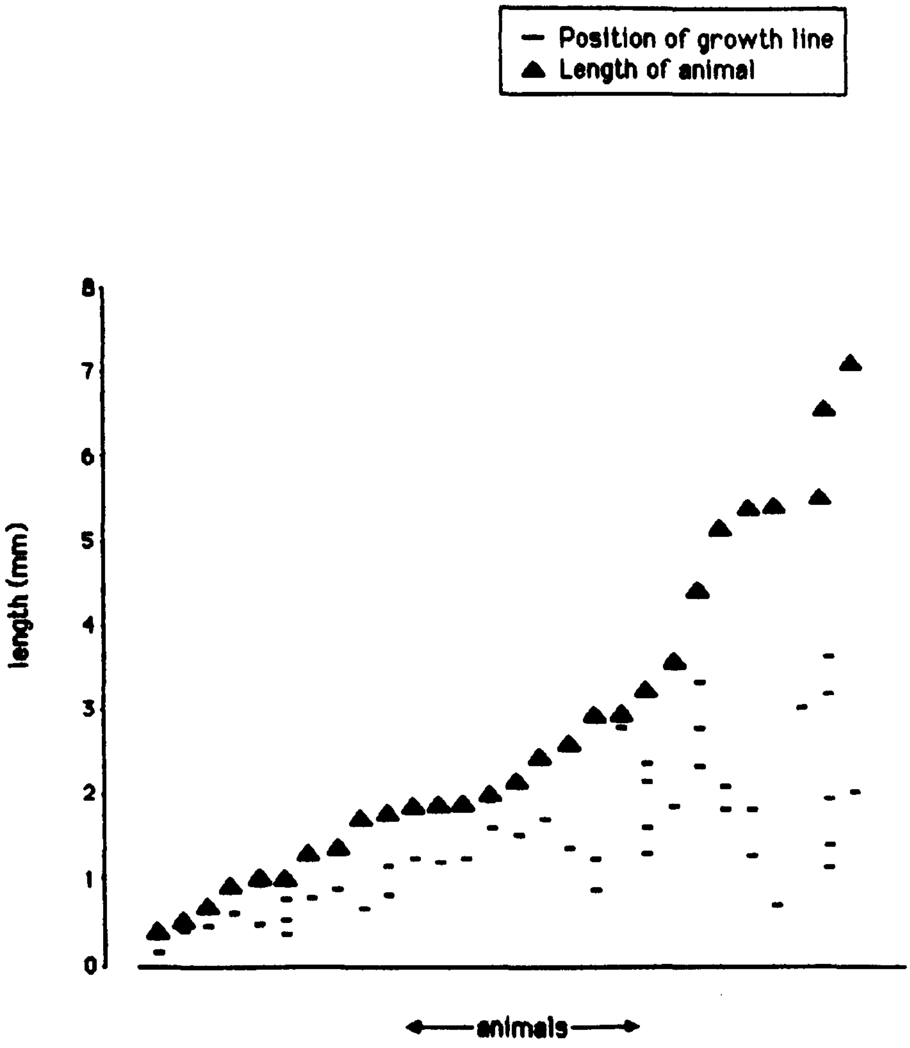
Monitoring the growth of individuals, has restricted application, as handling poses problems for measuring recently settled post-larvae and limits the depths at which such studies can be satisfactorally conducted.

### Size frequency distributions

Disassembling of size-frequency distribution of a population requires an

Figure I 4.1

Major growth lines present on small T. retusa



accurate census of the whole population and discontinous cohorts, with independant checks on the periodicity of recruitment.

### Radiometric dating techniques

Radiometric techniques enabling the ageing of adult shells (eg. Dodge & Thomson, 1974; Cochran & Turekian, 1981) have yet to be used on articulate brachiopods but may prove useful if used in conjunction with the methods outlined above.

## I 4.2 GROWTH RATE

### I 4.2.1 METHODS

Length frequency histograms for seasonal samples were produced both for the whole population and for sub-2 mm individuals. The length-frequency histograms were constructed with octaves as small as possible to present the maximum amount of information; stem and leaf plots of all histograms were produced to ensure that no distortions were introduced as a result of the corrections applied to the graticule measured lengths.

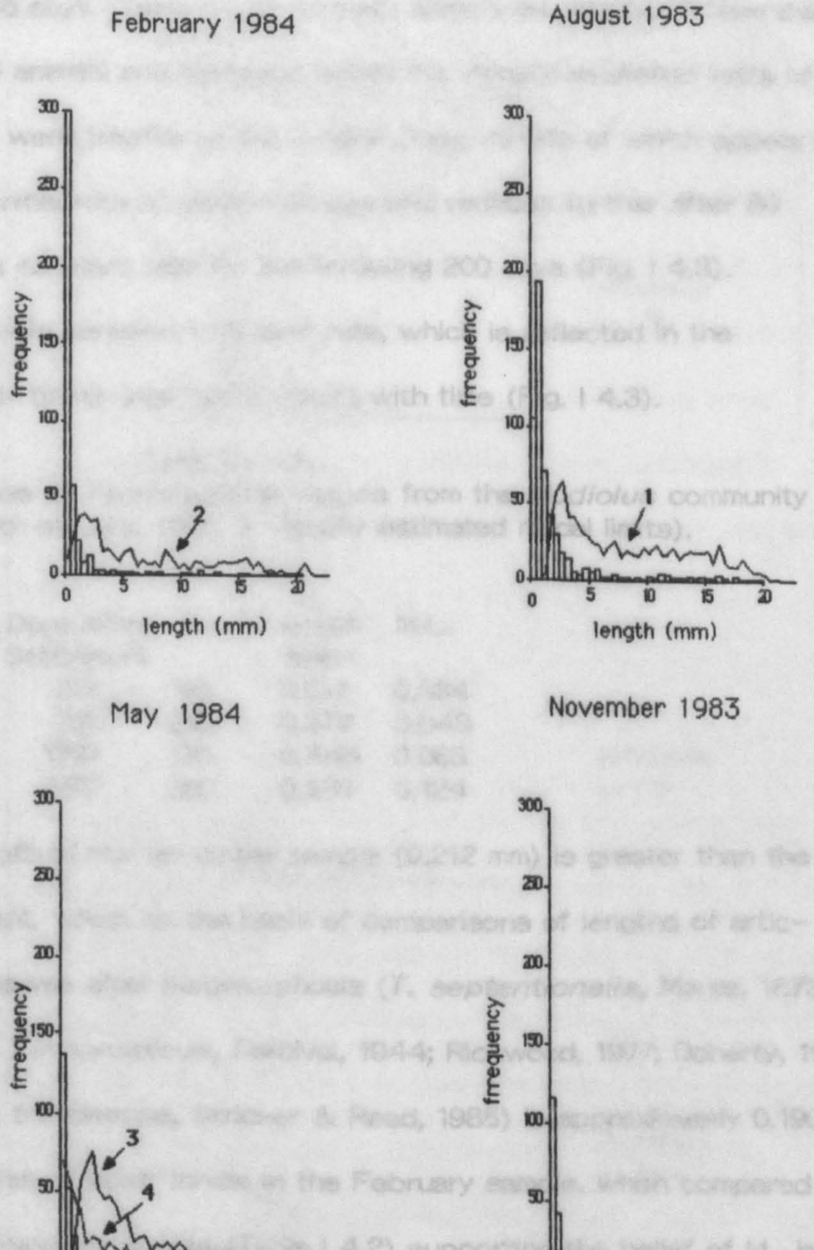
### I 4.2.2 RESULTS

#### Growth Rate

During the early stages of growth brachiopods have brephic shells (the first formed, non ribbed juvenile shell; Stricker and Reed, 1985) which as well as being small (< 0.300 mm) are transparent, and the brachiopods often settle cryptically. Surveys of living 0-year class animals were both painstakingly slow and finally unsatisfactory; attempts to improve recognition by vital staining of living animals was also unsuccessful. Brephic individuals could only be picked out satisfactorily, if the material was first fixed and stained, and the substrate thoroughly dried (Plate 1a) and then only with the aid of a binocular microscope. Satisfactory recovery of the 0-year class brachiopods was only possible as all the substrates were small and could easily be manipulated under the binocular microscope. The process was nevertheless

Figure I 4.2

Length frequency histograms for T. retusa from the Firth of Lorn (data from Curry 1982 superimposed (1 = 22/8/77, n= 830, 2= 12/1/79, n = 209; 3 = 5/5/77; 4 = 24/5/77, n = 554)



laborious, the average time between discoveries of brephic *T. retusa* was in the order of 7 minutes.

## Analysis of time series

Throughout the year, sub-1 mm brachiopods with brephic shells dominate the population (Fig. I 4.2). The population structure is strongly left skewed (*sensu* Curry, 1982) and histograms of sub-2 mm animals show a distinctive cohort (Fig. I 4.3), which slowly increases in mean size (from 0.212 mm to 0.539) over 246 days (Table I 4.1). Growth rates were produced from the mean values of all animals encompassed within the visually estimated limits of this cohort which were treated as the 0-year class, details of which appear in Table I 4.1. The initial rate of growth is slow and reduces further after 80 days maintaining a constant rate for the following 200 days (Fig. I 4.3). There is considerable variation in growth rate, which is reflected in the increasing width of the 0-year class cohort with time (Fig. I 4.3).

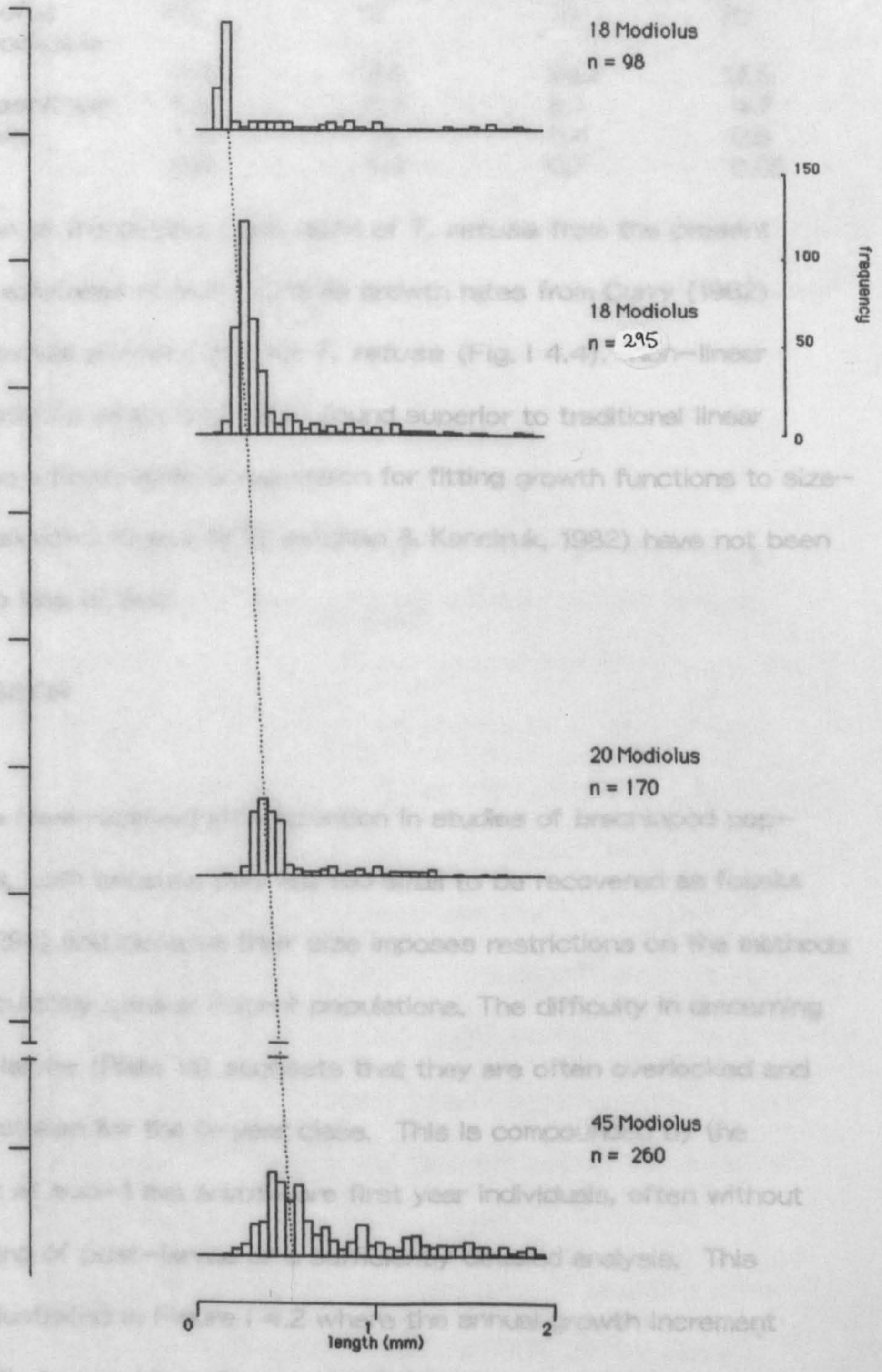
TABLE I 4.1
Size increase of *Terebratulina retusa* from the *Modiolus* community in the Firth of Lorn. (M.L. = visually estimated modal limits).

| Date of Collection | Days after Settlement | No. | length mean | M.L. |
|---|---|---|---|---|
| 29/11/83 | 10? | 98 | 0.212 | 0.034 |
| 10/02/84 | 76? | 295 | 0.374 | 0.048 |
| 23/05/84 | 173? | 170 | 0.443 | 0.066 |
| 24/08/83 | 256? | 260 | 0.539 | 0.124 |

The mean length of the November sample (0.212 mm) is greater than the length at settlement, which on the basis of comparisons of lengths of articulate brachiopod larvae after metamorphosis (*T. septentionalis*, Morse, 1873; *Terebratella. (W.) inconspicua*, Percival, 1944; Rickwood, 1977; Doherty, 1979; and *Terebratalia transversa*, Stricker & Reed, 1985) is approximately 0.190 mm. The higher densities of post-larvae in the February sample, when compared with the proceeding November sample (Table I 4.2) supporting the belief of M. James (*pers. comm.* 1986) that settlement extends beyond the November 29th sampling date. The slow acquisition of data precludes the production of meaningful length-frequency histograms of animals longer than 2 mm because the absolute

**Figure I 4.3**

Length frequency histograms of small (< 2.0 mm) animals arranged by date —— indicates the position of the estimated mean of each cohort .



numbers are too low (Fig. I 4.2). The author is therefore grateful to G. Curry who made available his raw data from populations sampled in May and August of 1977 and January, 1978 which are superimposed on the relevant length-frequency histograms (Fig. I 4.2).

TABLE I 4.2
Faunal settlement density on *M. modiolus*

| | MONTH | | | |
|---|---|---|---|---|
| | 23 Aug. 1983 | 29 Nov. 1983 | 10 Feb. 1983 | 24 May 1984 |
| No. of *M. modiolus* | 45 | 18 | 18 | 20 |
| Ratio sp./*M. modiolus* | | | | |
| *T. retusa* | 5.8 | 12.6 | 24.2 | 12.5 |
| *Modiolus phaseolinus* | 5.5 | 6.4 | 6.1 | 4.7 |
| *Crania anomala* | 1.8 | 1.0 | 0.4 | 0.6 |
| *Anomia* sp. | 0.8 | 1.4 | 0.7 | 0.05 |

Incorporation of the 0-year class rates of *T. retusa* from the present study, with the estimates of post-juvenile growth rates from Curry (1982) generates a sigmoidal growth curve for *T. retusa* (Fig. I 4.4). Non-linear regression techniques which have been found superior to traditional linear methods such as a Ford-Walford regression for fitting growth functions to size-at-age data (Gallucci & Quinn, 1979; Vaughan & Kanciruk, 1982) have not been employed due to lack of time.

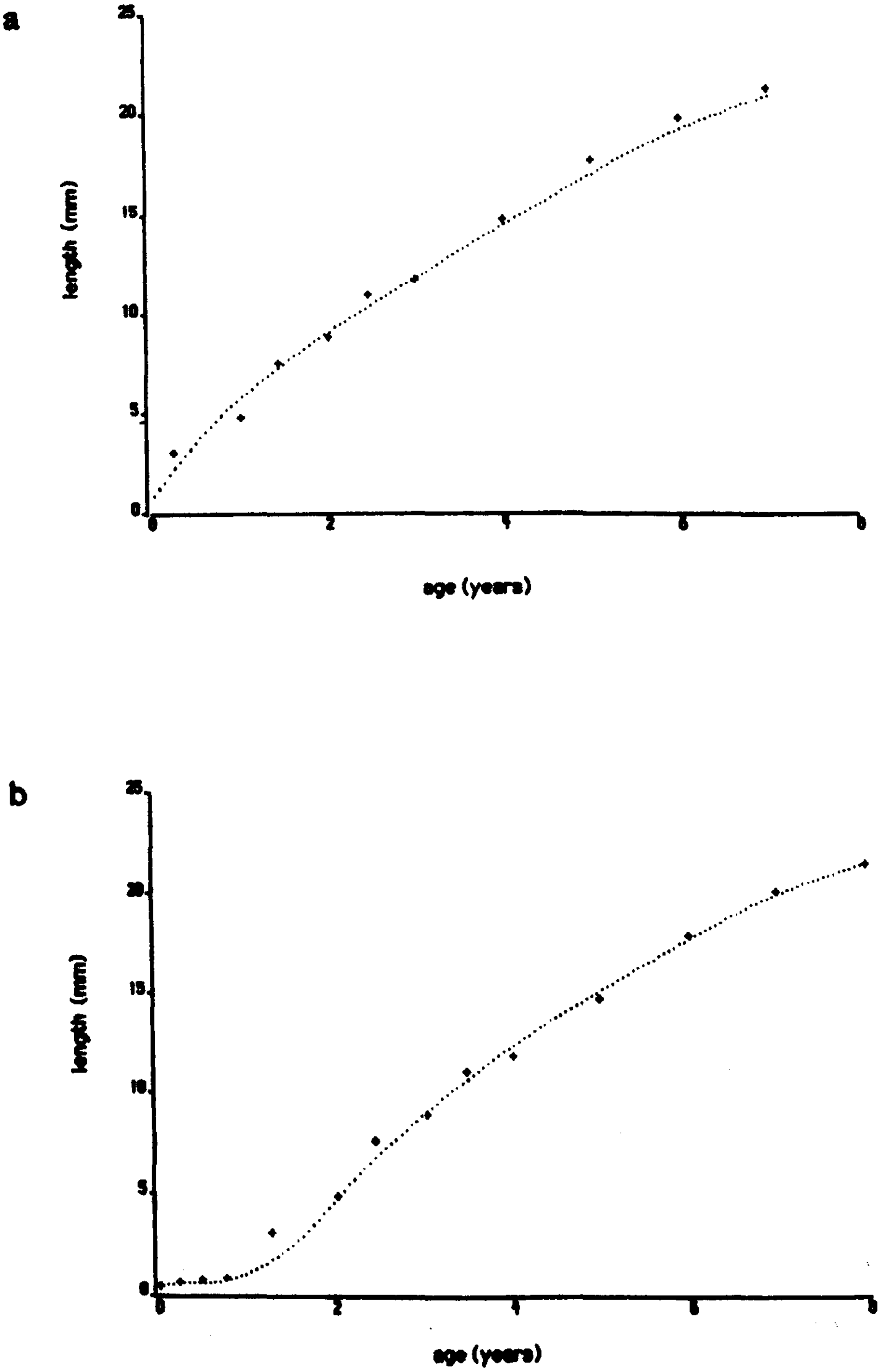
### I 4.2.3 DISCUSSION

Methodology

Post-larvae have received little attention in studies of brachiopod population dynamics, both because they are too small to be recovered as fossils (Boucot, 1981: 290) and because their size imposes restrictions on the methods employed to accurately census Recent populations. The difficulty in discerning the small post-larvae (Plate 1a) suggests that they are often overlooked and older animals mistaken for the 0-year class. This is compounded by the assumption that all sub-1 mm animals are first year individuals, often without adequate sampling of post-larvae or a sufficiently detailed analysis. This latter point is illustrated in Figure I 4.2 where the annual growth increment of *T. retusa* fails to provide a discernable shift in 0-year class modal peak

Figure I 4.4

Growth curves for T. retusa
a) from Curry (1982)
b) modified from (a) with the addition of early lag phase (see Fig I 4.3)



because of the use of over-wide octaves.

## Comparison with Curry (1982)

Curry (1982) who undertook a more detailed study of the population dynamics of the same population of *T. retusa*, derived a logarithmic growth curve (Fig. I 4.4a), and detected a sequence of twin peaks from length-frequency histograms which were attributed to bi-annual spawning periods. The results of the present study suggest that there is only one major period of settlement (the autumn settlement of Curry 1982) and a sigmoidal growth curve, with a lag phase following settlement (Fig. I 4.4b).

All the size frequency distributions presented in this study, with the exception of the August sample were derived from a single grab sample. Rudwick (1962) criticizes the population structure produced by Percival (1944) because all the animals were collected from a very small area (totalling 0.023 $m^2$) which fails to reflect the fact that brachiopod distribution is patchy. To counter this possibility an additional 3 samples were also observed to check that the size range in a random sample of 30 sub-1 mm individuals did not differ significantly from the pattern observed in corresponding seasonal sample.

Differences in the method of collection may also account for some of the variation, Curry (1982) dredged his populations in contrast to this study in which the samples were collected by grab. It has been observed that the over sampling of a population of brachiopods in Lyttleton Harbour, first sampled by Percival (1944) has altered the population structure, the numbers of mature adults decreasing (D.E. Lee. *pers comm.* 1984). The destructive sampling of the *T. retusa* population structure by clam dredge began in March 1977, two months before Curry's samples. By May 1984 sampling had been conducted on an irregular basis for a period of seven years, the different population structures may therefore reflect different patterns of recruitment.

Confirmation of spawning periods and the possibility of brooding (which was not observed) awaits a full investigation of the reproductive cycle of *T. retusa*. Brooding of larvae in the mantle cavity just prior to metamorphosis (for reviews see Thayer, 1975; Noble & Logan, 1981) is a K-selective reproductive strategy resulting in a patchy distribution of larvae with a high proportion of post-larvae successfully attached near the adult. This resulting heterogeneous distrbution would complicate sampling of the population, and may account for the discrepencies between the estimated population structure of *T. retusa* of Curry (1982) and this study. It has been suggested (Comely, 1978) that the area acts as a sink for larvae from other areas in the Firth and it is possible that the presence of small individuals within this population throughout the year may be the consequence of allochthonous inputs.

### Rates of growth

Attempts to rationalize the size frequency polygons within the framework of established articulate brachiopod growth rates (Fig. I 4.5a) would require the presence of at least four major, isolated settlements a year, (falling at steadily lengthening periods from each successive collection), which do not coincide with any known environmental 'cues' and which also experience catastrophic rates of mortality. Neither the data on settlement density with a February peak, nor the results of a study of changes in oocyte size (M. James, unpublished data) which implicates a single winter spawning event, lend support to such a view and while such a pattern cannot be completely ruled out it is less satisfactory than a re-interpretation of the growth curve.

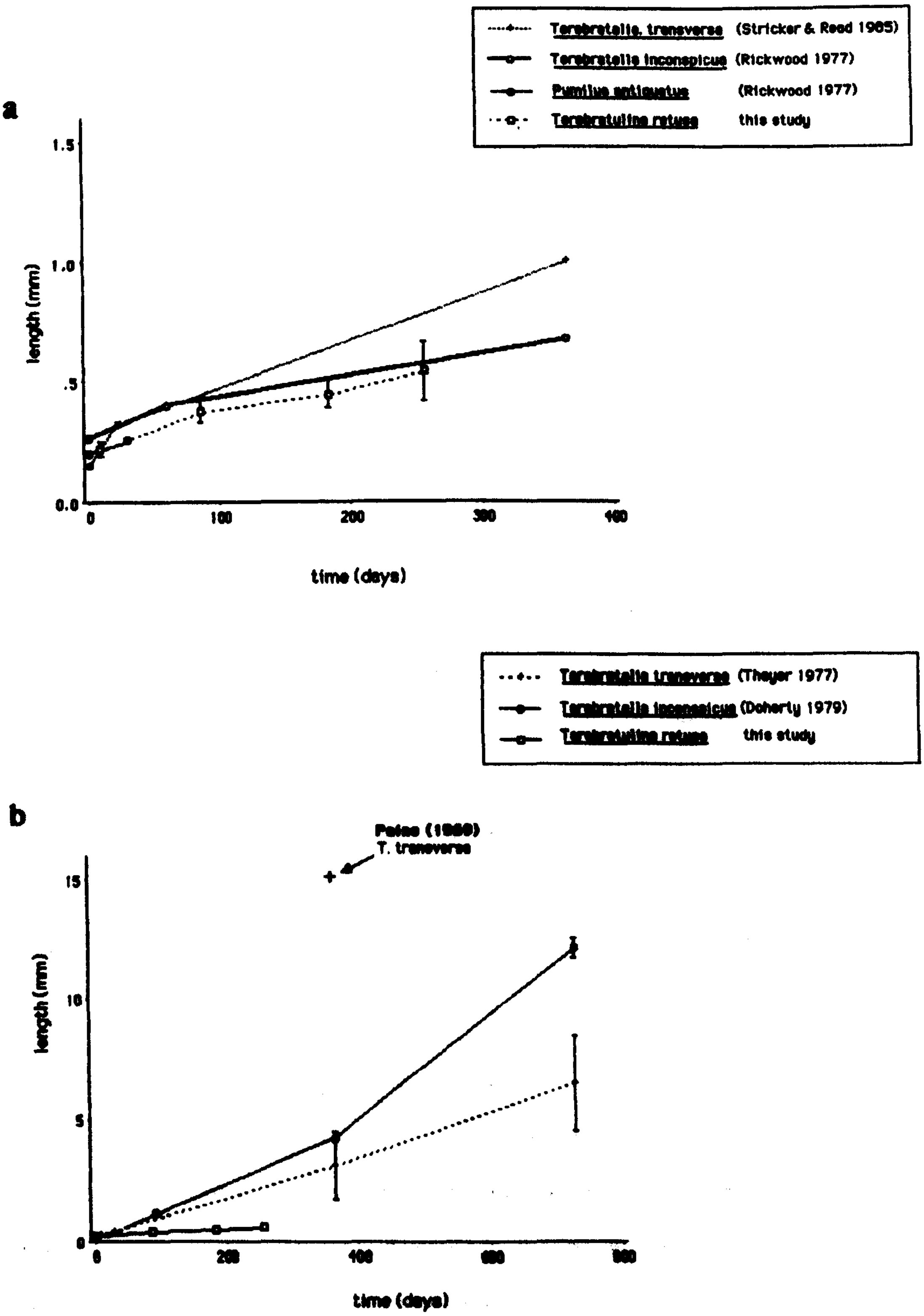
A sigmoidal growth curve destroys the previous concensus, evident for articulate brachiopod studies (Paine, 1969; Schumann, 1976; Rickwood, 1977; Thayer, 1977; Doherty, 1979; Curry, 1982), which was in broad agreement with the logarithmic growth model of Levington & Bambach (1969). A sigmoidal growth curve is, however in support of a parallel study by Muss (1973) on temperate water bivalves which stemmed from a similar concentration on very small post-larvae, in that case, quantitative investigations of meio-fauna (animals with a body-length of 0.2-2.0 mm) from the Oresund.

Muss (1973) noted that the date when bivalve spat 'appear' (and therefore

Figure I 4.5

Brachiopod growth rates

a) Laboratory studies; present field study included for comparison
b) Field studies



estimations of post-settlement age and growth rate) had depended in earlier work almost solely upon the size of meshes used in the sieving gear. Of eleven species examined by Muss, the maximum estimated growth rate was approximately 0.5 mm per month (*Venus striatula*) but more typical, were rates slightly in excess of 0.1 mm per month (shared by six species) (Muss, 1973: Table 4.).

It is dangerous to make direct comparison with bivalve mollusc studies as there are not only differences in the biology of the animals, but also in the methods employed in the analysis arising from the alternate use of settlement and recruitment (see Keough & Downes, 1982), recruitment describing the record of settlement events. The methods used to census newly metamorphosed bivalve molluscs are different because they are typically collected by sieve retention and many species have the potential for post-larval re-dispersal (eg. Sigurdsson *et al.*, 1976).

### Variations in growth rate

The increase in the width of the 0-year class cohort from November to May, (Fig. I 4.3) and the associated increase in standard deviation (Table I 4.1) probably represent variations in growth rate. The absence of a second cohort on the 0-2mm histogram (Fig. I 4.3) and the scattered tail of the same distribution, (partly an artifact of the extended scale), could also be attributed to the increased within-population variation during a rapid growth phase (Paine, 1969; Thayer, 1977; Doherty, 1979). Considerable variation in the incremental growth within a single cohort has also been observed by Rickwood (1977) and Doherty (1979).

### Comparison with other articulate brachiopod studies

Paine (1969) and Thayer (1977) estimated growth rate of *Terebratella transversa*. Paine's study only provides information on the *maximum* rate of growth, but the 0-year growth rates from both studies are much higher than the estimate for *T. retusa*. The results of both studies are equivocal, as in both cases, because of the constraints of discerning and measuring small animals in the field and they were restricted to animals greater than 1 mm. Studies which have monitored growth from settlement are (with the exception of Doherty, 1979) confined to the animals grown-on in aquaria (Fig. I 4.5a). The growth rates of laboratory reared brachiopods are similar to those estimated for *T. retusa* from this study (Fig. I 4.5a).

The detailed study by Doherty (1979) of *Terebratella (Waltonia) inconspicua* from a subtidal canyon wall (N. Island, New Zealand) is unique in that it included measurements of growth from settlement in both the field and laboratory and provides the strongest rebuttal to the hypothesis that the slow growth rate observed for *T. retusa* is universal amongst articulate brachiopods. Doherty placed out asbestos settlement panels which once settled by brachiopods were periodically recovered to measure growth increments over known periods of time. These results were contrasted with the growth rates of juveniles raised in the laboratory. Growth rates from the field population were rapid (Fig. I 4.5b) the mean size increasing from 0.188 mm at settlement to 1.11 mm after 90 days. The laboratory reared animals had substantially slower growth rates (27% of field populations after 24 months). If this 73% stunting is applied to the other laboratory results then these rates are elevated to the field estimates.

The ultra slow growth rate of *T. retusa* post-larvae has considerable implications for the autecology of this species, but with the limited information presently available it is difficult to predict how widespread the phenomenon of slow initial growth may be. There is a genuine disparity between the growth rates estimated for *T. retusa* from this study and the work of Doherty (1979).

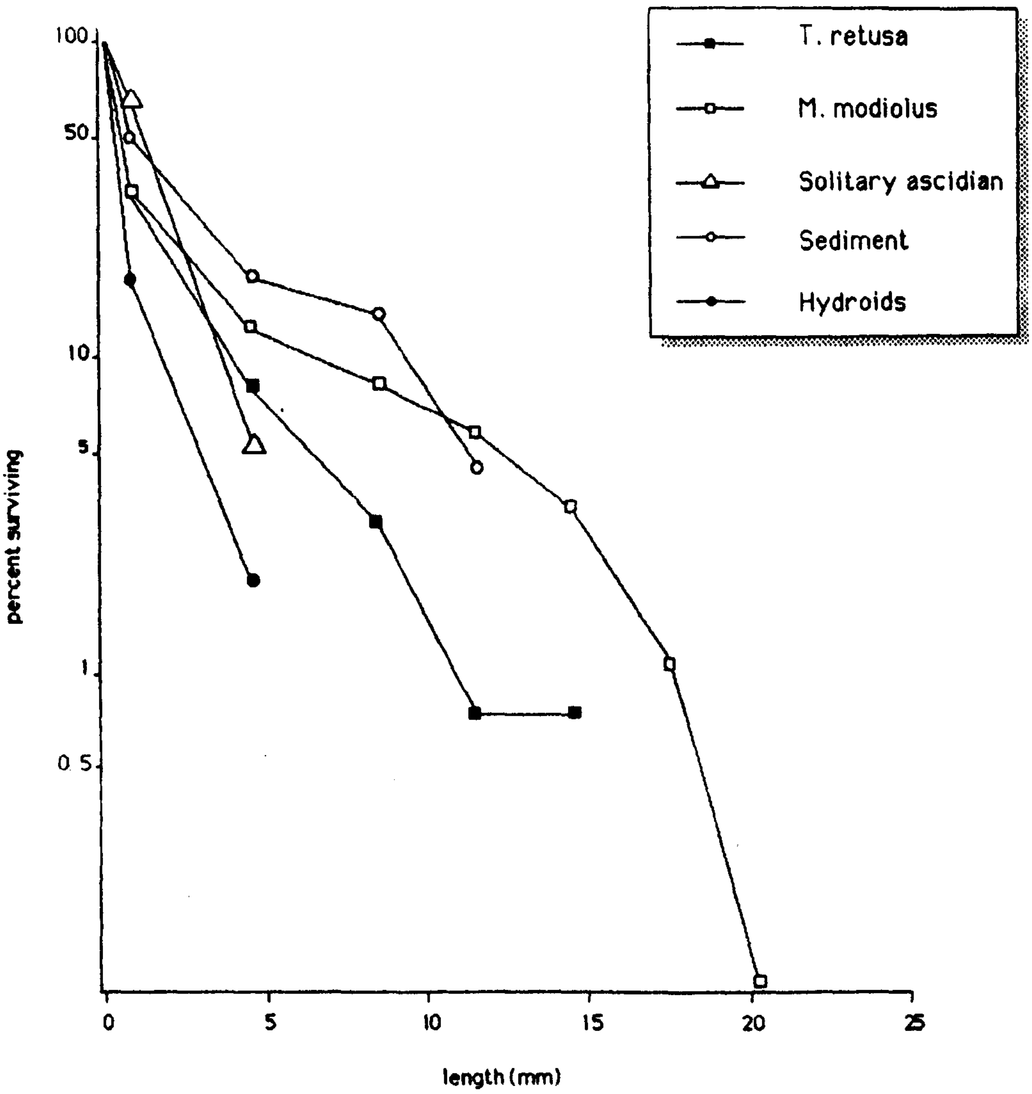
There are considerable environmental differences between a canyon wall in the shallow sub-littoral of North Island, New Zealand and endobyssate *M. modiolus* clumps at 180 m in a deep depression off the west coast of Scotland. However, there is no indication of nutrient or oxygen depletion in the water overlying the Firth of Lorn population, indeed the circulation pattern may serve to enrich these deep basins (Grantham *et al.*, 1983). *M. modiolus* from this community are stunted, reflecting sub-optimal conditions (Comely, 1978) and there is some evidence of stunting in *Terebratulina retusa*, compared with animals collected at 25 m. from rock walls in Loch Fyne (Argyll, west coast Scotland; Curry *pers comm.* 1986). It seems improbable that environmental controls alone could dictate such a marked difference in growth rates. Similarly, although *T. retusa* is a smaller brachiopod than the New Zealand *Terebratella (Waltonia) inconspicua*, the size differences are not great. There are differences in internal organisation and autecology (eg. settlement strategy, *T. inconspicua* settle on con-specifics and therefore clump, *T. retusa* on *M. modiolus*), but without further work the reasons for the disparity in growth rate will remain uncertain.

Although the growth rates of *T. retusa* and *T. (W.) inconspicua* are dissimilar, two common themes emerge from these studies. The first of these is that inclusion of juvenile post-larvae into the analyses of both bivalve and brachiopod growth rates (Muss, 1973; Doherty, 1979; Curry, 1982) alters the predicted growth pattern from a logarithmic decline to sigmoidal curve. This has profound implications for the autecology of articulate brachiopods. Also significant (because of the implications for the interpretation of population dynamics) is the apparent variation in growth rate of individuals from the same macro-environmental setting. Koehn (1984) in the discussion paper, singled out population growth rate (and the genetic component) as an area where our knowledge is "virtually non-existant", although such variation complicates the interpretation of length frequency diagrams.

Rates of mortality of *T. retusa* and other species (Doherty, 1979; Witman & Cooper, 1983) are strongly size dependant, being highest when the brachiopods are young (Fig. I 4.6). It is probable that rapidly-growing animals are at a selective advantage (with respect to predation, disturbance and/or the occupation of a habitat space). It is therefore possible that although slow growing brachiopods dominate the 0-year class, it is the fast growing 'super brachiopods' which are not analysed that are the important members of the adult

Figure I 4.6

Mortality curves for T. retusa with different attachment sites



breeding population. In such a case, depending on the level at which a population was analysed, different interpretations would be produced of the dynamics of the same population. That such a fanciful interpretation can be considered to explain the disparity between this study and the earlier work of Curry (1982) demonstrates our lack of understanding of growth rate, and the important role that untested assumptions play in our interpretation of data.

Assuming that a slow 0-year class growth rate is a feature common to many articulate brachiopods, (which cannnot be determined until further work has been undertaken) then it may have been a constraint in the evolution of paedomorphic brachiopods. Paedomorphs have had a long geological history (Racki 1985) occuring predominately today in the warm waters (see Asgaard & Stentoft, 1985 for a review of distribution) where they are a common member of the cryptic fauna, typically of platey corals. Jackson *et al.* (1971: 625) state that "competition for space on coral undersurfaces is extremely intense, and almost every square centimeter of older sections of the larger plate like corals is usually occupied." In space limited environments an *r*-selective strategy is necessary for poor spatial competitors. It could be argued that paedomorphic brachiopods are the expression of an adaptive requirement for early reproduction, constrained by a slow initial growth rate. While it is large brachiopods which appear to be better spatial competitors (Doherty, 1979), in these environments all the articulates are paedomorphic. If these species had the ability to grow to 15 mm within a year of settlement such size constraints would be absent.

Until such time as an accurate method for ageing living shells is developed or measurement of the growth rate from settlement of individuals *in situ* is combined with studies of the genetic determinants of growth, it will not be possible to adequately interpret rates of growth and by implication the dynamics of living populations.

### TABLE I 4.4a

### Substrate selectivity, numbers of *T. retusa* in size groups

| SUBSTRATE | SIZE GROUPS (mm.) .256 | .340 | .367 | .403 | .43 | .47 | .52 | .588 | .73 | .95 | 1.24 | 1.69 | 2.8 | 5.87 | 10.0 | 15.0 | 20 | Total | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Modiolus* | 67 | 75 | 86 | 51 | 79 | 51 | 53 | 51 | 58 | 56 | 48 | 43 | 32 | 47 | 31 | 36 | 25 | 891 | 58.0 |
| crevice | - | - | - | - | - | 1 | - | 1 | - | 1 | - | 1 | - | - | - | - | - | 4 | 0.3 |
| perost. | - | - | 2 | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | - | - | - | - | 17 | 1.1 |
| /hydroid | - | 1 | - | 2 | - | 1 | 1 | 1 | 1 | - | - | 2 | 3 | 1 | - | - | - | 12 | 0.9 |
| /poly. tube | - | - | - | 1 | - | - | - | - | - | 2 | - | - | - | - | - | 2 | 1 | 6 | 0.4 |
| Periostracal hair | 4 | 4 | 2 | 2 | 3 | 9 | 8 | 7 | 3 | 1 | 5 | 1 | 1 | 1 | - | - | - | 51 | 3.3 |
| Ascidian | 1 | - | 4 | - | 8 | 3 | 11 | 10 | 11 | 10 | 18 | 17 | 25 | 18 | 1 | - | - | 137 | 8.9 |
| *T. retusa* | 2 | - | 3 | 3 | 3 | 8 | 4 | 5 | 8 | 6 | 5 | 10 | 8 | 6 | 7 | 2 | 1 | 80 | 5.3 |
| /poly. tube | - | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | 2 | 0.1 |
| Hydroid | 5 | 3 | 5 | 3 | 2 | 3 | 3 | 2 | 5 | 1 | 3 | 4 | 8 | - | 1 | - | - | 48 | 3.1 |
| /mod. | - | - | - | 2 | 3 | 1 | - | 1 | 2 | 1 | 1 | 5 | 2 | 2 | - | - | - | 20 | 1.3 |
| Polychaete tubes | | | | | | | | | | | | | | | | | | | |
| Carbonte | 4 | 7 | 5 | 1 | 5 | 4 | 5 | 3 | - | - | 3 | 3 | - | - | - | - | - | 43 | 2.8 |
| /Mod | - | - | - | 1 | 2 | 3 | 3 | - | - | 1 | - | 1 | - | - | - | - | - | 11 | 0.7 |
| (Dead) | 1 | - | 1 | - | 1 | 3 | - | 1 | - | 1 | - | 2 | 4 | 3 | - | - | - | 17 | 1.1 |
| Sediment | 1 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 3 | 0.2 |
| *Filograna* | 1 | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | 3 | 0.2 |
| Bryozoa | - | 1 | 1 | - | 4 | 1 | 1 | 3 | - | 3 | 1 | - | - | - | - | - | - | 14 | 0.9 |
| planar | 1 | - | 2 | - | - | - | 1 | - | - | 1 | - | - | - | - | - | 1 | - | 5 | 0.3 |
| arbourescent | - | - | - | - | 1 | 1 | 1 | 1 | - | - | 1 | 1 | 1 | - | - | - | - | 7 | 0.5 |
| tabular | - | - | 2 | 1 | - | 1 | - | - | 1 | - | 1 | - | - | - | - | - | - | 6 | 0.4 |
| *Anomia* | 3 | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 6 | 0.4 |
| *Musculus* | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | 0.1 |
| *Verruca* | - | 1 | 3 | - | 3 | - | 3 | 2 | 1 | 1 | - | - | - | - | - | - | - | 14 | 0.9 |
| *Balanus crenatus* | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 0.1 |
| Poly pachment | - | - | - | - | - | - | - | - | - | 1 | - | 1 | 1 | 1 | - | - | - | 4 | 0.3 |
| Sponge | - | - | - | - | - | - | 2 | 2 | - | - | 1 | - | - | - | - | - | 1 | 6 | 0.4 |
| Sediment | - | - | 1 | 1 | 4 | 2 | 1 | - | 2 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | - | 22 | 1.4 |
| Unknown | - | - | - | - | - | - | - | 1 | - | 1 | 4 | 4 | 6 | 10 | 4 | 1 | 2 | 34 | 2.2 |
| TOTAL | 91 | 94 | 117 | 71 | 130 | 96 | 104 | 100 | 99 | 92 | 103 | 100 | 100 | 99 | 55 | 52 | 30 | 1536 | |

### TABLE I 4.4b

### Substrate selectivity, numbers of *M. phaseolinus* in size groups

| SUBSTRATE | SIZE GROUPS (mm.) .256 | .340 | .367 | .403 | .43 | .47 | .52 | .588 | .73 | .95 | 1.24 | 1.69 | 2.8 | 5.87 | 10.0 | 15.0 | 20 | Total | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Modiolus* | 2 | 8 | 6 | 5 | 6 | 8 | 10 | 16 | 21 | 42 | 50 | 29 | 25 | 13 | 8 | 2 | - | 256 | 44.5 |
| crevice | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 0.2 |
| perost. | - | - | - | - | - | - | 1 | 1 | - | - | 3 | 1 | 1 | - | - | - | - | 6 | 1.4 |
| /hydroid | - | - | - | - | 1 | 1 | - | - | 2 | 1 | 3 | 5 | - | 1 | - | - | - | 13 | 2.3 |
| /poly. tube | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | 0.2 |
| Periostracal hair | - | - | - | - | - | - | 1 | - | 1 | - | - | 2 | 2 | 1 | - | - | - | 13 | 2.3 |
| Ascidian | - | 1 | 2 | 1 | 2 | 3 | 3 | 5 | 10 | 10 | 17 | 9 | 13 | 6 | 3 | - | - | 79 | 13.7 |
| *T. retusa* | - | - | - | - | - | - | 1 | - | 2 | 4 | - | 3 | 1 | - | - | - | - | 11 | 1.9 |
| /poly. tube | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 0.0 |
| Hydroid | - | - | 1 | - | 5 | - | - | 3 | 1 | 7 | 13 | 9 | 2 | 2 | 1 | 1 | - | 45 | 7.8 |
| /mod. | - | - | - | - | - | 1 | - | 1 | - | 1 | 4 | - | 3 | - | - | - | - | 10 | 1.8 |
| Polychaete tubes | | | | | | | | | | | | | | | | | | | |
| Carbonate | - | - | 1 | - | - | - | - | - | - | 2 | 1 | 1 | - | 2 | - | - | - | 0 | 0.0 |
| /Mod | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 0.0 |
| (Dead) | 1 | - | - | - | - | - | - | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | 6 | 1.0 |
| Sediment | - | - | - | - | - | - | - | - | 1 | - | 4 | 1 | 1 | 1 | - | - | - | 8 | 1.4 |
| *Filograna* | - | - | - | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | 2 | 0.3 |
| Bryozoa | - | - | - | - | - | - | 3 | - | - | 2 | 1 | 1 | 1 | 1 | - | - | - | 9 | 1.6 |
| planar | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 2 | 0.2 |
| arbourescent | - | - | - | - | - | - | - | - | - | - | 3 | 3 | 2 | - | - | - | - | 8 | 1.4 |
| tabular | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 0.0 |
| *Anomia* | - | - | - | - | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | 3 | 0.5 |
| *Musculus* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 0.0 |
| *Verruca* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 0.0 |
| *Balanus crenatus* | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 1 | 0.2 |
| Poly pachment | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 0.2 |
| Sponge | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 2 | - | - | - | 3 | 0.5 |
| Sediment | - | - | - | - | - | 1 | - | - | - | 2 | 3 | 4 | 1 | 1 | - | - | - | 12 | 2.1 |
| Unknown | - | 3 | - | 1 | 1 | 3 | 1 | 1 | 1 | 3 | 5 | 4 | 8 | 16 | 5 | - | - | 47 | 8.2 |
| TOTAL | 4 | 11 | 10 | 7 | 14 | 17 | 22 | 31 | 47 | 83 | 117 | 75 | 66 | 47 | 17 | 3 | - | 575 | |

## TABLE I 4.5

### Settlement summary

(*Terebratulina retusa*, *Modiolus phaseolinus* & *Crania anomala*.

| | *T. retusa* | | | | *M. phaseolinus* | | | | *C. anomala* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L(max) | L(mean) | N | % | L(max) | L(mean) | N | % | L(max) | L(mean) | N | % |
| *Modiolus* | 20.9 | 2.04 | 891 | 58.0 | 12.3 | 1.38 | 256 | 44.5 | 13.3 | 3.148 | 110 | 86.6 |
| crevice | 1.32 | 0.766 | 4 | 0.3 | | 4.27 | 1 | 0.2 | | 0.917 | 1 | 0.8 |
| perost. | 2.20 | 0.715 | 17 | 1.1 | 1.87 | 1.31 | 6 | 1.0 | 8.7 | 3.392 | 4 | 3.1 |
| /hydroid | 2.52 | 1.076 | 12 | 0.9 | 3.71 | 1.28 | 13 | 2.3 | | | - | |
| /poly. tube | 16.0 | 6.565 | 6 | 0.4 | | 2.5 | 1 | 0.2 | | | - | |
| Periostracal hair | 5.73 | 0.667 | 51 | 3.3 | 1.98 | 0.957 | 13 | 2.3 | | | - | |
| Ascidian | 8.40 | 1.570 | 137 | 8.9 | 7.18 | 1.626 | 79 | 13.7 | | | - | |
| *T. retusa* | 16.9 | 2.06 | 80 | 5.3 | 1.76 | 1.048 | 11 | 1.9 | | | - | |
| /poly. tube | | | 2 | 0.1 | | | - | | | | - | |
| *C. anomala* | - | - | - | - | - | - | - | - | | | 3 | |
| Hydroid | 5.88 | 0.95 | 48 | 3.1 | 10.4 | 1.522 | 45 | 7.8 | | | - | |
| /mod. | 5.19 | 1.31 | 20 | 1.3 | 2.65 | 1.286 | 10 | 1.8 | | | - | |
| Polychaete tubes | | | | | | | | | | | | |
| Carbonate | 4.96 | 0.700 | 43 | 2.8 | 4.96 | 1.834 | 7 | 1.2 | | | | |
| /Mod | 1.23 | 0.542 | 11 | 0.7 | | | | | | | - | |
| (Dead) | 4.89 | 1.608 | 17 | 1.1 | 1.50 | 0.804 | 6 | 1.0 | | | - | |
| Sediment | 4.27 | 1.822 | 3 | 0.2 | 2.94 | 1.308 | 8 | 1.4 | | | - | |
| *Filograna* | 0.611 | 0.442 | 3 | 0.2 | 0.86 | 0.734 | 2 | 0.3 | | | - | |
| Bryozoa | 1.01 | 0.575 | 14 | 0.9 | 2.17 | 0.944 | 9 | 1.6 | | | - | |
| planar | 11.5 | 2.58 | 5 | 0.3 | 0.57 | 0.377 | 2 | 0.2 | | | 1 | 0.8 |
| arbourescent | 1.85 | 0.885 | 7 | 0.5 | 2.79 | 1.531 | 8 | 1.4 | | | - | |
| tabular | 1.12 | 0.564 | 6 | 0.4 | | | - | | | | - | |
| *Anomia* | 1.06 | 0.446 | 6 | 0.4 | 0.83 | 0.697 | 3 | 0.5 | | | - | |
| *Musculus* | | | 1 | 0.1 | | | - | | | | - | |
| *Verruca* | 0.844 | 0.471 | 14 | 0.9 | | | - | | | | - | |
| *Balanus crenatus* | 0.330 | 0.266 | 2 | 0.1 | | | 1 | 0.2 | | | - | |
| Poly pachment | 4.20 | 2.027 | 4 | 0.3 | | | 1 | 0.2 | | | - | |
| Sponge | 17.8 | 3.513 | 6 | 0.4 | | | 3 | 0.5 | | | - | |
| Sediment | 14.4 | 2.640 | 22 | 1.4 | 4.05 | 1.401 | 12 | 2.1 | | | 2 | 1.6 |
| Unknown | 20.1 | 4.703 | 34 | 2.2 | | | 47 | 8.2 | | | 6 | 4.7 |
| TOTAL | 20.9 | | 1536 | | | | 575 | | | | 130 | |

## TABLE I 4.3

### Substrate groupings combined in SRM analysis

| | |
|---|---|
| *Modiolus*<br>crevice<br>periostracum<br>/hydroid<br>/polychaete<br>tube | } *Modiolus* |
| Periostracla hair | Periostracla hair |
| Hydroid<br>/modiolus | } Hydroid |
| Polychaete tubes<br>Carbonate<br>/Modiolus<br>(Dead)<br>Sediment<br>Filograna | } *Pomatoceros* |
| Bryozoa<br>planar<br>arbourescent<br>tabular | } Bryozoa |
| Solitary ascidian | Solitary ascidian |
| *Verruca*<br>*Balanus* | } Barnacles |
| *Terebratulina*<br>/polychaete tubes | } *Terebratulina* |
| Sediment | Sediment |
| Unknown | Unknown |
| *Anomia*<br>*Musculus*<br>'Parchment like' polychaete tube<br>Sponge | } Ignored |

## 4.3 SETTLEMENT

### I 4.3.1 METHODS

Substrate related mortality (SRM) is defined as mortality which is a direct or indirect consequence of the failure of the substrate. Direct consequences include die-back and shedding of substrate, eg. the loss of *M. modiolus* periostracum; indirect SRM includes the removal of substrate by either predation or competition and substrate failure caused by epifaunal overloading (e.g. the inability of a small hydroid to support the weight of an adult *T. retusa*).

No description of substrates was attempted prior to data collection. A total of 37 substrate types were logged, but of these only one species (*Crania anomala*) was attached conspecifically, six were incorporated within the remaining 30 (Table, I 4.4); for most analyses these were further combined to form a total of 10 ecologically distinct substrate types (Table I 4.3). Although unable to re-attach once settled (Thayer, 1975), the genus *Terebratulina* is notable amongst brachiopods for the variety of attachment strategies, as expressed in the variable development of pedicle rootlets in this species (Surlyk, 1974; see Curry, 1981 for an extreme example). The ability of the rootlets to extend beyond, or penetrate through one substrate and attach to another was recognized in the delimination of substrate types. Therefore *T. retusa* attatched to an unstable substrate 'A', in very close proximity to a larger 'more stable' substrate 'B' was for the purposes of substrate related mortality considered to be functionally attached to the latter and was recorded as 'B/A' (ie *T. retusa* attached to the base of a hydroid was classed as *M. modiolus*/hydroid).

An accurate estimation of substrate selection by brachiopod larvae was not possible for two reasons. As with all sessile epi-fauna, substrate selection occurs at the larval stage. Mortality is strongly size dependant (Doherty, 1979; Witman & Cooper, 1983) therefore settlement strategies can only be determined experimentally or under unusual circumstances from 'wild' populations (where settlement is discrete and the substrate is sampled before any significant mortality has occurred). It is probable that even with the most rigourous methodology the results will under-estimate the density of settlement on complex surfaces where the very small post larvae are difficult to see. The problems associated with estimating the area of a heterogeneous surface are great and (as fractual mathematics demonstrates) become exaggerated when dealing with the settlement of small animals.

The problems of estimating substrate selectivity were circumvented by analysing trends in a combined sample incorporating all the data logged from four seasonal samples (without correcting for sample size). The substrates and lengths of *T. retusa* were split into 17 size groups, with approximately 100 individuals in the first 14 (length less than 2.8 mm) and 50, 50 & 30 in the final three groups (Table I 4.4). No animals of the same measured length were put into seperate groups and the wide variations in the splits of sub 0.5 mm animals (Table I 4.4) reflect the large number of individuals of identical measured length. The numbers for each split were recalculated as pecentage utilization of various substrates and by plotting the relative proportions of the total substrate in each of the subgroups it was possible to establish trends in substrate related mortality, independant of pre-sampling losses.

To enable comparison with *T. retusa*, all other epifaunal species were split into the same 17 size groups, but only the mytilid *Modiolus phaseolinus* (n = 575) occured in sufficiently large numbers for meaningful comparison.

### I 4.3.2 RESULTS

The density of settlement of *T. retusa* cannot be accurately estimated as it is not possible to evaluate the surface area of an ellipsoid analytically and because clumping reduces the potential area of settlement making the area more difficult to interpret. Settlement density was therefore expressed as average number of *T. retusa* attached per *M. modiolus*, with no correction for area. The absolute numbers of *T. retusa* per *M. modiolus* is broadly related to the size of the latter (Fig. I 4.7), overlaid by absolute settlement density

Figure I 4.7

Density of T. retusa on individual M. modiolus from all grab samples

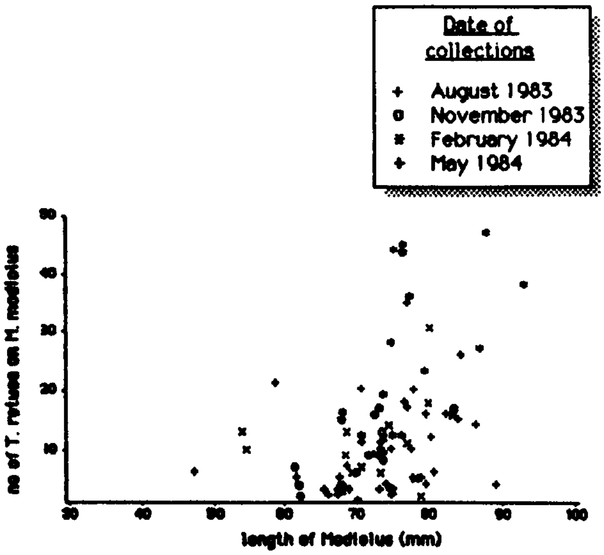
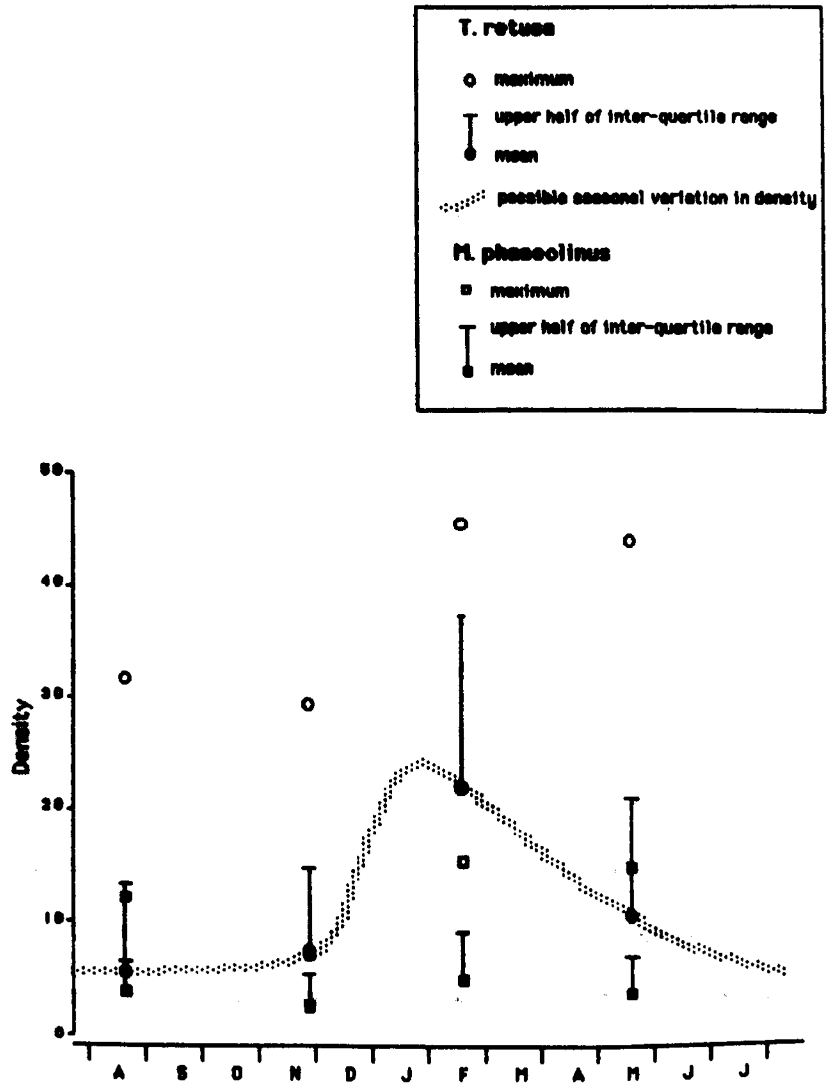


Figure I 4 .8

Seasonal changes in density of T. retusa and M. phaseolinus from grab samples



which was highest in the Febuary sample (Fig. I 4.7, 4.8; Table I 4.2).

The peak settlement density of *T. retusa* is unlikely to be a collection artifact as it is not paralleled by *M. phaseolinus* (Fig. I 4.8) or by the other epifauna (Table I 4.2).

The maximum recorded density of *T. retusa* on a single *M. modiolus* (47; Fig. I 4.8) is only slightly higher than the 30 recorded by Curry (1982). As the mean number per *M. modiolus* was considerably higher than that of Curry (15 per *M. modiolus* as against 2–3 observed by Curry, 1982) it is possible (by extrapolation) that *T. retusa* from the Firth of Lorn may reach densities of 150 per *M. modiolus*. A single 0.1 $m^2$ grab sample from the Feb. 1984 sampling trip contained 436 brachiopods giving a total density of 4360/$m^2$. The mean density for the whole year was 2466/$m^2$ , but this was mainly 0–year class individuals, the density of animals > 6 mm in length is approximately 100/$m^2$.

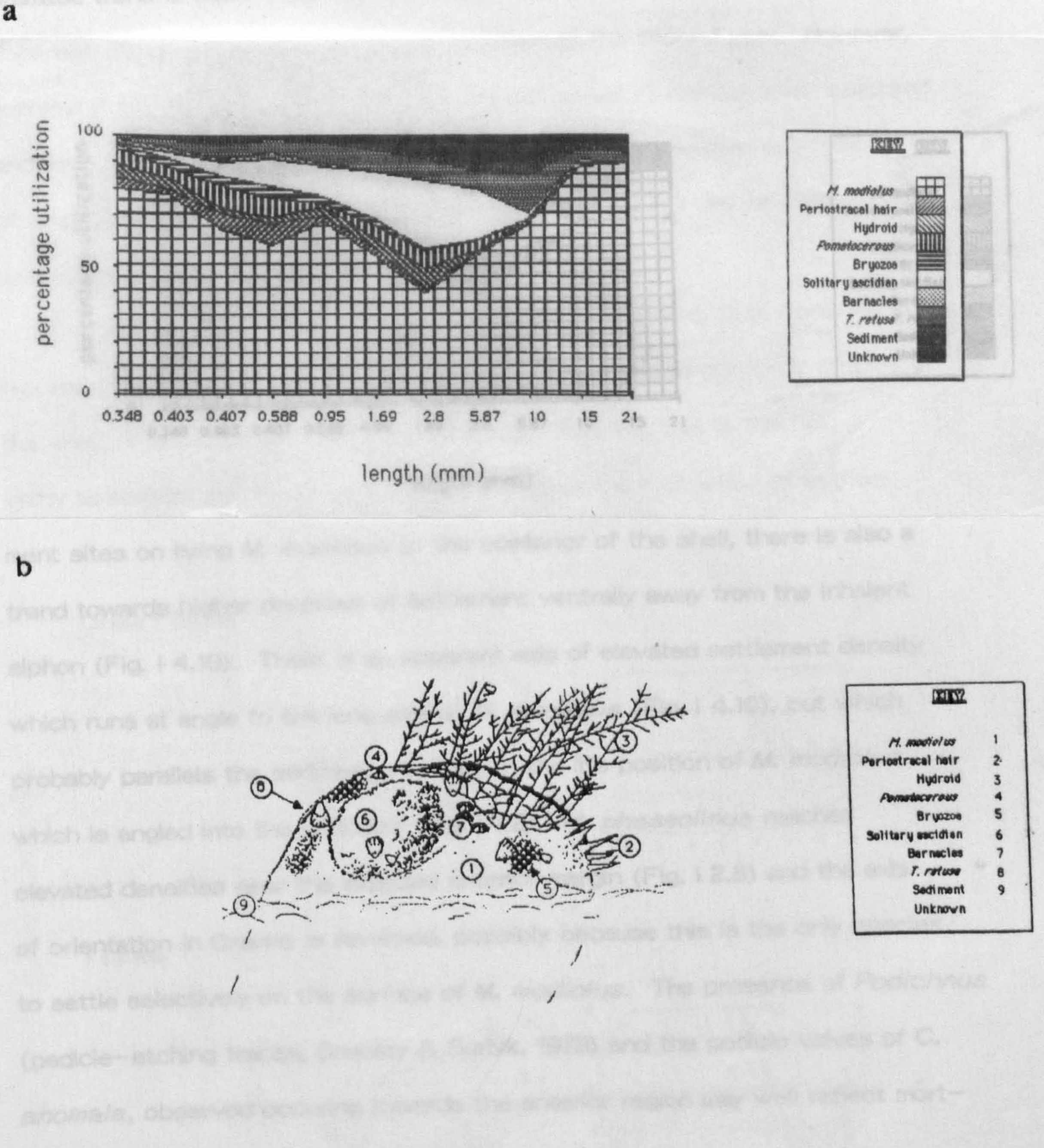
Although it was not possible to analyse substrate selectivity, the wide range of substrates utilised by both *T. retusa* and *M. phaseolinus* does not require the rejection of the hypothesis of an absence of selection in either of these species. *Crania anomala*, (which is believed to have an extended planktonic phase; Rowell, 1960) appears to be highly selective, 98% of the logged animals were cemented to *M. modiolus* (Table I 4.4).

Excluding those *T. retusa* whose site of attachment is unknown, there is a clear distinction between the survivorship curve (Fig. I 4.6) for *T. retusa* settled on *M. modiolus* and other substrates. This contrast is reflected in the trends of substrate utilisation.

The percentage substrate utilisation for the 17 size splits, plotted for the 10 ecologically equivalent substrates (Fig. I 4.9) indicates a fall in the percentage of *T. retusa* attached to *M. modiolus* from settlement (77%) to a length of > 1.69 mm (32%). This decline is naturally contrasted with a concomitant rise in the percentage attached to other substrates, most notably the tests of solitary ascidians which account for 8.9% of total substrate, rising from approximately 4% for sub–5 mm animals to 25% in the size split 1.69–2.8 mm

Figure I 4.9

a) Relationship between substrate, length and mortality
b) Diagrammatic representation of potential substrates utilized by T. retusa



thereafter declining rapidly (Table I 4.4a; Fig. I 4.9).

This transition in substrate utilization is illustrated by a distinctive inflection (at > 1.69 mm) turning about a former decline in percentage survival on *M. modiolus* (Fig. I 4.9). The decline may in-part reflect an undersampling of newly settled post-larvae on complex substrates, as a similar, although less dramatic trend is seen in *Modiolus phaseolinus* (Table I 4.4b) and there is an apparent rise in settlement density on ascidians in the second year. However, extreme care was taken to ensure that all post-larval *T. retusa* were collected and for > 0.5 mm individuals the author believes that the relative proportions of substrate utilization are accurate, although *M. modiolus* may be overstated as a substrate in smaller individuals.

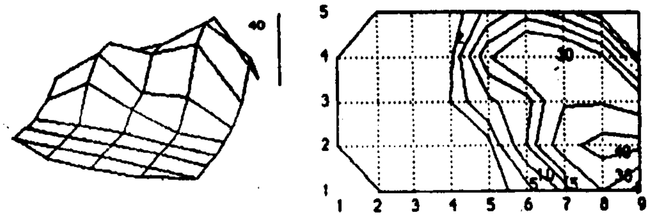
The clumping of *M. modiolus* has been long recognized, (e.g. Ford, 1927) as has the concomitant restriction of epifauna to the exposed posterior regions of the shell, (Fig I 4.10, see also Fig I 2.5, I 2.8, I 2.9) but this is the first study to analyze positional density. In addition to the restriction of settlement sites on living *M. modiolus* to the posterior of the shell, there is also a trend towards higher densities of settlement ventrally away from the inhalent siphon (Fig. I 4.10). There is an apparent axis of elevated settlement density which runs at angle to the long axis of *M. modiolus* (Fig. I 4.10), but which probably parallels the sediment interface in the life position of *M. modiolus* which is angled into the sediment (Fig. I 1.2). *M. phaseolinus* reaches elevated densities near the exposed anterior margin (Fig. I 2.8) and the axis of orientation in *Crania* is reversed, possibly because this is the only species to settle selectively on the surface of *M. modiolus*. The presence of *Podichnus* (pedicle-etching traces, Bromley & Surlyk, 1973) and the pedicle valves of *C. anomala*, observed occuring towards the anterior region may well reflect mortality as a consequence of re-orientation or burial.

The distribution of *T. retusa* on particular substrates is typically random, a restricted distribution (e.g. periostracal hairs) reflecting a non-random distribution of the substrate, significantly *Terebratulina* is one of the

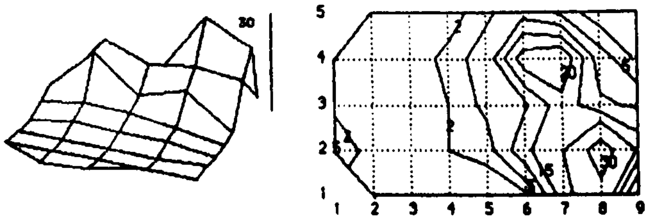
Figure 4.10

Contour and density plots of _T. retusa_ attachment sites on the _M. modiolus_ (left and right valves combined).
Details of positions are given in Fig. I 1.3 & details of the orientation of _M. modiolus_ in Fig. I 1.2.

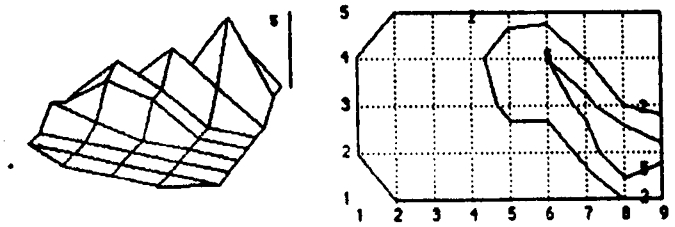
**< 0.5 mm**



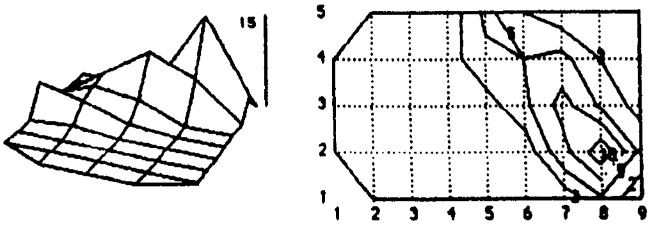
**0.5 mm - 1.5 mm**



**1.5 mm - 7.0 mm**



**> 7.0 mm**



few brachiopod genera which is able to attach to soft materials, such as algal stems, ascidians and agglutinated worm tubes (Jeffreys, 1863, Rudwick, 1965).

### I 4.3.3 DISCUSSION

It was thought that substrate-related mortality (SRM) would be the major cause of death of *T. retusa* from the Firth of Lorn. Doherty (1979: 334) was probably the first author to recognize and comment upon mortality of brachiopods as a consequence of substrate failure "when an individual at the base of a cluster dies, or is torn loose ..(con-specifically attached brachiopods)...are simultaneously dislodged and will also die." An alternative source of indirect mortality, the cropping of the substrate has been noted by Witman & Cooper (1983) who recovered polychaete tubes with small brachiopods still attached, from the stomachs of cod.

The hypothesis that SRM would be the major source of mortality in this population was based on a number of observations and assumptions:-

Observations

a) Adult *T. retusa* are almost totally restricted to direct attachment to *M. modiolus*, while juvenile *T. retusa* exploit a wide range of substrates.

b) Substrate failure typically leads to death of articulate brachiopods (Doherty, 1979) if they fall into a fine clogging sediment.

Assumptions

a) predation is not a major source of mortality in articulate brachiopods

b) because the community was well below the photic zone competition and disturbance are not significant sources of mortality.

c) *M. modiolus* is the most stable substrate because the latter have shorter lifespans, are subject to selective cropping, and in many cases are not sufficiently robust to support a fully-grown brachiopod, and will fail.

Figure I 4.11 illustrates the predicted change in substrate utilization with increasing age, based on the SRM hypothesis. The hypothesis predicts that there is a gradual rise in the dominance of *M. modiolus* as substrate for *T. retusa*, as those animals attached to other substrates, experience elevated levels of mortality, corresponding with die-back and substrate failure.

The predictions were not supported by analysis of the data. The increasing dominance of *M. modiolus* is only apparent after *T. retusa* reaches lengths in excess of 1.69 - 2.8 mm, prior to this *M. modiolus* is sub-optimal relative to most other substrates (Fig. I 4.9). The pattern of the data suggests that *T. retusa* reaches a size refuge at 2 mm from a source of mortality more extreme than the selective cropping, die back, and failure, believed to account for mortality of brachiopods attached to other substrates (assumption c). The results echo the view of Richards and Bambach (1975: 786) that a length of 2 mm is "apparently the critical size for the survival of many brachiopds".

The failure of the predictions to accurately describe the pattern of substrate utilization suggests that one or more of the assumptions upon which the hypothesis is based is incorrect.

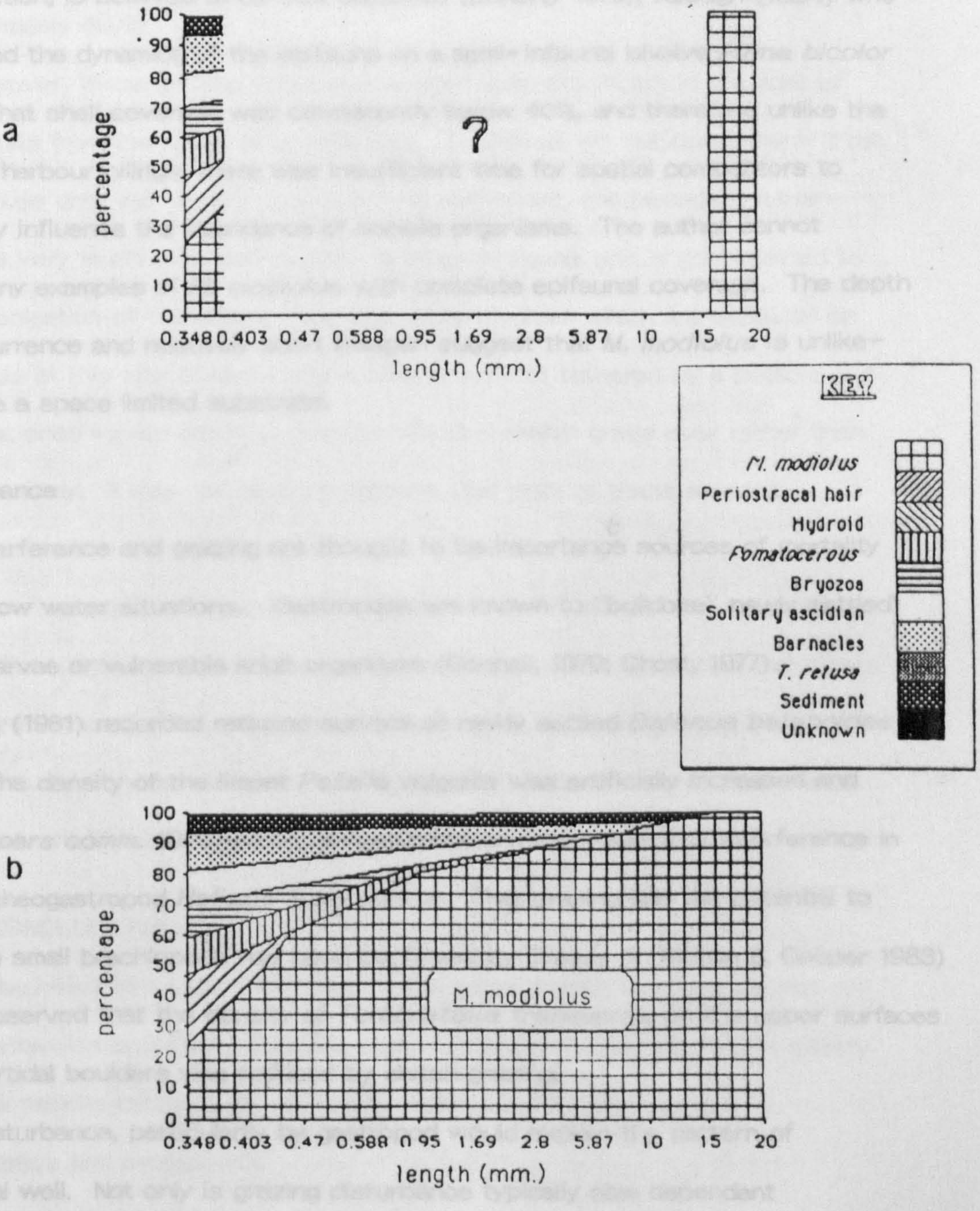
### Predation

Indirect evidence of predation has been supplied by a number of authors, (asteroids, Young, 1926; crabs, Atkins, 1960, Paine, 1969; gastropods, Poulicek 1981; fish, Couthouy, 1838; Habib, 1977, Witman & Cooper 1983). Asteroids have been observed to eat brachiopods under experimental conditions (McCammon, 1972; Thayer, 1981) and in the field (Witman & Cooper, 1983; Witman *pers comm.*). Although reports of gastropod predation on brachiopods are relatively common in the palaeonotolgical literature (eg. Smith *et al.*, 1985), only Logan (1977; 79), Noble & Logan (1981) and Witman & Cooper (1983) have provided evidence of such predation of Recent articulates.

Curry & Ansell (1986) demonstrate that brachiopods provide a poor rate of return to most predators and Thayer (1981, 85) further suggests that the tissues of brachiopods may be noxious and only consumed as a last resort.

Figure I 4.11

Theoretical implications of substrate related mortality for substrate utilisation
a) Substrate utilisation of post-larvae & adults
b) Theoretical decline of T. retusa attached to substrates with limited lifespans



Evidence for predation as a major source of mortality is therefore equivocal and furthermore it would seem unlikely that selective predation could account for the selective mortality of small < 2 mm *T. retusa* attached to the surface of *M. modiolus*.

## Competition

Although mortality of articulate brachiopods, as a consequence of spatial competition, is believed to be size selective (Doherty 1979), Keough (1984) who examined the dynamics of the epifauna on a semi-infaunal bivalve *Pinna bicolor* found that shell coverage was consistently below 40%, and therefore unlike the nearby harbour pilings, there was insufficient time for spatial competitors to strongly influence the abundance of sessile organisms. The author cannot recall any examples of *M. modiolus* with complete epifaunal coverage. The depth of occurrence and relatively short lifespan suggest that *M. modiolus* is unlikely to be a space limited substrate.

## Disturbance

Interference and grazing are thought to be importan~~ce~~t sources of mortality in shallow water situations. Gastropods are known to "bulldoze" newly settled post-larvae or vulnerable adult organisms (Connell, 1970; Choat, 1977). Connell (1961) recorded reduced survival of newly settled *Balanus balanoides* when the density of the limpet *Patella vulgata* was artificially increased and Peck (*pers comm.* 1986) has observed a similar (inter-specific) interference in the archeogastropod *Haliotis tuberculata*. That grazing has the potential to remove small brachiopods has been confirmed by Thayer (in Witman & Cooper 1983) who observed that the density of *Terebratalia transversa* on the upper surfaces of intertidal boulders was reduced by chiton grazing.

Disturbance, particularily by gastropod would explain the pattern of survival well. Not only is grazing disturbance typically size dependant (Connel, 1970, Choat, 1977), thereby explaining the survival of > 2 mm long animals, but is it also substrate selective, Akpan (1981) notes that the chiton

*L. asellus* tend to avoid grazing near complicated worm encrustations and were not observed to graze across bryozoan colonies.

Grazing disturbance was not thought to be a significant control in the Firth of Lorn, because grazing pressure is much reduced below the photic zone (where the highly productive algal films occur). The small polyplacophoran *Lepidopleurus asellus* is the only important grazing organism in the *Modiolus*–brachiopod community of the Firth of Lorn and only occurs in densities of approximately 40/m$^2$.

However, these grazing pressures appear more significant in the light of the results from the study of growth rate. *T. retusa* will not reach the > 2 mm size refuge until the second year following settlement, the period of vulnerability is very much extended relative to other epifauna, and is compounded by the organisation of the animal. The two other bivalves which are epifaunal on *Modiolus* at this site (*Crania* and *Anomia*), are not tethered by a pedicle, but have flattened valves which *L. asellus* would probably graze over rather than bulldoze away. It may not be a coincidence that both of these species penetrate further into shallow water than *T. retusa*.

Selective mortality reduces the numbers of *T. retusa* attached directly to the surface of *M. modiolus* (the substrate of reproductively mature individuals) and therefore as grazing pressures increase (with decreasing depth) a stage will eventually be reached when none of these *T. retusa* survive this crucial phase, at which point the breeding population ceases to exist.

### I 4.4 CONCLUSIONS

The belief in a rapid early growth rate for articulate brachiopods has drawn attention away from the early post-settlement phase of the life history when all sessile epifauna are especially vulnerable to disturbance, interference and overgrowth.

The perceived distribution of mature articulate brachiopods is a reflection of the survival of the vulnerable early stages and therefore a competent explanation of brachiopod distribution controls should also account for the pattern of SRM in the Firth of Lorn.

Overall, distribution is broadly consistent with the belief of Noble *et al.* (1976) that larval settlement is light controlled. The distribution of articulate brachiopods is generalized as being 'cryptic' in the photic zone (eg. Jackson *et al.* 1971; Pajaud, 1974; Noble *et al.* 1976; Logan, 1975, 77; Cooper, 1977; Noble & Logan, 1981; Farrow *et al.* 1983; Witman & Cooper, 1983; Asgaard & Stentof, 1985) gradually emerging onto exposed surfaces as light levels decrease with depth (Logan, 1977), although exceptions to this generalized distribution pattern do occur (Grange *et al.*, 1981; Willan, 1981; Witman & Cooper,1983).

It is generally believed that articulate brachiopods are poor spatial competitors (eg. Doherty, 1979) and it is argued that as competition for space decreases with depth and like predation (Stanley, 1974; Witman & Cooper, 1983) is reduced in cryptic environments, the distribution of brachiopods may therefore reflect a withdrawal from the effects of intense spatial competition and predation (e.g. Jackson *et al.* 1971; Logan 1977, 79; Witman & Cooper, 1983). This explanation only offers an indirect explanation for negatively phototactic larvae (Witman & Cooper, 1983), and cannot account for the pattern of mortality in the Firth of Lorn. In addition, although competition dominates ecological thinking, there is little hard data to support it (Simberloff, 1984).

Noble *et al.*, (1976: 10) were the first to recognize that disturbance might significantly control brachiopod distribution "algae predominate on the upper surface of rocks, together with a vagile benthos of browsers, while the sub-boulder surfaces are relatively free of algal encrustations and a rich and varied attached and vagile benthos is able to be established." Disturbance, particularily by grazing gastropods is an attractive proposition as a distributional control, because it accounts for the perceived distribution in areas of low light intensity, grazing being most intense in illuminated areas where algal films can develop.

Another line of evidence supporting the view that disturbance is an important distributional control is the rugophilic behaviour of larvae. Settlement on structurally complex substrates is common amongst brachiopods. Wisley (1969) Thayer (1975) and Doherty (1979) report rugophilic behaviour in articulate brachiopod larvae, Percival (1944), Wisely (1969) and Stewart (1981) notes the extent to which the ribbed shells of *Notosaria nigricans* area commonly settled by both con-specifics and larvae of *T. inconspicua*. The rugophilic settlement of *T. inconspicua* observed by Doherty (1979: 336) "inside or amongst the dead tests of a barnacle" attached to settlement plates is particularily intriguing as it follows failure of brachiopod larvae to settle on the panels during three earlier spawnings over the preceeding eighteen months. Although rugophilic behaviour can be explained in terms of reduced predation or spatial competition, a stronger case can be made for its occurrence as a response to the reductions in grazing pressure experienced by structurally complex areas (eg. Akpan, 1981), or to the selective removal of post-larvae from smooth surfaces by un-impeded grazers.

Recruitment onto or near to conspecifics is characteristic of a number of shallow water brachiopods (Mattox, 1955; Hartmann, 1966; McCammon, 1973; Foster, 1974; Thayer, 1975; Doherty, 1979; Richardson, 1981; Stewart, 1981) but although sub-optimal has only been commented upon in terms of recruitment strategy and adult orientation (Thayer, 1975). Conspecific settlement will lead to an increase in substrate complexity, thereby reducing grazing pressures and enabling penetration into exposed shallow water areas. The vertical orientation of *Thecidellina* and *Lacazella* (Jackson *et al.*, 1971) with the anterior margin held far away from the substrate, and the rapid elongation of the post-larval shell of *Terebratalia transversa* following settlement (Stricker and Read, 1985) are also features which may be related to the avoidance of grazing disturbance.

The relationship between a sigmoidal-growth rate and grazing disturbance has not been established by this work. It will be necessary to undertake further *in-situ* growth studies of post-larvae (cf. Doherty, 1979) to determine growth rates and controls on rate (ie, genetic or environmental). Similarily, the role of grazing disturbance as a distributional control could be determined using experimental manipulations and exclusion experiments.

A slow initial growth rate, if not confined to *T. retusa*, has considerable evolutionary implications, as it will increase the vulnerability of articulate brachiopods to both grazing disturbance and spatial competition. Stanley (1974) suggested that the decline of brachiopods in the late Mesozoic could be attributed to the evolution of advanced Mesozoic predators. This appears somewhat unlikely as predation cannot drive a species to extinction even when both predator and prey are experimentally confined within very small areas (Utida, 1957). Witman & Cooper (1983) modified Stanley's (1974) hypothesis by recognizing the significance of indirect disturbance, concomitant with the shift to cryptic habitats during the Mesozoic. The evolution of potential disturbance organisms other than the bony fish discussed by Witman & Cooper (1983) are also consistent with the late Mesozoic decline. The camarodont Echinoidea evolved at the end of the Cretaceous (Asgaard & Stentoft, 1985) and fossil molluscan grazing traces have been reported from the Upper Jurassic (Voigt, 1977) although as the geological record of the patellaceans extends back into the Triassic, earlier traces may come to light (Akpan *et al.*, 1982).

# PART II
# DEATH ASSEMBLAGE

## II 1.1 INTRODUCTION

Active palaeontologists attempt the equivalent of a sociological survey of village life by the analysis only of the graveyard, for apart from the occasional organism preserved in life position, the majority of fossil assemblages contain a biota which has been abraded and transported to a greater or lesser degree. These fossil mixtures can have little palaecological significance if it is not possible to reconstruct the events leading to their formation (Johnson, 1962) and herein lies the potential value of biostratinomic studies.

The most usual type of investigation compares the composition of living and accumulating dead assemblages, to determine which features of living community are faithfully transmitted to the sediment. The majority of such assemblage-similarity studies have been conducted in shallow marine environments, probably because of the difficulties of sampling in deeper water, thus studies have included rocky sub-littoral (Noble *et al.*, 1976) shallow coastal lagoons, bays and estuaries (Johnson, 1965; Cadée, 1968; Evans, 1968; Warme, 1969; Petersen, 1976; Bosence, 1978; McCall & Tevesz, 1983), and intertidal flats (Habe, 1956; Van Stratten, 1960; MacDonald, 1969a, b; Wilson, 1967; Antia, 1977). A few deep water studies have observed the relationship between the living community and the dead shells (Birkett, 1959; Holme, 1965), but rigorous analysis of the relationships have only been conducted by a few authors (Hertweck, 1972; Stanton 1976; Warme *et al.* 1976; Wilson, 1983; Carthew & Bosence, 1986).

The main analytical tool in such studies is quantification of 'similarity' to distinguish faunal associations. The palaeontological value of such studies therefore turns on the ability to recognize a faunal assemblage. Most studies are optimistic that this can be done (eg. Johnson, 1965; Cadée, 1968; Warme, 1969; Petersen, 1976; Stanton 1976; Warme *et al.*, 1976; Carthew & Bosence, 1986) but use species associations based on animals with carbonate exoskeletons or in some cases only molluscan bivalves. The work of Bosence (1979a, b) which include soft bodied organisms demonstrate poorer homology, and an inability to reconstuct trophic nuclei, unsurprising when the abundance and generally higher P/B ratios of soft-bodied organisms (Craig & Jones, 1966; Robertson, 1979) and their role in altering sediment quality are considered. Indeed Bosence (1979b) challenges the optimistic consensus by proposing three unflattering alternatives for the apparent dichotomy, either fossil communities were more distinct than the present day examples, that reconstructed palaeocommunities are not the same units as Recent communities, or possibly that the results from palaeocommunity analysis are fortuitous.

Recognition of assemblages, and exotic species are strongly allied to the scale of community definition. The assemblages of Bosence (1979a) from Mannin Bay, Eire which fail the test of similarity are in many cases little over 500 yards in extent. Perhaps the absence of exotic species in assemblages identifed from grab samples (Warme *et al.*, 1976; Carthew & Bosence, 1986) or which span a 2 km section of bay (Warme, 1971) has less to do with an absence of taphonomic biasing and is more a reflection of the scale on which the limits of recognizable 'comunities' are defined.

A more valuable contribution of such studies is the recognition of short-term cyclicity in community composition and the realization that the death assemblage is an ecologically significant, time-averaged, resource (Peterson, 1976, 77; Carthew & Bosence, 1986).

Of more palaeontological value are those studies which having recognized that the death assemblage is a selective accumulation of the preservable components of the living community, attempt to characterize the features of the selective processes. Examples of such studies include biased valve ratios (Martin-Kaye, 1951; Boucot *et al.*, 1958; Lever, 1958, 61; Lever & Thijssen, 1968; Craig, 1967; Behrens & Watson, 1969; Clifton, 1971) and features of abrasion (Pratje, 1929; Klahn, 1932, Driscoll, 1968), dissolution (Driscoll, 1970; Alexandersson, 1978, Aller, 1982) and bioerosion (Boekschoten, 1967, 68; Akpan *et al.*, 1982).

A third, potentially useful area attempts to predict the nature of the potential bias from the type of skeletal carbonates (eg. Chave, 1964; Hallam, 1965; Eisma, 1968; Lefort, 1970; Fuetterer, 1978a, b, c), unfortunately such studies have been typically confined to the laboratory or the swash zone.

The following section (section II) is of this third type and compares the estimates of production from section I with the composition of the death assemblage, to determine the degree of biostratinomical bias. Experimental investigations (section III) further attempt to explain some of the biasing phenomenon in terms which will hopefully be generally applicable.

## II 1.2 PROCEDURES

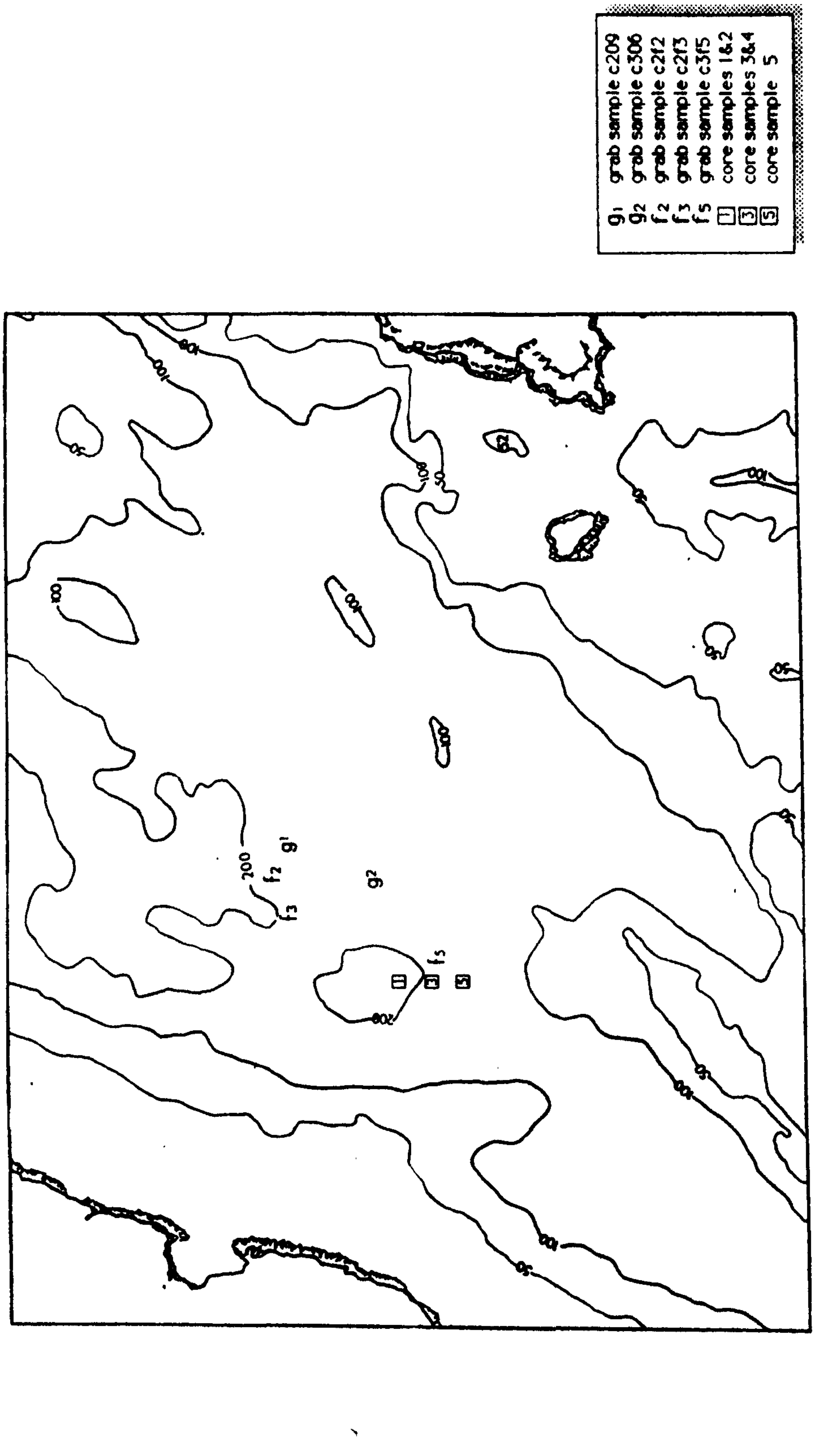
### II 1.2.1 Sampling Sites

Originally it was intended to make a series of two replicate core samples at each of five sites from the centre of the depression to the base of the slope, (Fig. II 1.1), however the box corer was lost after only five samples had been collected, and grain analysis of two grab samples (c209 & c306) collected from within the *Modiolus* community was also undertaken (Table II 1.1). A further three grab samples of sediment collected at depths in excess of 180 m, which contained no *M. modiolus* clumps and little other living fauna, and which were believed to be equivalent to the 'fossil *Modiolus*' facies of the video survey, were also analysed to the > 2 mm fraction (c2f2, c2f3 & c3f5; Table II 1.1).

Sediment from the box corer was split on deck into three lengths (0–6, 6–12 and 12–18 cm) and subsequently stored prior to analysis at 4°C. The absence of core boxes and the loss of the gear prevented attempts to estimate the degree of core compression, (cf. Allen *et al.*, 1979). The lengths of the splits were chosen because they adequately covered the penetration of the core in this sediment, and the division into short-term and long-term death assemblages (*sensu* Powell *et al.*, 1982). An additional advantage of these splits is that the upper fraction (0–6 cm) corresponds to a grab sample of six litres.

Figure II 1.1

a) Positions of sampling sites for sediment analysis



## TABLE II 1.1
### Details of cores and grabs used in sediment analysis

| sample | >9mm | >4mm | 4-2mm | 2-1mm | date | depth (m) | vol. (l) | temp °C |
|---|---|---|---|---|---|---|---|---|
| | | GRAB SAMPLES | | | | | | |
| (c202 | 996(1) | 174.9(1) | 165.1 | 151.2 | 22/08/83 | 151 | 6 | 12.5) |
| c209 | - | 785.5(1) | 113.2(5) | 118.5(100) | 22/08/83 | 174 | 5 | 12.0 |
| c306 | - | 396.4(1) | 87.2(10) | 213.8(100) | 29/11/83 | 188 | 10 | 11.5 |
| c2f2 | 776(1) | 394.2(10) | 418.3(25) | 595.5(50) | 29/11/83 | 183 | 8.5 | 11.5 |
| c2f3 | 930(1) | 335.4(10) | 475.2 | 897.5 | 29/11/83 | 183 | 6 | 10.9 |
| c3f5 | 280(1) | 361.0(20) | 192.4(5) | | 23/05/84 | 190 | 7 | 9.0 |
| | | CORE SAMPLES | | | | | | |
| 1a | - | 36.21(1) | 21.1(1) | 4.30(10) | 11/01/85 | 210 | | |
| 1b | - | 50.44(1) | 8.2(4) | 2.98(15) | 11/01/85 | | | |
| 1c | - | 137.01(1) | 11.3(5) | 1.20(50) | 11/01/85 | | | |
| 2a | - | 157.23(1) | 11.4(2) | 1.49(20) | 11/01/85 | 210 | | |
| 2b | - | 94.66(2) | 7.0(6) | 3.35(10) | 11/01/85 | | | |
| 2c | - | 213.83(1) | 38.8(2) | 1.10(40) | 11/01/85 | | | |
| 3a | - | 92.30(1) | 12.6(2) | 1.81(20) | 11/01/85 | 208 | | |
| 3c | - | 48.31(1) | 10.2(2) | 2.30(20) | 11/01/85 | | | |
| 4a | - | 45.07(1) | 5.5(10) | 7.22(10) | 11/01/85 | 208 | | |
| 4c | - | 46.55(1) | 22.4(2) | 2.31(20) | 11/01/85 | | | |
| 5a | - | 93.20(1) | 6.6(1) | 1.85(5) | 11/01/85 | 170 | | |
| 5c | - | 52.40(1) | 11.0(4) | 3.66(20) | 11/01/85 | | | |

## TABLE II 1.2
### Grain size distribution of samples

| | Gravel | | | Sand | | | | Mud |
|---|---|---|---|---|---|---|---|---|
| | > 4 | - 2 | - 1 | - .5 | -.25 | -.125 | - .0625 | < |
| | | | | CORES | | | | |
| Core 1 | | | | | | | | |
| 0 - 6 | 3.2 | 6.2 | 39.6 | 16.5 | 0.1 | 1.7 | 21.7 | 10.9 |
| 6 -12 | 1.2 | 6.7 | 49.4 | 2.4 | 0.4 | 2.7 | 9.1 | 28.1 |
| 12-18 | 2.0 | 9.0 | 30.5 | 0.7 | 0.5 | 2.4 | 38.2 | 16.6 |
| Core 3 | | | | | | | | |
| 0 - 6 | 7.7 | 5.2 | 9.7 | 21.9 | 5.4 | 5.2 | 5.6 | 40.8 |
| 6 -12 | 7.7 | 4.5 | 6.9 | 5.9 | 11.2 | 6.6 | 3.0 | 54.2 |
| 12-18 | 11.8 | 4.95 | 5.6 | 13.7 | 19.5 | 8.6 | 2.3 | 32.9 |
| Core 2 | | | | | | | | |
| 0 - 6 | 26.4 | 3.9 | 4.8 | 10.6 | 17.1 | 5.1 | 2.6 | 29.6 |
| 6 -12 | 21.7 | 4.6 | 5.1 | 2.0 | 6.0 | 3.2 | 0.83 | 56.6 |
| 12-18 | 17.9 | 6.5 | 5.2 | 12.9 | 26.3 | 6.0 | 3.3 | 22.0 |
| Core 3 | | | | | | | | |
| 0 - 6 | 17.1 | 4.3 | 6.8 | 13.4 | 25.8 | 6.6 | 5.6 | 20.6 |
| 12-18 | 10.6 | 5.11 | 4.1 | 6.5 | 14.3 | 4.9 | 1.5 | 53.2 |
| Core 4 | | | | | | | | |
| 0 - 6 | 14.4 | 3.7 | 4.6 | 1.1 | 3.0 | 1.8 | 2.8 | 68.6 |
| 12-18 | 6.0 | 6.8 | 6.2 | 11.0 | 31.5 | 5.3 | 2.1 | 31.2 |
| Core 5 | | | | | | | | |
| 0 - 6 | 12.7 | 5.0 | 6.9 | 17.9 | 34.4 | 4.6 | 1.9 | 16.8 |
| 12-18 | 6.4 | 5.6 | 4.0 | 16.2 | 32.6 | 3.6 | 2.2 | 29.6 |
| | | | | GRABS | | | | |
| c205 | 0.1 | 0.12 | 3.28 | 17.1 | 29.3 | 25.4 | 14.3 | 10.4 |
| c201 | 10.7 | 4.3 | 4.7 | 14.5 | 23.9 | 11.7 | 3.7 | 26.6 |
| e106 | 13.0 | 5.2 | 5.7 | 12.0 | 21.4 | 5.5 | 2.9 | 34.2 |

### II 1.2.2 Sediment Analysis

Sieveing technique

Early analysis used the standard technique of wet sieve analysis outlined by Buchanan & Kain (1971) using a sieve shaker. Subsequently, a modified wet sieveing technique was employed which more adequately dealt with the large volumes of sediment collected in the core samples, and was also more rapid and gave more consistent results.

Warm tap-water with a small amount of detergent, (to act as a wetting agent) was added to the sediment which was gently agitated inside the re-sealed plastic containers in which the sediment had been stored. The resulting thixotropic mixture was poured into the sieve tower and the process repeated until most of the sediment had been removed, the remainder being washed into the first sieve with excess water. The sieve tower was standing in a deep basin, which retained all the water poured through it. Once sufficient water had been passed through the tower the sieve was transferred to a second basin half filled with water and gently agitated by moving up and down through the water surface. Once the sediment was adequately sieved, it was given a final wash through tap water and oven dried at 95°C. The water and residue from the second basin were then poured through the next sieve (2 mm mesh) which was standing in a third (empty) basin and the process repeated.

Once all the fractions had been collected the remaining suspension (ie. that containing all the material to have passed through the 62.5 $\mu$m sieve) was left to settle in a large basin until the overlying water had cleared. The water was siphoned off, and the mud fraction transferred to a pre-weighed beaker which was oven dried and reweighed. No attempts were made to improve sample dispersion, and it is possible that distribution across the finer fractions was slightly distorted.

Sub-samples of fractions < 1 mm were analysed for carbonate, the organic fraction being first removed by ignition at 495°C, before acid digestion using cold HCl. Total carbonate was estimated in the coarser fractions from grain analysis (Table II 1.4).

Sediment classification

The classification of Folk (1954), a modified form of the earlier Wentworth (1922) classification was adopted (Fig. II 1.2) for this study. Sediments are primarily classed under three main groupings – gravel, sand and mud (Table II 1.2), modified by sub-dividing the sediment according to the percentage of gravel and the sand:mud ratio. Mud is defined according to Folk (1954) (ie. a grain size $< 62.5\ \mu m$; including the clay and silt grades of Wentworth, 1922). Sand and gravel were classified as Wentworth (1922), sand ranging from 0.0625 – 2.0 mm and the gravel fractions including all grains in excess of 2 mm.

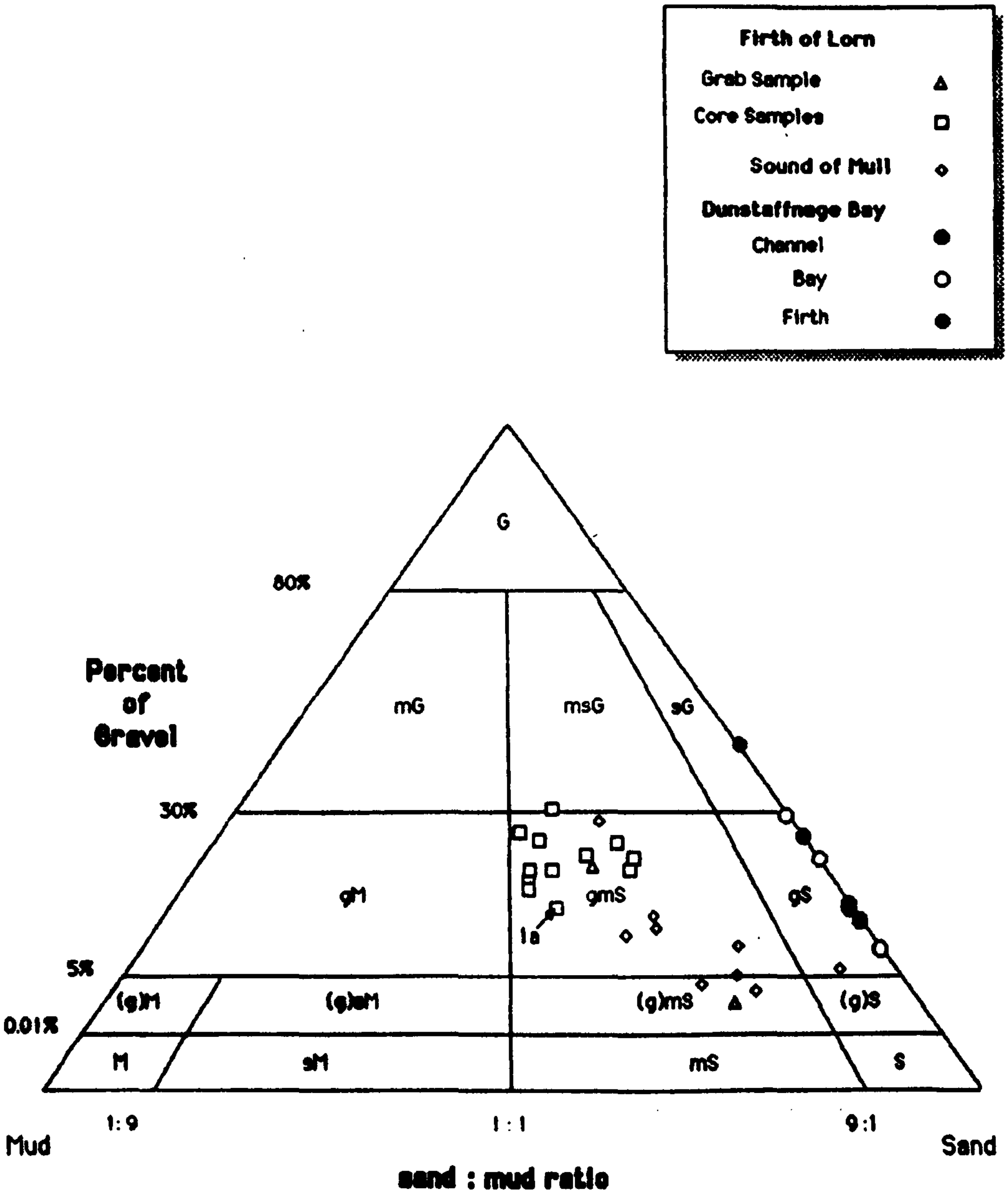
Grain analysis

Grain analysis was conducted by size fraction, routinely all the sediment in the coarsest fraction was surveyed, and splits taken of the smaller fractions (Table II 1.2). An additional sub-fraction, all those grains trapped by the byssal threads of living *M. modiolus*, was taken from the two grab samples collected from within the *M. modiolus* community (c209 & c306).

Only subsamples of the grains in the remaining fractions were analysed, all the grains being seperated and identified under a binocular microscope. All fragments were identified by dentiton where possible although with practice most coarse fragments could usually be assigned. For valves and shells an estimate was made of the degree of completness of those to which some damage had been sustained and a figure of 90% was chosen as the arbritary division between whole particles (be they gastropod spires, bivalve valves or articulated shells) and fragments. Length was measured as described in section I 1.2.2, using dial calipers for those items larger than 7 mm, and a binocular microscope and graticule, for the remainder; the diameter of countersunk borings were also recorded.

The sediment from fractions smaller than 1 mm was examined by binocular

Figure II 1.2
Folk classification



microscope and scored according to the criteria of Milliman (1974). Two alternative approaches were taken to determine composition, either point counting, or totalling numbers from known sub-fractions of the total. Although the former technique furnishes only relative densities of identifiable components it is preferable to the letter approach, which is laborious due to the large number of unrecognizable grains present in very small subfractions (0.5 - 1). Absolute composition was therefore only determined for the larger splits (1 - 0.5 and 0.5 - 0.25 mm). Summary details of each autochthonous carbonate are given in the text.

Totals are given as absolute numbers of valves recorded from core and grab samples, (ie not corrected for subfractioning of smaller samples). Estimated densities of living animals and carbonate production are supplied to contrast with the percentage contribution of the species to the total weight of sediment. Taphonomic bias is given in the form of the percentage change between the fraction of carbonate production and the fraction of autochthonous carbonate in the death assemblage, (ignoring those species for which estimates of production were not made; eg. bryozoa).

Taphonomic bias can be described in either absolute or relative terms. The most typical absolute measure is half-life of a particle within the sediment, first used by Powell *et al.* (1982). Half-life is valuable because it is easy to visualize although it has drawbacks both because it is very difficult to determine accurately and because it is yet to be demonstrated to be a meaningful measure. The alternative method, presenting changes in compostion as relative percentages (Noble *et al.* 1976; Powell & Stanton 1985) of the living community and death assemblage, is used in this analysis.

The changes themselves can either be presented as an absolute change relative to the whole community, or as percentage changes relative to the individual carbonate producer. The latter method has the advantage that if one species dominates production, dramatic changes in less important species are still highlighted, and is for this reason preferred for this study. This ability to highlight relatively small absolute swings is also a drawback however, as percentage changes are typically greatest for those species contributing least to the carbonate production (see Table II 1.13).

Percentage articulation was calculated by dividing the total number of articulated valves, (including those with very minor damage either of the valves) by the sum of the articulated valves and which ever of the disarticulated valves was most numerous.

The figure for 'percentage predation' reflects the number of animals killed by boring gastropods. It is derived from the number of valves carrying counter-sunk boreholes (*Oichnus*), divided by two, where relevant. Percentage predation was estimated from absolute numbers of predated and non-predated valves, no corrections being made for the lower numbers of smaller valves collected, because of the problems associated with multiplying up small subsamples. The absence of any corrections means that where predation is size selective (eg. *Anomia*) the extent of gastropod predation will be incorrectly estimated. Maximum and mean figures of all valves and predated valves are supplied.

Estimates of age by retention of stain

All grab sample collections were preserved with approximately 4% buffered seawater formalin, to which the stain, rose-bengal had been added. Consequently the shells from the death assemblage were variously stained pink, the depth of the stain reflecting the amount of organic material still present within the shell (cf. Boekschoten, 1967; Cadée, 1968). The depth of colour is therefore assumed to remain constant while the shells remain in formalin, as the organic material is fixed.

The residence time of *T. retusa* and *M. modiolus* shells was estimated by scoring from one (the youngest), to five using the following criteria:-

*Terebratulina*

1 Shells are strongly stained pink and are very 'clean'.
2 Shells are have a pink 'blush' and are typically fresh in appearance
3-5 No pink colour is visable in the shell

3 Shells are white and still retain a 'fresh' appearance
4 Shells are fawn in colour
5 Shells are dark brown/black and appear old

*Modiolus*

1 Periostracum & ligament present, shells have a hint of pink colour.
2 Periostracum present, no ligament or colour, shells still look fresh, nacreous layer is bright
3 Periostracum absent, the nacre is dulled
4 Shells appear old, the nacreous layer is dull
5 Shells appear very worn and 'moth eaten'

The method, being very subjective was aided by having a series of reference shells available and by dividing the complete sample into the respective groups rather than scoring each shell in sequence.

### II 1.2.3 Data analysis

Analysis was conducted using the S data-analysis package running under UNIX on a Vax II. Two data files were constructed for sediment analysis, both are available to readers on request from the author. The summary data files hold details of the 94 sediment types for each sample, as vectors (Table II 1.3). Additional details of length and estimated ages (Table II 1.3) were supplied in a second series of matricies.

TABLE II 1.3
Construction of data files for sediment

SUMMARY FILE

| Vectors |
|---|
| Site |
| Sample no |
| Number of whole shells |
| Weight of whole shells |
| Number of left valves |
| Weigth of left valves |
| Number of right valves |
| Weight of right valves |
| Number of left fragments |
| Weight of left fragments |
| Weight of right fragments |
| Weight of right fragments |
| Number of unidentifiable fragments |
| Weight of unidentifiable fragments |
| Number of non bivalve fragments |
| Weight of non bivalve fragments |
| Number of predator borings |

FILE FOR ALL COMPLETE SHELLS & VALVES

| Row | Variable |
|---|---|
| 1 | Site |
| 2 | Fraction |
| 3 | Species |
| 4 | Valve |
| 5 | Magnification factor |
| 6 | Length |
| 7 | Width |
| 8 | Height |
| 9 | Colour |
| 10 | Diameter of countersunk boring |

## II 1.3 RESULTS & DISCUSSION

### II 1.3.1 General description of sediments

The UWTV survey showed a bottom topography characterized by the presence of dense clumps of *M. modiolus* across much of the slope, which may account for the absence of any sedimentary structures. The UWTV survey also suggests a decrease in faunal abundance and diversity towards the centre of the depression (section I 2.2) and the development of an intermittant shell pavement. The sediment surface appeared clean, the majority of *M. modiolus* shells lay in the hydrodynamically stable concave-down position.

Surprisingly, although the sediment in the *Mellinnia* facies appears very 'muddy', all core samples are in the gravelly muddy sand (gmS) category of Folk (1954) (Fig. II 1.2), containing 16 - 56% mud. However, if the agglutinated sediment tubes of *Mellinia* are excluded from the gravel fraction, sediment in the two upper fractions of core 1 from the *Mellinia* facies is re-categorized as muddy sand (mS). The two grab samples from within the *Modiolus* community contained less mud (12 & 26%) although the difference may simply reflect a washing out of fines during recovery.

Carbonate concentration varies between 10% and 93%, being generally lower in the core and 'fossil' grab samples collected from close to the *Mellinia* facies (Table II 1.4, 1.5). The two most significant fractions are the contribution of the biomass dominant, *M. modiolus* (see section I 3.3) and terrigines, the latter being variably composed of two subfractions, the agglutinated sediment tubes of polychaetes (the '*Mellinia*-tubes fraction') and pebbles, stones and clinker (the 'stones' fraction). Echinoderm and barnacle debris are not as significant in this sediment (3.0 - 7.9%) as they are in the shallow water carbonates described by Farrow *et al.* (1979) from this area. Carbonate polychaete tubes, foraminifera, corals, chiton plates, fish otoliths and crab debris, recorded in Table II 1.4 as 'Others', individually account for less than 1% of any sample but can account for almost 20% of the total weight in some instances.

## TABLE II 1.4
Composition of sediments
(A *Terebratulina retusa*; B *Crania anomala*; C Bivalve molluscs excluding D *Modiolus modiolus*; E Gastropods; F Echinoderms; G Barnacles; H Others; I Terrigines.)

| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| | | | | GRABS | | | | | |
| c2f2 | 1.00 | 0.0 | 24.4 | 13.8 | 11.4 | 3.0 | 7.9 | 10.1 | 28.4 |
| c2f3 | 1.8 | 1.0 | 16.0 | 39.0 | 1.2 | 0.3 | 2.6 | 18.6 | 9.5 |
| c3f5 | 1.4 | 0.0 | 6.4 | 7.7 | 0.2 | 0.4 | 3.8 | 4.1 | 76.0 |
| e106 | 5.6 | 0.1 | 11.0 | 5.4 | 1.2 | 1.8 | 4.1 | 18.5 | 52.3 |
| c209 | 4.9 | 0.2 | 9.3 | 55.2 | 2.8 | 1.8 | 1.7 | 14.0 | 10.1 |
| c306 | 9.9 | 0.1 | 13.9 | 59.5 | 1.7 | 0.8 | 0.9 | 15.6 | 2.6 |
| | | | | CORES | | | | | |
| Core 1 | | | | | | | | | |
| 0 – 6 | 0.2 | 0.0 | 2.2 | 2.4 | 0.1 | 0.2 | 0.9 | 3.9 | 90.0 |
| 6 –12 | 2.2 | 0.0 | 15.8 | 17.9 | 1.8 | 1.3 | 1.6 | 6.0 | 53.4 |
| 12–18 | 5.6 | 0.1 | 11.0 | 5.4 | 1.2 | 1.8 | 4.1 | 18.5 | 52.3 |
| Core 2 | | | | | | | | | |
| 0 – 6 | 3.2 | 0.1 | 6.2 | 39.6 | 16.5 | 0.1 | 1.7 | 21.7 | 10.9 |
| 6 –12 | 1.2 | 0.0 | 6.7 | 49.4 | 2.4 | 0.4 | 2.7 | 9.1 | 28.1 |
| 12–18 | 2.0 | 0.1 | 9.0 | 30.5 | 0.7 | 0.5 | 2.4 | 38.2 | 16.6 |
| Core 3 | | | | | | | | | |
| 0 – 6 | 5.7 | 0.3 | 14.8 | 24.0 | 1.2 | 0.9 | 4.3 | 14.8 | 34.0 |
| 12–18 | 3.0 | 0.1 | 15.2 | 29.4 | 1.3 | 1.1 | 3.6 | 8.3 | 38.1 |
| Core 4 | | | | | | | | | |
| 12–18 | 0.8 | 0.0 | 8.3 | 35.9 | 1.2 | 1.7 | 1.8 | 21.5 | 28.8 |
| Core 5 | | | | | | | | | |
| 0 – 6 | 3.8 | 0.3 | 16.6 | 44.8 | 1.4 | 1.3 | 2.0 | 23.0 | 6.8 |
| 12–18 | 1.7 | 0.0 | 15.0 | 35.9 | 1.2 | 2.4 | 2.5 | 25.4 | 15.9 |

## TABLE II 1.5
Weigth of sediment from within community species

| | | carbonates | | | terrigines |
|---|---|---|---|---|---|
| Core | total | autochonous | allochthonous | exotic | |
| Depth | 0 – 6 cm | | | | |
| 1 | 100.6 | 4.1 | 5.8 | 0.7 | 90.1 |
| 2 | 209.8 | 48.7 | 40.4 | 1.2 | 10.9 |
| 3 | 153.6 | 44.0 | 22.0 | 1.8 | 34.0 |
| 5 | 168.5 | 62.3 | 31.3 | 1.9 | 6.4 |
| Depth | 6 – 12 cm | | | | |
| 1b | 127.7 | 31.3 | 15.3 | 2.0 | 53.4 |
| 2b | 231.4 | 56.8 | 15.1 | 3.8 | 28.1 |
| Depth | 12–18 cm | | | | |
| 1 | 176.1 | 19.0 | 28.7 | 0.6 | 52.3 |
| 2 | 335.3 | 40.8 | 42.9 | 0.95 | 16.6 |
| 3 | 114.6 | 42.1 | 19.8 | 2.1 | 38.1 |
| 4 | 137.7 | 42.3 | 28.9 | 1.46 | 28.8 |
| 5 | 144.3 | 49.8 | 34.3 | 1.45 | 15.9 |

Sediment from the Sound of Mull by contrast was dominated by a sand fraction, which accounted for 50 – 85% of the total weight. The reduced gravel components of these sediments result in some being characterized as slightly gravelly, muddy sand, fraction of Folk (Fig. II 1.2).

### II 1.3.2 Terrigines

Terrigines are most significant in cores taken from the *Mellinia* facies (Table II 1.6). The agglutinated sediment tubes of the polychaete *Mellinia* (*cristata?*), which form a dense palisade which projected above the sediment surface in core 1 accounted for 90% of the total weight of the 0 – 6 cm sediment fraction, but were less common in deeper fractions (Table II 1.6).

Concomitant with the fall in the contribution of polychaete tubes is an increase in the core of pebbles and stones (Table II 1.6), a heterogenous mixture of glacially derived quartz minerals, sandstones, shale and basalt, with more recently introduced clinker and coal. The increase is perhaps an indication of bioturbation working down the coarse sediment to a zone of accumulation below the depth of the living community.

TABLE II 1.6
The changing composition of the non-carbonate dominants (percentage by weight) in the sediment at site 1 *Mellinia* facies.

| | Core 1 | | Core 2 | |
|---|---|---|---|---|
| | Mellinia | Stones | Mellinia | Stones |
| 0 – 6 | 90.4 | 0.2 | 4.0 | 18.8 |
| 6 –12 | 65.7 | 2.5 | 1.5 | 63.4 |
| 12–18 | 5.1 | 87.0 | 0.2 | 55.5 |

In the second core taken at the same station as core 1, a similar trend was observed in the decline of *Mellinia* tubes as a component of the sediment down the core, although they make a much smaller overall contribution (Table II 1.6). The marked differences in the contribution of *Mellinia* tubes in the two samples, in addition to highlighting the difficulties of re–sampling the same station could be the result of a patchily distributed facies, although the UWTV surveys were unable to confirm this. The greater proportion of stones in the 6 – 12 cm fraction of core 2 may reflect a shallower limit to bioturbation concomitant with a reduced density of bioturbators.

The proportion of pebbles and stones appears to decrease away from the *Mellinia* facies, the means of the upper and lower fractions from the two stations are 40% and 48% respectively, higher than the 15% estimate from core 5, and the two grab samples from within the *Modiolus* community (2.6 – 10%; Table II 1.4). Pebbles and stones account for a particularly small fraction (0.7%) of the sediment entrapped within the byssal threads from living *M. modiolus* clumps. The variation between the 'sub-fossil facies' samples f202, f203 f305 is much greater (5.7 – 72.7%; Table II 1.4), one sample with an estimated penetration of 6 cm recovered 1242 g of pebbles and stones alone. This variation is perhaps a reflection both of an absence of autochthous carbonate production (Table II 1.5) and the failure to sample fractions finer than 2 mm.

### II 1.3.3 Autochthonous carbonate

Bivalves (including *M. modiolus*) constitute the major source of carbonate within the sediment, of which *M. modiolus* alone accounts for between 29 and 88% (Table II 1.7).

TABLE II 1.7
Contribution of bivalves (and the percentage of this fraction which is *M. modiolus*) to the carbonate fraction of the > 1mm fraction.

| Depth | CORES % Bivalve (*% of bivalve as Modiolus*) | | | | |
|---|---|---|---|---|---|
| (cm) | 1 – | 2 | 3 – | 4 | 5 |
| 0 – 6 | 50.5(*51.6*) | 62.9(*29.4*) | 58.7(*61.8*) | – | 65.8(*73.0*) |
| 6 –12 | 72.3(*53.1*) | 78.1(*87.9*) | | | |
| 12–18 | 34.2(*32.4*) | 46.6(*79.2*) | 72.0(*65.9*) | 65.1(*81.2*) | 60.5(*70.5*) |
| mean of 0–6 & 12–18 | 42.3(*42.0*) | 54.7(*54.3*) | 65.3(*63.8*) | 65.1(*81.2*) | 63.5(*71.7*) |
| | GRABS | | | | |
| | c306 | c209 | | | |
| 0 – 6 | 73.2(81.0) | 64.5(85.8) | | | |

There is an apparent increase in both the proportion of bivalve mollusc shells and *M. modiolus* towards the *M. modiolus* community (ie further from the '*Mellinia*' facies). *M. modiolus* accounts for 55–59% of the sediment > 1 mm in the two grab samples taken within the *M. modiolus* community (Table II 1.7).

I 3.3.1 Mollusca

*Modiolus*

*Modiolus modiolus*:

Total number collected in (a) cores & (b) grabs: (a) **89** (b) **29**; Mean percentage in (a) cores & (b) grabs: (a) **32.1** (b) **57.3**; Density of living species /m²: **177**; Carbonate biomass estimate (g/m²/yr): **2219**; Carbonate production estimate (g/m²/yr): **126.6**; % change in sediment: **+98**; Maximum length recorded (mm): **89.1**; Whole valve/fragment ratio in (a) cores & (b) grabs: (a) **11.82** (b) **1.34**; Left/right valve ratio: **1.05** ; Percentage predation: **0**.

*Modiolus phaseolinus*:

Total number collected in (a) cores & (b) grabs: (a) **166** (b) **49**; Mean percentage in (a) cores (a) & grabs (b): (a) **0.97** (b) **0.17**; Density of Living species /m²: **479**; Carbonate biomass estimate (g/m²/yr): **1.9**; Carbonate production estimate (g/m²/yr): **2.45**; % change in sediment: **+99**; Maximum length recorded (mm): **15.0**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **11.8** (b) **1.3**; Left/right valve ratio: **0.95**; Percentage predation: **1.8**; Mean length of shells (mm): **5.03**; Maximum length of predated shells (mm): **13.0**; Mean length of predated shells (mm): **11.36**

The population structure of *M. modiolus* within the death assemblage is strongly bimodal (Fig. II 1.3), unlike the polygon for living animals (Fig. I 3.2). The accumulation of small valves in the death assemblage supports the view expressed in section I 3.3.1 that juvenile mortality is extreme. The size-frequency distribution of *M. phaseolinus* from the death assemblage is strongly left-skewed (Fig. II 1.4), and corresponds closely to the polygons for living animals (Fig. I 2.7).

One unusual feature of the distribution of *M. phaseolinus* valves is the substantially higher densities of valves in the upper core fractions. Although the reverse trend is seen in the infaunal bivalves *Parvicardium ovale* (Fig. II 1.9) and *Venus ovata* (Fig. II 1.10), this distribution is not a feature of other valves. The disparity in patterns of distribution of these valves may be related to their contrasting epifaunal/infaunal life positions, or to the selective preservation of the relatively robust *Parvicardium* and *Venus* valves or perhaps to succession resulting from the coarsening of the sediment, with the gradual dominance of epifauna. The comparative ratios of numbers of *M. phaseolinus* and *P. ovale* in upper and lower core fractions of 1.2 : 1 and 1 : 7.5 respectively are striking and suggest that more comparisons of this kind should be undertaken.

**Figure II 1.3**

Length frequency of valves of all M. modiolus recovered from the death assemblage

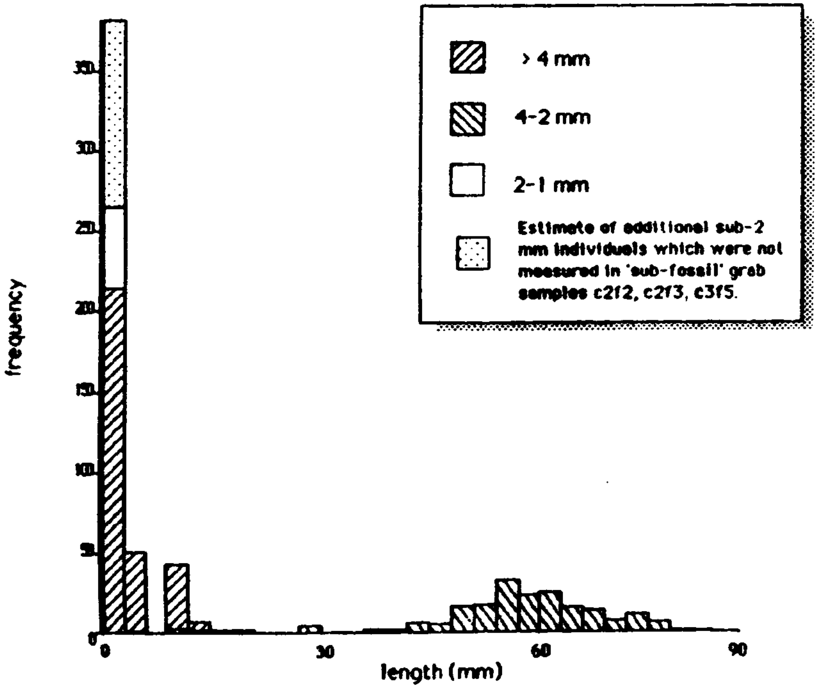
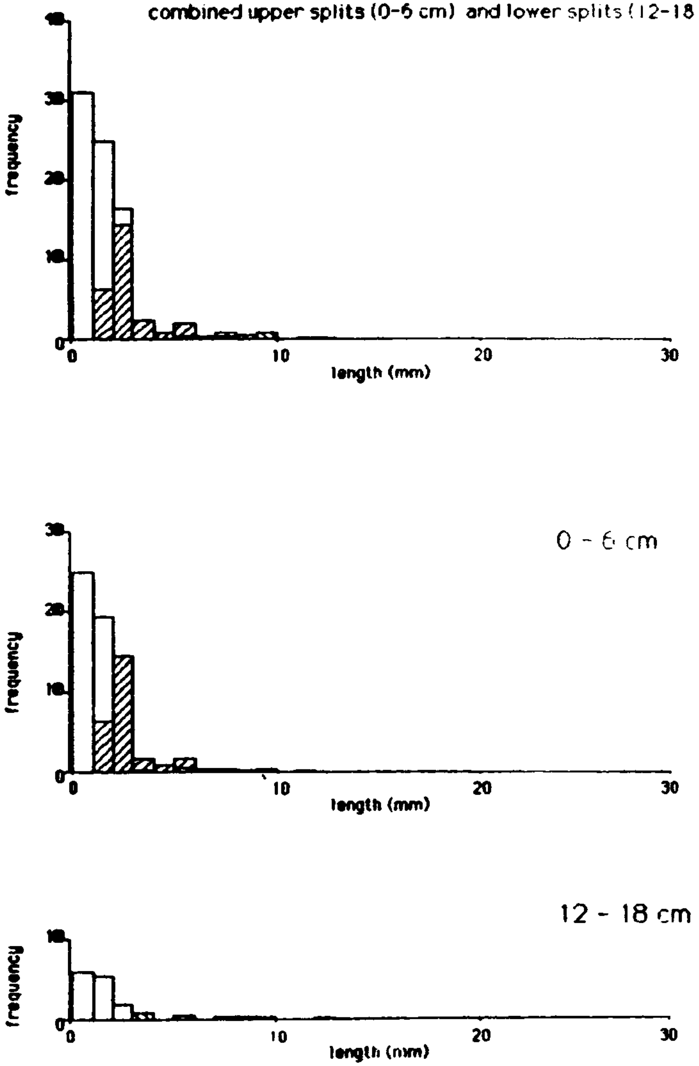


**Figure II 1.4**

Length frequency of whole valves of Modiolus phaseolinus recovered from cores.

(Lower two histrograms denote size-frequency distributions in the combined upper splits (0-6 cm) and lower splits (12-18 cm) of the cores



Attempts were made to estimate the age of *M. modiolus* valves using the technique of stain retention (discussed in section II 1.3.4.3). The distribution of shell groupings is similar to *T. retusa*, but the numbers of available valves was much lower (Table II 1.8).

Table II 1.8
Residence time of mature *M. modiolus* valves

| | 'Age' categories 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| c209 | - | 15 | 19 | 3 | 5 |
| c306 | 1 | 7 | 28 | 6 | 2 |
| TOTAL | 1 | 22 | 47 | 9 | 7 |

The shells of living *M. modiolus* were too robust to be used in the point-loader designed for *T. retusa*, it was thus not possible to estimate half-life of *M. modiolus* using this method. The presence of an intact ligament was used to distinguish goup 1 *Modiolus*, and as this was not lost over a 420 day field trial it is probable that this group is older than the equivalent *T. retusa* group 1 (section II 1.3.4.3), in which case the solitary individual in this *Modiolus* group is possibly significant.

The absence of determinable cohorts within the living *M. modiolus* population makes it difficult to estimate the rate at which large shells of *M. modiolus* would input into the sediment. However, assuming a lifespan of 20 - 40 years, the deaths of 4 - 8 adult *M. modiolus* /m$^2$/yr would be required to maintain the population of adult animals at the present levels of 164/m$^2$. 239 complete valves were recovered from five grab samples (total area 0.5 m$^2$) giving an estimated density of 478 valves/m$^2$, which would take 30 - 60 years to accumulate assuming that none of the valves were destroyed.

The ratio of fragments to whole shells is much higher in core samples (11.8 : 1) than in grabs (1.3 : 1). Although this must, at least in part, reflect the increased likelihood of the corer splitting valves during sampling and recovery, it may also stem from the positions of the respective samples relative to the centre of *Modiolus* production. The ratio for both is slightly increased because of the potential inclusion of *M. phaseolinus* fragments (sect-

**Figure II 1.5**

Length frequency of whole valves of Astarte recovered from cores

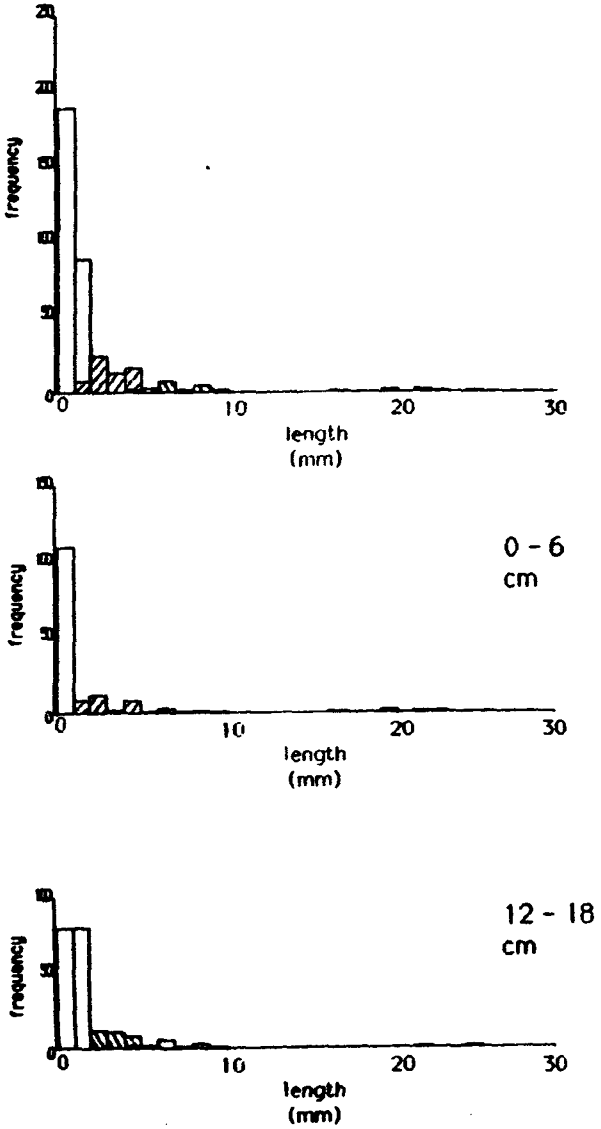
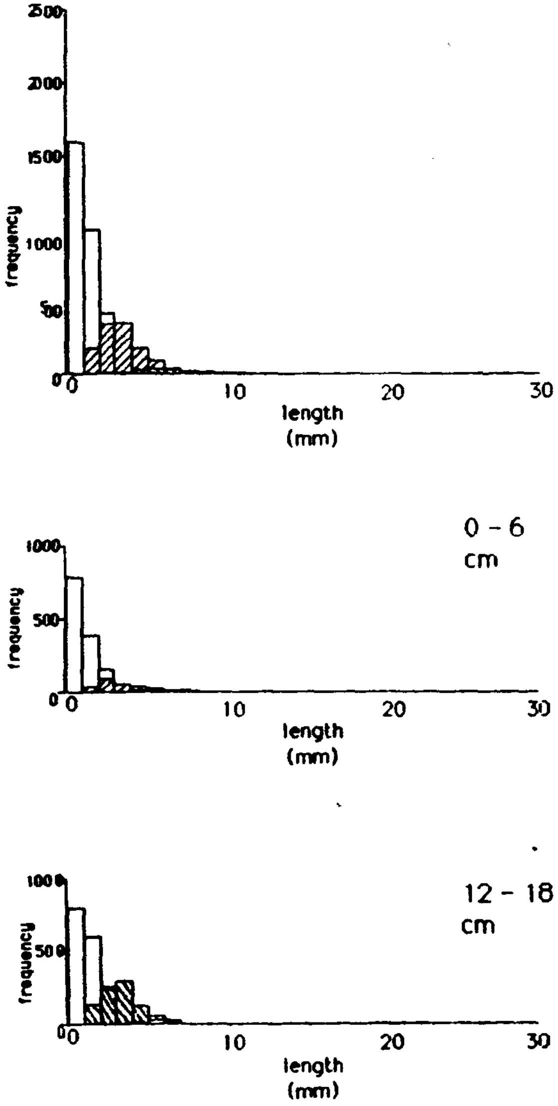


**Figure II 1.6**

Length frequency of whole valves of Anomia recovered from cores



▨ > 4 mm

▧ 4-2 mm

□ 2-1 mm

ion I 3.2) which accounts for approximately 0.6% by weight of total sediment analysed.

Although no X-ray radiography was conducted (c.f Farrow *et al.*, 1984), a number of dead shells had characteristic signs of sponge boring (Plate 1b), probably *Cliona vastifica* Hancock (Akpan, 1981). 50% of a random sample of 20 valves were bored by *Cliona*, which may acount for the observation that many of the valves in the sediment were more fragile than their living counterparts. Farrow *et al.* (1984) have noted that *M. modiolus* shells from North Orkney were degrading rapidly. Occasional blistering on the inner surface of valves indicated that some of this infestation had occurred during the life of the animal.

*Astarte* spp.

Total number collected in (a) cores & (b) grabs: (a) **89** (b) **29**; Mean percentage in (a) cores (b) grabs: (a) **1.39** (b) **1.75**; Density of living species $/m^2$ : **37**; Carbonate biomass estimate ($g/m^2/yr$): **59.5**; Carbonate production estimate ($g/m^2/yr$): **70.2**; % change in sediment: **-335**; Maximum length recorded (mm): **25.4**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **3.08**; Left/right valve ratio: **1.15**; Percentage predation: **4.7**; Mean length of shells (mm): **6.6**; Maximun length of predated shells (mm): **9.2**; Mean length of predated shells (mm): **4.3**

Unlike the living population in which the size/frequency distribution is bimodal, (Fig I 3.4) in the death assemblage there is an accumulation of small specimens (Fig. II 1.5), which is even more marked in finer fractions where *Astarte* shells were more common than all other valves combined. Crude estimates suggest that an additional 300 - 600 valves are present in the 1 - 0.5 mm core fractions (mean = 430, SD = 150, n = 3) and 600 in the 0.5 - 0.25 fraction (n = 1) or approximately 1 075 00$/m^2$. In contrast, the valves of adult *Astarte* are relatively uncommon in the sediment (Fig II 1.5) and total carbonate is under-represented in relation to the estimates of production.

Many of the adult valves were heavily bio-eroded, particularily by *Cliona* (Plate 1b-d), and a characteristic feature of many valves was the almost complete excavation of the body of the shell (Plate 1b) in a manner similar to that illustrated by Milliman (1974: plate XXIXa).

*Anomia* sp.

Total number collected in (a) cores & (b) grabs: (a) **671** (b) **203**; Mean percentage in (a) cores & (b) grabs: (a) **1.78** (b) **1.01**; Density of Living species /$m^2$: **71**; Carbonate biomass estimate (g/$m^2$/yr): **0.10**; Carbonate production estimate (g//$m^2$/yr): **0.12**; % change in sediment: **+11 120**; Maximum length recorded (mm): **28.2**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **2.48** (b) **1.01**; Left/right valve ratio: **9.2**; Percentage predation: **18.5**; Mean length of shells (mm): **4.74**; Maximun length of predated shells (mm): **11.7**; Mean length of predated shells (mm): **3.77**

*Anomia* sp. was the most abundant valve present in the sediment, a total of 927 valves being collected, representing 836 animals. The population is strongly left skewed (*sensu* Raup & Stanley, 1978) (Fig. 1.6). The highest estimated density of *Anomia* was 53 820/$m^2$ from sample c2f2, with the majority of estimates between 3 000 and 5 000/$m^2$, while the estimated density of living *Anomia* sp. was 71/$m^2$. To contribute such numbers to the death assemblage would therefore require between 70 and 700 years.

The ratio of 9.2 upper (left) valves to 1 lower valve is not abnormal, because of the differential thickening of the two valves, the lower (right) valve being very thin. *Anomia* experiences the highest levels of gastropod predation of any valves in the Firth of Lorn, 17.3% of the upper valves carry counter-sunk boreholes (*Oichnus parabolodies*). The predated shells are significantly smaller (p. > 0.5, 1 tailed t-test) than the sample of the total population. The spined surface of the 'rough' *Anomia* does not appear to be a successful anti-predatory device as counter-sunk borings were more common in this form (Table II 1.9)

TABLE II 1.9
Comparison of relative size and degree of predation
of *Anomia* vavles.

| | Population | | | Predated *Anomia* sp. | | | |
|---|---|---|---|---|---|---|---|
| | n | max | mean | n | max | mean | % |
| *Anomia* (rough) | 221 | 21.0 | 6.3 | 7 | 7.5 | 3.8 | 21 |
| *Anomia* (smooth) | 615 | 28.2 | 5.1 | 98 | 11.7 | 4.0 | 16 |

*Chlamys opercularis*

***Total number collected in (a) cores & (b) grabs:*** (a) **106**, 11 (b) **91**, 1; Mean percentage in (a) cores & (b) grabs: (a) **2.09** (b) **2.67**; Density of living species /$m^2$ : **< 1**; Carbonate biomass estimate (g/$m^2$/yr): **ND**; Carbonate production estimate (g/$m^2$/yr): **ND**; % change in sediment: Maximum length recorded (mm): **ND**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **10.59** (b) **3.902**; Left/right valve ratio: **1.28**; Percentage predation: **0**; Mean length of shells (mm): **ND**

Seven pectinaceans were identified from the death assemblage, (Table II 1.10) although only *Chlamys opercularis* which makes up 61% of the fragments was recovered alive (see section I 2.5 & section II 1.4).

TABLE II 1.10
Details of pectinacea in the death asemblage

| | % by weight of cores | n | length max | mean | predated |
|---|---|---|---|---|---|
| *C. opercularis* | 2.093 | ND | – | – | – |
| *C. striata* | 0.497 | 47 | 16.9 | 7.5 | 0 |
| *C. distorta* | 0.346 | 42 | 22.5 | 7.63 | 0 |
| *C. septemradiata* | 0.125 | 12 | 20.5 | 9.89 | 0 |
| *Similipecten similis* | 0.115 | 51 | 7.32 | 3.93 | (2 8%) |
| *C. nivea* (incl *C. varia*) | 0.020 | ND | – | – | – |
| Unrecognised pectinacea fragments including *C. tigerina* | 0.205 | ND | – | – | – |
| Total Pectinacea | 3.426 | | | | |

The size-frequency distribution of *Chlamys opercularis* valves is strongly left skewed (Fig. II 1.7). The majority of other pectinacea valves in the death assemblage were also small, light and typically derived from epifaunal life-positions, thereby increasing the chances of transport by current drifting. *Similipecten similis* was one of the species believed by Brown (1979) to be transported into and along deep channels in the Sound of Jura.

If much of the material was allochthonous it would be expected that the ratio of fragments to whole shells would be high, and this is indeed the case, *C. opercularis* having a ratio of 10.6:1 in the cores, the combined figure for *Chlamys* being an even higher 13.4:1. However, of the three species measured for shell softening (section III 2) *C. opercularis* suffered the least 'softening' and it is possible that fragments of pectinaceans are also more resistant to comminution than other types of shells. The high surface area/volume ratio of pectinacea valves will theoretically increase the degree of abrasion (Driscoll & Weltin, 1973) and dissolution (Flessa & Brown, 1983), but is likely to limit the degree of infestation by *Cliona*.

**Figure II 1.8**

Length frequency of whole valves of Nuculana recovered from cores (articulated valves plotted below axis)

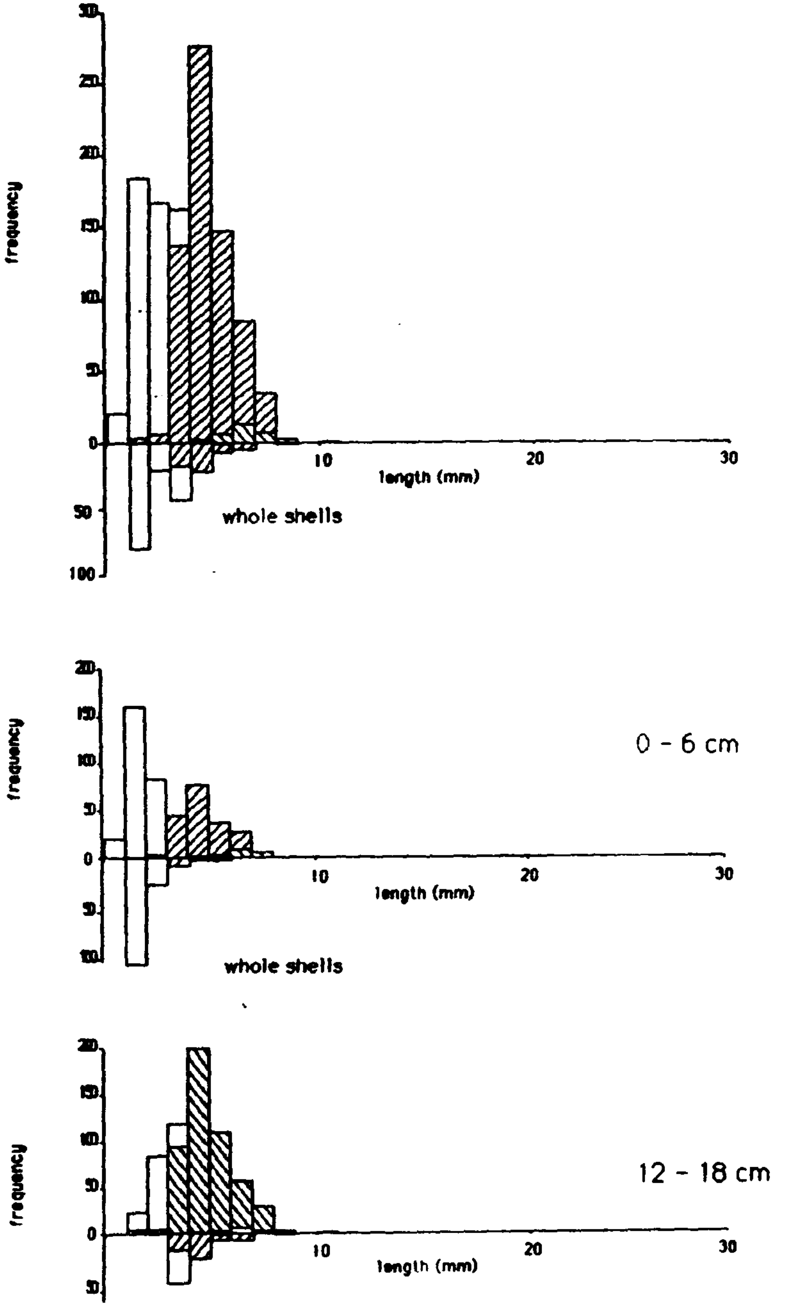
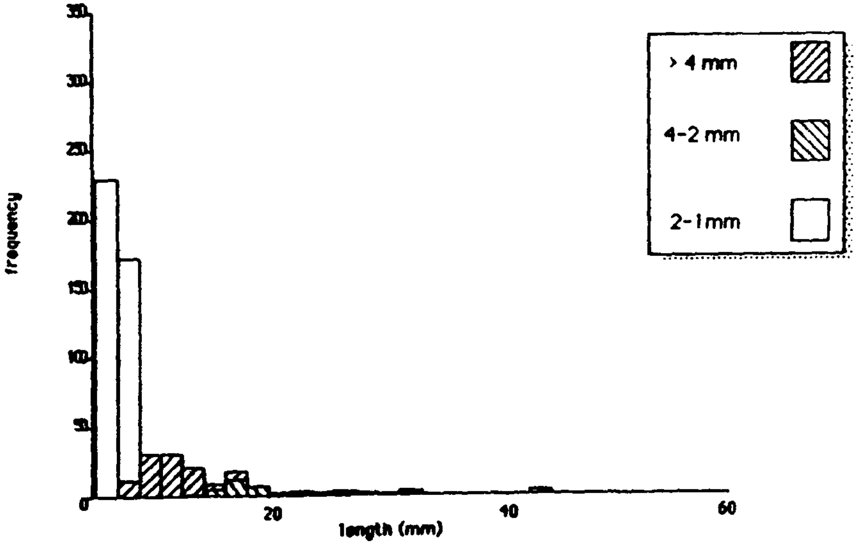


**Figure II 1.7**

Length frequency of whole valves of Chlamys recovered from cores



*Nuculana minuta*

Total number collected in (a) cores & (b) grabs: (a) **293**, 11 (b) **134**, 1; Mean percentage in (a) cores & (b) grabs: (a) **0.906** (b) **2.11**; Density of Living species /m²: **6**; Carbonate biomass estimate (g/m²/yr): **0.046**; Carbonate production estimate (g/m²/yr): **0.032**; % change in sediment: **+32 810**; Maximum length recorded **11.1**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **1.8** (b) **4.8**; Left/right valve ratio: **1.106**; Percentage predation: **8**; Mean length of shells (mm): **6.08**; Maximum length of predated shells (mm): **7.33**; Mean length of predated shells (mm): **5.41**.

*Nuculana minuta* is the most over-represented of the autochonous carbonate producers, being 32 810% more common, than would be predicted from estimates of carbonate production.

The population structure for *Nuculana minuta* is less left-skewed than most other species in the death assemblage, with a peak density of 4–5 mm long animals. The lower frequencies of smaller *Nuculana* may be because the shell is elongate and may pass through the 1 mm mesh. Surprisingly if the frequencies of the cores are split into upper and lower fractions, it is clear that this accumulation of 4–5 mm animals is peculiar to the deeper sediments (Fig. I 1.8).

*Nuculana* like *Nucula* has closely fitting dentition and margins, and therefore the valves can remain together for considerable periods (c.f. Boyd & Newell, 1972; Bosence, 1979a). Whole valves account for 12% of the total dead shell population, a figure similar to *Nucula* (15%) and as with *T. retusa* (section II 1.4), the degree of articulation of *Nuculana* diminishes with increasing size (Fig. I 1.9).

Countersunk borings are not uncommon on the valves of either *Nucula* or *Nuculana* and there is no apparent selection for small valves in either case.

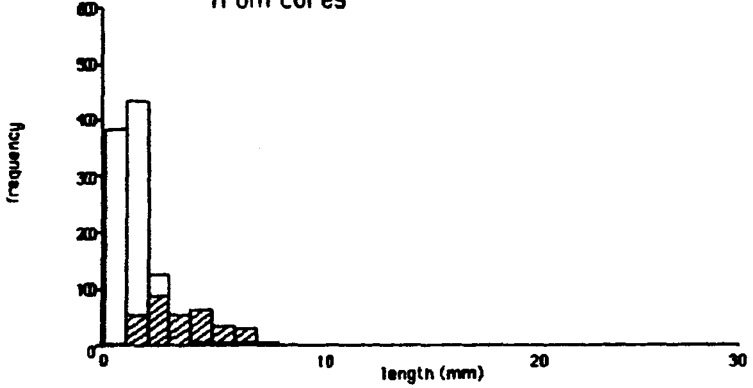
Other bivalves

*Parvicardium ovale*:

Total number collected in (a) cores & (b) grabs: (a) **168**, 11 (b) **36**, 1; Mean percentage in (a) cores & (b) grabs: (a) **0.55** (b) **0.41**; Density of Living species /m² : **5**; Carbonate biomass estimate (g/m²/yr): **0.03**; Carbonate production estimate (g/m²/yr): **0.033**; % change in sediment: **+12,760**; Maximum length recorded (mm): **9.7**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **4.13** (b) **ND**; Left/right valve ratio: **0.96**; Percentage predation: **18**; Mean length of shells (mm): **4.08**; Maximum length of predated shells (mm): **7.78**; Mean length of predated shells (mm): **3.45**.

**Figure II 1.9**

Length frequency of whole valves of Parvicardium recovered from cores



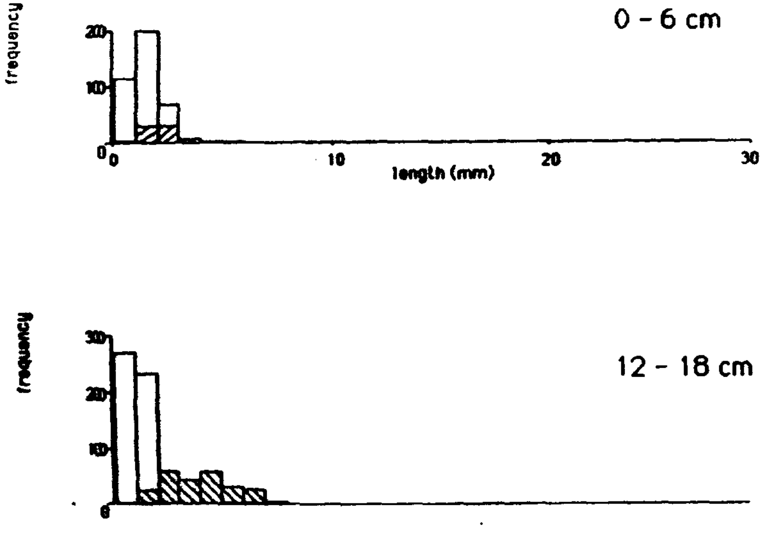


**Figure II 1.10**

Length frequency of whole valves of Hiatella arctica recovered from cores

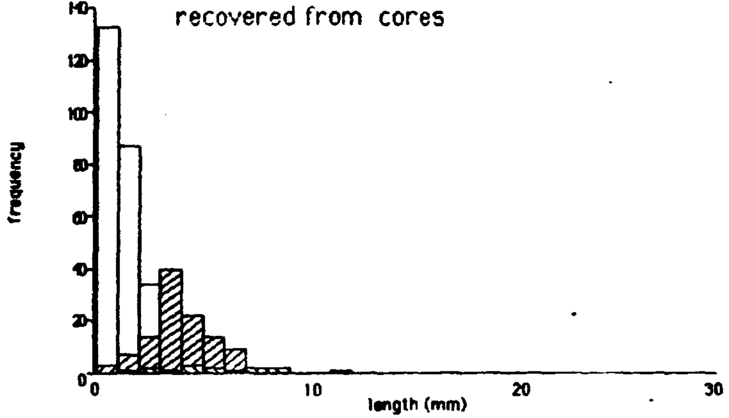
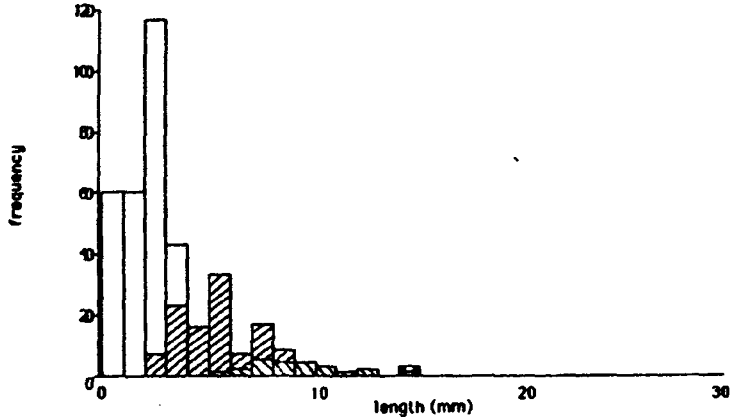


**Figure II 1.11**

Length frequency of whole valves of Abra alba recovered from cores



*Abra alba*:

Total number collected in (a) cores & (b) grabs: (a) 77 b) 22; Mean percentage in (a) cores & (b) grabs: (a) **0.59** (b) **0.28**; Density of Living species /m²: **4**; Carbonate biomass estimate (g/m²/yr): **0.06**; Carbonate production estimate (g/m²/yr): **0.066**; % change in sediment: **+27,167**; Maximum length recorded (mm): **12.0**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **217.3** (b) **2.9**; Left/right valve ratio: **9.2**; Percentage predation: **0**; Mean length of shells (mm): **5.2**.

*Hiatella arctica*:

Total number collected in (a) cores & (b) grabs: (a) **74**, 11 (b) **22**, 1; Mean percentage in cores (a) & grabs (b): (a) **0.35** (b) **0.009**; Density of Living species /m²: **51**; Carbonate biomass estimate (g/m²/yr): **0.58**; Carbonate production estimate (g/m²/yr): **0.68**; % change in sediment:**+285**; Maximum length recorded (mm): **15.9**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **2.15** (b) **1.19**; Left/right valve ratio: **0.89**; Percentage predation: **6**; Mean length of shells (mm): **6.81**; Maximum length of predated shells (mm): **7.48**; Mean length of predated shells (mm): **6.10**.

*Venus ovata*

Total number collected in (a) cores & (b) grabs: (a) **70**, 11 (b) **7**, 1; Mean percentage in cores (a) & grabs (b): (a) **0.64** (b) **0.29**; Density of living species per /m²: **0**; Carbonate biomass estimate (g/m²/yr): **0.03**; Carbonate production estimate (g/m²/yr: **0.033**; % change in sediment: ND; Maximum length recorded (mm.): **15.3**; Whole valve/Fragment Ratio: **0.991**; Left/rigth Valve Ratio: **1.34**; Percentage predation: **0**; Mean size of shells (mm.): **5.76**

*Hiatella Abra* and *Parvicardium* were all valves that were elevated relative to production estimates, all had left skewed length – frequency distributions (Figs. II 1.9–11) and all except *Hiatella* are infaunal. *Hiatella*, the only epifaunal species in this group was the least elevated of the carbonates. *Abra* was unusual in that although comprising a significant proportion of the sediment, few whole valves were recovered. Indeed *Abra* had the highest whole shell/fragment ratio of any carbonate fraction, presumably because the thin shelled valves are easily fragmented.

The size and morphology of *Venus ovata* and *Parvicardium ovale* valves are simliar, as were their contribution to the sediment (*Venus ovata*, 75% of total weight of *Parvicardium ovale*). The elevated densities of *Parvicardium* and *Venus* in the lower core splits (Fig. II 1.9 & 12) has already been noted (see discussion of *Modiolus* fraction). Although *Venus ovata* was not recovered alive in the survey, *Parvicardium* was only recovered at low densities and it is possible that *Venus* is also autochthonous.

**Figure II 1.12**

Length frequency of valves of Venus ovata recovered from cores

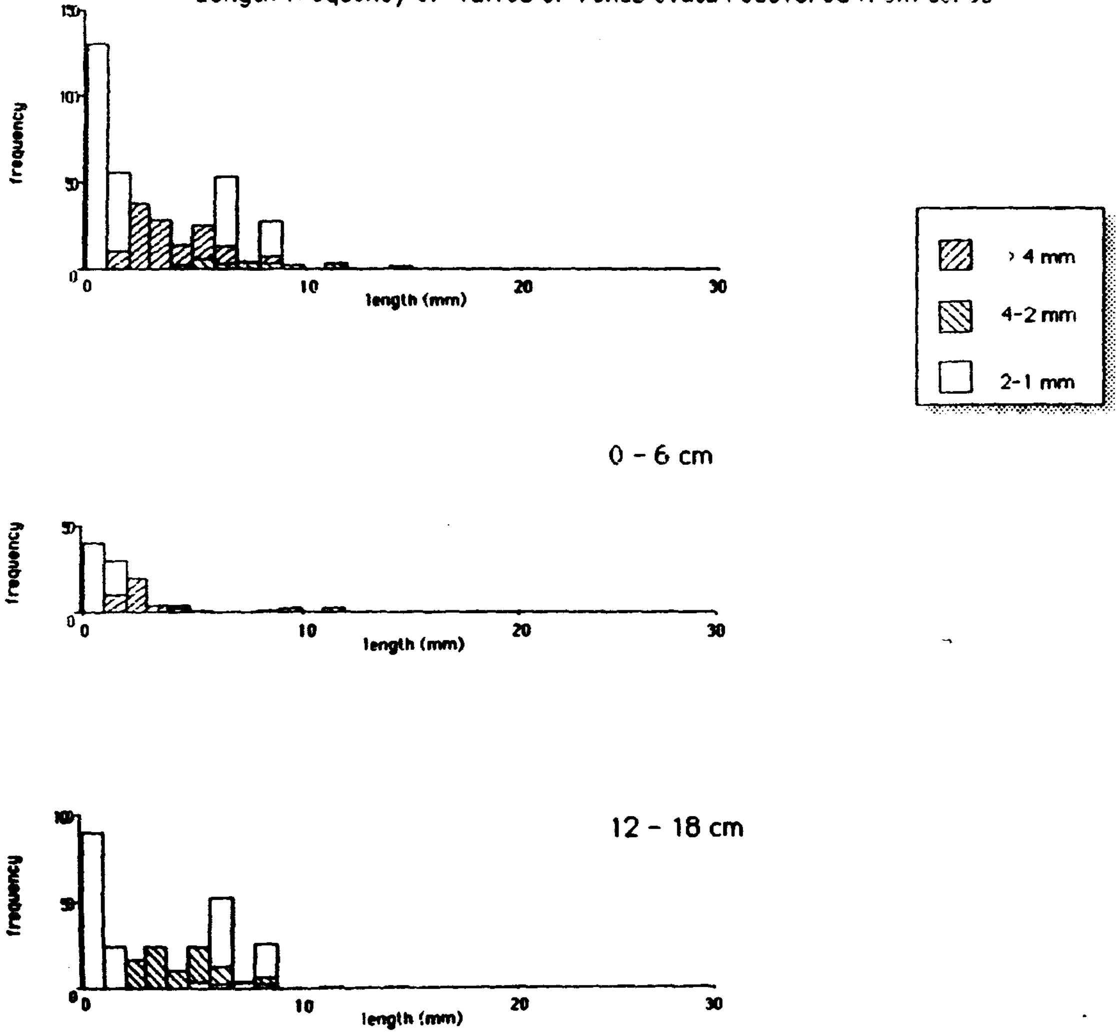
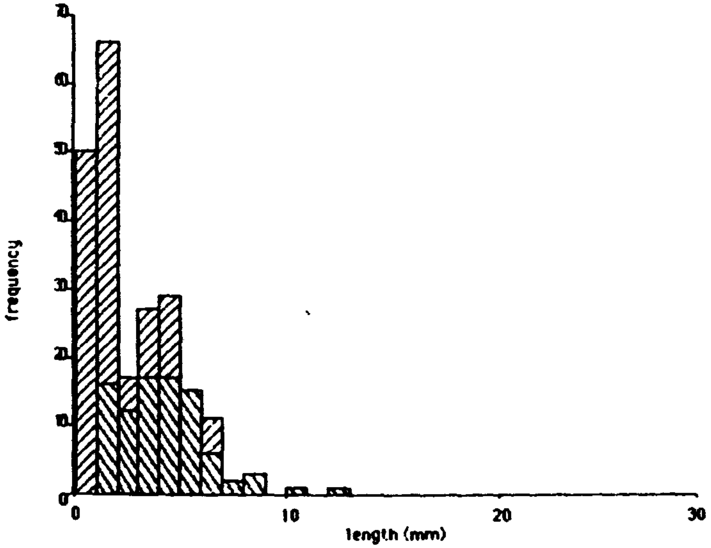


**Figure II 1.13**

Length frequency of whole valves of Crania recovered from cores



#### Gastropoda

Gastopods only account for a relatively small fraction of the sediment (Table II 1.4) and many of these are believed to be exotic (see section I 1.3.4). Gastropod shells are also typically more robust than bivalves of equivalent size (Chave, 1964). Of all the gastropod shells recovered only two *Propalium* shells had countersunk borings.

### II 1.3.3.2 Brachiopoda

(*Terebratulina* is discussed in section II 1.3.4.3)

#### *Crania anomala*

Total number collected in (a) cores & (b) grabs: (a) **23**, 11 (b) **8**, 1; Mean percentage in (a) cores (b) grabs: (a) **0.11** (b) **0.14**; Density of living species /m²: **115**; Carbonate biomass estimate (g/m²/yr): **4.4**; Carbonate production estimate (g/m²/yr: **5.2**; Ratio of estimate to actual:**-733**; Maximum length recorded (mm): **13.3**; Whole valve/fragment ratio in (a) cores (b) grabs: (a) **2.64** (b) **0.39**; Percentage predation: **0**; Mean lenght of shells (mm): **6.93**

The death assemblage is left skewed (Fig. II 1.13), like the living population (Fig I 2.9a), but unlike the accumulation of dead valves recovered by Cadée (1968), which was believed to indicate a transported assemblage. All the whole valves recovered from the sediment were robust (there was no evidence of 'softening' of the carbonate as seen in *Terebratulina*, section III 2). It is unusual therefore that no whole valves were recovered in the 2-1 mm fraction (Fig. II 1.13) and that even *Crania* debris was uncommon within the 2 - 1 mm fraction even though the microstructure is very distinctive. It is possible that the punctae, which anastomose throughout the body of the valve, weaken fragments increasing rates of comminution.

### II 1.3.3.3 Echinoidea

#### Spatulate spines

Regular echinoderm plates contributed 0.46 to the total weight of sediment, regular spines, 0.227% and the tests of the clypeasteroid, *Echinocyamus pusillus*, 0.37% of the mean total from grabs and cores.

Spatulate spines of irregular echinoderms, similar to those figured by Farrow *et al.* (1985: plate 2a) accounted for 0.03% of the > 1 mm fraction, although no irregular echinoderm fragments were recovered. In the 1 – 0.5 mm fraction the estimated density of spatulate spines (1300 – 1700 / 6 cm core split, n = 5) was similar to the estimated density of regular echinoderm spines of 1400 – 2100. Although irregular spines are typically more abundant per animal (the irregular urchins *Spatagnus purpureus* and *Echinocardium cordatum* bear 31,300 spines and 12,300 spines respectively, whereas *Echinus esculens* bears 5790 spines and *Psammechinus* only 2100 (Schafer, 1972), the absence of irregular urchin fragments suggest that the spines have been winnowed in.

*Ophiothrix fragilis*

Ophiuroid debris accounts for only 0.408% by weight of the > 1 mm sediment fractions, of which 49.4% were ossicles, spines accounting for 4.4% and shields and plates the remainder. There are no readily definable trends in the concentration of ophiuroid debris although there is considerable consistency through most cores (Table II 1.11). The distribution of ophiuroid remains within the sediment size fractions is unsurprisingly the most skewed of all the carbonates examined, reflecting the small size of the elements, 91.5 % of the total weight being present in the 2 – 1 mm fraction.

TABLE II 1.11
Ophiuroid ossicles (and total ophiuroid fragments) by core as
a percentage by weight of total carbonate

| Depth (cm) | Core 1 | Core 2 | Core 3 | Core 4 | Core 5 | mean |
|---|---|---|---|---|---|---|
| 0 – 6 | .70(.903) | .053(.069) | 0.20(.238) | | 0.06(.175) | 0.25(.346) |
| 6 – 12 | .58(.580) | .048(.074) | | | | |
| 12 – 18 | .36(.534) | .087(.135) | 0.39(.394) | 0.65(.775) | 0.22(.662) | 0.26(0.431) |
| mean | .53(.719) | .007(.102) | 0.29(.316) | 0.65(.775) | 0.14(.419) | |

The disintegration of ophiuroids is discussed by Schaefer (1972), the skeleton of a ophiuroid is made up of large numbers of very small elements joined only by skin or connective tissue and fifteen hours after death of the ophiuroid the arms begin to disintegrate and fall apart.

The skeleton of the arms consists of an internal row of vertebral ossicles, their size decreasing towards the tips of the arms, and an outer skeleton of shield-like plates. The lateral plates of *Ophiothrix fragilis* generally carry seven arm spines on the distal margin (Mortensen 1938). According to Mortensen (1938) the isolated skeletal parts are not classifiable, and all were attributed to *O. fragilis* in this study.

An attempt was made to estimate the contribution of *O. fragilis* ossicles to the sediment. Initially the ratio between arm-length and ossicle number was determined from *O. fragilis* collected by grab sample from the Firth of Lorn and Port Appin. The disc diameter and arm length of anaesthetized animals were measured with dial calipers, ossicles were counted on both oral and aboral sides. Of 60 arms measured (12 animals) only six arms were judged to be complete. Equations for the relationships between arm length and disc diamter and ossicle number are relatively crude due to the small sample sizes;

(II i) Arm length = 5.94 (+/- 2.6) x disc diameter + 1.59(+/- 0.37)
(n = 6; r = .813)

(II ii) Ossicle number = 7.67(+/- 1.83) x arm length (mm) - 0.39(+/- 0.02)
(n = 6; r = .902)

It is possible from these crude estimates to determine that in a medium sized ophiuroid with a disc diameter of 8 mm, the arms are approximately 50 mm long, giving 376 ossicles per arm and 1881 ossicles in total. It therefore follows that it is also possible to estimate total production of ossicles/$m^2$/yr, from estimates of elimination production (Table II 1.12). This estimate is relatively unsatisfactory because the sample was collected in late August just prior to spawning, and the numbers of 0 - 3 mm animals is small, giving a negative production figure.

TABLE II 1.12
Estimation of ophiuroid ossicle production based on lengths of arm (n number; A mortality; B mean disc length; C mean number of arm ossicles from equation; E total number of ossicles.)

| length (mm) | n | A | B | C | D | E |
|---|---|---|---|---|---|---|
| 0 - 3 | 10 | -121 | 1.5 | 10.53 | 80.4 | -48,626 |
| 3 - 7 | 131 | 40 | 5 | 27.5 | 210.5 | 42,100 |
| 7 - 16 | 91 | 91 | 11.5 | 69.9 | 535.7 | 243,736 |
| TOTAL | | | | | | 237,209 |

Given that disc weight accounts for 33.8% of the total AFDW (SD = 6.0), and that AFDW is higher in arms (77.4%, n = 6, SD = 6.0) than in the disc (65.5, n = 5, SD 5.9) it is also possible to derive crude estimates of the total weight of each ossicle. If it is assumde that ossicles acount for 80% of the total AFDW of the arm, then the mean ossicle weight is approximately 0.46 mg. Total AFDW production, split into arm and disk production on this basis of the figures outlined above, derives a second estimate of ossicle production of 139 008/m$^2$/yr. This second estimate could be improved by empiracle determinations of mean ossicle weight.

The estimated density of ophiuroid ossicles/kg of autochthonous carbonate (> 1 mm) in the death assemblage is 10 022 ossicles, or 5% of estimated annual production per year. Clearly a considerable quantity of production will be present within finer sediment fractions, however, examination of finer fractions, produce estimated densities of 1800 – 10 000 additional ossicles/kg of sediment (x = 4300, n = 4, SD = 3380). Using the maximum figure for ossicle density would suggest that in the absence of destruction or transport of ossicles, annual production would be dispersed through 10 kg of sediment, which contrasts with total estimated autochthonous production of 330g/m$^2$/yr!

### II 1.3.3.4 Crustacea

#### Cirripeda

Ring plates, scuta and terga were common in the sediment, forming betwen 0.8 and 3.9% of the total, the greatest percentage of *Verruca* occurs surprisingly at the base of the *Mellinia* facies.

Although the anomurans and brachyurans are important members of the living community which shed their exoskeletons between each growth stage, extensive decalcification of the cuticle leaves a soft exoskeleton which soon decays. In the sediment only crab claw tips, and fragments of the carapace are present and these are uncommon.

### II 1.3.3.5 Bryozoa

Bryozoa only account for 0.5 – 0.7% of the total weight of sediment. In the analysis they were subdivided into chained stoloniferous arbourescent forms ('arborescent 1', *eg. Scrupocellaria* sp., *Crisia* sp., *Bugula* sp.) contigous arbourescent forms such as the cheilostomata *Sertella* sp. (arborescent 2), mound, and encrusting forms (Table II 1.13). Mound and chained stoloniferous arbourescent forms were the most important contributors to the sediment. All these forms were observed epifaunally on *M. modiolus*.

TABLE II 1.13
Summary of the composition of bryozoan debris in the sediment
('fossil' = grab samples, c2f2, c2f3,c3f5, Grabs = grab samples c209, c306)

| Species | 0–6 | 6–12 | 12–18 | Cores | 'fossil' | Grabs |
|---|---|---|---|---|---|---|
| Bryozoa arborescent (1) | 42 | 11 | 47 | 0.207 | 0.501 | 0.224 |
| Bryozoa arborescent (2) | 20 | 51 | 29 | 0.119 | 0.007 | 0.127 |
| Bryozoa mound | 18 | 51 | 32 | 0.342 | 0.100 | 0.353 |
| Bryozoa incrusted | 12 | 10 | 78 | 0.019 | 0.049 | 0.016 |
| Bryozoan debris | – | – | – | 0.008 | 0.177 | 0.010 |
| Total bryozoa | – | – | – | 0.694 | 0.834 | 0.506 |

## II 1.3.4 BIOSTRATINOMY OF *TEREBRATULINA RETUSA*

Total number collected in (a) cores & (b) grabs: (a) **671** (b) **203**; Mean percentage in (a) cores (b) grabs: (a) **2.6** (b) **7.4**; Density of living species /m²: **2466**; Carbonate biomass estimate (g/m²/yr): **0.10**; Carbonate production estimate (g/m²/yr): **0.12**; % change in sediment: **+ 40**; Maximum length recorded (mm.): **28.2**; Whole valve/fragment ratio (a) cores (b) grabs: (a) **7.8** (b) **2.3**; Pedicle/brachial valve ratio: **0.6**; Percentage predation: **0**.

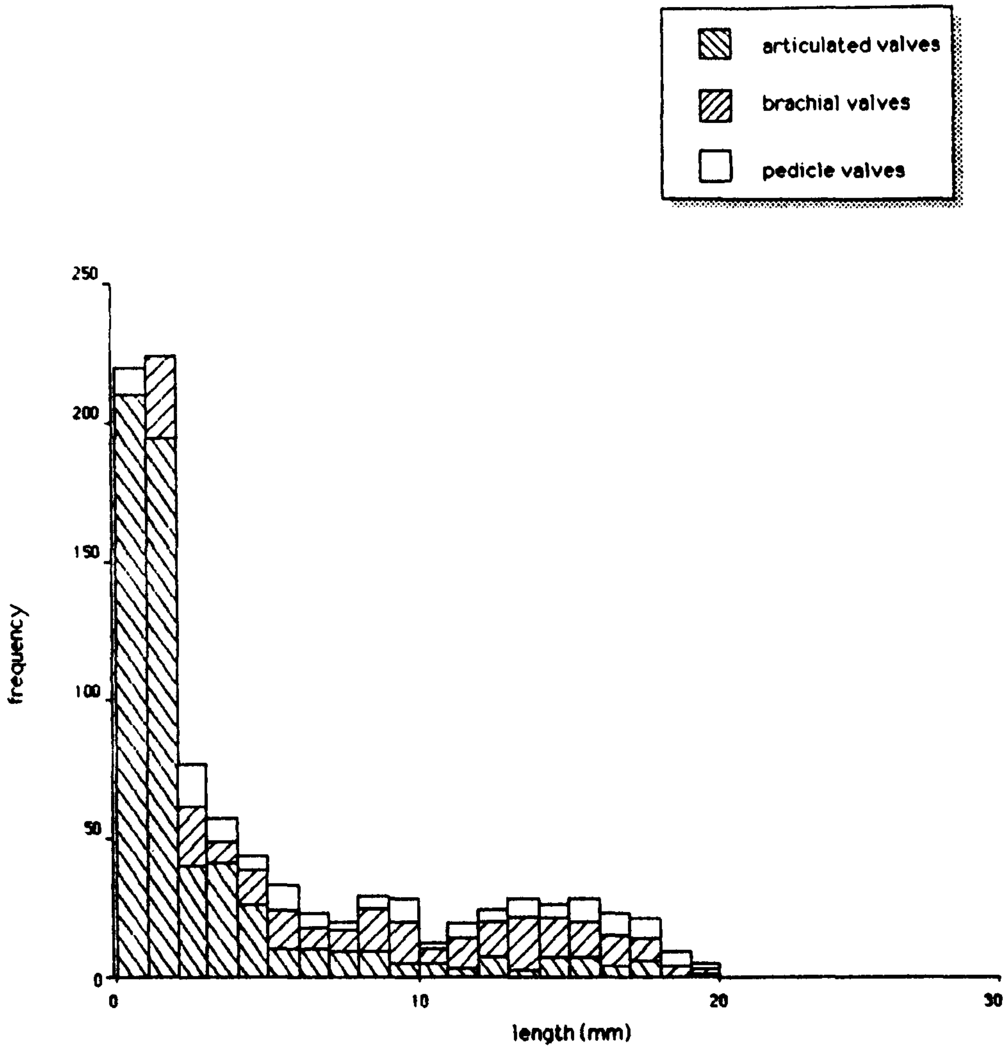
Although a considerable quantity of *Terebratulina* carbonate is probably allochthonous, derived from the 'cliff facies' where *Terebratulina* is abundant, the underestimation observed by Caulet, (1967) and Noble *et al.* (1976) and predicted in section III 2 was not readily apparent. *Terebratulina* debris was extensively bored (Plate 1e & f, Plate 3d), but there was no evidence of dissolution of the shell fabric (cf. Plate 3h).

### II 1.3.4.1 Population structure

The population structure of *T. retusa* in the death assemblage, although left-skewed has an accumulation of large shells producing a weakly bimodal polygon (Fig. II 1.t.1), very similar to that of the Ordovician Strophomenacian

Figure II 1.t.1

Length frequency of articulated and disarticulated valves of Terebratulina recovered from the death assemblage



*Onniella meeki* illustrated by Richards & Bambach (1974). Although the secondary peak is overstated in Figure II 1.t.1, because the polygon is a composite of valves and articulated shells, the accumulation of adult shells is a feature common to each of the fractions if plotted in isolation. The left skewed population structure of *T. retusa* contrasts with the indeterminate distribution of *Macandrevia* (Fig. 1.t.2b), and *Gryphus*, where large shells dominate both the living and death assemblage (Fig. 1.t.2a)

The accumulation of small shells and valves of *T. retusa* is similar to the Recent accumulations investigated by Noble & Logan (1981) and Stewart (1981) and most of the silicified upper Ordovician brachiopods investigated by Richards & Bambach (1975). The results are, however at odds with *Gryphus* and *Macandrevia* material examined during the course of the study (Table II 1.t.1, see Emig, 1985 for additional details of Corsican sites) and the published size frequency distributions of a number of other Recent & fossil brachiopod death assemblages (eg. Parkinson, 1952, 54; Veevers, 1959; Hallam, 1961, 72; Sheldon, 1965; Cadée, 1968; Neall, 1970; Brookfield, 1973; Richards & Bambach, 1975; West, 1977; Lee, 1978; Stewart, 1981).

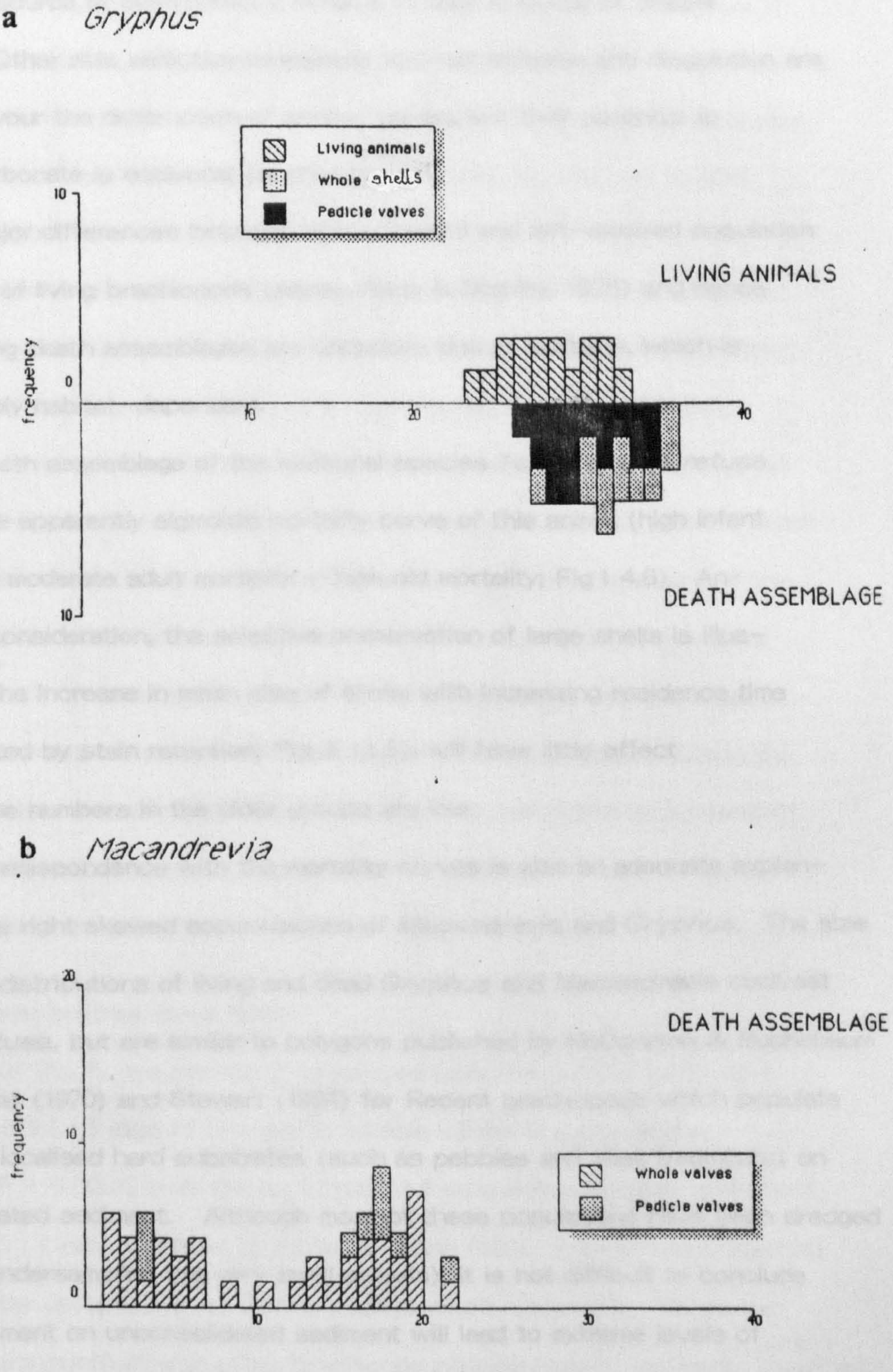
TABLE II 1.t.1
Details of sites from which brachiopod material was examined during the course of the study

| Site | Firth of Lorn | Hebrides Shelf | Corsica |
|---|---|---|---|
| Species | *Terebratulina retusa* | *Macandrevia cranium* | *Gryphus vitreus* |
| Latitude | 56°23'N | 56°43'N | 42°40'N |
| Longtitude | 05°38'W | 09°00'W | 08°50'W |
| Depth | 160–200 | 601 | 120–200 |
| Sediment | g(mS) | 'sandy mud' | g(mS)? |
| Collection | Day Grab | Box Core (22 cm) | Dredge |

Two alternative factors, size related preservation and mortality are responsible for the size–frequency distribution on accumulating dead shells. A number of contibutory factors have been forwarded to explain the loss of small shells, the absence of lag concentrations of smaller shells and the observ–

Figure II 1.t.2

Size frequency distributions of a) Gryphus and b) Macandrevia



ations of Stewart (1981: 206) and Noble & Logan (1981: 96) appear to rule out selective winnowing of smaller shells. The extent of bioerosion is believed to be inversely related to the degree of agitation of grains (eg. Bosence, 1978) and thus to hydrodynamic stability and size. However, where bio-erosion is a significant source of destruction it is liable to bias in favour of smaller particles. Other size selective processes such as abrasion and dissolution are liable to favour the destruction of smaller valves, but their potential to destroy carbonate is equivocal (section II 1.42.).

The major differences between right-skewed and left-skewed population structures of living brachiopods (*sensu* Raup & Stanley, 1978) and hence accumulating death assemblages are undoubtly due to mortality, which is demonstrably habitat-dependant.

The death assemblage of the epifaunal species *Terebratulina retusa*, reflects the apparently sigmoidal mortality curve of this animal (high infant mortality - moderate adult mortality - high old mortality; Fig I 4.6). An additional consideration, the selective preservation of large shells is illustrated by the increase in mean size of shells with increasing residence time (as estimated by stain retention; Fig. II 1.t.5), will have little effect because the numbers in the older groups are low.

The correspondence with the mortality curves is also an adequate explanation of the right skewed accumulations of *Macandrevia* and *Gryphus*. The size frequency distributions of living and dead *Gryphus* and *Macandrevia* contrast with *T. retusa*, but are similar to polygons published by McCammon & Buchsbaum (1968), Neall (1970) and Stewart (1981) for Recent brachiopods which populate very small localised hard substrates (such as pebbles and shell fragments) on unconsolidated sediment. Although most of these populations have been dredged (thereby undersampling the very small animals), it is not difficult to conclude that settlement on unconsolidated sediment will lead to extreme levels of juvenile mortality, and therefore right skewed population structures when contrasted with those attached to solid substrates (cf. Stewart, 1981). Surlyk

(1974) noted similar differences in population structures of peduncally attached and 'free-lying' Cretaceous articulate brachiopods. Surlyk (1974) further suggests, on the basis of growth lines, that brachiopods living on unconsolidated substrates have much higher initial growth rates than small pedunculate species to reduce the period of vulnerability to disturbance. An almost identicle conclusion (rapid early growth rate and delayed maturity) was reached by Seed & Brown (1978) to account for the population of living *M. modiolus* although in this case it was predation and not disturbance which caused elevated levels of juvenile mortality.

In addition to elevated substrate related mortality (SRM) of unconsolidated sediment, an increasingly significant factor since the end of the Palaeozoic due to the acceleration in biogenic disturbance (Thayer, 1979, 83), morphological adaptations to brachiopods to survive in shifting sediment will also increase selective preservation of adults shells. The most common adaptation of brachiopods living in unconsolidated sediment, the thickening of the posterior regions of the valve (to lower the centre of gravity and therefore improving hydrodynamic stability; eg. *Gryphus*, *Neothyris*) and the small or occluded foramen, will potentially increase the half-life of dead shells in the sediment. When this thickening is achieved by the production of a prismatic ('tertiary') layer, the rate and degree of shell softening will also be reduced, further increasing the potential half-life (section III 2).

### I 3.4.2 Pedicle/brachial valve ratios

62.2% of the *T. retusa* valves recovered from the Firth of Lorn were brachial, the 1.6 : 1 ratio of brachial to pedicle valves is a significant deviation ($P > 0.0001$) from the expected 1 : 1 ratio and is in close agreement with the 1.5 : 1 ratio obtained by Noble & Logan (1981) from an untransported shallow water accumulation of *Terebratulina septentrionalis*. These two accumulations contrast with other brachiopod bearing Recent sediments examined during the course of the study (Table II 1.t.1), where pedicle valves and characteristic pedicle valve fragments are more abundant (Table II 1.t.2; Fig

II 1.t.2; Plate Ic).

TABLE II 1.t.2
Comparison of pedicel/brachial valve ratios
of Recent articulate brachiopods
,(site details given in Table II 1.t.1)

| | Whole | | | Fragments | | |
|---|---|---|---|---|---|---|
| | whole | pedicle | brachial | pedicle | brachial | debris |
| *Gryphus* | 18 | 12 | 1 | 90 | 29 | 6 |
| percent | *58* | *38* | *3* | *85* | *9* | *ND* |
| *Macandrevia* | 34 | 9 | 0 | 20 | 12 | ND |
| percent | *79* | *21* | - | *34* | *36* | *32* |
| *Terebratulina* | 350 | 178 | 286 | ND | ND | ND |
| percent | *43* | *22* | *35* | *39* | *16* | *45* |

Boucot *et al.* (1958) following the work of Menard & Boucot (1951) on current drifting and Boucot (1951) on the recognition of death assemblages, were the first to employ pedicle-brachial valve ratios for environmental interpretation. Boucot *et al.* (1958) assumed that variation of valves from a 1 : 1 ratio indicated selective redistribution and used valve ratios in Devonian deltidiodont brachiopods to interpret the extent of net transport away from a growth site. Similar distorted pedicle-valve ratios have been employed as palaeoenvironmental indicators since this pioneering work. Hanna (1986: 216) observed a selective bias towards the more robust pedicle valves (1.4-2.3 : 1) in stropheodontid brachiopods from the Ludlow (Silurian) of the Welsh Borderlands and Gotland. Similar biasing has also been observed by Dr. J. Lawson (*in* Hannah, 1986) in many other genera (e.g. *Kirkidium*, *Dayia*), from the Welsh Borderland and from the Ordovician of Norway (Worsley, 1971; Worsley & Broadhrst, 1975). Like Boucot *et al.* (1958), Hanna (1986) and Worsley & Broadhurst (1975) attribute this biasing to current-drifting and therefore use it as a palaeoenvironmental indicator.

Pedicle/brachial valve ratios are only valuable as an environmental indicator if the distorted ratio is the consequence of environmental factors. Seilacher (1968) describes two L. Devonian genera which have similarily thickened valves and a similar pattern of preservation to the Mediterranean *Gryphus*. Seilacher assumes that the destruction was mechanical and is forced to conclude, (in the absence of an exotic fauna) that the umbo fragments (c.f. Plate 2g) were produced by '*in situ* transport'.

Selective destruction of one valve, the alternative explanation for such occurrences, has only latterly been demonstrated, when Noble & Logan (1981) observed elevated numbers of brachial valves i~~s~~n a non-transported Recent death assemblage. Surprisingly their observation has not lead to investigations of the various factors liable to promote selective preservation, although this is a potentially valuable palaeoecological phenomenon.

The respective ratios of *Gryphus*, *Macandrevia* and *Terebratulina* appear to be related to the relative robustness of the two valves. Attempts to quantify the robustness of the valves of *T. retusa* by measuring the thickness at approximately the central point of each valve, produced no clear trend of increasing shell thickness with increasing size (r, 0.455; Fig. II 1.t.3b) although a better correlation between thicknesses of opposing valves (r = 0.706; Fig. II 1.t.3a). Shell thickness is a relatively poor measure of the robustness of valves, particularily when, as is in the case of *Gryphus* and *Macandrevia* there are considerable variations in thickness across the valve.

Attempts were therefore made to determine the relative weight of carbonate in opposing valves by estimating the difference in size of the two valves and then comparing the relative weights, corrected for differences in size.

### Estimate 1

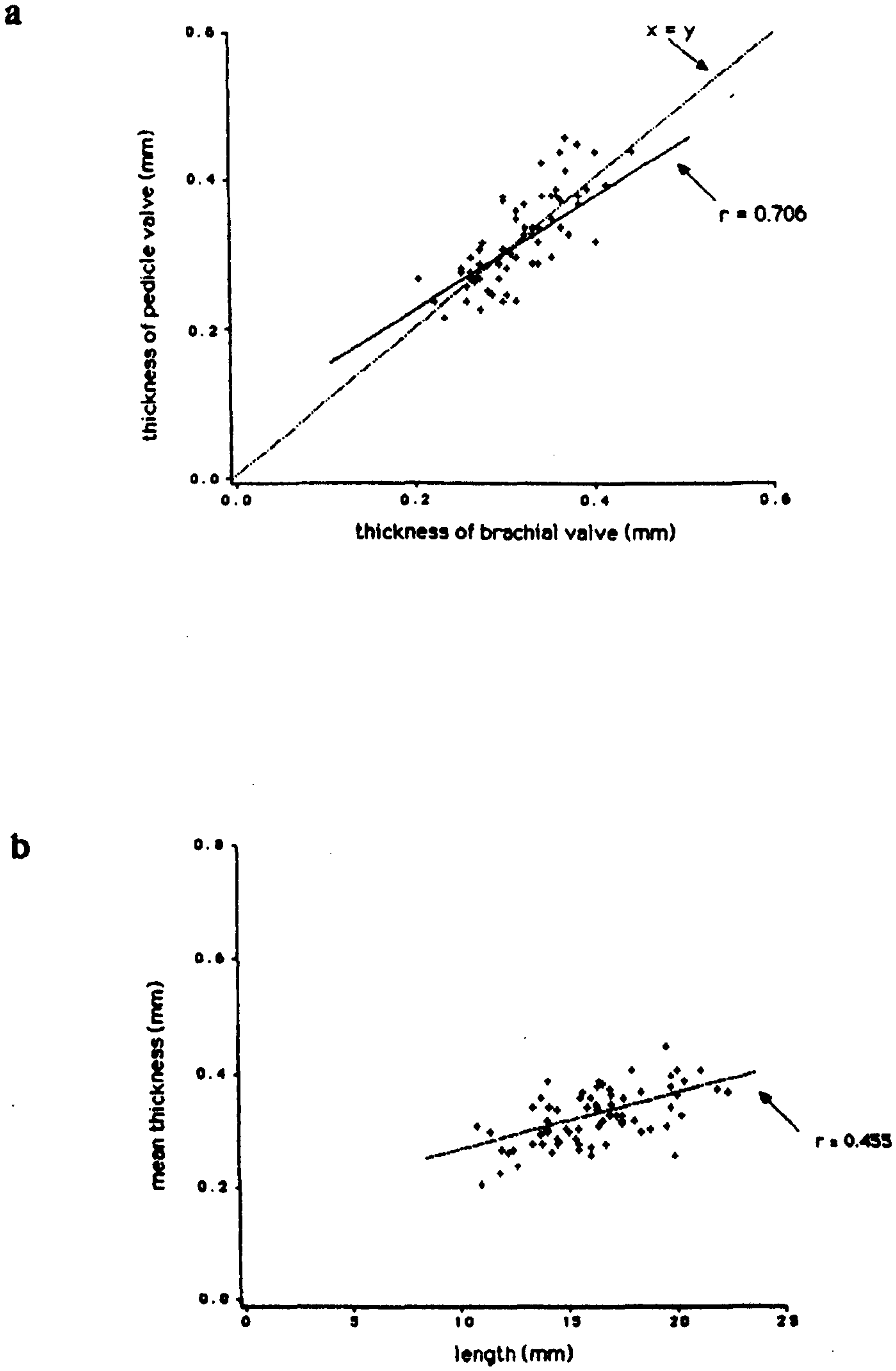
The ratio between the pedicle and brachial valves, was determined by multiplying the brachial valve by the ratio between the lengths of the pedicle and brachial valves. This method recognizes that there is no change in the width of the brachial valve, but fails to account for differences in shell curvature.

### Estimate 2

The degree of shell curvature was included in Estimate 2, for *Gryphus* and *Macandrevia* this was achieved using a modified version of the surface area

Figure II 1.t.3

Relative thickness of the valves of T. retusa
a) Comparison of brachial and pedicle valve thicknesses
b) Relationship between mean thickness and length



estimate supplied by Flessa & Brown (1983).

(II i) $$Vs = L \times H \times (1 + W/L))$$

where *Vs* is valve size and *L*, *H* and *W* are length, height and width respectively.

The valve areas of *T. retusa* was estimated from data supplied by G. B. Curry, which included as estimate of the curved length of each valve *cL*, but not valve height. The alternative estimate of valve size for *T. retusa* was derived from the equation:

(II ii) $$Vs = cL \times W$$

Estimate 2 resulted in larger standard errors (Table II 1.t.2a) probably reflecting the difficulties in accurately measuring the height of either valve. Regressions of shell length, against weight are also supplied (Table II 1.t.2b).

TABLE II 1.t.2a
Relative weights of pedicle and brachial valves

| Species | n | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|---|
| *Terebratulina retusa* | 82 | 1.135 | 0.001 | 1.118 | 1.029 | 1.181 | 0.914 | 0.006 |
| *Macandrevia cranium* | 19 | 1.114 | 0.006 | 1.007 | 1.102 | 1.402 | 0.904 | 0.027 |
| *Gryphus vitreus* | 19 | 1.115 | 0.007 | 0.725 | 1.131 | 1.593 | 1.153 | 0.025 |

A = Ratio of length of pedicle to brachial valve; B = SE of length; C = mean of estimate 1; D = mean of estimate 2; E = maximum of estimate 2; F = minimum of estimate 2; G = SE of estimate 2.

TABLE II 1.t.2b
Regressions of total weight against length; of the form
log10 length (mm) = a. log10 weight (mgs) − b).
(NB. values for *T. retusa* are given in Table I 3.1b)

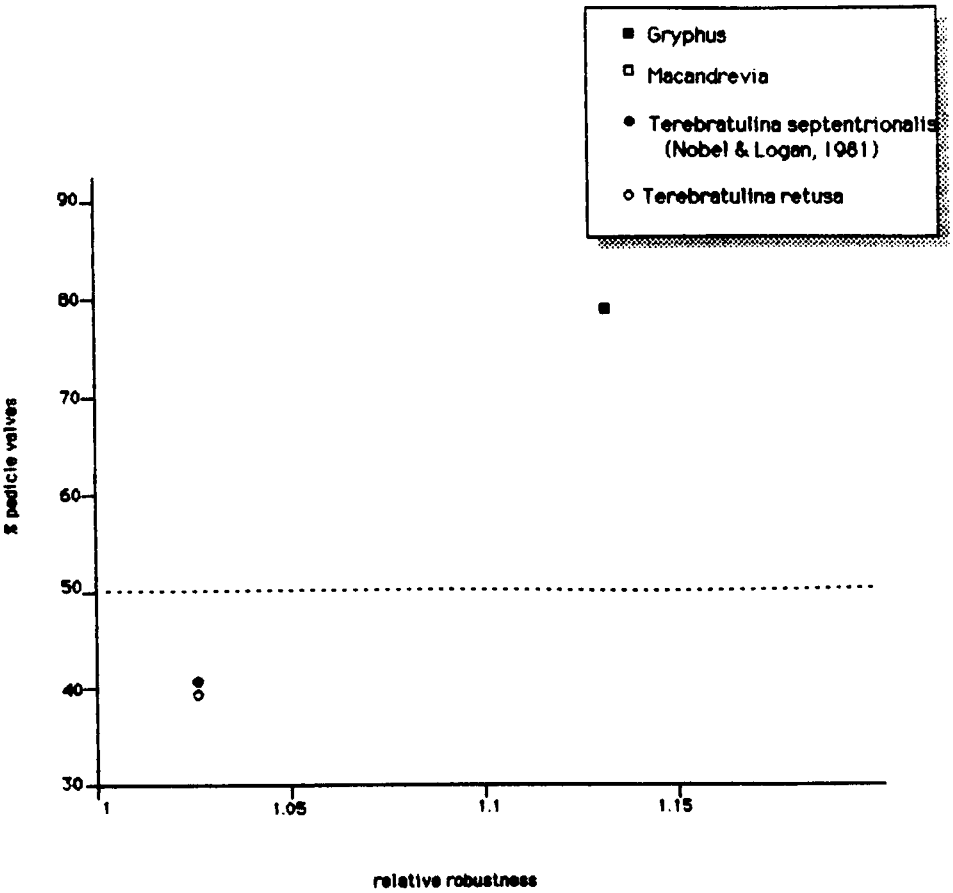
| | n | a | b | r | SE a | SE b |
|---|---|---|---|---|---|---|
| *Macandrevia cranium* | 19 | 0.241 | 2.202 | 0.883 | 0.765 | 0.283 |
| *Gryphus vitreus* | 19 | 3.081 | 3.142 | 0.849 | 1.589 | 0.474 |

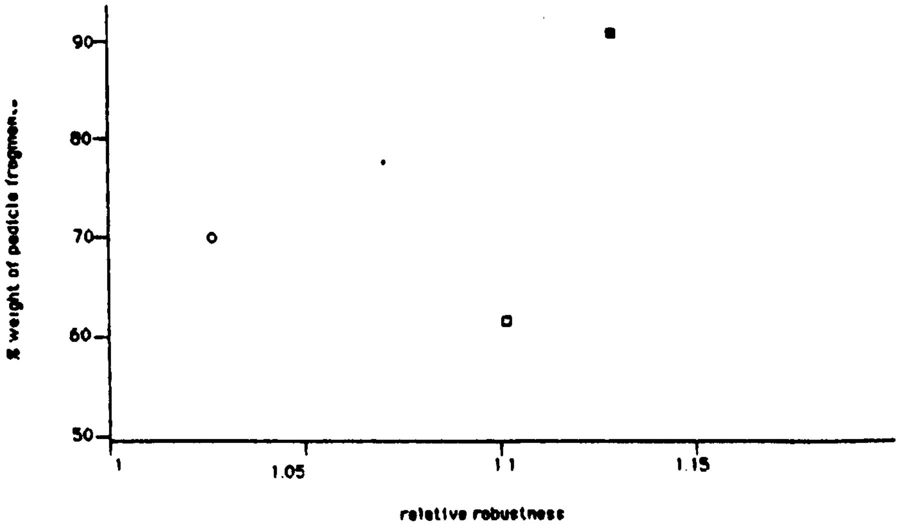
There is a clear trend towards increasing preservation of pedicle valves as the relative robustness of this valve increases (Fig. II 1.t.4). Although there is insufficient information on the environmental characteristics of the three sites (Table II 1.t.1), it appears unlikely that environmental factors alone could account for the variation in valve ratios.

Assuming that rates of destruction of both valves are equal, the single

Figure II 1.t.4

Relative preservation of valves of Terebratulina, Gryphus & Macandrevia, related to the 'robustness' of the valves





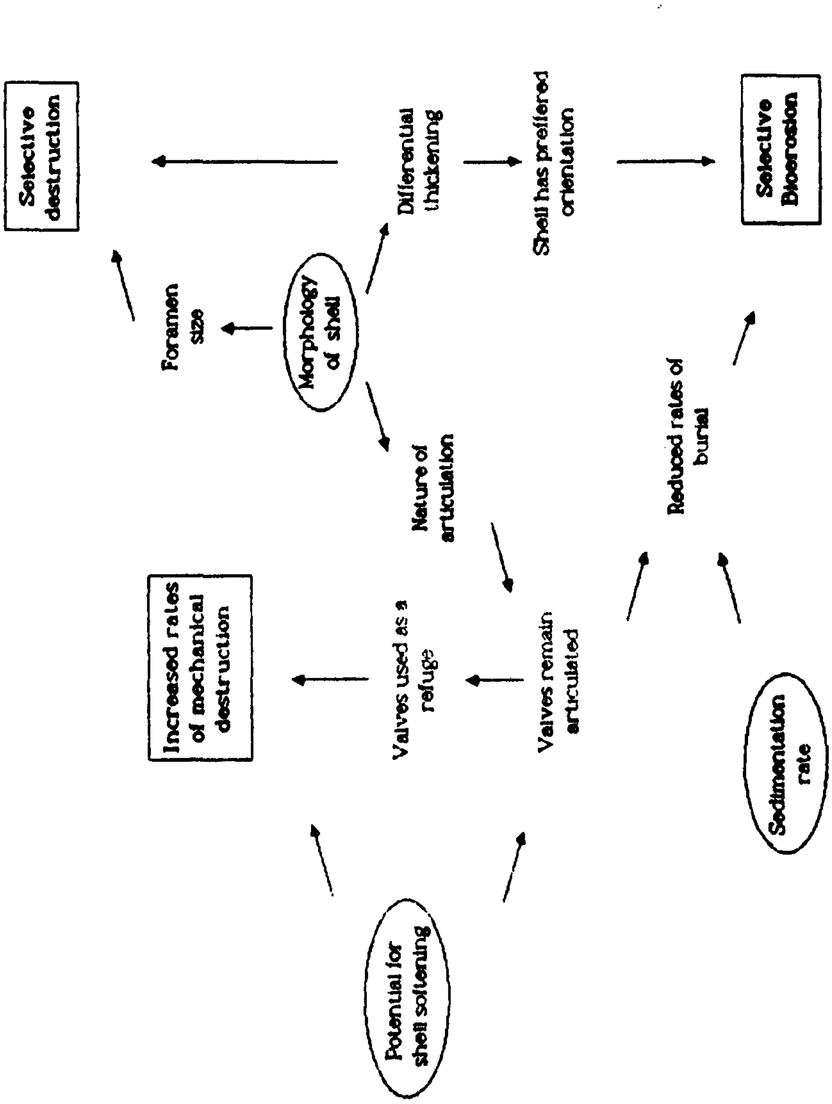
most important feature is the differences in the relative thickness of the two valves. Processes such as dissolution, abrasion and bioerosion which operate non-selectively on all items will take longer to reduce more substantial items such as the thickened posterior region of the pedicle valves simply because there is more carbonate to weaken or destroy.

More information is required on the mechanics of fragmentation and disarticulation of articulate brachiopod valves as these are also potentially relevant to the process of selective destruction. Pedicle valves will, for example, be more liable to fragment if they possess a large foramen and lack differential thickening (Fig. II 1.t.5). When the valves of *T. retusa* (particularily softened shells, section III 2) are opened overwide, the increase in effective distance between the sockets on the brachial valve causes the pedicle valve to split down the median axis. Although such a force is very unlikely to operate on shells in the sediment, similarly split fragments of pedicle valves are common in the sediment (Plate 2.a; Noble & Logan, 1981), perhaps because a crushing force operating on the posterior of the shell will have a similar effect.

Splitting down the medinal axis is less common in the *Gryphus* and *Macandrevia* and is only seen in brachial fragments. The presence of a delithyrum or occluded foramen will reduce the structural weakness of the pedicle valve (eg *Gryphus*; Fig. II 1.t.5) as will posterior thickening. In *Macandrevia* and *Gryphus* the most common fragments are parts of the thickened posterior of the pedicle valve (Plate 1g, 1h).

Rates of burial are lower in articulated shells than solitary valves (section III 1.4.4), increasing the chances of post-mortem bio-erosion. During life, a variety of orientations are adopted by species with posterior thickening if the centre of gravity is altered by the tethering pedicle. The hydrodynamically stable position for such shells following death, is lying upon the heavier pedicle valve, which is therefore less liable to infestation (Plate 2 e). There is no similar selective bioerosion of *T. retusa* shells, which have no

Figure II 1.t.5
Interrelated features leading to selective destruction



preferred orientation (Table III 1.6). If the degree of *Cliona* infestation is dependant upon the thickness of the carbonate, then infestaton will be more significant in those species with thickened, hydrodynamically stable, valves. Such selective bioerosion will weaken and hence further reduce the 'preservation potential' of the brachial valve (Fig. 1.t.5).

The large internal volume of *Gryphus* shells may provide an important refuge (see Dauer *et al.* 1982), 23% of conjoined valves of *T. retusa* held in cages on the seafloor for 83 days, had indications that organisms had been present within them and 3% (19) were recovered with polychaetes inside, the most numerous being an unidentified Neridiae and the phyllodocids *Eulalia viridis* and *Platyneris coccinea* (Plate 2d). Sediment worm-tubes and two polychaetes (one *Sylid* sp. and a member of the Terebellidea) were also collected from inside the closed valves of *Gryphus* (Plate 2d). The presence of these organisms within the valves could encourage bio-mechanical fragmentation by scavenging crustaceans, crushing the shell in order to gain access to the polychaetes. It is not possible to establish the palaeontological significance of such refuges, although in a fascinating paper, Brett (1977) describes a complete specimen of the trilobite *Phacops rana* Green in the enclosed valves of an atrypid, (cyrtomatodont) brachiopod *Pseudoatrypa* sp. The calcified brachidium of the atrypid is absent and Brett (1977) postulates that the brachiopod may have provided shelter or possibly food for the trilobite.

In the pulsed input experiments, crushing of articulated valves markedly reduced the half-life of *T. retusa* shells within the sediment and it is suggested that this may be related to the role of brachiopod valves as refuges (section III 1.4.4).

The microarchitecture of the shell both affects its strength during life (Currey and Taylor, 1974), and the rate of shell softening (Purdy, 1963; Collins 1986). The absence of a tertiary layer will lead to a rapid softening of the skeletal fabric enabling weaker forces to commute the valves, although the maximum claw gape of the largest anomuran recovered from the Firth of Lorn was only 9 mm (see section I 1.2.3.6), too small to grasp adult *T. retusa* shells. Skeletal architecture (especially ribbing) influences the crushing resistance of brachiopod shells (Alexander, *pers comm.* 1985).

The inter-relationship between the various factors outlined above and in Figure II 1.t.5) will increase the potential for selective destruction, although information presently available on the behaviour of brachiopod shells in the sediment is insufficient to predict distorted pedicle and brachial valve ratios. Stewart (1981) presents pedicle/brachial valve ratios for three species of New Zealand terebratulids from a variety of habitats which show no clear pattern of selective preservation.

### II 1.3.4.3 Half-life of *T. retusa* in the sediment

Attempts were made to estimate the residence time of shells from the retention of stain, using the guidelines outline in section II 2.2. Shells collected from the living community and the death assemblage show similar frequency distributions of the various categories, with shells in group 3 accounting for approximately 40% of the population (Fig. II 1.t.6). The percentage of group 1 shells is similar in both the within-community sediment and the sediment from areas lacking any living *Terebratulina* (c2f2; Table II 1.t.4), suggesting that, either there is considerable mixing of the shells across the living community or that living *Terebratulina* were present close to this sample.

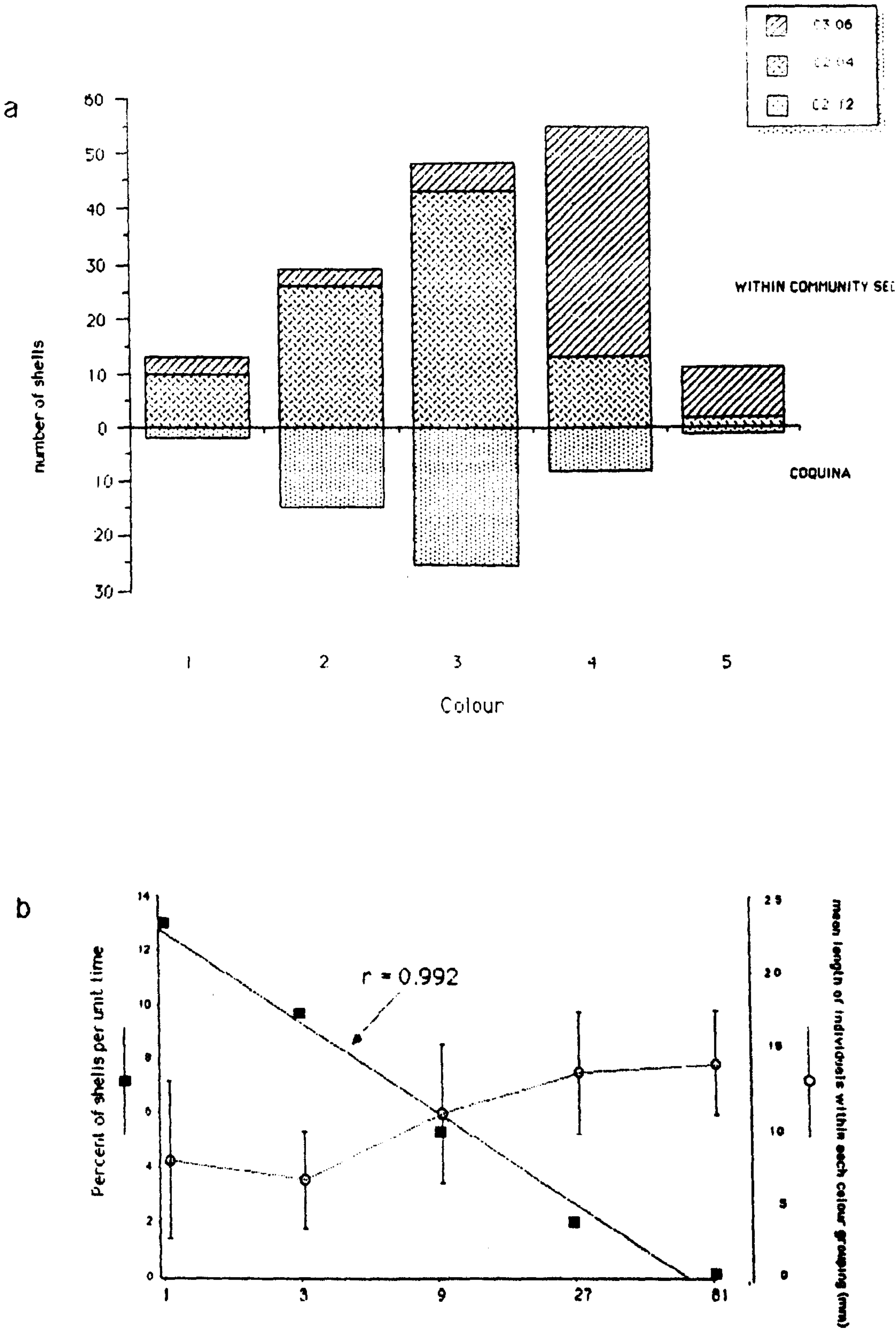
TABLE II 1.t.4
Results of the categorization of *T. retusa* into residence times within the death assemblage

| | Residence time of *T. retusa* valves | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| c2f2 | 3 | 25 | 42 | 13 | 2 |
| c204 | 10 | 26 | 43 | 13 | 2 |
| c306 | 3 | 3 | 5 | 42 | 9 |
| TOTAL | 16 | 56 | 94 | 72 | 18 |
| % | 6.6 | 23 | 38.6 | 29.6 | 7.4 |

An attempt was made to provide a half-life estimate (t1/2) for *Terebrat-*

Figure II 1.L.6

a) Distribution of valves by residence time
b) Decline in mean numbers of shells with increasing residence time (error bars 1 SD)



*ulina* in the death assemblage from the distribution of shells between colour groupings. The estimate assumes that the groups 1 – 5 represent a sequence of shells with increasingly long residence times, and that each age group spans a larger time interval than the previous one.

It is unlikely that shells will have been subject to processes which will significantly increase or decrease the rate at which the organic matrix is lost (see section III 2). It is also not unreasonable to assume that the time intervals encompassed within each group increase sequentially, for as processes alter the state of progressively older shells they require concomitantly longer time intervals to achieve each state change, due to the coarsening of the resolution. The same is equally true of other stochastic processes, such as estimates based on rates of radio-active decay.

The estimates of half-life can only be determined if a final crucial assumption also holds true, that the increasing time intervals are regularly spaced (ie that they are a sequence of base powers). If the process of ageing of carbonate fabric following death can be interpreted as a series of rate-independant stochastic events. As the scale on which such events are examined broadens, their predictability increases. The time taken to pass from one state to another is therefore governed by stochastic laws, and as long as the groupings are natural it is not wholly unreasonable to suggest that they are governed by an underlying symmetry.

Assuming the rate of destruction of biogenic particles is constant (*ie.* particles can be ascribed half-lives; Powell *et. al*., 1982, 84), then the number of shells in successively older year classes will diminish at a constant rate. Dividing the accumulation of shells in each colour grouping by the time interval of each colour grouping, yields an estimate of the mean number of shells per year class in each time interval, which should show a constant rate of decay. The correct base sequence (time interval) can then be determined by iteration, the best whole base approximation being given by base 3 (least sum squares regression r = 0.994; Fig I 1.t.6). The fit to the line is good, suggesting that the above assumptions may well be valid.

To determine half-life in the sediment, the next approximation was to ascribe times to each interval. The residence time of the colour groups 1 – 4 were estimated by measuring point loading force (see section II 2). Although the shells from colour groups 2 – 4 had mean strengths approximating to the minimum values measured (Fig. II 2.5), colour group 1 had strengths ranging from 52% – 11% of the estimated figure for living animals. Using the relationship derived from the point-loading experiments (equation III i.v ) gives an estimated mean residence time for group 1 shells of 122.5 days (assuming a similar rate of strength loss to the experimental animals).

The residence time of the first group is therefore 0 – 0.6 years giving estimates of 0.6–1.8, 1.8–5.4, 5.4–16.2 and 16.2–48.6 years for groups 2 through 5 respectively. The regression of this equation yields a half-life of approximately 5 years (see section III 1.2.5 for the derivation of this figure).

The summed totals of all brachiopod debris > 8.5 mm collected in six grab samples (0.6 $m^2$) with a total volume of 34 litres was 303 whole valves, 386 brachial ( > 9.37 mm) and 271 pedicle valves (all values/$m^2$), an estimated density of 689 brachiopod shells/$m^2$. Autochthonous carbonate production which accounts for approximately 49% of the total sediment is estimated to be approximately 330 g/$m^2$/yr, which can be interpreted as an accumulation of 1.3 mm/$m^2$/yr (section I.3). Rates of mortality estimated from the productivity estimates of *T. retusa* (Table I 3.8) predict that 45 animals in excess of 8.5 mm contribute to the death assemblage each year.

Autochthonous carbonate accounts for approximately 49% of the total sediment by weight in the > 1 mm fraction, of the remaining sediment 28% is terrigines and 23% exotic carbonate. Autochthonous carbonate is unlikely to account for such a high figure in the finer fractions where terrigines are more abundant. Assuming no winnowing of bio-erosion fragments into the deeper water *Mellinia* facies (cf. Young & Nelson, 1985) and no dissolution of carbonate as a result of bio-erosion (an unlikely scenario see Scoffin *et al.*, 1980) then the maximum possible sedimentation rate is approximately 2.4 mm/yr or 250 cm/1000 yrs. This estimate is significantly higher than the estimates of Matthew (1974) and Nelson (1978) for modern shelf sea carbonates of 10 - 100 cm/1000 years but not dissimilar to the estimates of Allen (1983). Using a more conservative figure (the maximum estimate of Matthews, 1974) for shelf sea carbonates of 1 mm/yr it will take 60 years to accumulate the 6 cm depth of sediment sampled in the grab and coreing programs giving a half-life of 4.6 years. Although the correspondance between the two independantly derived estimates of half-life is close, the maximum ages of shells at 17 - 48 years appears intuitively low.

However, Brown (1979) obtained radiocarbon dates for bivalves in the Colonsay Sea Area and the Sound of Jura ranging from 208+/- 70 to 478+/-70 years B.P. with a maximum age for a *Phymatolithon calcareum* dated at 3893+/- 70 from the Sound of Iona. The Firth of Lorn is bathymetrically similar to the Sound of Jura, and autochthonous carbonate production is believed to be high (section I 3.4.4) and suggest either rapid sedimentation or rapid destruction of carbonate within these areas.

### II 1.3.5 Exotic Species.

Exotic species were those recovered only as dead shells during the course of the study. On the basis of available autecological information (Tebble, 1966; Campbell, 1976; Brown, 1979 and references therein) and additional distributional information from sites on the west coast of Scotland (Gage, 1972 a & b, 74; Brown, 1979; Comely, *pers comm.*) the exotic components of the death assemblage were subdivided into allochthonous (ie. transported) and potentially autochthonous components (Table II 1.14 & 1.15; cf. Thomsen & Vorren, 1986).

### II 1.3.5.1 Potentialy autochthonous species.

Potentially autochthonous species comprise those which either were unsampled living animals or animals which were formerly living in the habitat but

## TABLE II 1.14
Exotic species believed to be autochthonous

| Species | Depth range (m) | Life position | Sediment |
|---|---|---|---|
| *Dentalium entalis* | 15 – 100 | shallow burrower | fine sand – shell gravel "even in dredging the bulk of shells taken are usually empty ...". (Young & Thompson, 1976) |
| *Emarginula reticulata* | LW – 265 | epifaunal | on rocks & under stones, rasping sponges, but also ingesting detritus. |
| *Natica alderi* | LW – 165 | infaunal | sand – gravel bottoms |
| *Didora apertura* | LW – 20 | epifaunal | on rocks & under stones, feeding on sponges. |
| *Propalium ancyloidea* | 7 – 170 | epifaunal | possibly a detrital feeder |
| *Nucula nucleus* | ELW – 146.5 | infaunal | muddy gravel – coarse sand, found alive by Comely (*pers comm.*) at station 25 at densities of 7/$m^2$. |
| *Chlamys distorta* | LW – 90 | epifaunal | attached to shells and similar hard substrates, one large right valve found attached to the inner valve of a stunted *M. modiolus*. |
| *Venus ovata* | 3 – 180 | shallow burrower | sand – shell-gravel, found alive by Comely (*pers comm.*) at stations 24 and 26 at densities of 7/$m^2$.. |
| *Myrtea spinifera* | 8 – 110 | infaunal | soft mud – muddy gravel |
| *Gafrarium minimum* | 7 – >200 | surface – shallow burrowing | sandy mud – medium gravel |
| *Corbula gibba* | ELW – >200 | infaunal | silty sand – muddy gravel, found alive by Comely (*pers comm.*) at station 26. |
| *Thracia phaseolina?* | ELW – 55 | deep burrower | sand – sandy gravel, *T. villosiuscula* found alive by Comely (*pers comm.*) at stations 25 & 26. |

## TABLE II 1.15
Exotic species believed to be allochthonous

| Species | Depth range (m) | Life position | Sediment |
|---|---|---|---|
| *Patina pellucida* | LW – 3 | associated with the algae *Laminaria saccharina*, *L. digitata*, *Rhodymania palmata* and fucoids. | |
| *Callistoma zizyphinum* | LW – 156 | associated with algae. | |
| *Gibbula* sp. | HWNT – 130 | associated with algae, one of the most common prosobranchs on rocky shores. | |
| *Littorina* sp. | LW – 140 | associated with algae although also a detrital feeder. | |
| *Onoba semicostata* | LW – 100 | epifaunal | under stones, among weeds & corallines, mussles, *Lima* nests & tunicates in shelly gravel but always where there are considerable quantites of silt. |
| *Hydrobia ulva* | intertidal | epifaunal | soft substrate esturine grazer |
| *Ocenabra* sp. | LW – 95 | epifaunal | on rocks and under stones |
| *Mytilus edulis* | LW – 88 | epifaunal | on rocks and similar hard substrates. |
| *Lima hians* | LW – 100 | nest builder | coarse sand – gravel, broken shells. |
| *Lima loscombi* | 10 – 180 | nest builder | mud – gravel, broken shells |
| *Dosinia exoleta* | ELW – 75 | deep burrower | muddy gravel – shell gravel |
| *Mya arenaria* | LW – 75 | deep burrower | mud – sandy gravel |
| *Mactra corallina* | LW – >200 | burrower | clean sand – (muddy gravel) |
| *Glycymeris glycymeris* | ELW – 75 | shallow burrower | muddy – shelly gravel |
| *Chlamys septemradiata* | 10 – 180 | epifaunal | deepwater muds |
| *Chlamys striata* | 7 – 160 | epifaunal | |
| *Chlamys tigerina* | ELW – 90 | epifaunal | |
| *Chlamys varia* | ELW – 80 | epifaunal, either free living or attached bysally | |
| *Chlamys nivea* (possibly a variety of *C. varia*) | | | |
| *Similipecten similis* | 4 – 55 | epifaunal | one of those species noted by Brown (1979) to be transported in deep-water channels associated with high surface currents. |

which were absent during the collection period. Ecologists have long recognized that it is typically not possible to sample all the members of a living community (Petersen, 1976; Powell *et al.*, 1982), indeed the rate of recovery of increasingly rare members of the live fauna has been exploited by ecologists to describe the pattern of diversity, so called 'rarefraction' (Sanders 1968).
The alternative, that the carbonate was derived from within the area, but by species which were rare or absent over the collection period as a consequence of long-term fluctuations in benthic diversity, is increasingly recognized as a possibility (e.g. Petersen, 1976; Powell *et al.*, 1984; Gray, 1981; Carthew & Bosence, 1986). Autochthonous 'exotic' carbonate of this kind is ecologically, but not palaeoecologically significant, as neither type of occurrence would be recognizable from a fossil horizon.

Bivalves known to inhabit shell-gravels comprise the largest fraction of potentially autochthonous (Table II 1.14). If they are indeed present in the sediment then failure to sample these animals alive may be explained by their occurrence at relatively low densities, or at depths too deep to recover by grab, or temporal fluctuations in abundance (c.f. Peterson, 1976; Gray, 1980; Buchanan, 1986; Carthew & Bosence, 1986).

### I 3.5.2 Allochthonous species

Allochthonous species are those which on the basis of available autecological information are unlikely to have derived from the *Modiolus* community. Their presence within the death assemblage suggests some mixing of communities. The recognition of mixed assemblages is important in palaeoecology, and is usually thought to indicate current drifting of material.

The *Modiolus* community in the Firth of Lorn has a hydrography and a bathymetry apparently well suited to the input of exotic carbonate and the allochthonous component of the exotic species includes a substantial number of littoral and sub-littoral epifauna (Table II 1.15). It is possible that all this material is transported from shore by bedload transport, but other processes should not be discounted. The estuarine gastropod, *Hydrobia ulva*, is an example of a shell well suited to flotation. In life *Hydrobia* has been observed floating both on the surface film (Newell 1962) and bouyed on a mucus raft (Fretter & Graham, 1978), Wilson (1967) has also observed post-mortem flotation. Other small gastropods (eg. *Onobia* and *Propalium*) could also be introduced in a similar manner, although this has yet to be proved.

Many of the exotic species are characterized by an association with macro-algae (Table II 1.15). Six of the ten species that Brown (1979) considered characteristic of shore to shallow water transport are herbivorous gastropods, and the association is common to many of the exotic shells of other studies (Johnson, 1962; Cadée, 1968; Akpan, 1981). The blades of macro-algae, which compromise a visually significant part of the detritus within the community (section I 2.3) and it follows that the epifloral component may have been associated with this detritus.

Macro-algal mediated transport is not a new concept, Van Regteren Altena, (1959) noted that under favourable conditions the sublittoral brown macro-algae *Himanthalia* was capable of transporting some of the epifauna from English and French Channel coasts towards Dutch beaches. The same algae was also implicated by Cadée (1968) in transport of shallow water epifauna into deeper waters in a Spanish Ria. Akpan (1981) suggested that the shells of the *Patella vulgata* and *Littorina littorea* recovered from 12 m of water may have been transported by the action of drifting algae, and Powell *et al.* (1982) note the import into a death assemblage of animals attached to sea grass blades.

*Mytilus* an exotic member of the death assemblage may also be prone to algal mediated transport. When a whole plant breaks free they tend to transport the clast to which they were attached, resulting in the eventual mortality of organisms within the clast (McKay, 1972; Dayton, 1973; Farrow *et al.*, 1979; Paine, 1979; Akpan, 1981; Witman 1984; A. Ansell *pers comm.* 1985), macro-algae have been implicated in the transport of pebbles forming the Chesil Bank by a similar process (H. Powell, *pers comm.* 1985). Although there are no records of *Mytilus* suffering this form of mortality, Witman (*pers comm.* 1985) considers this process to be that major source of mortality in the byssate bivalve *M. moidolus* at certain sites on the New England coastline.

Storms which have been noted to cause large accumulations of kelps may not be needed to uproot the algae and transport clasts since as they grow, they naturally get more bouyant through the larger surface area of the frond exposed to wave and current action (Farrow *et al.*, 1979).

The ratio of blade/clast transport will probably increase with distance from shore. A crude biological indicator of the ratio is the gastropod *Patina pellucida* which occurs in two forms, one *P. p. pallucida* is found on the surface of fronds and during the summer, whereas the other *P.p. laevis* is found in recesses in the holdfast (Graham, 1971). All the *P.pellucida* recovered in the study were of the *P.p. pellucida* form. Unfortunately this does not unequivocally demonstrate that all transport occurs on the blades of macro-algae, as the ratio is always going to be biased in favour of *P.p. pellucida* not simply because the blade has a shorter effective life (Thorson 1971: 108), but as the relative area of the shell mouth (and hence adhesion) of this form decreases with age (Fretter & Graham, 1978). In addition, both forms are capable of flotation, bouyed on a mucus raft (Fretter & Graham, 1978).

It is therefore possible that all of the shallow water component could have been introduced by some form of post-mortem flotation, particularily associated with macroalgal detritus ripped free during storms. Some of the gastropod fragments (most notably two shells of *Littorina* sp.) were well worn possibly related to an extended period of current-drifting across the seafloor rather than algal transport, gastropods are relatively resistant to mechanical destruction (Chave, 1964; Driscoll & Weltin, 1973) and are therefore liable to have a favourable preservation bias. The degree to which algal mediated transport may account for transport from shallow water is sadly almost impossible to determine although it is perhaps palaeontologically significant.

Excluding those species for which some form of post-mortem floating could account for the introduction, leaves a rump of bivalves including the pectinaceans (see section II 1.3.3.1), *Dosinia exoleta, Lima hians* and *L. loscombi* (recovered alive from current swept gravels outside Loch Don) and Mactra corallina and *Mya arenaria* (Table II 1.15), all which have probably been introduced by down-slope bedload transport.

### II 1.3.6 Composition of sediment trapped within the byssal threads

Pebbles and stones constitute only a very minor fraction of the sediment trapped within the byssal threads of living clumps of *Modiolus*. The trapped sediment is dominated by coarse fragments of *Modiolus*, elevated relative to the coarse ( > 4 mm) fraction of the remaining sediment (Table II 1.16). The significance of 'sibling' carbonate in stabilizing the clumps demonstrates a positive feedback within the *M. modiolus* community (cf Kidwell & Jabolinski, 1983).

As many of the valves become trapped within the byssal threads the high ratio of fragments of *M. modiolus* to whole valves in the sediment, may be in part due to the forces exerted by multiple byssal attachments and animals re-aligning within the clump.

TABLE II 1.16
Comparison between composition of byssal threads
& main community

| Species | %overall | %byssal | %change |
|---|---|---|---|
| *Capulus ungaricus* | 0.103 | 0.632 | + 513 |
| *Crania anomala* | 0.1 | 0.49 | + 390 |
| *Modiolus modiolus* | 72.8 | 86.3 | + 18.5 |
| *Terebratulina retusa* | 4.3 | 4.1 | - 4.6 |
| *Chlamys* sp. | 4.7 | 4.10 | - 12 |
| *Anomia* sp. | 1.25 | 0.91 | - 27 |
| Gastropoda | 1.8 | 1.0 | - 44 |
| *Astarte* sp. | 2.7 | 0.4 | - 85 |
| *Hiatela arctica* | 0.384 | 0.083 | - 36.0 |
| Stones | 11.9 | 0.68 | -1650 |
| *Modiolus phaseolinus* | 0.170 | 0.0 | ND |
| | | | |
| Total weight (g) | 1022 | 158.6 | |

(% overall = % composition, by weight in grab samples c209 & c306; % byssal = % by weight of sediment recoverd from byssal threads in grab samples c209 % c306)

The shells of *Capulus* and *Crania*, both species intimately associated with the *Modiolus* clumps, were also elevated in the byssal threads relative to the surrounding sediment, although other species which were also common epifaunal constituents (*Anomia Hiatella* and *M. phaseolinus*) were not (Table II 1.16).

### II 1.3.7 Comparisons between productivity and preservation

*M. modiolus* dominates the sediment and as a result because percentage comparisons are used to identify taphonomic biasing (section II 1.2.2) the 98% increase in *Modiolus* carbonate within the sediment (Table II 1.17) essentially delimits the 'no-change' position. This increase in the *M. modiolus* fraction within the sediment, relative to its' estimated contribution to production, is due to the virtual absence of ophiuroid debris in the sediment and the under-representation of *Astarte*. Farrow *et al.*, (1984) suggest that *Modiolus* carbonate on the Orkney shelf is rapidly degrading which if also true of Firth of Lorn will mean that carbonate which has increased relative to *M. modiolus* may simply be degrading at a more typical rate, and conversely carbonate showing a fall relative to *M. modiolus* is being destroyed even more rapidly.

TABLE II 1.17
Comparison of estimated carbonate production and composition within the death assemblage

| Species | n/$m^2$ | production | % pres | % change | Comely's stations | | |
|---|---|---|---|---|---|---|---|
| | | | | | 24 | 25 | 26 |
| *Nuculana minuta* | 6 | 0.01 | 3.291 | +32810 | – | 7 | 3 |
| *Abra alba* | 4 | 0.03 | 0.821 | +27167 | 20 | 203 | 27 |
| *Parvicardium ovale* | 5 | 0.01 | 1.286 | +12760 | – | – | – |
| *Anomia* sp. | 71 | 0.03 | 3.366 | +11120 | – | – | – |
| *Thyasira flexuosa* | 2 | 0.01 | 0.04 | + 300 | – | 13 | 23 |
| *Hiatella artica* | 51 | 0.2 | 0.769 | + 285 | – | – | – |
| *Modiolus phaseolinus* | 479 | 0.65 | 1.294 | + 99 | 10 | 50 | – |
| *Modiolus modiolus* | 171 | 37.8 | 74.85 | + 98 | – | 90 | – |
| *Terebratulina retusa* | 2466 | 6.6 | 9.25 | + 40 | – | – | – |
| *Astarte sulcata* | 37 | 20.9 | 4.8 | – 335 | – | – | 13 |
| *Crania anomala* | 115 | 1.5 | 0.18 | – 733 | – | – | – |
| *Musculus discors* | 58 | 0.73 | 0.104 | – 602 | – | – | – |
| *Ophiothrix fragilis* | 238 | 31.0 | 0.351 | – 8632 | 27 | 120 | – |
| *Amphiura chaijei* | 37 | 0.65 | – | | – | 20 | – |

(% pres = mean % composition of carbonate, by weight, relative to total weight of allochthonous carbonate within the death assemblage; % change = % change relative to production estimates; Details of Comely's stations given in Fig. I 2.3 & Appendix III)

*Nuculana, Abra, Parvicardium, Anomia* (and possibly *Venus ovata* which may be autochthonous, Table II 1.14) form a natural group, for all of which estimates of carbonate production markedly underestimates the presence of shells in the sediment (Table II 1.17). All are relatively small bivalves, and all but one (Anomia sp.) are shallow burrowing members of the infauna. Distribution of the carbonate within the sieve fractions reflects the small size of most of these species, little of the carbonate is present in the > 4 mm fraction. Estimated densities and therefore carbonate production of all these bivalves is relatively low, being highest for the epifaunal species *Anomia* sp. (as it is for *Hiatella* which occupies an intermediate position between these and *Modiolus*). This variation reflects an undersampling of small infauna, which unlike the epifauna were not retained, although production estimates for all four species are similar as the very small *Anomia* contribute little to production.

*M. modiolus and M. phaseolinus* are presented as a summed total in addition to being presented seperately because of their inter-relation in the analysis due to the difficulty of distinguishing debris with incomplete dentition. The percentage difference between the estimated production and carbonate within the sediment of *M. modiolus* & *M. phaseolinus* is almost identical (Table II 1.17).

*Terebratulina, Astarte, Crania, Musculus* are ophiuroid debris are all under-represented relative to *M. modiolus* in the sediment fraction. The production estimates of both *A. sulcata* and *C. anomala* are both crudely estimated by multiplying biomass by a P/B ratio derived from the bivalve equation of Robertson (1979, see section I 3.3). The production estimate of both species may be too high because of the lifespans supplied in the literature seem intuitively rather short. Recalculating estimated production on the basis of 12.5 year lifespans (P/B ratios dervied from equation 1 of Robertson 1979) reduces the disparities between production estimates and presence in the sediment but the values for *Astarte* and Crania are still 539 and 223% respectively, suggesting that inaccuracies in production estimates are insufficient to account for the under-representations of carbonate.

The values for *Musculus discors* and *Thyasira flexuosa* are discounted as the contribution to the sediment is so low that in both cases they are absent from one of the sediment fractions. The taphonomic history of *Musculus* will be complicated by its intimate association with solitary ascidians.

## II 1.4 CONCLUSIONS

### II 1.4.1 Population structures from the death assemblage

The common occurrence of normal distributions among fossil populations, as emphasised by Olson (1957) does not hold true for any of the death assemblage population structures. Although it is relatively easy to demonstrate the under-representation of small shells in a death assemblage the converse is more difficult to determine as it is time consuming to obtain accurate estimates of their density in the living population due to typically high rates of mortality (Powell *et al.*, 1984).

The size frequency distribution of valves of *M. modiolus* is bimodal (Fig. II 1.6) and like *T. retusa* (Fig. II 1.t.1) is thought to represent a sigmoid mortality curves (high infant mortality – moderate adult mortality – high old mortality; Boucot, 1981). Indeed, the delayed maturity and size selective predation of *M. modiolus* (Seed & Brown, 1978) is perhaps the most clearly defined example of this pattern of mortality, although other bivalves with similar curves have been described (eg. *Protothaca staminea*; Scmidt & Warme, 1969).

### II 1.4.2 Comparison of production estimates and preservation

The most striking loss of carbonate within the Firth of Lorn was *Ophiothrix fragilis*, which was estimated to account for 31% of total carbonate production, but composed only 1.7% of the autochthonous carbonate in the > 1 mm fraction. Although relatively more significant in finer sand fractions the preservation bias against ophiuroid ossicles is striking.

The relatively high contribution of ossicles to the carbonate fraction of core 1 of the Mellinia facies is not repeated in the replicate core and although it is possible the *Mellinia* facies may serve as a sink for ossicles there is no evidence presented from this work to suggest that the readily transported skeletal elements accumulate in this sink, unless the increased bioturbation is serving to promote solution of carbonate (cf. Aller, 1982). It is also unlikely that *O. fragilis* is prone to heavy cropping, the food value of *Ophiothrix fragilis* is low relative to molluscs or polychaetes (Holm 1953) and concentrated in the disc which is probably difficult to selectively crop because of interference by the bulky arms. In the study of Holm (1953) *Ophiothrix fragilis* occurred in the stomachs of 39% benthic fish examined, but unlike polychaetes and bivalves only rarely did the ophiuroid form an important part of the diet, usually just a few spines or portions of the arms being present. In the present study, although remains of *O. fragilis* were recovered from the stomach of *Scyliorhinus stellaris* and *Eupagurus* was one observed feeding a severed arm, it is unlikely that they are heavily preyed upon.

Although Schaefer (1972) states that occasionally coarse sands, infilling the gaps between boulders and shell fragments are rich in ophiuroid debris, the paucity of ophiuroid remains is one of the most striking features of this and other studies in the area. Farrow *et al.* (1978: 73-4) make the following relevant observations "After many underwater traverses in the Inner Hebrides, particularily between Mull and Coll, one is left with a vivid impression of the forests of ophiuroids and echinoids peppering the more bouldery areas. Their debris in the resulting sediments, however, is far less impressive, indeed we have yet to identify ophiuroid plates from over 100 samples so far examined: echinoderm plates and spines have never yet exceeded 10%. This is staggering when one considers that the Pennines are built largely of echinoderm debris in the shape of the Carboniferous Limestone."

The selective increase in the group of relatively small (mainly infaunal) bivalves in the sediment, can be accounted for either as a result of significant allochthonous additions or due to some form of selective taphonomic biasing. If the latter alternative is true then it should be possible to isolate some common feature of these particular bivalves.

Brown (1979) estimated the extent of transport from correspondance analysis in an equivalent deep water channel in the Sound of Jura, and concluded that a number of species not recovered in the living community were transported down the steep slopes into deep water, as were *Lima* and *Dosinia* in the Firth of Lorn. Of the species whose density is elevated in the sediment it is possible that some *Anomia* (and to a lesser degree *Hiatella*) are allocthonous, being introduced from exposed hardgrounds of the near vertical cliff walls to the south of the community, the inability to sample this facies make estimates of potential production difficult. A total of 18.5% of the *Anomia* and 6% of *Hiatella* were predated by an epifaunal predatory gastropod such as *Ocenabra*. As no living predatory gastropds were collected and the sediment analysis yielded only a single *Ocenabra* shell, it is not unreasonable to assume that these predated valves have been introduced from the hardgrounds to the south. Densities of *Anomia* and *Hiatella* are relatively high in the community (71 & 51/$m^2$ respectively) the area needed to supply the shortfall in autochthonous production (assuming equivalent densities) is approximately 75 times that of the *Modiolus* community for *Anomia* and a more credible 2.6 times the area for *Hiatella*.

Table II 1.18 includes data supplied by Comely (*pers comm*) for three stations close to the study area (Fig. I 2.3), which may be feeding carbonate into the death assemblage. Of the relevant species Comely only records *Abra alba* and *Nuculana minuta*. The estimated density of *Abra* from the study area is considerably lower than Comely's nearest station (station 25) and also lower than the other two sites. *Abra alba* is a deposit feeding infaunal bivalve and it is possible that it was undersampled by the grab. Multiplying the production estimated by the maximum density of Comely (station 25; 203/$m^2$) produces a production estimate well above that needed for parity with the sediment.

TABLE II 1.18

Distribution of autochthonous carbonate across size fractions

| | % in each size fraction | | | % in | frag/whole |
|---|---|---|---|---|---|
| | >4mm | 4–2mm | 2–1mm | sediment | valve ratio |
| *Nuculana minuta* | 7 | 49 | 45 | 1.43 | 3.311 |
| *Abra alba* | 9 | 19 | 72 | 0.59 | 2.492 |
| *Parvicardium ovale* | 14 | 31 | 55 | 0.88 | 4.136 |
| *Anomia* sp. | 36 | 20 | 44 | 2.62 | 1.631 |
| *Hiatella artica* | 24 | 43 | 33 | 0.56 | 1.673 |
| (*Thyasira flexuosa* | 80 | 20 | – | 0.22 | 0.061) |
| *Modiolus phaseolinus* | 36 | 23 | 41 | 1.54 | 4.219 |
| *Modiolus modiolus* | 75 | 15 | 10 | 50.95 | 6.581 |
| *Modiolus* combined | 74 | 15 | 11 | 52.49 | 6.540 |
| *Terebratulina* | 30 | 31 | 40 | 3.94 | 5.031 |
| *Astarte* sp. | 90 | 6 | 4 | 1.74 | 1.662 |
| *Crania anomala* | 75 | 18 | 71 | 0.14 | 1.514 |
| (*Musculus discors* | 2 | 83 | 15 | 0.02 | 19.364) |

(% in sediment = weight of carbonate as a % of the total weight of sediment)

The densities of the shallow burrowing *Nuculana minuta* recorded by Comely are very close to the figures from this study. *Nuculana minuta* is one of those species thought by Brown (1979) to be indicative of transport in this kind of hydrodynamic regime, and *Nuculana penderi* (Dall & Bartsch) was one of Johnson's (1962) exotic species. It is possible that *Nuculana* is a species prone to current drifting, although being infaunal this would appear unlikely. Alternatively the low overall density of living animals coupled with a positive selection bias may lead to its recovery only as dead shells (which is possibly true of *Venus ovata* from this study). The latter explanation appears more reasonable as the survey conducted by Comely (*pers comm*) does not highlight a potential source population. Ansell *et al.* (1978) who surveyed the distribution of *Nuculana* in the Firth of Clyde, reported maximum densities in Lower Loch Fyne, with a mean density of the area of 61/m$^2$ and a maximum density of 210/m$^2$. Given that suitable *Nuculana* grounds with similar elevated densities occurred in the Firth of Lorn and assuming that all the *Nuculana* from this site were transported, the area would have to be in the order of five to thirty times the size of the carbonate sink.

Comely does not record the presence of *Parvicardium ovale* in his survey (Appendix III), although it was recovered by Gage (1972a, b, 74) using similar sampling equipment. It may have been undersample by grab but it difficult to believe that the muddy gravel sand could support an additional 400 unsampled animals/$m^2$.

*Venus ovata*, which was not collected alive in this survey may have been transported into the community, Comely (*pers comm.*) also fails to record *Venus ovata* from his equivalent station (25) but collects the species in low densities (3 – 13/$m^2$) from the two sites which straddle the central depression (Table II 1.18).

The alternative interpretation of the results is in terms of a pattern of selective preservation. If ophiuroid debris and the two most minor components of the sediment *Thyasira flexuosa* and *Musculus discors* are excluded from the analysis, a striking trend is elicited by plotting as a triangular diagram the percentage contribution of the remaining carbonates bivalve in each of the three fractions (Table II 1.18; Fig. II 1.14). As the mean size of the contributing carbonate coarsens, the preservation potential decreases (Fig. II 1.14), although it is usually assumed that smaller shells are under-represented.

This apparent relationship between distribution within the three sub-fractions and preservation bias, may be accounted for in one of four ways;

a) Under-estimation of production

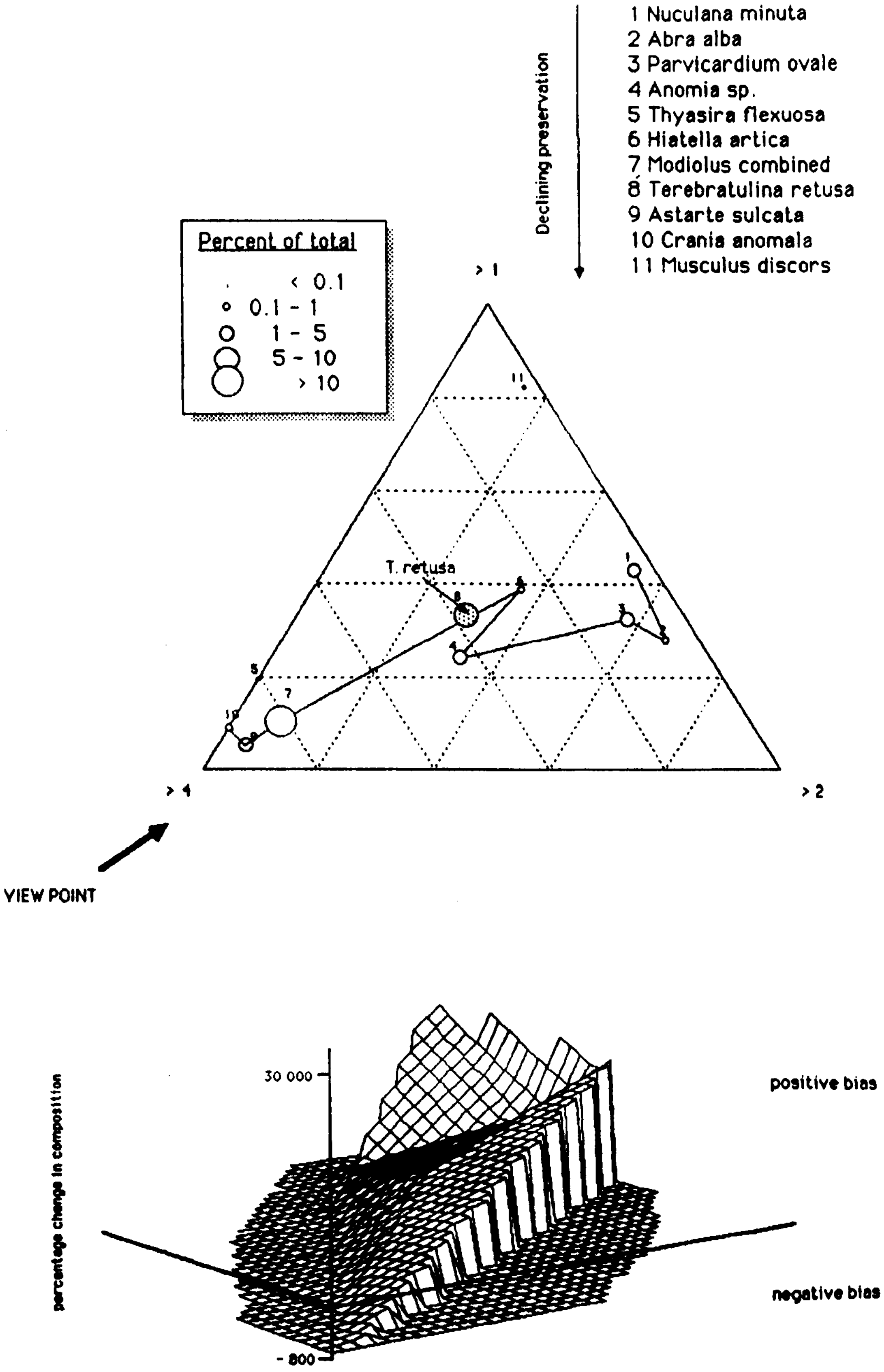
Many of the small items are infaunal, poor grab penetration may under-estimate the density of these species, particularly if they are deep burrowing forms. In addition, production estimates may underestimate production of larger, longer lived species.

b) Over-estimation of the importance of smaller fractions

Smaller fractions were sub-sampled and estimates of density obtained by multiplying up the results form this fraction by the relevant amount, a constant error towards the overestimation of the importance of smaller fractions may account for the bias, this possibility can only adequately be dis-

Figure II 1.14

Relationship between size and preservation bias



counted by independant analysis.

c) Winnowing into the community of smaller items

The bathymetry and hydrography of the region suggest that there is probably a degree of allochthonous input and as smaller items have lower component velocities than larger but otherwise identicle counterparts (eg. Cadée, 1968), it is not unreasonable to expect some selective input of smaller items. The degree of under-representation of some items is such however, that to account for the changes it would require massive inputs from large, highly productive source areas. The difficulty in accounting for such large influxes of exotic carbonate can be reduced if autochthonous production has been under-estimated and occurrence in the sediment fraction, over-estimated.

d) Selective destruction of larger items.

Rates of destruction by abrasion and chemically mediated dissolution were determined experimentally. A total of 2748 items of biogenic carbonate representing the main bivalve groups within the death assemblage, where held in a total of 12 cages at three seperate sites, ranging in depth from 9 to 18 m (Fig. III 1.1) for a total of 223 days. Rates of weight-loss attributed to abrasion were monitored in the cages, and summary results relative to *Modiolus* are given in Table II 1.19. Relative rates of weight loss by dissolution in distilled water of 225 items were also monitored over 447 days, and the summarised in Table II 1.19. These two manipulatons do not exhibit parallel trends to the observed biasing (Table II 1.19), nor is there any evidence from SEM analysis of sediment grains to suggest that either chemical dissolution or mechanical destruction are significant processes in this community.

The alternative source of taphonomic bias relevant to such early taphonomic stages is bio-erosion. Although the bio-eroding community is believed to be impoverished in cooler climates (Bromley & Hanken, 1981), Young & Nelson (1985) have concluded that *Cliona* is a major agent of shell destruction in temperate skeletal deposits. Other bio-eroders may be equally significant, Scoffin *et al.* (1980) in a study of carbonate sedimentation on Rockall Bank suggest that bioeroders which dissolve carbonate in non-supersaturated waters may account for as much as 10 – 20% of production.

TABLE II 1.19
Comparison between taphonomic bias and relative rates of destruction

| | A | B | C |
|---|---|---|---|
| *Nucluana minuta* | +335 | −1.6(1) | −4.7(1) |
| *Abra alba* | +277 | −0.45 | −8.2 |
| *Anomia* sp. | +113 | −0.34 | −9.4 |
| *Modiolus modiolus* | 0 | 0 | 0 |
| *Terebratulina retusa* | −0.4 | −0.10 | −6.7 |
| *Astarte sulcata* | −3.4 | +2.46 | +6.4 |
| *Crania anomala* | −7.5 | −1.34 | −3.2 |

A Preservation relative to production with *M. modiolus* (98% increase) as baseline. B Rates of dissolution in distilled water, with *M. modiolus* 7.15% decrease over 477 days) as baseline (1) figure for *Nucula*. C Half-lives from rates of weight loss by abrasion, (with M. modiolus, 176 years) as baseline.

Significantly, a number of authors propose that the extent of infestation is controlled by two factors; the degree of agitation of the carbonate grains and the rate of sedimentation. Boekschoten (1966) attributed the absence of *Cliona* borings in several hundred *Venus striatula* shells collected from Dutch beaches, but infestation in 6 of 48 specimens from 33 m on the Dogger Bank, to these two factors. Scoffin *et al.* (1980) also observed that grains collected in shallow water (100 m) at the top of Rockall bank were rounded, polished and unbored, whereas at 150 – 300 m many grains were severely bored by sponges and unidentified filaments, and concluded that "this observation endorses the contention that frequent agitation is an excellent preservative for marine carbonate grains" (Scoffin *et al.*, 1980: 349).

The degree of agitation is related to a variety of environmental factors including turbulence, sea-bed roughness and water velocity (section III 2). Within a single environment all these variables are approximately constant and the extent of agitation of particular grains will be a function of their hydrodynamic stability, itself a combination of several factors, including shell shape, density and above all size.

Bosence (1978: 466) studying taphonomic processes in Mannin Bay, Co. Clare was probably the first to state that the post-mortem history of bivalve shells depended largely on size. "Large shells (greater than about 2 cm diameter, e.g. some Mytilacea, Ostracea, Pectinacea, some Cardiacea, Veneracea, Mactracea and Solenacea) are frequently bored, encrusted, abraded and fractured, whereas small shells (less than about 2 cm diameter, eg. some Mytilacea, Astartacea, Lucinacea, Erycinacea, some Cardiacea, and Tellinacea) are not encrusted and bored at the macroscopic level, but are abraded and fractured. This is thought to be because the larger shells are less frequently transported than the small shells and can therefore, be colonized and bored." The critical size suggested by Bosence was later echoed by Akpan (1981) who noted that *Cliona* borings were found mainly on dead molluscan shells, and there was an apparent preference for shells in excess of 20 mm in length. Semi-quantitative comparisons of the degree of bio-erosion from this study would support this conclusion.

If there is some form of bias operating, it is difficult to visualize any other process which would selectively bias aganst such large and robust items such as *Astarte* and *Modiolus modiolus* valves. This selection would also explain the disparity between the low estimated densities of juvenile *Astarte* in the living community and their super-abundance in the death assemblage.

The carbonate of *Terebratulina retusa* is an outlier to the general trend when plotted in the triangular diagram (Fig. II 1.14), its distribution on the triangular plot would suggest that if the apparent trend is real, *T. retusa* should be much more common than it is in the sediment, possible reasons for this are discussed in section III 2.

# PART III
# EXPERIMENTAL SECTION

## III 1 ANALYSIS OF A PULSED INPUT

### III 1.1 INTRODUCTION

Boucot's seminal paper of 1953 proposed a number of criteria which could be used to recognize a current drifted assemblage of marine bivalves. Various authors have added and subtracted from this basic analysis but broadly the criteria remain as follows, changes in the population structure as a consequence of 'winnowing', increased disarticulation, valve sorting, the introduction of exotic species, fragmentation and evidence of mechanical abrasion.

The criteria were based on little empirical evidence, and whereas some of the assumptions were later supported by experiments and observations conducted in the swash zone (Martin-Kaye, 1951; Holme, 1965; Craig, 1967; Behrens & Watson, 1969; Lever, 1958, 61; Lever & Thijssen, 1968; Clifton, 1971; Trewin & Welsh, 1972; Farrow, 1974; Antia, 1977; Lawrence, 1979) others were later challenged (eg. Johnson, 1962; Trewin & Welsh 1972).

By 1981 Boucot (1981: 323) was forced to conclude (mainly on the basis of correspondance analysis, see section II 1) that "most shells, although not all suffer very little postmortem net transport". Omitted from Boucot's (1981) review however, was a very basic line of evidence, studies investigating the nature, extent and type of subtidal transport of biogenic particles. This begs the question of what other taphonomic processes account for the criteria which Boucot (1953) and subsequently others have used to recognize current drifted assemblages. Therefore, in tandem with empirical evidence based on the living and death assemblages from the Firth of Lorn (section II), this study investigates the short term taphonomic history of a pulsed input of 4 types of biogenic particle to a shallow sub-tidal facies.

### III 1.2 PROCEDURES

#### III 1.2.1 Site

The experiments were conducted in a small marine embayment, Dunstaffnage Bay, at a depth of 9 m (Fig. III 1.1, site a). The site was chosen as a compromise between a deep-water site, with hydrographic conditions comparable with the Firth of Lorn and one which was both accessible and experienced current speeds within the range encompassing the estimated component velocities of biogenic particles. Sediment for sieve analysis was collected by diver operated hand corer. Suction sampling revealed that the sediment was stabilized by large numbers of the tubicolous polychaete *Lanice conchilega* (Phallas) (Plate 2g &h).

The area is subject to a complex current regime, tidal flows are reduced and topographically streamed by the small island *Eilean Mor* which constricts the north west of the bay. Loch Etive, a large sea loch (estimated low water volume of 939.8 M. m ; A. Edwards *pers comm.* 1986) has a significant influence on the hydrographic regime of Dunstaffnage Bay. The entrance to the loch is constricted by a shallow sill at Connel Falls, two miles to the east of the Bay, which experiences a mean current speed of 172 cm/sec. Within the bay a clockwise gyre is initiated by the interaction of the tidal flows with the outflow from this sea loch.

### III 1.2.2 Environmental factors

Soil analysis of both the sediment and the tubes of *Lanice conchilega* (Pallas) was conducted as outlined in section II 1.2.2, the *Lanice* tubes being soaked in a weak solution of sodium hypochlorite solution overnight.

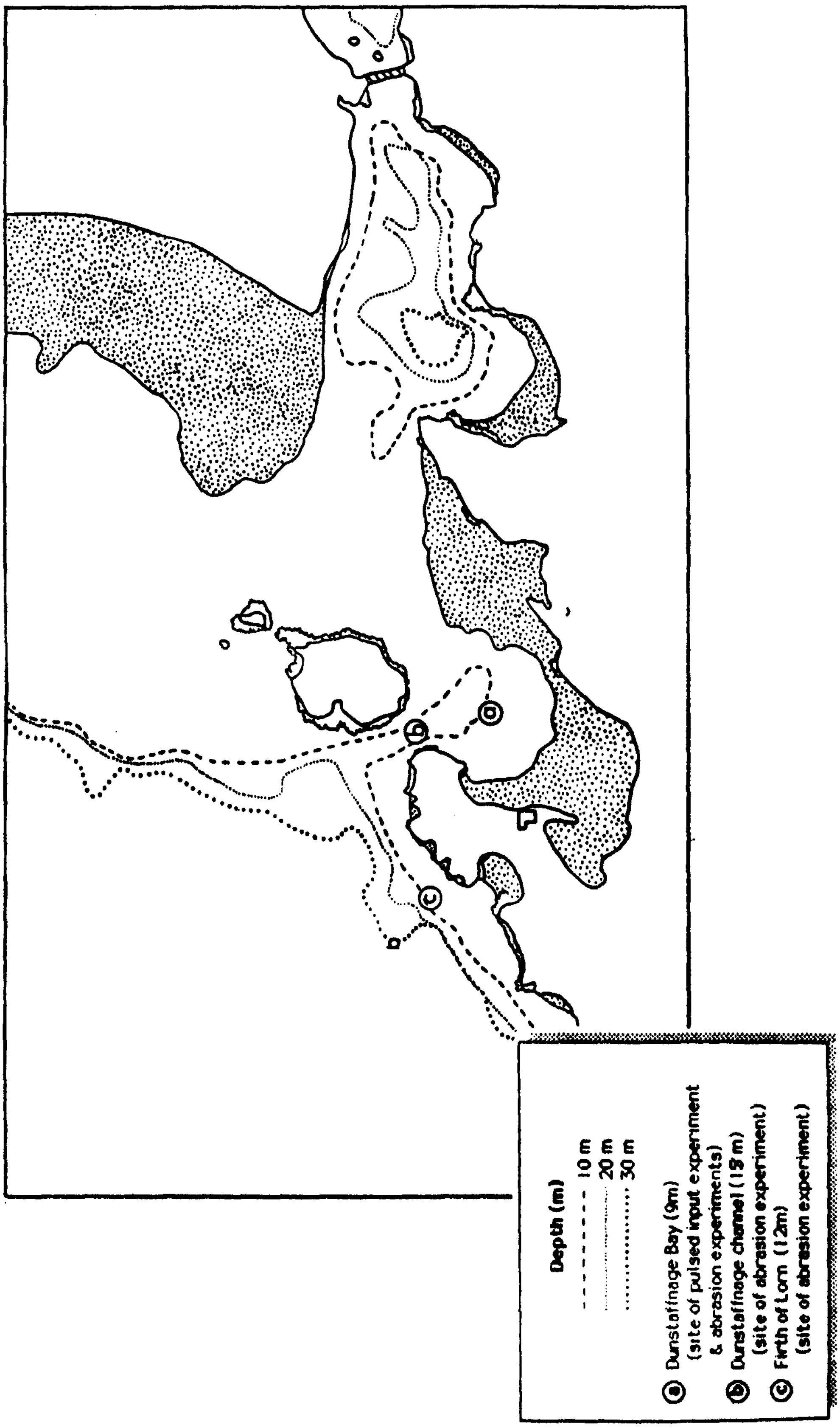
The water movement in Dunstaffnage Bay and at a contrasting site in the Channel (site b: Fig 1.1) were measured using an Aanderaa current meter, with no directional fin. A mounting was made for the meter from 'Dexian' aluminium pieces, bolted together with plastic bolts, (brass at the critical load bearing points). This mounting was fixed to a frame designed to support a large box corer and the meter fixed so that the current speed was measured one meter from the bed.

Current speed at the sediment water interface was estimated from the logarithmic profile method, equation 16 of Soulsby (1983);

$$U = (u* / k) \ln(z / z0) \qquad \text{(III 1.i)}$$

**Figure III 1.1**

Map of site



where U = mean current velocity (cm/sec) and $U_{100}$ current velocity 1 m above the seabed; u* = friction velocity; k= Von Karman's constant; z = height above the sediment–water interface; $z_0$ = seabed roughness length (an indication of friction exerted by the sediment) was estimated from values measured from logarithmic profiles given in Heathershaw (1981); u* = was estimated from equation 19 of Soulsby (1983).

(III 1.ii) $$C_{100} = \frac{k}{\ln(100/z_0)}$$

using the approximation for C100 provided by Charnock (1959).

if $$C_{100} = (u* / U_{100}) \qquad \text{(Charnock, 1959)}$$

then

(III 1.iii) $$u* = U_{100} \times \frac{k}{\ln(100/z_0)}$$

A Von Karman's constant of 0.4, was used, this is within the range established from a number of field and laboratory studies (Soulsby, 1983). Current speed was monitored at the site over a two week period from 14/4/85 to 3/5/85, encompassing one half of a tidal cycle allowing estimates of the annual tidal regime (Fig III 1.2).

However, the values of u*, the threshold velocities are only weakly correlated with grain size and do not correlate well with various shape factors, threshold shear velocities u* range from 0.4 – 1.0 cm/sec. (Yound & Mann 1985).

### III 1.2.3 Biogenic carbonate

Four species of marine bivalves dredged from the Firth of Lorn and Loch Spelve were killed by exposure, partially rotted, shucked, rinsed and dried. Three of the species chosen *M. modilus*, *T. retusa* and *A. sulcata* dominate both the biomass and production in the Firth of Lorn. The thin shelled infaunal bivalve *A. alba*, is not abundant in the Firth of Lorn but was chosen because it provided a thin shelled contrast to the other three species. The shells of *Terebratulina retusa* were soaked overnight in a weak solution of sodium hypochlorite, to ensure complete removal of organic matter. A total of 209 biogenic particles were used in the experiment (Table III 1.1).

TABLE III 1.1

Composition of biogenic carbonate

| | | No. | Length (mm) | | | Weight (gms.) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Max. | Min. | Mean | Max. | Min. | Mean | SV |
| *Abra* | re-conjoined | 20 | 19.7 | 12.5 | 17.2 | 0.245 | 0.048 | 0.164 | 9.8 |
| | left & right | 16 | 19.7 | 13.3 | 15.8 | 0.149 | 0.035 | 0.069 | 19.7 |
| *Terebratulina* | conjoined | 58 | 21.4 | 10.2 | 16.1 | 0.783 | 0.112 | 0.418 | 3.4 |
| | pedicle | 20 | 20.7 | 10.4 | 14.9 | 0.362 | 0.082 | 0.179 | 6.7 |
| | brachial | 20 | 19.8 | 9.6 | 15.4 | 0.466 | 0.075 | 0.174 | 7.4 |
| *Astarte* | conjoined | 10 | 26.7 | 19.9 | 23.0 | 4.193 | 2.049 | 2.775 | 1.0 |
| | left & right | 10 | 25.0 | 19.9 | 21.7 | 1.645 | 0.861 | 1.257 | 2.0 |
| *Modiolus* | conjoined | 10 | 87.6 | 71.4 | 80.02 | 22.01 | 12.86 | 17.69 | 2.0 |
| | left & right | 10 | 83.4 | 63.9 | 73.04 | 22.51 | 9.58 | 15.41 | 1.9 |

The cleaning and preparation of the shells prior to the addition of identification markings caused some damage to the ligament. Cracks appeared in the ligament of *A. alba* and when re-wetted the valves parted very easily. The larger ligaments of *A. astarte* and *M. modiolus* were less affected, possibly because they did not dry out completely. The valves of Abra alba were re-conjoined with a small amount of rubber-solution glue placed in the ligament pit. Although the adhesive had resilient properties, as it was not under compression, the valves remained closely apposed for the duration of the experiment and can therefore be considered crude analogs of thin shelled cyrtomatodont brachiopods. The valves of *Astarte sulcata* and *Modiolus modiolus*, having retained the original elastin ligament remained 'butterflied' apart over the duration of the experiment (Plate 2h).

Twenty undamaged disarticulated *Terebratulina* valves were produced to examine way-up criteria. As disarticulation of cyrtomatodont brachiopods (*sensu* Jaanusson, 1971) typically involves stress to the shell and damage to the hinge structures (Thompson, 1927), it was necessary to destroy the opposing valve to obtain one which was undamaged. The presence in a death assemblage of undamaged disarticulated brachiopod valves was primarily a Palaeozoic phenomenon, as disarticulation, not requiring damage to the hinge structures was believed to be a feature of those brachiopods possessing a deltidiodont dentition (Sheehan, 1978), a characteristic of members of the Orthida, Strophomenida and Pentamerida, (Jaanusson, 1971).

The size of the pedicle foramen in 31 of the 58 *T. retusa* shells was altered by covering over the foramen with an epoxy-resin ('Araldite') and then drilling three diameters of artificial foramen; 1(7), 2(5) and 2.5 mm (4) (numbers in brackets refer to number of treated shells). The resin prevented splitting of the valves during drilling, but had the drawback of restricting the articulation of the valves. The foramen in a further 15 shells was sealed by covering with a thin skin of a vinyl paint.

The rational behind the alteration of foramen size in shells lying on the sea floor followed a pilot study (in which *T. retusa* shells with artificially enlarged foramen held in in 3 $mm^2$ nylon mesh bags were buried to a depth of 15 cm in a sub-tidal sand gravel) which demonstrated a correlation between foramen size and rate of infill in buried shells ($r = 0.670$; $n = 8$). The effective density of brachiopod shells has a bearing on the rate of transport (Menard & Boucot, 1951), but sediment infill will only modify the component velocity if it occurs prior to burial or if an infilled shell is exhumed.

In a second experiment, run concurrently (experiment I2), a total of 147 shells were modified in similar fashions, both infill experiments failed to provide any results as consequence of unexpected destruction of the shells by an unknown process.

All shells were marked clearly with a water-insoluble black marker pen, the darker shells of *Astarte sulcata* and *Modiolus modiolus* had white numbers with a contrasting black stripe, to enhance identification on the photographs (Plate 2f).

The ratio of surface area to volume of the biogenic particles was crudely estimated using the formula;

(III 1.iv) $$SV = \frac{L \times 2}{(wt / 2.72)}$$

where *SV* is the surface area to volume ratio, *L* is length in mm, wt is weight in mg and 2.72 is the density of calcite.

### III 1.2.4 Position recording and recovery

One of the principal difficulties with such a study is the problem of identification and recording of the position of the shells on the sea bed, without disturbance or modification to the conditions on the sea floor. All the shells were deposited within a metre square of heavy gauge steel wire which lay partially buried in the sediment (Plate 2h). The position of shells was recorded at intervals on a photographic mosaic. No attempt was made to attach the meter square to the sea floor and it was noted that between 47 and 196 days following initiation of the experiment it moved to the north east by approximately 1 cm. Such movement could easily be prevented by the positioning of small staples at each corner and would be recommended if this experiment were to be repeated.

To minimise the problems of producing an accurate photographic mosaic an oblong frame (200 x 170 mm) was mounted to the front the camera, this size of frame enabled the whole surface of the square to be covered in a 5x6 mosaic using a standard 36 print film, a single flash unit provided relief shadow. Successful mosaics of shells were taken at intervals of 1, 8, 25 and 47 days after the shells had first been placed onto the sediment surface. Orientation and position were recorded relative to the sides of the meter square, orientation of the long axis of the shell was only measured where this proved axiomatic.

Recovery involved first recording all the shells which had been transported outside the meter square. Distance was measured from a stake planted in the centre of the square using a line marked at 20 cm intervals attached to a freely rotating collar. The area was searched to a distance of 5 m from the stake in a spiral pattern, the distance from the stake and compass position relative to the centre of the square was recorded for each shell recovered. All shells remaining on the surface within the square were collected by hand, a vacuum operated suction sampler was used to recover buried shells. The first dive removed approximately the top 5 cm of the sediment from within the metre square. The second dive two days later, using a more powerful sampler removed a further 10 cm of sediment.

Distance moved by the shells was calculated geometrically from positional changes in successive photographic mosaics.

### III 1.2.5 Half-lives of biogenic particles

The percentage recovery of various types of carbonate was described in terms of the half-life *(t1/2)* of each biogenic particle. The half-life is inversley proportional to the rate constant of taphonomic loss, (*k*) which was determined from equation (III 1.v);

(III 1.v)
$$k = \frac{2.303}{t} \cdot \log \frac{[A]0}{[A]}$$

where *t* is the time in days, [A]0 is the initital concentration of shells and [A] is the final concentration. The half-life is thus determined by substituting *k* into equation III 1.vi.

(III 1.vi)
$$t\,(1/2) = \frac{0.693}{k}$$

## III 1.3 RESULTS

### III 1.3.1 Environmental factors

The sediment was a sand gravel (Fig. II 2.2) 63% of which was retained by a 0.5 mm sieve. (gravel 3.21%, sand 95.0%, mud 0.79%). The sediment was partially stabilized by the Sand Mason Worm, *Lanice conchilega* (Plate 2g), which occurred at densities of approximately 150/$m^2$. The *Lanice* tubes consisting of 98% sand sized grains, reflecting the composition of the surrounding sediment.

Menard & Boucot (1951) demonstrated that all sizes of *Terebratulina septentrionalis* were moved by currents with velocities of 11.7 to 15.1 cm/sec. The actual component velocities will be lower than those stated by Menard & Boucot (1951) by virtue of the drag exerted by the sediment. The maximum

~~Boucot (1951) by virtue of the drag exerted by the sediment. The maximum~~ recorded current speed in Dunstaffnage Bay at 1 m was 28.05 cm/sec, and speeds in excess of 15 cm were recorded on 28 of 40 tides, the speeds therefore appear to be of the same order of magnitiude.

The current meter readings for Dunstaffnage Bay were collected over a period with high tides 86% of springs, suggesting that maximum current speeds corresponding to the spring neap would be in the range of 20–30 cm/sec at 1 m above the seabed. The logarithmic model of current speed predicts maximum speeds in the order of 11 cm/sec at 1 cm above the seabed, with a *U100* of 25 cm/sec (Fig. III 1.2; Table III 1.2).

TABLE III 1.2
Current Profile (Logarithmic model)

| Site | *U100* | *z0* | u* | Velocity (cm/sec) at depth (m) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 0.5 | 1 | 5 | 10 | 25 | 50 | 100 |
| Channel | 75 | 0.3 | 5.3 | 7 | 16 | 37 | 46 | 59 | 68 | 77 |
| Bay | 25 | 0.03 | 1.25 | 9 | 11 | 16 | 18 | 21 | 23 | 25 |

### III 1.3.2 Recovery

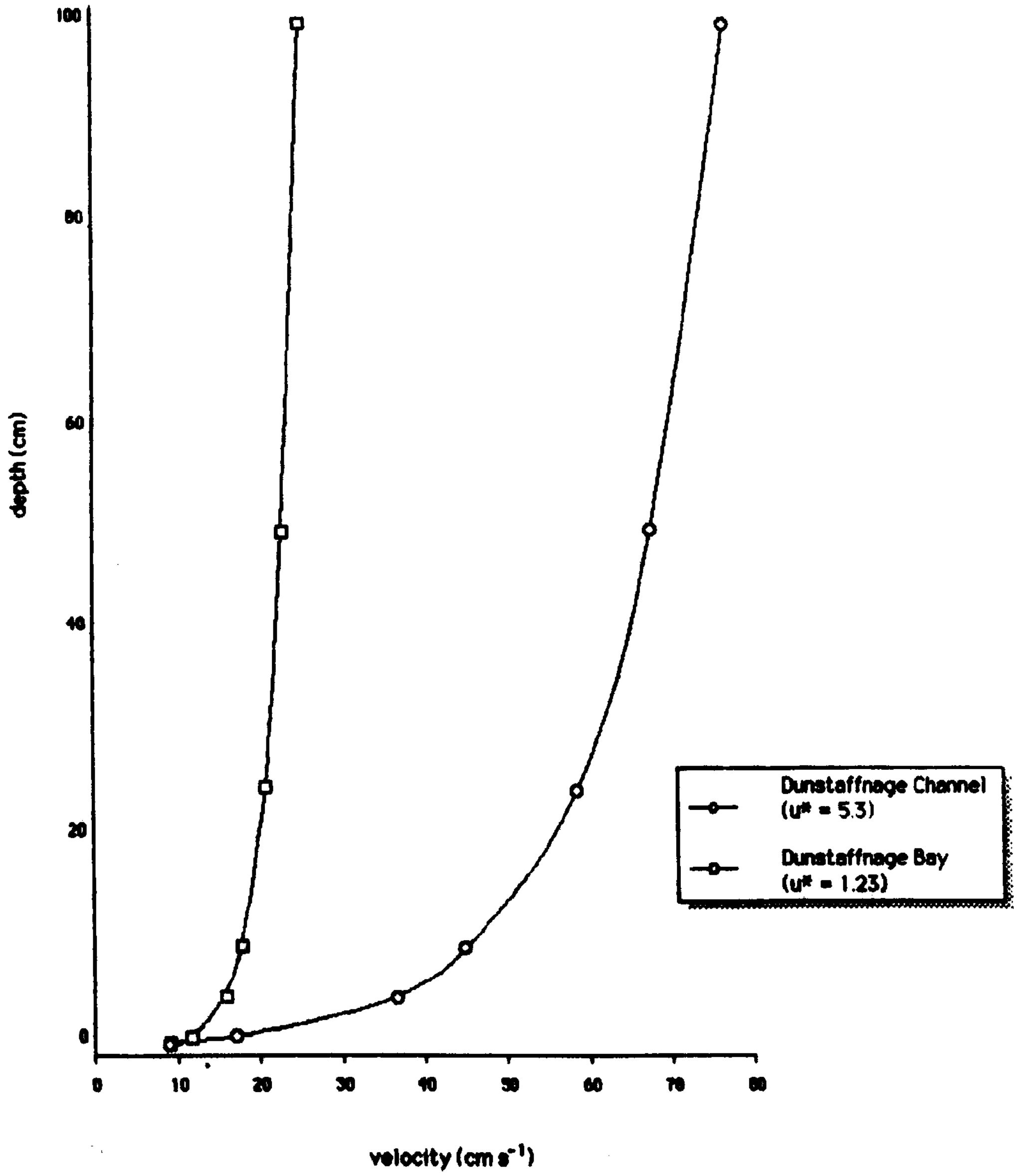
24% of the biogenic particles were neither observed in a photographic matrix, or recovered following the termination of the experiment, 87.5% of these were single valves of either *T. retusa* or *A. alba*. 53.5% of the initial shells were recovered either as whole shells or recognizable fragments (Table III 1.2). The compositional changes are summarised in Table III 1.3 and Figure III 1.3a.

Assuming that the initial figures given in Table III 1.3 reflect the composition of the carbonate producing macro-fauna, then relative changes in abundance can be seen as taphonomic biasing and can be calculated as half-lives

Of the original 'community' of 160 organisms, 14 (8%) were preserved in their original condition, either as whole shells or valves, a further 72 valves were also present, attributed to either 36 or 38 organisms depending on the measure of the valve re-composition applied, (22.5% or 23%) with an additional

## Figure III 1.2

Current profile



29 valves recognizable from valve fragments (18%), giving a maximum total estimate for the community of 47.5% (Fig. III 1.3a).

TABLE III 1.3
Recovery of biogenic carbonate

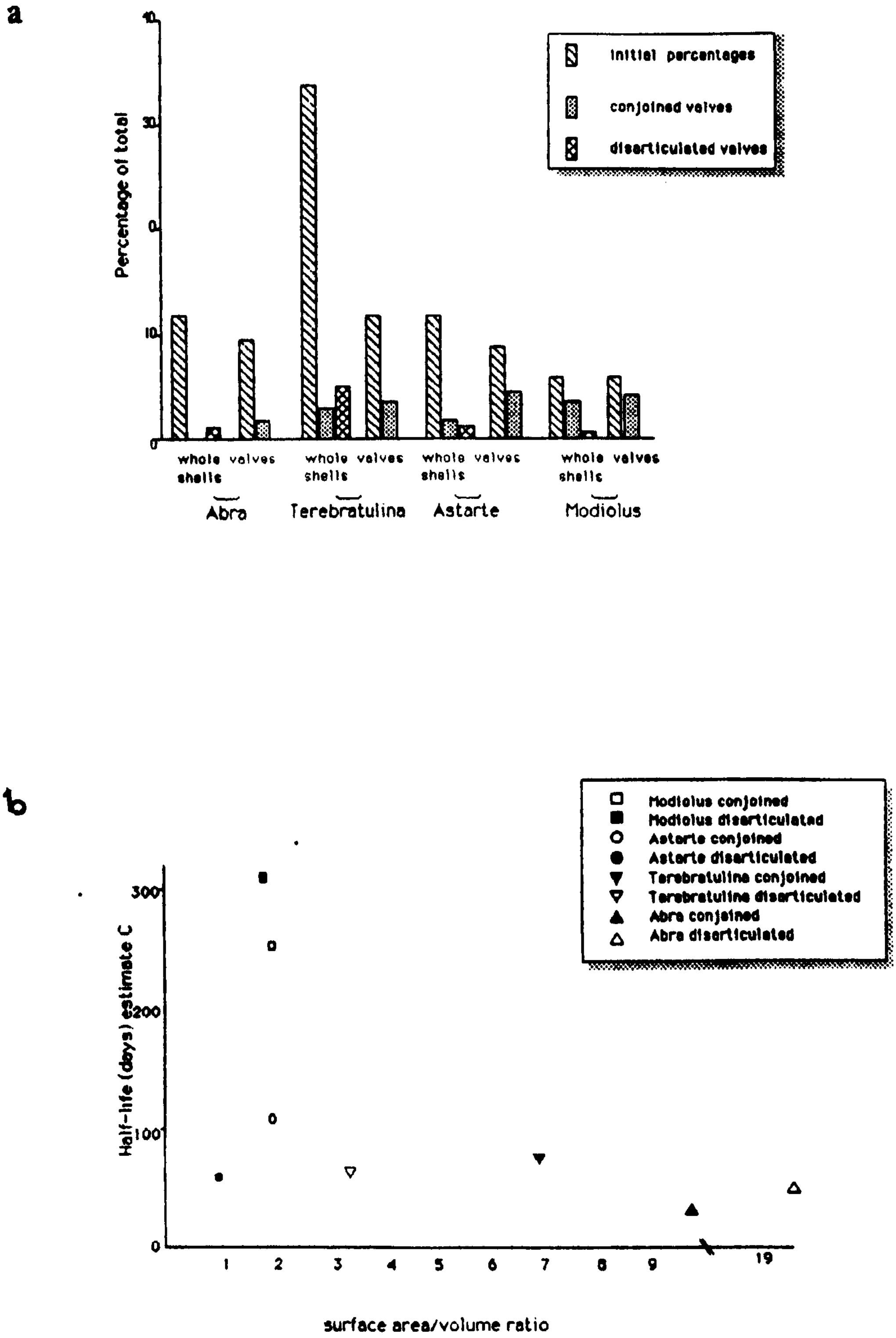
| Carbonate | Valves | Initial | | Recovered | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | No | % | A | B | C | D | E | F |
| *A. alba* | conjoined | 20 | 11.9 | 0 | 1.5 (2) | 4 | 1 | 0.5 | – |
| | seperated | 16 | 9.5 | | 2.5 (3) | 0 | 2.5 | – | – |
| *T. retusa* | conjoined | 57 | 33.9 | 5 | 10 (11) | 10 | 6 | 6 | 3 |
| | seperated | 20 | 11.9 | | 6 (6) | 0 | 4.5 | 0.5 | 2.5 |
| *A. sulcata* | conjoined | 20 | 11.9 | 3 | 2 (2) | 0 | 1 | 2 | 2 |
| | seperated | 15 | 8.9 | | 6.5 (8) | 0 | 2.5 | 3 | 1 |
| *M. modiolus* | conjoined | 10 | 6.0 | 6 | 1 (1) | 0 | 1.5 | 0.5 | 5 |
| | seperated | 10 | 6.0 | | 7.5 (8) | 0 | 2.5 | – | 5 |
| | | 168 | 100.0 | 14 | 36 (38) | 14.5 | | | |
| (Expt 12 | | | | | | | | | |
| *T. retusa* | conjoined | 147 | 100.0 | 12 | 11.5 (17) | ND | 21.5 | | 1 ) |

Totals of 'seperate' valves unless stated, refer to the number of seperated valves / 2. Composition of recovered material, A = whole valves; B = seperated valves, the figure in brackets is the total of the most abundant valve; C = identifiable fragments. Occurrence of recovered fragments, D = Buried, (ie recovered by suction sampler; E = on surface, within square; F = on surface, outwith square.

Half-lives can be calculated in a variety of ways depending upon the way that this experiment is used to model the dynamics of a real death assemblage. The total of biogenic particles remaining after 130 days can be calculated either by subtracting the number of shells recognized as fragments (ie those definately destroyed; half-life A of Table III 1.4) or the number of shells recovered. The latter number can also be treated in one of two ways, reflecting the nature of transport within the community. Typically, if shells are transported small distances prior to burial, and the living community extends over a considerable area of the seafloor, then for most of this area export of particles by current drifting would be in equilibrium with import from other areas within the community. The half-lives of particles in such a situation can be estimated from the figure for the total of all shells collected (half-life C of Table III 1.4). If the community is more localized however, then transport will result in a net loss of autochtharous carbonate, half-lives including loss by transport are in this example estimated from using the number of shells remaining within the metre square (half-life B of Table III 1.4).

Figure III 1.3

Recovery of carbonate
a) Comparison between initial and final compositions of pulsed input
b) Comparison between preservation and surface area/volume ratio



Half-lives were calculated using equations III 1.v & 1.vi, the half-life of conjoined valves being calculated from the total of conjoined shells and half the sum of seperated valves. Results are presented in Table III 1.4 and Figure III 1.4.

TABLE III 1.4
Half-lives of biogenic particles (see text for methods of calculation)

| | | t *1/2* (days) | | |
|---|---|---|---|---|
| | | A | B | C |
| *A. alba* | conjoined | 3559 | 35 | 35 |
| | seperated | 2840 | 49 | 49 |
| *T. retusa* | conjoined | 468 | 58 | 67 |
| | seperated | oo | 52 | 75 |
| *A. sulcata* | conjoined | oo | 48 | 65 |
| | seperated | oo | 70 | 108 |
| *M. modiolus* | conjoined | oo | 56 | 253 |
| | seperated | oo | 65 | 313 |

### III 1.3.3 Articulation and Fragmentation

The pattern of preservation of the material recovered by suction sampler, suggested a dichotomy between the more robust shells of *Astarte* and *Modiolus*, for which the only observed 'damage' inflicted was seperation of conjoined valves and those of the two less resiliant bivalves (*T. retusa* and *A. alba*). In the latter group only a small proportion (30%) of the recovered shells remained intact (Table III 1.3). Such a difference would be predicted but the process of fragmentation did not appear to be random for while only 16% (5) of the articulated brachiopod valves recovered remained articulated and 76% (50) were recognized from valve fragments, all the inititally disarticulated valves of both *T. retusa* and *A. alba* recovered (16) remained undamaged.

These figures for recovery and fragmentation are very similar to those from Experiment I2. Of the 147 shells used, 74 were recovered and of these only 13% (10) remained articulated and only 31% (20) of the remaining valves were undamaged. The above figures only include recognizable fragments which formed a minimum of the recovered material.

### III 1.3.4 Distance & direction moved

Distance and direction are illustrated in the rosette diagrams, Figures III

1.4 & 1.5, by originating the paths from a single position, each path corresponding to the distance and direction moved by that shell across the mosaic. It is difficult to summarise this data graphically because not all shells are present in each mosaic (Fig. III 1.5) therefore while a path with three vectors clearly indicates that a position was recorded in all four mosaics, those paths with only one or two vectors may represent any one of ten time possible time intervals between recording (ie present in mosaics 1,3 & 4 or 1,2 & 4 or 2,3 & 4 etc.). An attempt has been made in Figure III 1.5 to summarise the data for the articulated valves of *M. modiolus*, which is the most straightforward of these rosette diagrams.

It is apparent from these plots, that the shells of *M. modiolus* (there being no significant difference between atriculated shells and valves) move distances considerably in excess of either *T. retusa* or *A. sulcata*. There is also some directionality, eight of twenty paths moving in a broadly N NW direction (Fig. III 1.5). There is however, no apparent directionality in either the plots of *A. sulcata* or *T. retusa* (Fig. III 1.6).

Summarising the minimum distances furnishes (ie 3!) possible time intervals between observations depending on their combination (7, 17, 22, 25, 39 & 46 days; Table III 1.5). Minimum distance measures further complicate the comparison of distance, as a shortest distance measure will usually increase with the inclusion of intermediate dates as a result of erratic paths (Fig. III 1.5 & 1.6). 46-day-minimum disance, a distance calculated from the position of shells in the first and last photographic mosaics, calculated without reference to intermediate positions (Table III 1.5) were used to provide a larger data set to furnish more meaningful comparisons of distances moved by various biogenic particles. It was only possible to provide a 46-day-minimum distance for those shells present in both the first and last mosaics, a second mean distance was therefore calculated from all the available data, as this ignored time-intervals, the time intervals which compose the data set are also included (Table III 1.5).

**Figure III 1.4**

Rosett of movement of M. modiolus
a) Whole valves
b) Single valves

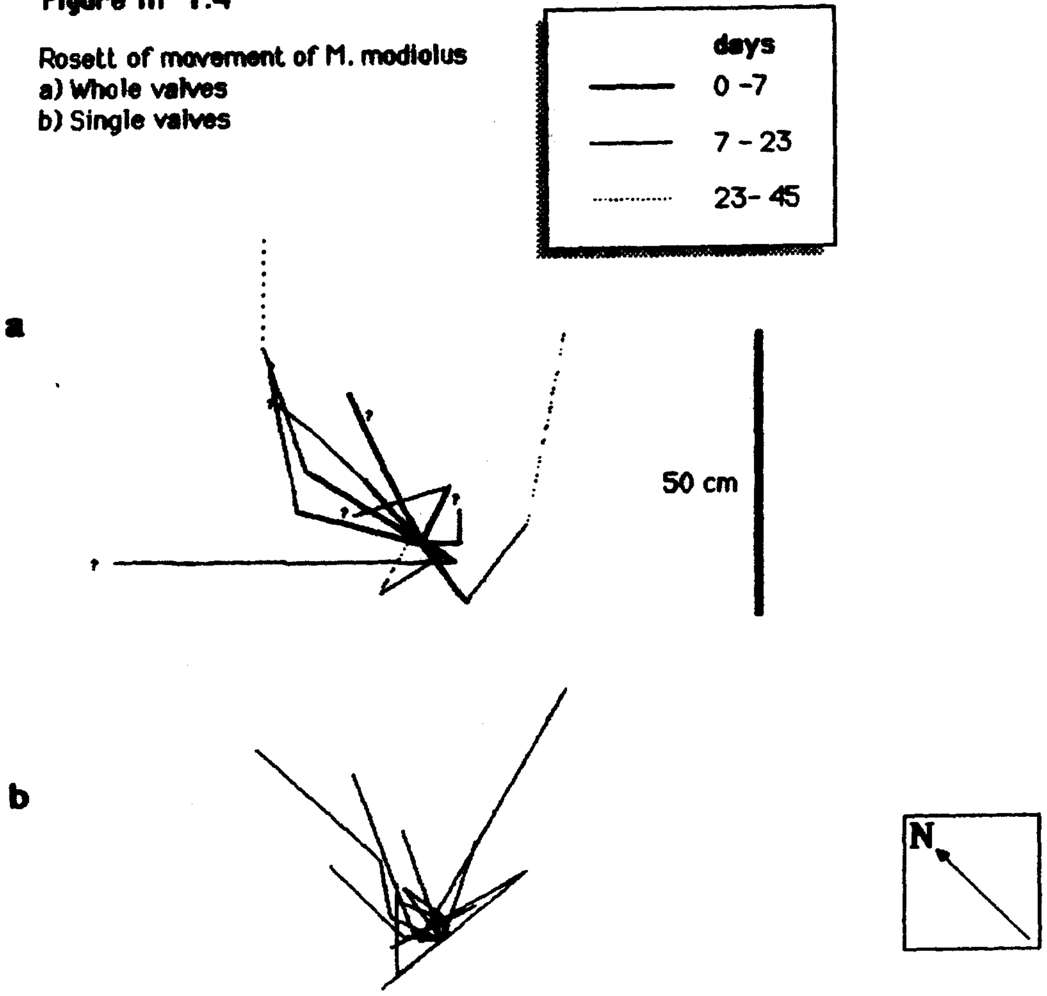
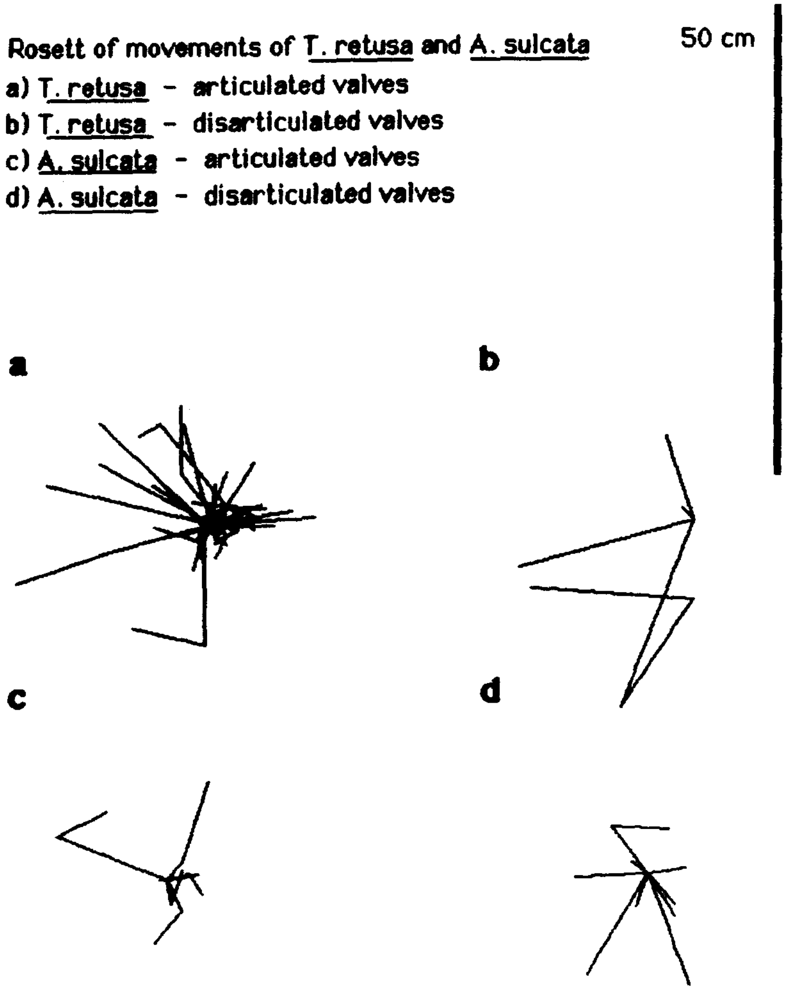


**Figure III 1.5**

Rosett of movements of T. retusa and A. sulcata
a) T. retusa - articulated valves
b) T. retusa - disarticulated valves
c) A. sulcata - articulated valves
d) A. sulcata - disarticulated valves



Only the mean of total distances are significantly different, the 46-day-minimum distances, although greater, are not significant as the size of comparative data-sets are small. However, there is a striking contrast between the distance travelled by the three small particles and *M. modiolus* (Fig III 1.4 & 1.5).

TABLE III 1.5a
Distance moved by biogenic particles (46-day-minimum & total results)
(NA = data not available; NS = not significant)

| | Distance moved (cm) | | | | Time (days) over which distances measured | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 46-day-minimum | | All | | | | | | | |
| | No. | distance | No. | distance | 7 | 17 | 22 | 25 | 39 | 46 |
| *A. alba* | NA | NA | 8 | 14.5 | 4 | 1 | 2 | – | – | 1 |
| *T. retusa* | 16 | 41.0 | 36 | 20.2 | 10 | 1 | – | 5 | 4 | 16 |
| *A. sulcata* | 7 | 36.9 | 16 | 16.6 | 5 | – | – | 2 | 2 | 7 |
| *M. modiolus* | 15 | 203.3 | 23 | 52.6 | 1 | – | – | 7 | – | 15 |

TABLE III 1.5b
t-test of distances moved

| | all distances | | | composite of 46-day minimum | | |
|---|---|---|---|---|---|---|
| | *T. retusa* | *A. sulcata* | *M.modiolus* | *T. retusa* | *A. sulcata* | *M.modiolus* |
| *A. alba* | NS | NS | .05 | NA | NA | NA |
| *T. retusa* | – | NS | .025 | – | NS | NS |
| *A. sulcata* | – | – | .05 | – | – | NA |

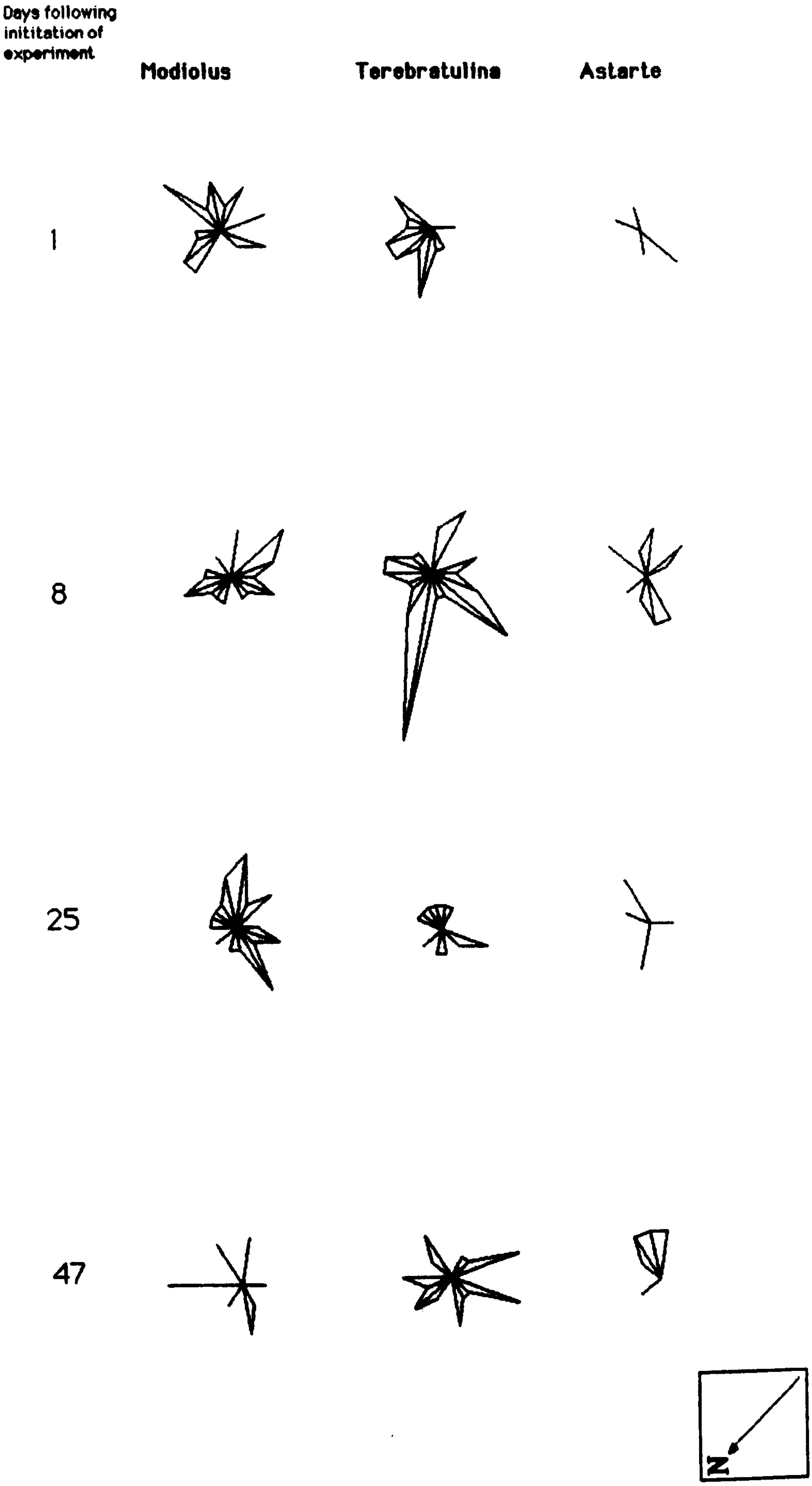
The failure to identify many of the single valves of either *T. retusa* or *A. alba* following inititaion of the experiment, suggests that these light particles were rapidly moved outside the metre square, although those single valves which remained did not move very much. There are three factors which possibly have an effect, the nature of the valve articulation (disarticulated, conjoined but apart, or conjoined and opposed), surface area-weight ratio and absolute weight. The expected correlation between absolute weight and distance transported appears to hold good. The heaviest of the two similarly sized particles (ie *Astarte* & *Terebratulina*) moved a shorter mean distance, although the differences are not significant (Table III 1.5).

### III 1.3.5 Orientation

Star plots (Fig. III 1.7) do not indicate any significant changes in the

Figure III 1.6

Star plots of orientation of shells of each species in each photographic mosaic



orientation of shells, except for a marked NE-SW trend in *T. retusa* at 25 days, and a less marked trend of similar orientation of *M. modiolus* at 8 days. It was not possible to relate current direction to orientation as the current meter only monitored current speed and temperature. Comparison with direction of movement, suggest that there is little correlation.

Convex-up convex-down orientation was also recorded from the photographic mosaics (Table III 1.6).

TABLE III 1.6
Combined totals of orientation observed in photographic mosaics

| | Days following inititation of experiment | | | |
|---|---|---|---|---|
| | 1 | 8 | 25 | 47 |
| *T. retusa* | | | | |
| Conjoined - lying on pedicle valve | 11 | 12 | 8 | 6 |
| Conjoined - lying on brachial valve | 20 | 14 | 3 | 10 |
| Disarticulated - concave-up | 8 | 13 | 4 | 8 |
| Disarticulated - convex-up | 1 | 6 | 4 | 2 |
| *M. modiolus* | | | | |
| Disarticulated - concave-up | 20 | 12 | 12 | 11 |
| Disarticulated - convex-up | 0 | 2 | 4 | 4 |
| *Astarte* | | | | |
| Disarticulated - concave-up | 9 | 9 | 6 | 6 |
| Disarticulated - convex-up | 5 | 5 | 2 | 6 |
| *Abra* | | | | |
| Disarticulated - concave-up | 6 | 1 | 3 | 3 |
| Disarticulated - convex-up | 0 | 3 | 0 | 1 |

Trends plotted for *T. retusa, A. sulcata* and *M. modiolus* (Fig. III 1.8) indicate that there is a decline in the number of concave-up shells. Analysis of the trend for individual shells is hampered by the inability to identify partially infilled shells lying concave-up (eg. Plate 2g & h), in only one case was a concave-down shell (of *T. retusa*) identified overturned in a later photographic mosaic. Initially more shells were lying concave-up (Table III 1.6), the preferred orientation as the shells fell through the water column, having been shaken free of the container. The trend of all three shell types is to a flattening out of the curve between 8 and 25 days, suggesting either that equilibrium is achieved or that once orientated concave-down (the hydrodynamically stable position), the shells remain so. The inability to identify all concave-up shells hinders an attempt to prove or disprove either hypo-

**Figure III 1.7**

Changing ratio of concave-up to concave down orientation of single valves

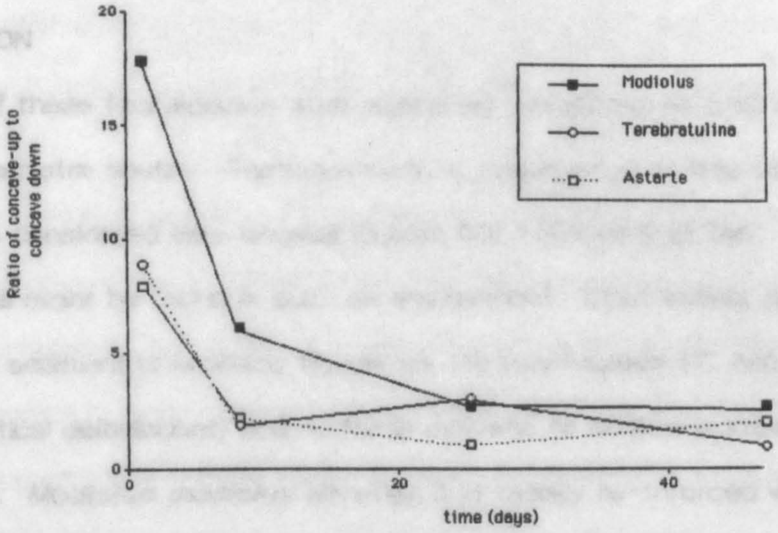
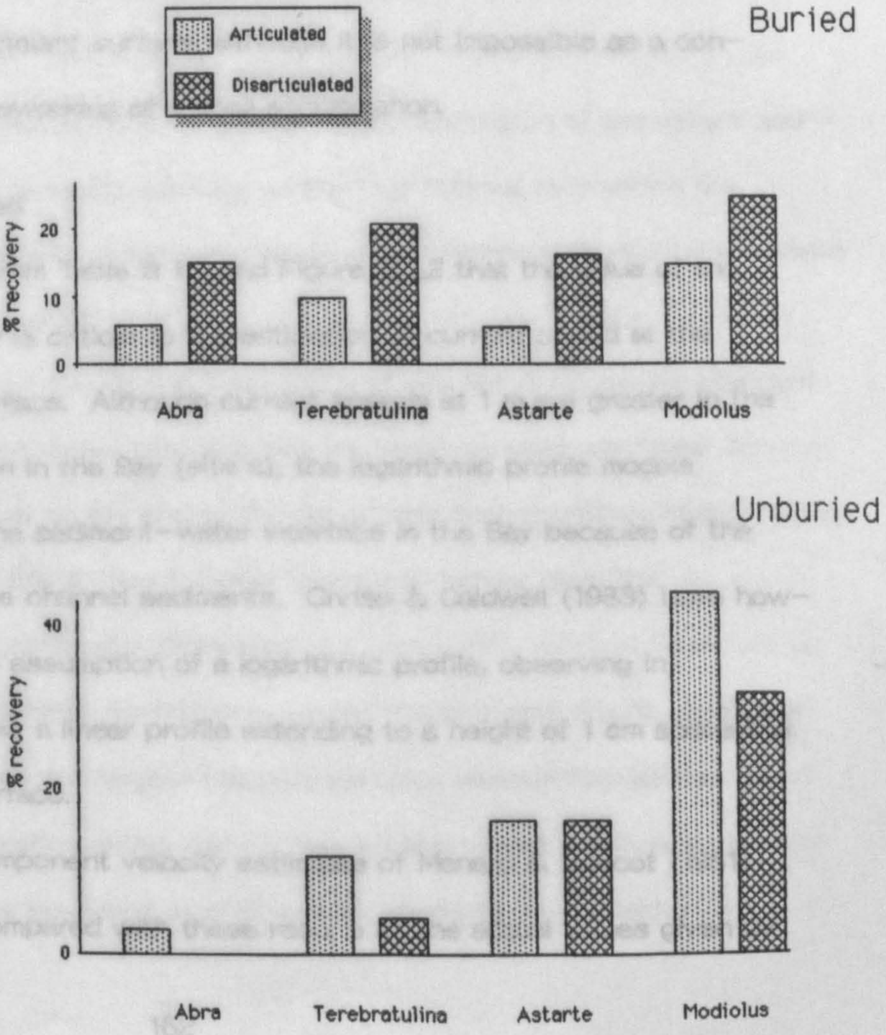


**Figure III 1.8**

Percent recovery of valves buried and on the surface



thesis, but the suggestion that the shells reach an equilibrium position is supported by the fact that it was not always the same shells which were identified as concave-down in each mosaic.

### III 1.4 DISCUSSION

The shells of these four species were scattered across the seabed within the confines of a metre square. Taphonomically, a pulsed input of this composition must be considered very unusual indeed, but individually all the biogenic particles might be found in such an environment. Input initially onto the surface of a sediment is probably typical for the brachiopods (*T. retusa* and the hypothetical deltidiodont) and *Astarte sulcata* (a shallow burrower; Salueddin, 1965). *Modiolus modiolus* although it is bysally re-inforced within the clump could be introduced onto the surface of the sediment if the clump becomes disturbed (eg. Farrow *et. al.,* 1979; J. Witman *pers comm.* 1983) or if repeated failure of succession renders the whole clump senile. The infaunal life position of *Abra alba* reduces the chance of an input of the shells of this species onto the sediment surface, although it is not impossible as a consequence of storm reworking of a shell accumulation.

### III 1.4.1 Current Speed

It can be seen from Table III 1.2 and Figure III 1.2 that the value of the roughness length $z0$ is critical to the estimation of current speed at the sediment water interface. Although current speeds at 1 m are greater in the Channel (site b) than in the Bay (site a), the logarithmic profile models greater speeds at the sediment-water interface in the Bay because of the friction of the coarse channel sediments. Chriss & Caldwell (1983) have however, challenged the assumption of a logarithmic profile, observing in smooth turbulent flow a linear profile extending to a height of 1 cm above the sediment water interface.

Similarily the component velocity estimates of Menard & Boucot (1951) cannot readily be compared with these results as the actual values given by these authors refer to a mean velocity within the flume calculated on the basis of dividing the discharge by the cross-sectional area of the flow. As the depth of the flume is not given, it is impossible to estimate a velocity profile, although values are probably lower, as within a flume friction will be exerted on the sides as well as the base of the tank and water depth is typically less than 1 m, the depth at which most field current speeds are estimated.

Comparisons between laboratory flumes and field studies are unrealistic as the former are usually artificial. Erodability of sediment is dependant upon flow strength, turbulence, bed roughness and cohesion, grain density and shape, the major compromise in flume studies being in the nature of the sediment, which is often unrealisitically homogenous but much more significantly it is not biologically stabilized (c.f. Nowell *et al.*, 1985). In the field the cohesion of the sediment is elevated by the presence of bacterial mucus (Nowell *et al., in press*), algal mats and infauna including nematodes, tubiculous polychaetes and phoronids (cf. Medows, 1986).

### III 1.4.2 Transport

The study does not provide a very meaningful estimation of the extent and type of transport of biogenic particles as the time interval over which the study was conducted was short, and therefore the distances moved by the shells were correspondingly small.

Over the period of 130 days the valves of *M. modiolus* moved the greatest distances, a mean net distance of 2 m. Furthermore, as relatively fewer *M. modiolus* were buried by the end of the experiment than any other kind of valve, (Table III 1.3, Fig. III 1.8) it would appear that these valves have the potential to move considerable distances.

A possible explanation for this unexpected result is that the *M. modiolus* shells being physically the largest biogenic particles impinge further into the greater current velocities above the viscous sublayer. The significance of projection above the boundary layer is variably related to the velocity

profile, increasing as the velocity
gradient is compressed more closely to the sediment-water interface (c.f Table III 1.2).

Projection into higher current velocities is only adequate as an explanation of selective transport for the articulated valves of *M. modiolus*, which project above the sea-bed, it does not explain the greater relative distances transported by the single valves of *M. modiolus*, whose height above the seafloor was not significantly different from the articulated valves of *T. retusa*.

It was clear, prior to the completion of the experiment that *M. modiolus* shells would have been moved most extensively. On later dives particular attention was paid to the possible causes of this unexpected phenomena, hermit crabs (Plate 2g) which were common in the area (three were present on the four mosaics), were observed to 'investigate' the larger particles, one instance of a large hermit carb *Pagurus* sp. rocking a shell as it moved past was noted, the larger shells were also used as refuges by small goby-like fish.

From the photographic records it would appear that very many *Abra* and *Terebratulina* valves were already missing after 24 hours, suggesting perhaps a rapid winnowing of the light valves following their inital dispersal onto the experimental square. This possibility is supported by the suggestion of Boucot *et al.* (1958; Fig. 6) that disarticulated valves have lower component velocities than whole shells. This suggestion is in conflict with the subsequent observations of the photographic mosaics, where the numbers of single valves present fluctuates very little. Two alternative explanations which may explain this apparent contradiction are firstly the force of suction, which holds particles onto the seabed (C. Griffiths *pers comm* 1986), the suction builds up over a period of time, which could account for the apparent dicotomy between winnowed and unwinnowed particles. A similar gradual rise would be expected for the phenomenon of biological binding of particles, which was observed most dramatically when recovering the particles two *Modiolus* valves were bound together by a solitary ascidian. Binding was also a common feature of unreported abrasion experiments and is perhaps very significant in restricting the transport of biogenic particles.

### III 1.4.3 Orientation

In only one instance, day 8 (Fig. III 1.6) was there any indication of a preferred orientation. The majority of *T. retusa* shells were on this occasion, orientated with their long axis perpendicular to the main vector of transport, the orientation which Menard & Boucot (1951) observed most articulated shells to move when rolling over the sand bed in their flume studies. There appears to be correlation between the orientation of valves and direction of transport (Fig. III 1.4 – 1.6). Menard & Boucot (1951: 149) reach a similar conclusion "the Terebratulina shells moving over an immobile sand bed came to rest at random orientation relative to the direction in which the current was moving."

Convex-up, convex-down orientation of concavo-convex brachiopod and molluscan bivalve valves have been used to orientate strata (see Clifton, 1971). On shelf sediments valves lie dominantly in a concave-up position (Emery, 1968) apparently as a result of bioturbational rotation, a conclusion supported by the experimental studies of Clifton (1971). Bosence (1979a) inferred that most large shells in the high energy 'clean algal facies' occurred in the hydrodynamically stable concave-down position, and it is proposed that in high energy environments, shells settle concave-up to be flipped over during periods of water turbulence (eg. Menard & Boucot, 1951; Johnson, 1957; Clifton, 1971; Bosence, 1979a). Johnson (1957) describes field observations and experimental investigations which suggest that the majority of transport takes place in shells orientated concave-up.

The trend towards the reduction in numbers of concave-up valves (Fig. III 1.7) does not conclusively demonstrate that an equilibrium between orientations, driven in opposite directions by bio-turbation and current activity has been inititated, as only one instances of repeated re-orientation was documented.

### III 1.4.2 Biostratinomic biasing

#### Burial

Futterer (1978) has demonstrated that current activity on loosely consolidated material may result in the filling of concave-up valves with sediment prior to burial and this was observed in this study (Plate 2g & h). Johnson (1957) and Menard & Boucot (1958), in flume studies, noted that burial of single valves always occurred in a concave-down attitude, but this observation not supported in the field experiments of Clifton (1971). It is clear, however, from these studies that disarticulated valves are more rapidly buried than articulated shells, a view supported by the results from this experiment (Fig. III 1.8). It therefore follows that valves which are less prone to disarticulation are also less prone to burial, and therefore more liable to infestation by bio-eroders.

#### Articulation & Fragmentation

It is assumed by Boucot *et al.* (1958) that "disarticulation of the shell changes exponentially with distance, and that current flow was the only force acting to disarticulate the shells", but this appears to be highly artificial. The approximate distance moved by articulated *Terebratulina* shells over the 103 day period, was by extrapolation 1 m, and although the majority of valves recovered were disarticulated, the mechanism did not appear to have been passive (Plate 2b), in only two instances were both valves recovered intact. The behaviour of articulated valves is in marked contrast to the absence of evidence of fragmentation for those valves which had been disarticulated prior to the inititation of the experiment (Table III 1.3; Fig III 1.3).

There are three possible reasons for the differing histories of the two types of particle; a) the suction sampler selectively fragments articulated valves, this would appear to be very unlikely (indeed single valves are intuitavely less resiliant than articulated shell); b) when a disarticulated intuitavely less resiliant than articulated shell); b) when a disarticulate~~d~~ valve fragments, it breaks into smaller (un-identifiable) fragments, than do the equivalent conjoined valves (again an unlikely senario); c) the force acting to crush the fragments is only operable on the conjoined valves. The last alternative appears on the surface rather an illogical proposition, unless the possibility of bio-mechanical destruction is considered.

Fractures perpendicular to the median axis, and the presence of isolated punctures (Plate 2b), were both features exhibited in valves crushed by *Cancer* (Plate 2c). Bio-mechanical fragmentation is a feature common to many arthropods, benthic feeding fish, asteroids and in the intertidal environment birds (Wilson, 1967; Farrow, 1974); field observation suggest that in this area there is extensive reworking of the sediment by crabs. The reasoning for the destruction in this instance, is however problematic as the organic content of the shell had previousely been removed. Conjoined valves are less likely to be buried than articulated valves, and the conjoined valves of brachiopods have been used as micro-habitats by small errant and tubicolous polychaetes ~~and possibly even trilobites~~ (section III 1.3.4.2). Crustaceans from the experimental area would rarely come across conjoined valves which were not inhabited by living bivalves. There have been few relevant studies of the behaviour of potential destructors, although Elner & Hughes (1979) and others have demonstrated that crabs will handle potential food items and assess size. In the laboratory, crabs would crush both living animals and empty brachiopod shells.

Sixteen of the 20 undamaged brachiopod valves recovered from the aborted infill experiment (experiment I2), were brachial, although a preponderance of intact brachial valves was not noted in the transport experiments (Table III 1.5). Such a result would be expected if *T. retusa* were crushed between the claws of a small crab, because the pedicle valve is more liable to fail, S. Ackerly (*pers comm.* 1985), (see section II 1.3.4.2). If this were the case, valve softening (section III 2) would effectively increase the range of arthropods and other animals capable of fragmenting valves.

One of the consequences of the fragmenation of *T. retusa* shell material, was a low half-life. The range of figures for half-life estimate C (Table III 1.4) are of the same order of magnitude as the estimates supplied by Powell *et al.* (1982, 4). Half-life is much greater in the more robust particles (Fig. III 1.8b), although the relationship between half-life and surface area/volume ratio is poor.

The experimental approach used, inputing a discrete pulse of shells, all of similar size, should provide better estimates of relative half-life than the monitoring techniques employed by Powell *et al.* (1982, 84). The interpretation of the absolute values from was too heavily dependant upon recovery rather than rates of destruction, an effect that could be reduced by increasing both the numbers of particles and the size of the study area.

## III 1.5 CONCLUSIONS

The experiment was initially designed as an adjunct to studies of rates of abrasion (see section II 1.5) to enable comparison between the surface architecture of sand-blast (ie caged) abrasion and more typical friction abrasion, and also to estimate the equivalent distances travelled by the carbonate within the cages and the relative probability of burial. In the event, the insignificance of abrasion in sublittoral enviroments altered the emphasis of this part of the study.

As an estimate of the relative degree of transport, the study, was only a qualified success. Most direct observations regarding shell movement have been confined to beaches, tidal flats, or similar areas near the strand line, which is a vertical zone where physical energy is concentrated by tidal and other currents, waves, and wind (Martin-Kaye, 1951; Holme, 1965; Craig, 1967; Behrens & Watson, 1969; Lever, 1958, 61; Lever & Thijssen, 1968; Clifton, 1971; Trewin & Welsh, 1972; Farrow, 1974; Antia, 1977; Lawrence, 1979). This study illustrated that larger, heavier particles can be moved as much, or more than smaller lighter particles in areas where physical energies are less extreme.

The over-use of physical process to explain biostratinomic features is also illustrated in the short-comings of flume studies. It is apparent from this study that biological systems played a significant role in interfering with physical processes. The work highlights the need for improved modelling of velocity profiles at the structurally complex sediment-water interface, the significance of biological stabilization of sediment and the significance of and reasons for, biological reworking of apparently unproductive sediment by macro-fauna. The experiment was too limited to demonstrate the relative significance of physical and biological processes, although it does implicate the latter in the biasing of death assemblages forming below the littoral fringe.

## III 2 SHELL SOFTENING

### III 2.1 INTRODUCTION

The under-representation of articulate brachiopod carbonate in the death assemblage (section II 1.3.4.3) parallels a Canadian study of the *Terebratulina septentrionalis* (Couthouy) community from the rocky subtidal (Noble *et al.*, 1976) and equates with the observations of Caulet (1967) and Brown (1979). In all these studies, brachiopods were poorly represented in the death assemblage, in Canada strikingly so (*T. septentrionalis* was over five times more abundant in the living community than in the sediment). The authors of the Canadian study suggest that the under representation of brachiopods may be "to some extent due to fragmentation". Mundlos (1978) has noted that "Recent terebratulids become, after a few months so fragile that they break under very weak pressures", and this dramatic phenomenon, observed in all *T. retusa* valves recovered from sediments off the West Coast of Scotland, contrasts with bivalve carbonate and the shells of living brachiopods. Such loss of strength will have repercussions for a wide variety of taphonomic processes and may result in higher than expected rates of comminution of affected shells.

### III 2.2 PROCEDURES

### III 2.2.1 Point loading

Theory

Shell strength was expressed as the ability of a valve to resist point loading of an area of approximately 0.25 $mm^2$. Point loading was chosen in preference to a measure of crushing force, as used by authors investigating durophagous predation (Roberts, 1975; Alexander, *pers comm.* 1986) and shell compaction (Allen, 1974) because the experiment was solely concerned with quantification of the observed loss of structural integrity with time. Whilst the results are less biologically and taphonomically relevant, a number of advantages accrue to this method, the most significant being the ability to make multiple determinations. Additionally morphological features (eg. foramen size, costation, articulation) are less likely to influence point loading values. An alternative method pioneered by Currey and Taylor (1974) was inapplicable to relatively thin shelled brachiopods.

The force required to puncture the shell is dependant upon only two factors, the thickness of the shell and its 'structural coherence'. The force required to crush a shell is also dependant upon the gross morphology and to a lesser extent, surface architecture (eg ribbing) and articulation as well as pathological factors and damage inflicted by bio-eroders. In addition, punching a hole leaves the rest of the shell intact and therefore enables a second or even third determination to be made. Wide variations in the forces required to penetrate the same shell suggest that the results of the particular determination are unreliable.

## Design

The design for the brachiopod point loader, was essentially a lever to which an increasing force could be applied. The force was transmitted via a point to the surface of a brachiopod valve which eventually failed, punching a hole in the valve. The lever had an arm made of aluminium rod, hinged in the vertical plane, the pivot designed to restrict lateral movement, (Fig. III 2.1). The height of the pivot being adjustable to ensure that the arm was horizontal (and hence the point vertical) with respect to the median axis of the shell.

The point was a blunted brass drawing pin with a flattened top, selected for its surface area which approximated to 0.25 mm$^2$, mounted in resin, set into a threaded holder. The holder was screwed into a fixing on the aluminium arm, which could be moved along the arm to various pre-set positions. By varying the distance of the mounting from the pivot, it was possible to vary the range of force applied.

## Operation

*Terebratulina retusa* and *Chlamys opercularis* for shell strength experiments were periodically collected from the Firth of Lorn, (Site 1 of Curry, 1982) and carefully selected to exclude bored or damaged shells. *Mytilus edulis* were collected from a single 0–year class clump from the Ardchattan Fish Farm, Loch Etive. All animals were killed by exposure and placed in 6 x 6 mm plastic mesh containers, which were held in a large external tank with slowly exchanging seawater, monitored to ensure that there were no significant changes in pH.

*Terebratulina retusa* and *Chlamys opercularis* for comparison of shell strength and for examination under the scanning electron microscope (S.E.M.) were collected from the sediment, at a depth of 203 meters from the short term death assemblage (sensu Powell *et al.*, 1982) by hand picking material from benthic grab samples, rinsing in one change of tap water and two rapid changes of double distilled water to remove salts, before air drying and storing in cotton wool. Prior to point loading experiments this sedimentary material was immersed in seawater for 24 hours.

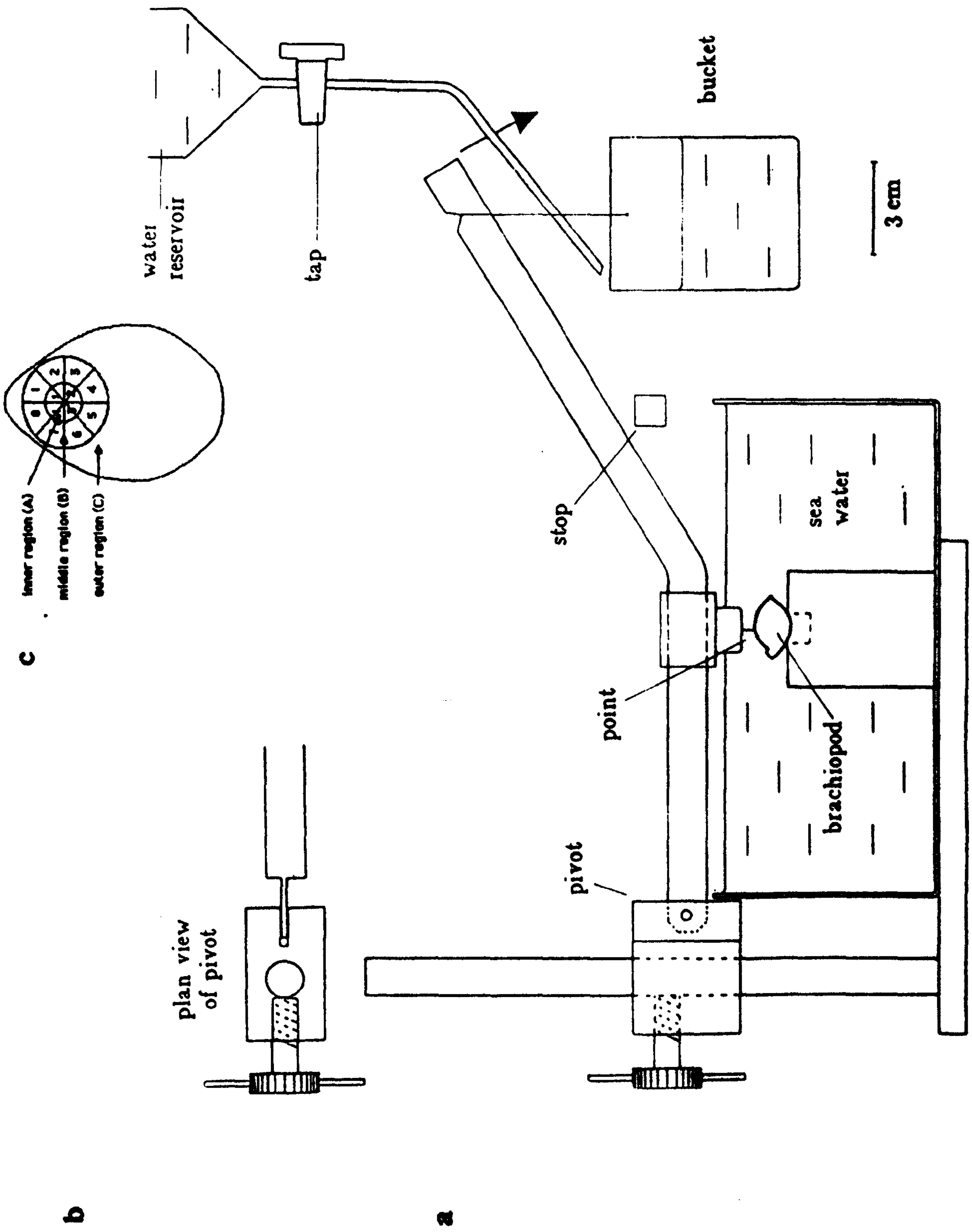
The value of staining as a means of determining the interrupted residence time of biogenic carbonate in the death assemblage (Section II 1.3.4.3) was investigated by comparing the point loading values of shells of *T. retusa* aged by this method.

Strength determinations were made with shells immersed in seawater. Spheroidal shells were seated in a hole 8 mm in diameter in the centre of the supporting platform. Force was applied at a standardized rate by means of a stream of water, progressively filling and therefore weighting a container hanging from the far end of the arm (Fig. III 2.1). A stop was used on the arm to prevent the momentum of the arm from entirely crushing the shell and also because excessive movement might have caused water to slop from the bucket. The point loader was calibrated by hanging known masses from the end of the arm, and reading the force directly from a top pan balance, the arm height adjusted so that the arm was parallel with the depressed pan.

Variability as measured by multiple determinations of the point loading

Figure III 2.1

a) Side view of brachiopod point-loader
b) Plan view of pivot assembly
c) Point position (plan view of pedicle valve)



resistance of a piece of card was low for such a crude device, (mean 1535.9, min 1144.5, max 1717.6, SD = 136.6, 8.8% of mean).

The 'strength' of each shell was routinely measured twice, the first determination being made on the brachial valve, the point being positioned posterio-medianally at the point of maximum curvature. The length, width and height of each shell was measured with a pair of dial callipers to the nearest 0.1 mm, and the between-rib thickness of the shell adjacent to this site measured with a modified micrometer. Selected shells were subsequently examined under the SEM to confirm that no dissolution of the shell fabric had occurred.

Any shell which gave results which varied by a factor of two or more was disgarded. This was a valuable attribute of the system, as pathological damage, repair and positioning of the point (Table III 2.1) could all potentially alter the force required to puncture the shell.

TABLE III 2.1
Effect of point position on the strength determination
Deviation from mean (%) of point loading values for *T. retusa*
(for positions on valves see See Fig III 2.1)

| position | | n | mean |
|---|---|---|---|
| brachial valve | A | 53 | -3.05 |
| brachial valve | B | 16 | 11.63 |
| pedicle valve | A | 45 | -2.28 |
| pedicle valve | B | 18 | 4.95 |
| pedicle valve | C | 3 | 9.13 |

### III 2.2.2 Scanning electron microscopy

Sediment grains were dehydrated by taking up through a sequence of acetone solutions of increasing concentration. Adhering particles were removed with jets of air; the samples were not cleaned ultrasonically, because of possible disaggregation effects.

All specimens were splutter coated with gold to a thickness of 75 $\mu$m.

Preparation of the protein sheaths of the secondary layer involved double fixation of the matrix. The initial fix based on the 'low osmium mixed prefixative technique' developed by Einsmann and Alfert (1982) enabled the efficient penetration of glutaraldehyde into the tissues (the presence of osmium tetroxide rendering the plasma membranes of cells freely permeable to glutaraldehyde). In *T. retusa* the outer epithelium is the only surface through which fix can pass into the deepest regions of the shell and it is therefore important to improve mobility. The second fix (incoporating a tanning agent) reduced flexibility and increased the 'strength' of the matrix exposed at the surface of the section.

The organic matrix was exposed by sectioning the shell with a slow speed diamond saw and then fixed a second time using a seawater-glutaraldehyde fixative containing 4% tannic acid. Sections were then gently polished, with 0.05 $\mu$m alumina grit, etched and critically point dried.

### Materials

#### Prefixation

Glutaraldehyde to which 0.005% $OsO_4$ had been added immediately before use.

#### Fixation

Same fixative without $OsO_4$ added fixed for one hour.

#### Main fixative

4% Glutaraldehyde
0.2 M Na Cacodylate
0.1 M NaCl pH 7.2 with 0.2 M HCl
0.35 M Sucrose

#### Post Fixative

1% $OsO_4$
0.3 M NaCl pH 7.2 with 0.2 M HCl
0.2 M Na cacodylate

### Methods

Prefix prepared by adding a small measured volume of post fix to the main fix (0.5 ml to 10.00 ml of main fix). Pre-fix mixed within five minutes of the time it is used, material pre-fixed for 5-10 minutes. Buffer rinse consists of two changes (5-10 min each) of 0.3 NaCl on 0.2M Na cacodylate, pH 7.2. Material held in a third change of rinse overnight, then transferred to post-fix (with one change) for 1 hour.

The shell material was then rinsed in three rapid changes of distilled water and taken through the alcohols, (30%, 50%, 70%, 90% and three changes in absolute) and then transferred to polypropylene oxide (1,2 epoxypropane), two changes of five minutes each, one change of 10 minutes, for this final change samples being split into individual containers.

The shell material was tumbled for seven hours in sealed containers, with a half mix of araldite and propylene oxide, the tops of the containers were removed and the containers tumbled overnight. The material was embedded in araldite and hardened for 48 hours at 60°C. The resin was trimmed and sectioned with a slow speed diamond saw at 80 r.p.m. producing sections approximatly 1 mm thick.

These sections were re-fixed and tanned in 15% fix with 0.6 gm tannic acid for 30 minutes, and rinsed in changes of fix and distilled water. The section was polished gently with 0.03 $\mu$m alumina powder until shell section appeared smooth under a binocular microscope (x 50), rinsing frequently with distilled water; finally being etched in 0.05% E.D.T.A. and taken up rapidly through the alcohols, ensuring that a meniscus of liquid was retained on the specimen surface during each transfer. Early sections were taken up through acetone, but the reaction of acetone with unpolymerised araldite marred the results.

### III 2.2.3 Organic Content

The organic content of shells was determined by ashing at a temperature of 480°C for a period of 36 hrs (Price *et al.*, 1976)

## III 2.3 RESULTS

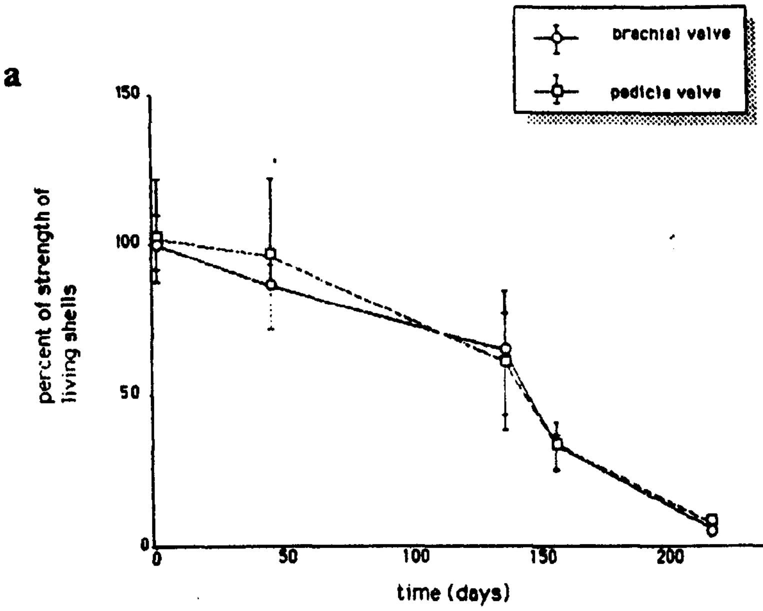
### III 2.3.1 Shell strength

#### *T. retusa*

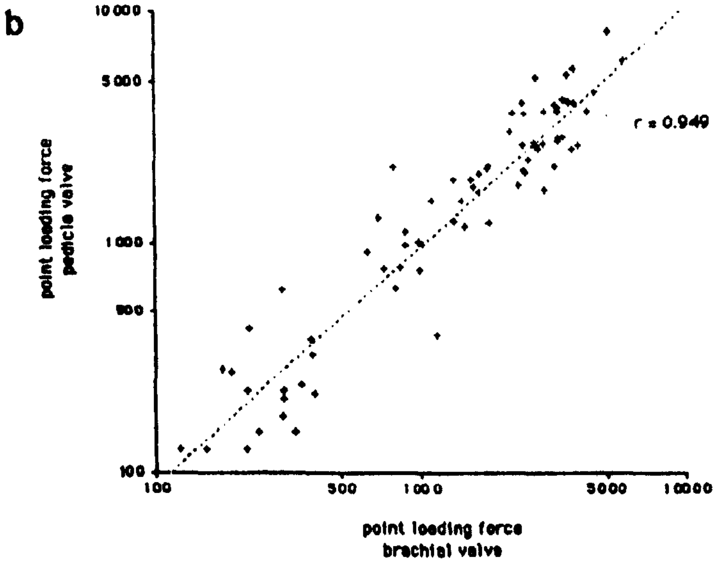
The results from the point loading experiments demonstrate a rapid decrease in the resistance to point loading of the skeletal fabric of *T. retusa* (Fig. III 2.2), the mean falling to 7% of the strength of living shells 218

Figure III 2.2

a) Decline in shell strength of T. retusa.



b) Comparison of the point loading values of the brachial and pedicle valves of T. retusa.



## TABLE III 2.2
## Results of shell softening experiments

| Species | Time (days) | No. | Length Mean | Length Min | Length Max | Length S.D. | Force as a % of living Mean | Force as a % of living Max | Force as a % of living Min | Force as a % of living S.D. |
|---|---|---|---|---|---|---|---|---|---|---|
| *T. retusa* | 0 | 16 | 15.21 | 10.4 | 22.4 | 3.24 | 100 | 130.0 | 71.0 | 25.8 |
| (brachial) | 45 | 13 | 15.78 | 10.8 | 20.0 | 2.43 | 86.4 | 113.5 | 47.3 | 23.5 |
| | 137 | 8 | 19.09 | 16.5 | 21.9 | 1.91 | 65.3 | 119.7 | 19.0 | 30.6 |
| | 157 | 21 | 16.64 | 13.8 | 19.8 | 1.46 | 34.4 | 55.3 | 9.2 | 14.2 |
| | 218 | 13 | 14.77 | 11.9 | 19.8 | 2.39 | 7.7 | 11.9 | 3.7 | 2.5 |
| *T. retusa* | 0 | 21 | 15.21 | 10.4 | 22.4 | 3.24 | 101.5 | 179.9 | 52.1 | 35.1 |
| (pedicle) | 45 | 13 | 15.78 | 10.8 | 20.0 | 2.43 | 96.1 | 153.2 | 55.0 | 28.2 |
| | 137 | 8 | 19.09 | 16.5 | 21.9 | 1.91 | 61.5 | 117.9 | 26.6 | 28.1 |
| | 157 | 19 | 16.64 | 13.8 | 19.8 | 1.46 | 33.9 | 63.2 | 11.4 | 15.5 |
| | 218 | 13 | 14.77 | 11.9 | 19.8 | 2.39 | 6.1 | 8.1 | 3.7 | 2.6 |
| Sub fossil | Colour 1 | 3 | 12.17 | 10.8 | 14.9 | 2.28 | 37.2 | 52.2 | 11.2 | 22.6 |
| (brachial) | Colour 2 | 3 | – | – | – | – | 10.9 | 12.5 | 10.5 | 11.3 |
| | Colour 3 | 10 | – | – | – | – | 9.7 | 13.5 | 3.7 | 3.2 |
| | Colour 4 | 9 | – | – | – | – | 8.7 | 19.5 | 3.7 | 5.7 |
| Sub fossil | Colour 1 | 1 | 12.17 | 10.8 | 14.9 | 2.28 | 56.8 | – | – | – |
| (pedicle) | Colour 3 | 4 | – | – | – | – | 6.9 | 9.4 | 3.7 | 2.4 |
| *Mytilus edulis* | 0 | 14 | 19.50 | 17.9 | 22.2 | 1.45 | 100 | 133.0 | 53.3 | 28.3 |
| | 45 | 11 | 21.93 | 19.6 | 25.9 | 2.37 | 134.0 | 185.8 | 47.5 | 49.1 |
| | 282 | 19 | 21.41 | 14.6 | 26.0 | 3.41 | 67.0 | 105.6 | 15.2 | 25.8 |
| *Chlamys opercularis* | | | | | | | | | | |
| Living | 0 | 32 | – | – | – | – | 100 | 110.7 | 73.8 | 42.4 |
| Sub–fossil | ND | 8 | – | – | – | – | 84.2 | 149.4 | 48.8 | 31.6 |

## TABLE III 2.3
## Regressions of the relationships between length and point loading values, fitting the equation length (mm) = *a* . point loading vaue + *b*

| | days | n | b | a | r | t–test |
|---|---|---|---|---|---|---|
| *T. retusa* | | | | | | |
| Brachial valve | | | | | | |
| length | 0 | 16 | 1032.3 | 148.7 | 0.627 | .01 |
| thickness | 0 | 14 | 1675.9 | 5269.8 | 0.320 | NS |
| length | 45 | 20 | −1463.0 | 154.2 | 0.473 | .05 |
| thickness | 45 | 13 | 693.2 | 7044.6 | 0.397 | NS |
| length | 137 | 13 | 2979.1 | −5.8 | 0.018 | NS |
| thickness | 137 | 8 | −2443.2 | 12541.5 | 0.281 | NS |
| length | 157 | 8 | 7805.7 | −294.6 | 0.564 | NS |
| thickness | 157 | 21 | 488.0 | 1782.3 | 0.344 | NS |
| length | 218 | 13 | 150.0 | 7.2 | 0.204 | NS |
| thickness | 218 | 13 | −9.6 | 911.2 | 0.426 | NS |
| Pedicle valve | | | | | | |
| length | 0 | 21 | 1256.5 | 140.4 | 0.391 | NS |
| thickness | 0 | 17 | 2963.4 | 1283.7 | 0.067 | NS |
| length | 45 | 20 | 2117.1 | 69.4 | 0.179 | NS |
| thickness | 45 | 13 | 1900.4 | 4353.2 | 0.216 | NS |
| length | 137 | 8 | 237.7 | 95.3 | 0.199 | NS |
| thickness | 137 | 7 | 5397.8 | −8411.8 | 0.369 | NS |
| length | 157 | 18 | −1324.8 | 143.0 | 0.435 | NS |
| thickness | 157 | 16 | 330.1 | 2151.5 | 0.193 | NS |
| length | 218 | 10 | 280.2 | −3.1 | 0.086 | NS |
| thickness | 218 | 13 | −5.3 | 745.7 | 0.412 | NS |
| ***M. edulis*** | | | | | | |
| | 0 | 14 | −764.6 | 108.21 | 0.410 | NS |
| | 45 | 10 | −558.3 | 112.72 | 0.464 | NS |
| | 282 | 19 | −672.2 | 73.50 | 0.725 | NS |

days after death (Table III 2.2).

A range of shell sizes was employed for each determination (Table III 2.2), but it is difficult to correct the results to a 'standard' length or thickness as some of the relationships between length and shell strength (as measured by point-loading) were poor (Table III 2.3). The wide confidence limits therefore reflect a range of valve sizes employed and a variation in absolute strengths. The poorest correlation between shell length and size occurred at 137 days, and the poorest correlation between shell length and thickness at 218 days (Table III 2.3).

The positioning of the point is another potential variable (Table III 2.1), loading figures measured outside an inner region (Fig. 2.1b), which when corrected for time, have a mean which is 14.41% higher than those results close to the preferred centre ($t = -1.9736$, t critical $= -1.9798$; Table III 2.1).

Multiple regressions were performed on a combined (non standardized) data set of brachial and pedicle valves, regressing length, time following death and shell thickness, against the dependant variable, force. Shell thickness was not a significant contributor to the equation.

TABLE III 2.4
Multiple regression analysis

| | coefficient | SE | t-value | p |
|---|---|---|---|---|
| Intercept | 1823.027 | 436.941 | 4.172 | >.0005 |
| Time | -14.636 | 0.788 | -18.572 | >.0005 |
| Length | 93.602 | 26.240 | 3.567 | >.0005 |
| Shell thickness | 592.344 | 1228.987 | 0.482 | NS |

the equation for the relationship is :-

(III i) $$F = 1823 + 93.602\ l - 14.636\ t$$

where $F$ = point loading force, $t$ = time in days, and $l$ = length (mm) $r = 0.858$

There is no significant difference in the resistance to point loading of 218 day experimental shells and the values obtained from samples collected from the sediment (Fig. III 2.3a & b). The presumed residence time in the natural environment, is much longer than the 218 days of the experiment, suggesting that the process causing the rapid decline in resistance to point loading is

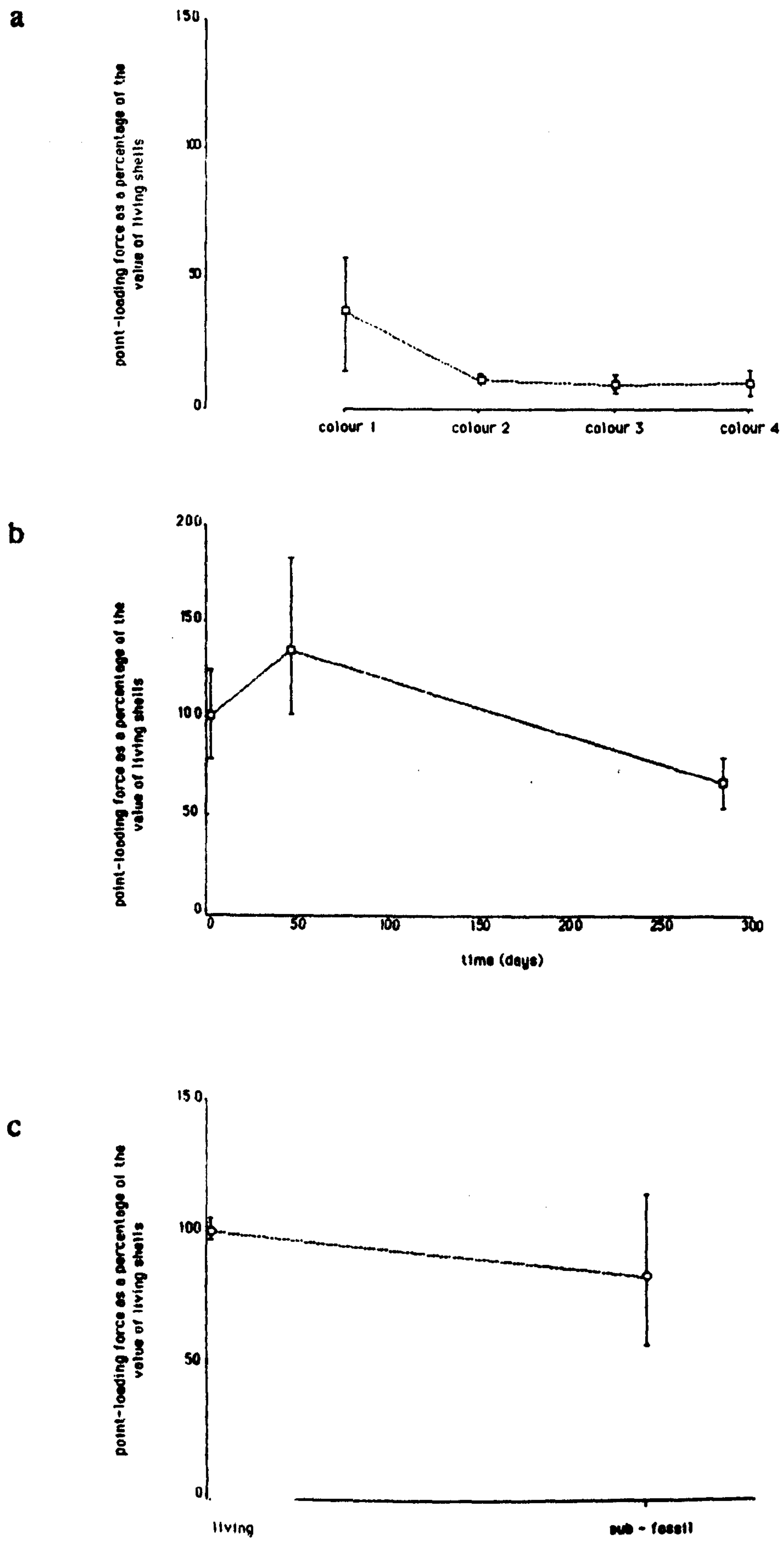
Figure III 2.3

Decline in shell strength of brachiopod and bivalve carbonate (for details see Table III 2.2)

a) T. retusa — sub-fossil shells, age estimates from retention of stain in shell fabric (see section II 1.3.4.3)

b) Mytilus edulis — living shells, and material rotted for 45 and 282 days

c) Chlamys opercularis — living and sub fossil shell material



complete by about this time, with a shell 'strength', 7% of that of a living shell, (although bio-erosion may serve to weaken the shells still further).

The stained shells from which residence times were determined (section II 1.3.4.3) show a decline in 'strength' corresponding to a reduction of stain retention and therefore organic material within the shell (Fig. III 2. b), but all those shells exhibiting the greatest stain retention (from which in one instance a complete spicule support was obtained; cf. Rowell & Rundle, 1967) have point-loading values similar to those found experimentally at 218 days and from unprepared sub-fossil material. The wide variation in the results of the three individuals aged as 'colour one' (Table III 2.2), attest either to the poor resolution of the process or the rapid rates of skeletal dissimilation.

### Bivalves

Both bivalves (*M. edulis* and *C. distorta*) undergo significantly lower reductions in the resistance to point loading than *T. retusa* (Fig. III 2. c & d; Table III 2.2). The greater degree of skeletal integrity is also reflected in the higher correlation coefficients in *M. edulis* (Table III 2.2). *M. edulis* shows an initial rise in strength from 100% to 141.6% (Fig. III 2.3c; Table III 2.2) with a reduction in strength to 65.8% of the initial force after 282 days). Sub-fossil shells of *C. opercularis* recovered from the sediment also retain a higher proportion (85.9%) of the strength of living shells than do the sub-fossil shells of *T. retusa*.

### III 2.3.2 S.E.M.

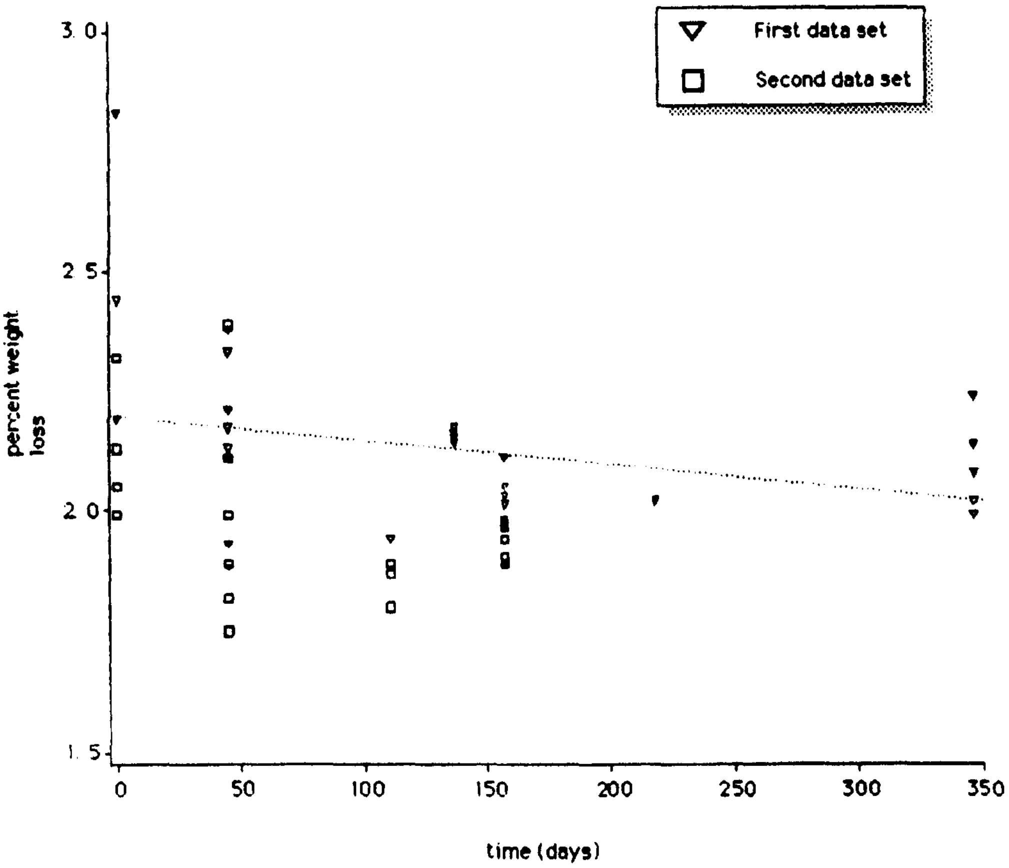
Fracture surfaces of 'fresh' (killed) and 'naturally aged' *T. retusa* shells collected from the sediment, have different appearances in hand specimen. The surface of a fracture in aged shells is ragged and ill defined, contrasting with the clean fractures of fresh shells.

Closer examination of the fabric under the S.E.M. reveals no apparent change in the dense primary layer, which is fractured cleanly in both living an aged shells. The difference in appearance is due to changes in the nature of

Figure III 2.4

Percentage weight loss of shells used in softening experiments following ashing.

(The two data sets are from the same experiments, but were determined 43 and 120 days after the point loading values had been determined. The shells dry in airtight containers following completion of point loading determinations.)



the secondary layer, the main structural unit of the shell which is composed of long fibres of calcite. The 'clean' appearance of fractures from fresh shells, results from the crisp breakage of fibres at right angles to the plane of the fracture (Plate 3a). This is in contrast to aged shells, in which the fibres are unevenly fractured and often partly disaggregated (Plate 3b), functioning as discrete units, rather than as a close packed, interlocking whole. The internal surfaces of old valves differ from the well ordered mosaic (Plate 3c) of fresh samples, large areas of mosaic are missing as terminal fragments snap free, exposing lengths of underlying fibres (Plate 3d).

The distinctive shapes and cross section of the fibres aids recognition of liberated fragments in sediment smears taken from the study area, where they form a common constituent (Plate 1d, 3e), not unlike the presence of needles from the fibrous layer of *Mytilus edulis* observed by Alexandersson (1978a) and Fitzgerald *et. al.* (1979). The presence of fibres in sediment smears is not surprising when it is considered that medium-large *T. retusa* (18 x 16 x 11 mm), with a secondary layer 0.4 mm thick, would yield approximatly 35,000 fragments of size, 15 x 5 x 100$\mu$m (typical of those found in the sediment) when totally disaggregated.

Preparations of the organic matrix from shells left to rot in experimental tanks reveals a concomitant loss in the structure of the protein sheaths of the secondary shell layer, over a period of 180 days (Plate 3f & g). No examination of the organic matrix of bivalves was undertaken.

### III 2.3.3 Organic content

Plots of percentage loss of weight indicates that there is a decline (Fig. III 2.4) but there is considerable scatter of points and the correlation coefficient is very poor (r = 0.313).

## III 2.4 DISCUSSION

### III 2.4.1 Shell Strength

Upon death, the shells of *Terebratulina retusa* soften rapidly and after approximately 200 days, have reached the limit of fabric weakening although bioerosion will serve to weaken the fabric further.

A variety of factors, poor measurment, valve thickness, skeletal architecture, point position and variable rates of softening will determine the rate of decline in the resistance to point loading. The good correlation ($r= 0.903$; Fig. III 2.2b) between the respective values obtained for brachial and pedicle valves suggest that the results are a fairly accurate estimate of shell 'strength'. The absence of a significant difference in the force required to puncture the brachial and pedicle valves (Fig. III 2.2b) suggests that valve thickness (for which there is no significant difference; section II 1.3.4.3) is more important to inherent strength than differences in morphology (although this is not necessarily true of resistance to crushing or fracture). The poor correlation between shell length and shell thickness reflects a policy of recording valve thickness close to the position of puncture, which was not inconsistent (see Table III 2.1). Nevertheless it is improbable that even if a strong correlation exits, the methodology used, could demonstrated such a relationship, because of variations in skeletal topography and architecture.

The higher correlation coefficient relative to the smoother valves of *M. edulis* is a reflection not of a stronger relationship but a larger data set (75 as against 10 data points). The wide variation in determinations implies that adequate seperation of the two factors, valve thickness and morphology would require more data.

The sharp rise in point loading resistance by *M. edulis* after 45 days (Fig. III 2.3c) must be seen in the light of the lower absolute force required to puncture the valves of living *M. edulis* when compared with *T. retusa* (mean valve 43%); larger average size of *M. edulis* used at 45 days (mean of day 0 = 19.5 mm; mean of day 45 = 21.93 mm) which when corrected for size reduces from 139% to 129%.

Skeletal organisation as a cause of shell softening

S.E.M. examination of sections through the shell only reveal changes taking place in the secondary layer. Examination of fracture surfaces demonstrates that the secondary layer has ceased to respond as a unit, and that the fibres have gained a degree of functional autonomy.

The process of softening in *T. retusa* is apparently a direct consequence of the architecture of the secondary layer (Fig III 2.5), the principal structural component of this species and the most common organization found in articulate brachiopod shells (Willams, 1968; Fig. III 2.6).

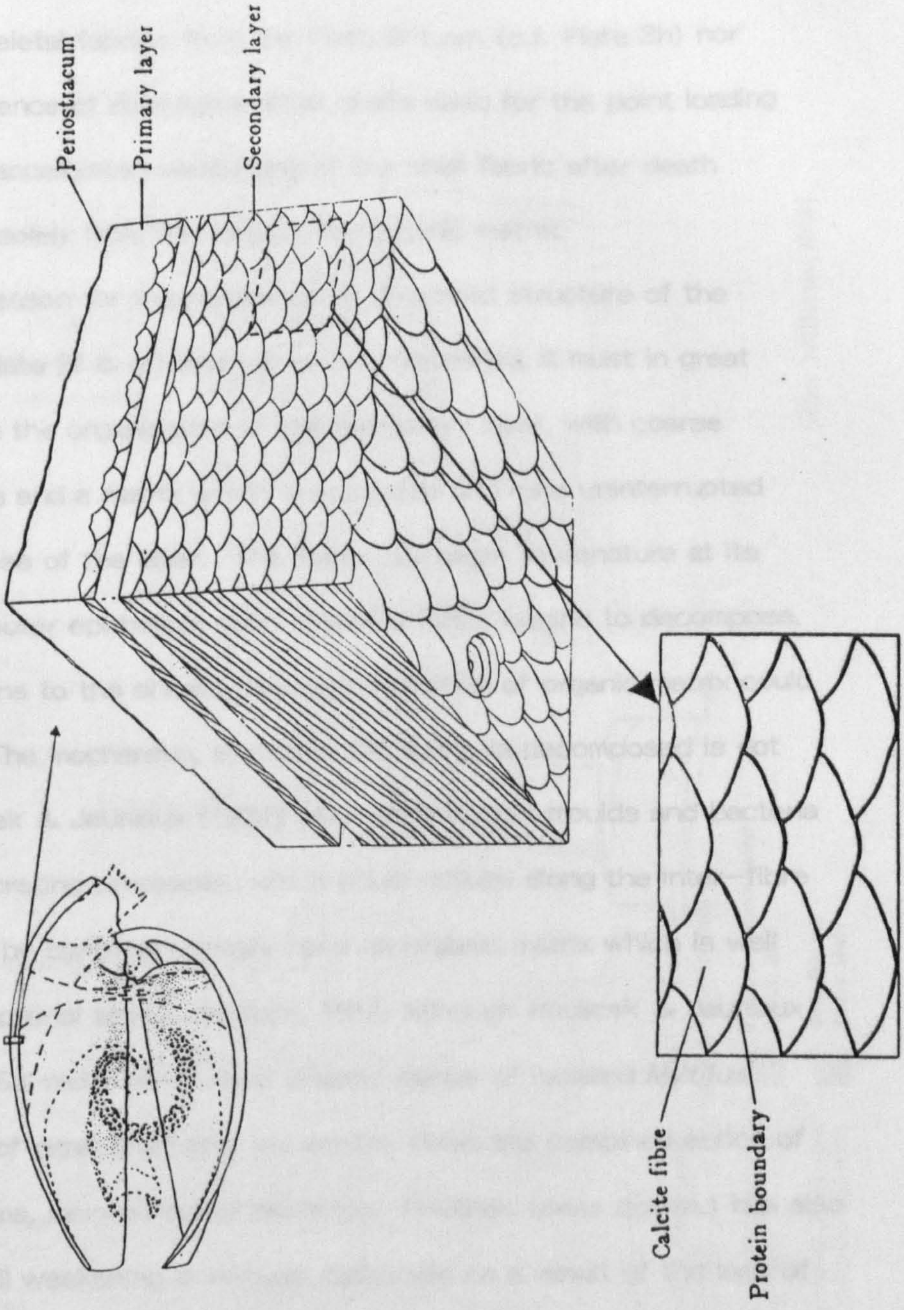
The loss of a functional organic matrix will alter the physical characteristics of the secondary layer in a variety of ways. The absence of a 'resilient bedding matrix' (Jope, 1977) will cause mechanical shock to be transmitted directly to the fibres and the shell therefore becomes more prone to mechanical destruction. The loss of the matrix would expose the fibres to chemical processes, which depending upon the saturation of calcium carbonate in the inter-fabric water, could lead to either dissolution or crypto-crystallisation (Poulicek *pers comm.*). The relationship between the organic and inorganic material of the secondary layer is analogous to that of a brick wall, the organic sheaths, a thin layer of 'mortar' seperating individual fibres or 'bricks'. The denaturing of the protein sheaths will effectively reduce the packing density of the fibres and like the loss of binding mortar from a brick wall, increase the functional autonomy of individual building blocks. The overall response will be the weakening of shell structure as observed in the point loading experiments.

The hypothesis that loss of a functional organic matrix is responsible for the observed shell softening is strengthened by the observation that brachiopod shells steeped for prolonged periods in a weak solution of sodium hypochlorite (which selectively digests away the matrix) are good analogues for those which have undergone softening.

Alexandersson (1978a,b, 79) has witnessed the alteration of 'hard glossy

Figure III 2.5

Organization of brachiopod shell fabric

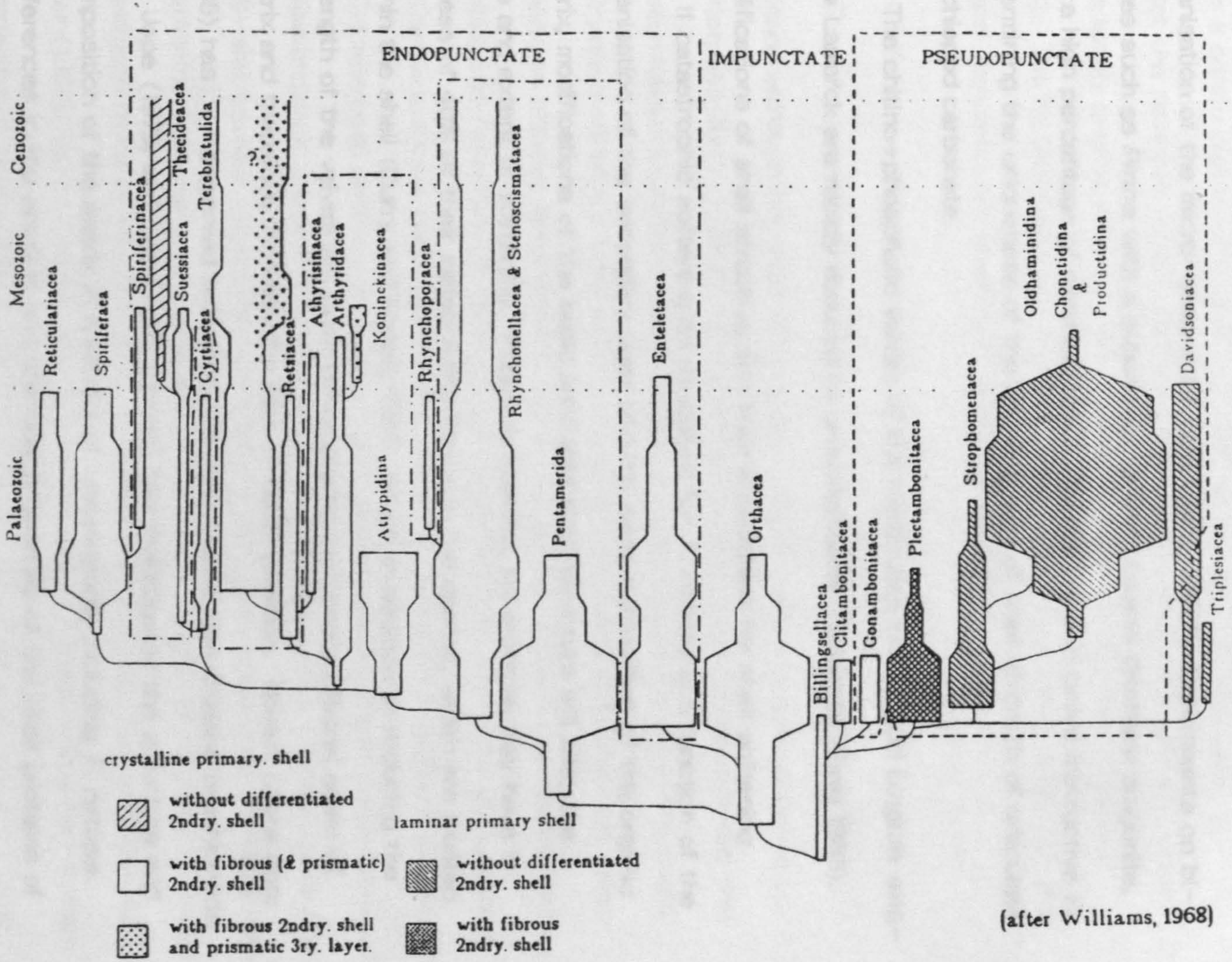


shells into weak and fragmented parts' from sediments of the Skagerrak and elsewhere, through "partial dissolution of the mineral phase, and decomposition of the organic phase" a process he termed 'maceration', but dissolution, was not observed in skeletal fabrics from the Firth of Lorn (c.f. Plate 3h) nor was there any evidence of dissolution from shells used for the point loading experiments. The accelerated weakening of the shell fabric after death apparently results solely from the loss of the organic matrix.

Although the reason for the rapid loss of observed structure of the protein sheaths (Plate 3f & g.) has yet to be determined, it must in great measure stem from the organisation of the secondary layer, with coarse structural elements and a matrix which is accesible and runs uninterrupted across the thickness of the layer. The matrix will begin to denature at its junction with the outer epithelium soon after the latter begins to decompose. Without interruptions to the sheets, the decomposition of organic matrix could proceed rapidly. The mechanism, by which the matrix is decomposed is not known, but Poulicek & Jeuniaux (1982) have verified that moulds and bacteria are capable of secreting proteases, which could diffuse along the inter-fibre spaces. Bivalves by contrast normally have an organic matrix which is well protected from bacterial attack (Hudson, 1967) although Poulicek & Jeuniaux (1982) record a 65% reduction in total organic matter of isolated *Mytilus edulis* L. mother of pearl after only six months (from the combined action of endolithic organisms, meiofauna and bacteria). Poulicek (*pers comm.*) has also demonstrated shell weakening in mollusc carbonate as a result of the loss of matrix and a similar process has been reported by Lewy (1975). The description by Lewy (1975) of shells of *Artica islandica* collected from the Baltic Sea, is in close agreement with the observations of brachiopod shells from the Firth of Lorn. Although lacking any signs of carbonate dissolution the shells were found to be mechanically weak with a chalky nature, easily broken and tending to split apart parallel to growth lines. The shells of *A. islandica* were collected by Lewy (1975) from within a core, and not from the surface of the

## Figure III 2.6

Phylogenic relationships of shell fabric



(after Williams, 1968)

sediments, which suggest that although loss of the organic matrix will result in a similar weakening of bivalve carbonate, the process occurs less readily. This assumption is supported by the results of point loading of bivalve shells and the rates of skeletal disintegration observed by decomposition of the organic matrix in hydrogen peroxide. The rate of shell weakening is probably a combination of the refactory nature of the organic matrix, and the size and organisation of the micro-strucuture (see Purdy, 1963). Experiments on bivalves such as *Pinna* with a substantial layer of coarse prismatic aragonite, and a high percentage of organics within the shell would prove instructive in determining the uniqueness of the dramatic loss of shell strength of articulate brachiopod carbonate.

The chitino-phosphatic valves of the inarticulate brachiopod *Lingula anatina* Lamarck are rapidly reduced to unrecognisable fragments (Emig 1983).

## Modifications of shell structure and their implications for shell softening

If catastrophic softening as described for *T. retusa* is a function of the organisation of the secondary layer and the rapid destruction of the organic matrix, modifications of the basic articulate shell structure will alter the rate and extent of softening. Punctate species, for example, may have in excess of 40% of their metabolizing tissue in the caecae, which are located within the shell (Curry and Ansell, 1986), which in addition to reducing the strength of the valves will upon decomposition expose additional areas of matrix and therefore increase the rate of decomposition. Hovert (*pers com* 1985) has observed softening only in punctate New Zealand brachiopods.

Jope (1979; and references therein) has investigated the structure and composition of the matrix in a variety of brachiopods, including *T. retusa*. Differences in the physical and chemical properties of the shell proteins of terebratulids and rhynchonellids, demonstrated by Jope may have a bearing on the rate of decomposition.

Perhaps the most significant modification is the presence of the tertiary 'prismatic layer'. Although these prisms remain discrete, the interprismatic spaces are smaller than those in the secondary layer and do not contain protein sheets. It is probable that the prismatic layer will both restrict the entry of proteases, and strengthen the valve. The prismatic layer is present in some terebratulids, pentamerids and spiriferids (Williams, 1968; MacKinnon and Williams, 1974; Gaspard, 1978; Benigni, 1985) where it occurs sporadically and forms a continuous tertiary layer in koninckinaceans. It is impossible to predict the potential for shell softening of the extinct strophomenides, which had a totally original fibrous fabric derived from the primary layer (Williams, 1968). The thecidaceans, which lack a differentiated secondary layer, lack the skeletal organisation that leads to rapid shell softening.

### III 2.4.2 Evidence of post mortality softening

There have been no reports of softening of brachiopod shells in the literature, although the rapid destruction of dead shells has been noted by Brunton and Curry (1979: 2). Christian Emig (*pers comm.*) has confirmed that *Terebratulina* shells from Mediterranean sediments are soft, unlike the shells of *Gryphus vitreus*, a terebratulid with a well developed prismatic layer (MacKinnon and Williams, 1974; Benigni, 1985). Weakened shells of the terebratulid brachiopods *Terebratalia transversa*, *Terebratulina unguicula* and *Laqueus californianus* have been observed in sediments collected from Puget Sound (USA) (M.C. LaBarbera *pers comm.* 1985). Post mortality weakening has also been noted in *Macandrevia cranium* from Norwegian coastal waters (E. Thomsen *pers comm.* 1986) and the New Zealand terebratulids *Terebratella sanguinea*, *Terebratella (Waltonia) inconspicua* and *Neothyris lenticularis* but not in shells of the impunctate rhynchonellid *Notosaria nigricans* (W. A. Hoverd *pers comm.* 1985). Hillier (1986) figures a specimen of *Grammetaria africana* with a marked dis-association of fibres along a fracture surface.

The rapid softening of articulate brachiopod shells will result in an increased susceptibility to mechanical and bio-mechanical fragmentation, leading to an overall reduction in whole shells and valves with a concomitant increase in the number of fragments. In the Firth of Lorn, in the absence of high energy conditions, bio-mechanical fragmentation is probably the most important method by which whole shells and valves are comminuted. Once the shells are fractured the process of destruction is probably quite rapid. The ragged fracture surfaces of soft valves of *Terebratulina retusa* (Plate 3b) expose lengths of brittle fibres which are liable to snap free, liberating short pieces into the sediment (Plate 3e). This process which differs from straight forward fragmentation, as observed in the majority of bivalves (e.g. Trewin & Welsh, 1972) has been noted by Brown (1979: unpublished thesis 267) in *T. retusa* fragments from the Sound of Jura "Fragmentation of *Terebratulina* would seem to be by the loss of small fragments from the fibrous shell structure, rather than definite fragmentation as in many bivalves". Brown (1979) also notes that actual fragments "though not scarce are not as common as might be expected." Pieces of secondary fibre are also shed from the inner surfaces of articulated valves (Plate 3d), but this process, mediated by disturbance from sediment infilling or from organisms exploiting the micro-habitat afforded by the closed valves (section II 1.3.4.3), is probably too slow to have a significant effect when contrasted with the rapid disaggregation of the secondary layer at fracture surfaces.

The liberation of fragments of fibres from the secondary layer into the sediment is implicit in the softening process, and yet the author is unaware of any published reports of these distinctive fibres from sediment samples although the presence of aragonite needles in carbonate muds derived from the tropical calcareous algae *Halimeda* and the presence in suspension and sediment of aragonite crystallites from the fibrous layer of *Mytilus edulis* shell fabric are both widely reported (Alexandersson, 1978; Fitzgerald *et al.* 1979). Similarily Lowenstam (1963) records his surprise at the absence of records of fossil brachiopod spicules in the literature. A very limited survey of samples from Devonian to Tertiary was disappointing, the few positive records of fibres, observed by light microscope (from the Upper Leintwardine Fauna, from

Ludlow and from the Cornbrash of Ducklington, Oxford) were not confirmed by S.E.M. analysis of smears. These results may simply reflect the limitations of the methods employed to isolate fibres from the sediment, as J. Forsey (*pers comm.*, 1986) has observed numerous fibres in the 250 μm sieve fraction of Jurassic mudstones, often in samples lacking brachiopod macrofossils, although these provisional identifications are awaiting corroboration. Forsey (*pers comm.*) uses these fibres as supporting evidence for marine conditions, a role to which they are particularily well suited.

### III 2.4.3 Skeletal durability

When considering the importance of mechanical and biomechanical fragmentation, attempts have been made to provide estimates of the relative durability of biogenic carbonates (Chave, 1964; Hallam, 1967; Eisma, 1968; Lefort, 1970; Driscoll & Weltin, 1973). Although dependant on a variety of factors (architecture, microarchitecture, type of dentition and articulation) as illustrated by a consideration of the factors leading to distortion of the pedicle valve ratio (section II 1.3.4.2). Although point-loading resistance is a poor measure of skeletal durability, the fall of *T. retusa* relative to *Mytilus edulis*, from 243% to 17% over 217 days, suggests that the rate of shell 'softening' is undoubtedly one of the most significant contributors to durability, a factor which has not yet been recognized.

## III 2.5 CONCLUSIONS

The process of shell weakening will, under many circumstances contribute to an underestimation of articulate brachiopods in the death assemblage. In published studies, from both the west coast of Canada (Noble *et al.*, 1976) and the Algerian slope (Caulet, 1967), brachiopod carbonate is poorly represented in the sediment.

Post mortality strength loss is not restricted to the shells of *Terebratulina retusa*, nor indeed to those punctate articulate brachiopods that lack a tertiary layer, but both the rate and extent of weakening of different organic carbonates are difficult to predict. However, post mortality strength loss will alter the relative 'durability' of skeletal carbonate (a concept employed by a number of authors, eg. Chave, 1964; Hallam, 1967) and may therefore have an important effect, although as yet unquantified on the potential for preservation of different types of organic carbonate.

It must however, be recognised that the rate of softening is not the sole factor relevant to the rate of disintegration of carbonate. Additional considerations include, mineralogy, the quantity of both magnesium and aragonite adversely affect diagenetic stability (section IV). Interlamellar or intercrystalline conchiolin (Kennedy & Hall, 1967) may perform the same protective function, albeit on a microscopic scale, as that of the periostracum. Environmentally, pH, Eh and carbonate equilibria, the rates of deposition and burial, and habitats of organisms will all have a bearing on the potential for destruction.

# SECTION IV
# CONCLUSIONS

# IV CONCLUSIONS

Carbonate skeletal remains undergo a cycle of carbonate degredation (Fig. IV 1), all stages of which have the potential to distort the relationship between the living community and accumulating death assemblage.

## Mortality

Mortality can strongly influence the nature of the death assemblage, a mass mortality event will derive a very different assemblage from selective predation of the same community.

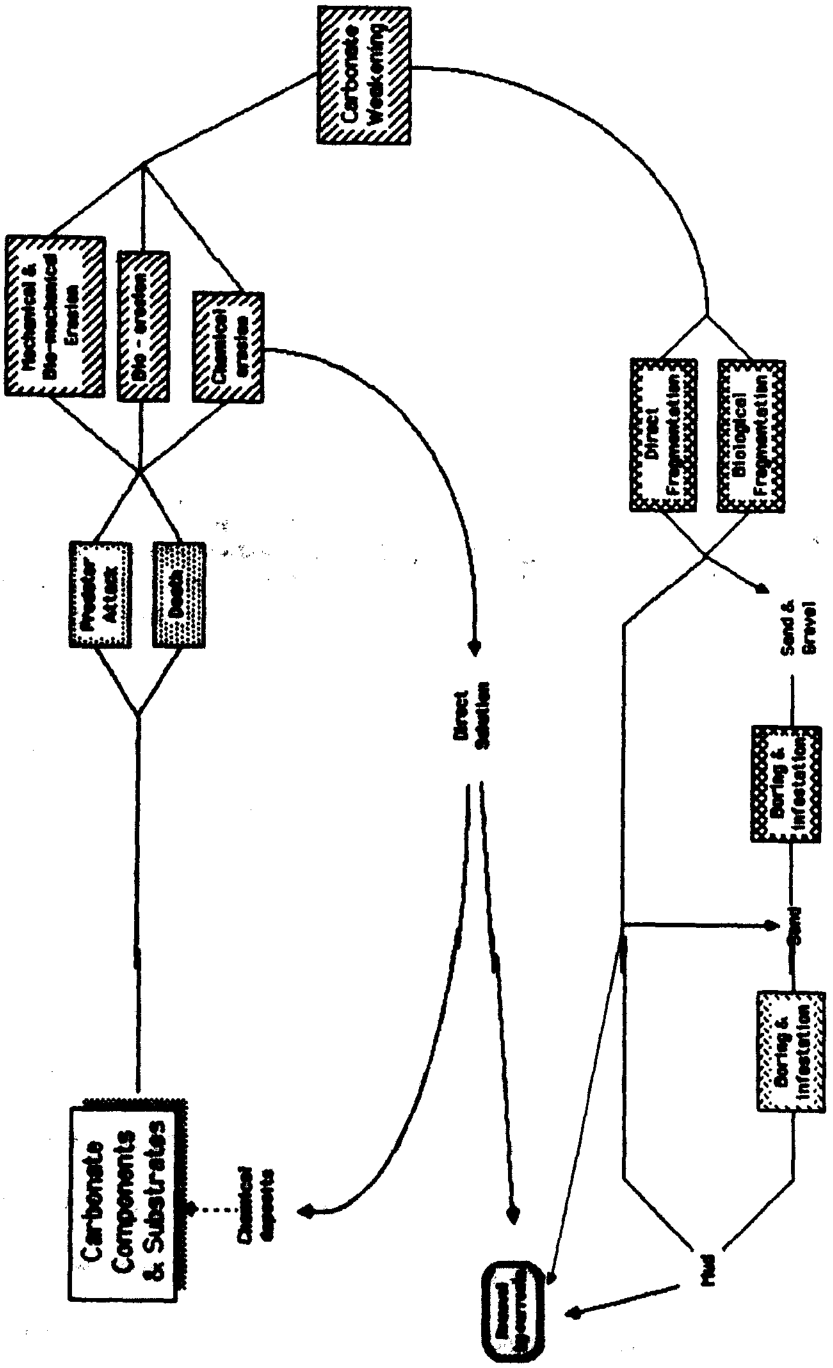
With occasional exceptions (eg. Boyd & Newell, 1972) the source of mortality is usually ignored, unless pathological damage is inflicated. Gastropods are 'ideal' fossil predators in this respect leaving clear evidence in the form of taxonomically significant, countersunk borings as well as macrofossil remins. Asteroids, in contrast, are enigmatic fossil predators, capable of consuming bivalves of their own body weight, but decaying to small plates. Although the forces exerted by asteroids can be considerable and may cause the prey's shell to fracture during feeding (Comely *pers comm.* 1985), most pathological damage is inflicted by durophagous predators such as crustaceans fish and birds, which may fracture shells in recognizable ways (section III 1.4.4). Hughes (1980) cites evidence of remarkably sophisticated selection by predators.

## Processes leading to carbonate weakening

Biogenic and biocalstic sediments do not always reflect the prevailing current activity of their environments (in contrast to transported sediments whose grain sizes are environmentally sensitive) and their textures are determined chiefly by the processes of skeletal breakdown. In the breakdown of skeletons to unrecognizable skeletal particles, three mechanisms are recognized, mechanical, chemical and biological (Fig. IV 1). Although these three mechnisms are each considered seperately, this is a stylistic constraint which does not accurately reflect the interplay between them. Scoffin *et al.*

**Figure IV 1**

Cycle of shallow water carbonate degredation (Milliman,1974)



(1980) illustrate how the processes of bio-erosion and dissolution are interrelated, Swinchatt (1965) cites an example from shallow water where boring algae promote mechanical destruction, and this study examines another biologically mediated process which reduces the structural integrity of biogenic carbonate (section II 2).

Mechanical comminution

Field studies have yet to demonstrate unequivocally processes of sub-tidal mechanical comminution. Pratje (1929), Klahn (1932) and Frey & Basan (1981) have documented examples of 'sand-blast' abrasion in the intertidal and Driscoll (1967, 70) compared the rates of destruction of shells from a moderate surf on both gravelly, and fine sand beachs with those observed from a low energy sub-littoral environment. The rates of destruction of *Mercenaria mercenaria* was two orders of magnitude greater on the fine sand beach and three orders of magnitude greater on the gravel beach.

Laboratory studies of the resistance of skeletal parts to physical destruction have been carried out using tumbling barrels (Chave, 1964; Hallam, 1965; Driscoll & Weltin, 1973; Hoskin *et al.* 1983), flumes (Eisma, 1968), and other forms of artificial agitation (Lefort, 1970; Trewin and Welsh, 1976) to simulate the effects of waves and currents. These simulations may distort the significance of mechanical breakdown as they model environments where physical processes dominate the destructive regime, an insignificant proportion of the depositional environments of bioclastic and biogenic limestones.

In an experimental study (section III 1), biogenic particles exposed on the sea floor, were extensively fragmented, unlike caged counterparts, leading to the conclusion that this destruction was biologically and not physically mediated (section III 1.4.4). Weight loss of carbonate held within cages was very slight and fragmentation minimal, much of the material being biologically bound together by polychaetes (section II 1.4.2).

The absence of convincing field studies means that the significance of physical destruction to taphonomic biasing in subtidal deposits is still equivocal, although the consensus (Swinchatt, 1965; Driscoll, 1967, 70; Turney & Perkins, 1972; Guntilaka 1977) is that biologically and chemically mediated processes are more important.

### Dissolution

Dissolution was traditionally thought to occur only in water under-saturated with calcium carbonate (c.f. Milliman, 1974) but dissolution is more extensive than classic stoichiometry would suggest because of the role of magnesium, and organic material in the organic geo-chemical cycle.

The significance of mineralogy is well known, but the inter-relationship between mineralogy and the partial pressure of $CO_2$ in oceanic seawater (ie the carbonate compenstion depth) has only recently been demonstrate (Cooke and Kepkay, 1984). The differences in solubility of aragonite and calcite are believed to be a function of the presence of magnesium (eg Walther & Morse, 1980). Little is known of the cation stoichiometry of magnesium calcite precipitation and dissolution, even though several authors (Morse et al., 1979; Wollast et al., 1980) have proposed that layers of magnesium calcite on what were originally pure calcite surfaces are involved in the complex phase equilibria with sea water. Compositional changes due to the surface reactions with aragonite are less pronounced (Berner, 1976). Precipitation of calcium carbonate may be inhibited by the presence of organic matter in the seawater (Chave & Suess 1970) either by complexing with ions or by poisoning of nucleation sites.

A number of authors have observed dissolution at low latitudes in shells below the sediment-water interface (Driscoll, 1970; Peterson, 1976; Aller, 1982; Reaves, 1986). Aller (1982) working in Long Island Sound noted the extent to which bioturbators can reduce the buffering effect of organic matter decomposition and how deposit feeders can promote dissolution by transfering iron sulfide rich, anoxic sediments, to the surface where they are subsequently oxidised releasing sulphuric acid (Aller & Yingst, 1978).

Biological comminution

Biological carbonate destruction is of two forms bio-erosion and bio-mechanical fragmentation, the former including those organisms which use skeletal carbonate as a source of nutrient (fungal hyphae), protection (the boring sponge *Cliona*), or as a means of anchorage (brachiopod *Podichnus*). There is some evidence that those species which use the shell as a source of nutrient are selective (see Milliman, 1974). Bio-eroding algae tend to be restricted to the photic zone (which on the west coast of Scotland is less than 30 m; Akpan & Farrow, 1985) although they have been recovered from surprising depths (eg. Fredj & Falconetti, 1979). Fungi are solely dependant upon organic matter for their nutrition, and are consequently not restricted to the photic zone.

Following death, bacteria and fungi secrete proteases which will hydrolyse the organic component of the skeleton, (Poulicek & Jeuniaux (1982). The loss of the organic matrix will reduce the effective durability of the skeletal carbonate (Purdy, 1963; Lewy, 1973; Collins, 1986) and expose it to chemical disintegration (section III 2).

Little attention has been paid to bio-mechanical destruction as a consequence of the biological reworking of sediments (section III 1) although the reworking of poorly sorted muddy sediments by the arthropods, *Hyas* and *Pagurus*, has been implicated in the fragmentation of brachiopod shells (Noble *et al.*, 1976), and Clifton (1971) has demonstrated the role of bio-turbators in the re-orientation of shells.

The sheer diversity of biological systems means that the potential to locally make significant, if unusual, contributions to biostratinomic processes is almost limitless. Examples of such processes include the transport of gastropod shells by hermit crabs (Arntz *et al.* 1976), use of valves as micro-habitats (section II 1.3.4.2), the possible fragmentation of material in byssal clumps (section II 1.3.6), and algal mediated transport (section II 1.3.5.2).

One of the goals of biostratinomical investigation should be the recognition of common trends, rather than isolated processes. Chave (1964) and others have attempted to identify those factors which affect the durability of biogenic carbonates. In addition to 'traditional' features such as morphology, architecture, microarchitecture (Chave, 1964), and shell chemistry (Cook & Kepkay, 1984), other aspects of the particle may be relevant in a biological context, such as the nature of the organic matrix (section III 2) and of articulation (eg. Fig II 1.t.5).

Comparisons of productivity and preservation (section II 1.4.2) suggest that size has a significant influence in this community. Broadly it would appear that the greater the proportion of shells in the > 4 mm fracton, the more heavily is the shell under-represented. It is proposed (section II 1.4.2) that this pattern is caused by selective ~~relationship size is infact related~~ to bio-erosion, the degree of infestation itself a function of those factors which will increase the period of exposure on the sea floor.

If bio-erosion is the major source of carbonate destruction and the degree of bio-erosion is related to hydrodynamic stability, then within any given community it should be possible to predict the degree of agitation of individual particles, once more robust models for predicting erosion velocities are available (eg. Yound & Mann, 1985).

If bio-erosion is dependant upon hydrodynamic stability then a number predictions follow, taphonomic biasing in favor of smaller particles will be more significant in low-energy environments and in shallow water. It appears crucial to the understanding of taphonomic biasing to identify the most important bio-eroders, to determine rates of bio-erosion and see if this alters as residence time increases. Akpan (1981) notes that *Echinus* grazings occur around the entrance of *Cliona* borings, housing living animals. If shells macerate (*sensu* Alexandersson, 1979) then older and thinner shells will provide reduced protection from the attentions of echinoids. The role of bio-eroders in taphonomic biasing could be determined in areas with similar hydrodynamic regimes with different degrees of infestation (ie at different depths or different sedimenation rates) with particular attention being paid to size-specific within species infestation. The great difficulty with such a study would be to demonstrate that juvenile shells are under-represented, requiring production and mortality estimates of juveniles.

Dispersal

The extent to which sediment has been moved across the shelf is difficult to predict on the basis of our present understanding. Today beach sands are derived from the winnowing of sediment from deeper waters; sabkha muds and sands are derived from the seaward lagoon; oolites characteristically migrate over the floor (Bathurst, *pers comm.* 1984). Most of the evenly-bedded, moderately to poorly sorted skeletal debris may have remained more or less where it formed biologically (Boucot, 1981), yet all but the most mobile sediments have been repeatedly re-worked by bioturbators and biological bull-dozers, especially since the end of the Palaeozoic (Thayer 1982). The attention given to transport phenomena far outweighs that given to bioturbation and bio-reworking of sediments although these biologically mediated processes appear much more significant, both for taphonomy and in determining sediment quality. Surprisingly little is known of the ways in which the sediment dwelling fauna influences sediment quality and stability (Meadows, 1986) but it may be significant that the preservation potential of storm-generated beds appears to have declined through the Phanerozoic (Sepkoski 1982; Larson and Rhoads 1983).

Algal mediated transport has been widely reported, but its significance in community mixing has yet to be determined.

The three, interrelated processes of biostratinomic bias, physical, chemical and biological, are in the most simplistic analysis, stratified within the marine environment. Physical energy is concentrated in the littoral fringe, and is observed to move, sort, abrade and fragment biological particles, although it is apparent that biological systems can replicate many of these features, which should therefore be treated with some caution when used for palaeoenvironmental interpretation. In water below the carbonate compensation depth, dissolution finally eliminates all carbonate remains leaving only siliceous biogenic deposits. Between these two extremes biological systems dominate, not simply bio-eroding and comminuting particles, but modifying conditions to promote or relegate the other two processes (eg. Aller, 1982; Nowell *et. al.* 1985).

It is understandable that biologically-mediated taphonomic and biostratinomic processes have played a less significant role in our interpretaion of taphonomic history. Physical and chemical processes are typically more dramatic and also more accessible to field and laboratory investigation, furthermore biologically mediated processes are much less predictable not only because they are so complex and inter-dependant, but because of the evolution of biological systems over the course of the Phanerozoic, including profound changes in the extent of bioturbation (Thayer, 1982) and durophagous predation (Vermeij, 1977).

# APPENDICIES

## APPENDIX I

Species List – *M. modiolus community* Firth of Lorn

Phylum Class

- Porifera
    - *Iophon nigricans*
    - *Iophon patterson*
    - *Placamionida ambigua* (Bowerbank)
    - *Cliona celata* Grant
    - *Hymadesmia* sp Blue sponge
- Cnidaria
    - Hydrozoa
        - *Diphasia margareta* (Hassall)
        - *Abietinaria abietina* Hincks
        - *Aglaophenia tubulifera* (Hincks)
        - *Tamarisca tamarisca* (L.)
    - Anthozoa
        - Actinaria
            - *Adamsia palliata* (Bohadsch)
        - Alcyonacea
            - *Alcyonium digitatum* (L.)
        - Zoantharia
            - Madreporaria
                - *Caryophyllia smithii* Stokes
- Echinodermata
    - Crinoidea
        - *Antedon bifida* (Pennant)
    - Ophiuroidea
        - *Amphiura chaiaje*
        - *Ophiocomina nigra* (Abildgaard)
        - *Ophithrix fragilis* (Abildgaard)
    - Asteroidea
        - *Luidia ciliaris* (Philippi)
        - *Henricia sanguinolenta* (Muller)
        - *Crossaster papposus* (L.)
        - *Anseropoda placenta* (Pennant)
        - *Solaster endeca* (L.)
        - *Asterias rubens* L.
    - Echinoidea
        - *Psammechinus miliaris* (Gmelin)
        - *Echinus esculens* L.
        - *Echinocyamus pusillius* (O.F. Muller)
- Mollusca
    - Polyplacophora
        - *Lepidoplerus asellus* (Gmelin)
    - Gastropoda
        - Prosobranchia
            - Fissurellidae
                - *Emarginula reticulata* (Sowerby)
                - *Didora apertura* (Montagu)
            - Capulidae
                - *Capulus ungaricus* (L.)
            - Eratoideae
                - *Trivia* sp.
                - *Clathrus clathrus* (L.)
            - Buccinidae
                - *Buccinum undatum* L.
                - *Neptunea antiqua*

- Bivalvia
  - Nuculidae
    - *Nucula nucleus* (L.)
    - ?*Nucula sulcata* Bronn
  - Nuculanidae
    - *Nuculana minuta* (Muller)
  - Arcidae
    - *Arca tetragona* Poli
  - Anomiidae
    - *Anomia epihhipum* L.
    - *Monia squamata* (Gmelin)
    - *Monia patelliformis* (L.)
  - Mytilidae
    - *Modiolus phasiolina* (Phillipi)
    - *Modiolus modiolus* (L.)
    - *Musculus musculus* (L.)
  - Pectinidae
    - *Chlamys opercularis* (L.)
  - Astartidae
    - *Astarte sulcata* (da Costa)
    - *Astarte elliptica* (Brown)
  - Thyasiridae
    - *Thyasira flexuosa* (Montagu)
  - Erycinacea
    - *Kellia suborbicularis* (Montagu)
  - Cardiidae
    - *Parvicardium ovale* (Sowerby)
  - Venerdiae
    - *Dosinia exoleta* (L.)
    - *Venus ovata* Pennant
    - *Venus casina* L
  - Scrobiculariidae
    - *Abra alba* (Wood)
  - Myacidae
    - *Hiatella arctica* (L.)
- Annelida
  - Polychaetae
    - Sedentaine
      - Amperetidae
        - *Melinna* sp. (cristata?)
      - Terebellidae
        - Amphitrite (*Polycirris*)sp.
      - Chloraemidae
        - *Diplocirris* sp.
      - Cirratulidae
      - Poronidae
        - *Paraonis lyra*
      - Serpulidae
        - *Pomatocerous triqueter* (L.)
        - *Protula* sp.
        - *Filograna implexa* Berkeley
      - Sabellidae
    - Errantes
      - Aphroditidae
        - *Lepidonotus squamata*
        - *Hermione hystrix* (Savigny)
      - Syllidae
      - Nepthyidae
      - Glyceridae

PAGE
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IN
ORIGINAL

# APPENDIX II

## *Modiolus* Communities

Author Site Depth Sampling Methods

Warwick & Davies Bristol Channel Day Grab

Species found at other sites which reach their greatest abundance on the mixed bottom (finer sediment) *Modiolus* community, as opposed to the *Modiolus* community prop characterised as occuring on hard bottoms with no admixture of soft sediments. Faunal analysis from hardground should be treated with caution because of the sampling inefficiencies of the Day grab on firm substrates. Many of the species found on the mixed bottoms also found in the *Abra* or *Venus* communities.

Amphipoda *Ampelisac spinipes*
*Stenothe marina*
Polychaeta *Lumbrineris latrelli*
Echinoidea *Echinocyamus pusilius*
Sipunchulida *Phascolion strombi* (distribution limited by availibility of old *Dentlium* and *Turritella* shells).

Other species, may be precluded from areas of strong erosion of *Modiolus* proper, eg the crustaceans :-
Crustaceana *Macropipus pusillius*
*Pilumnus hirtellus*
*Galathea intermedia*
*Galathea* spp.
*Pagurus prideauxi*
*Eurynome aspera*
*Ebalia tumefacta*
*Atelecyclus rotandus*
*Ianachus dorynchus*
*Pandulus montagui*
*Crangon crangon*
*Hippolyte varians*
*Modiolus modiolus* both environments
Crustaceana *Pagurus bernhardus*
*Eurystheus maculatus*
*Thoralus cranchi*
Echinodermata *Ophiothrix fragilis*
*Asterias rubens*
Polychaeta *Lepidonotus squamata*
*Lepidopleurus asellas*
Mollusca *Pisidia longicornis*
*Hiatella arctica*
*Calliatoma zizyphinum*

Comley 1981 Sullom Voe 15m Diver Collection
(Shetland Isles)
Echinodermata *Ophiothrix fragilis* (Abildgaard)
*Ophiopholis aculeata* (L.)(smaller numbers)
*Henricia sanguinolenta* (O.F. Muller)
*Asterias rubens* L.
*Psammechinus miliaris* (Gmelin)
Mollusca *Chlamys opercularis* (L.)
*Hiatella arctica*

Spark 1932 Faroes few 110m. Dredge
In channels swept by considerable current, also on open coasts, banks and shoals etc.

wherever the water is likely to be frequently renewed. In comparison with Petersen (1913, 18) greater abundance reduced diversity in the Faroes.

Echinodermata *Ophiothrix fragilis* (Abildgaard)
*Ophiopholis aculeata* (L.)(smaller numbers)
Crustaceana *Galathea nexa*
*Hyas corarctatus*
*Spirontocaris pusilosa*
*Eupagurus* spp.
*Balanus hameri*
Cnidaria (Hydrozoa) *Hydrallmannia*
Polychaeta *Lepidonotus squamata*
*Trophon plumosa*

Caddy 1970 Bay of Funday few 110m. Dredge
Constituent species of *M. modiolus* assemblage identified by Caddy
Cnidaria (Hydrozoa)
Crustaceana *Hyas coarctatus*
*Pagurus* spp.
*Balanus balanus*
Mollusca *Chlamys islandica*
*Hiatella artica*
*Buccinum undatum*
Echinodermata *Pteraster militaris*
*Henricia* spp.
Chordata (Tunicata) *Boltenia ovifera*
Porifera *Weberella bursa*
Additional dominant species (ie those regarded as abundant in at least one haul also containing abundant *M. modiolus*). Abundance from 0–3
Epifauna
Mollusca *Anomia* spp.
Echinodermata *Asterias rubens* L.
Brachiopoda *Terebratulina septentrionalis* (Couthouy)

Roberts 1975 Strangford Lough sub–littoral Scallop Dredge
Quadrate Survey, and by
hand sampling.
Dominant Associated fauna :–
Cnidaria (Hydrozoa) *Plumularia* spp.
Polychaeta *Sabella pavonia* Savigny
*Serpula vermicularis* L.
*Pomatoceros triqueter* (L.)
Crustaceana *Pagurus bernhardus* (L.)
*Hyas areneus* (L.)
*Macropipus depurator* (L.)
*Balanus balanus* (Ascan)
*Ianachus dorsettensis* (Pennant)
Mollusca *Buccinum undatum* L.
*Chlamys varia* (L.)
*Chlamys opercularis* (L.)
*Hiatella arctica*
Echinodermata *Ophiothrix fragilis* (Abildgaard)
*Ophiocomina nigra* (Abildgaard)
*Asterias rubens* L.
*Echinus esculentus* L.
Chordata (Tunicata) *Clavelina lepadiformis* (O.F. Mueller)
*Ciona intestinalis* (L.)
*Dendroda grossularia* (Van Benden)

Jones 1971 South Isle of Man sub-littoral Dredge, Van Veen and Grab
Dominant Associated fauna gravels and coarse sands, found in abundance on the south east *M. modiolus* occurs on all sediments except the very finest coast, in places forming a solid mass of shells, attached to one another by byssus. The bed seems to be outside the strongest currents, but in an area of considerable water movement.

Cnidaria (Hydrozoa) *Plumularia* spp.
Polychaeta *Lepidonotus squamatus*
*Syllis spongicola* (in sponges)
*Nereis pelagica* (L.)
*Serpula vermicularis* L.
*Pomatoceros triqueter* (L.)
*Filograna implexa*
Crustaceana *Perrierella audouiniana* (in sponges)
*Leucóthe* (in sponges)
*Pandulus montagui*
*Galathea intermedia*
*Galathea nexa*
*Eupagurus bernhardus*
*Eupagurus pubescens*
*Ebalia tuberosa*
*Xantho couchi*
*Euryonome aspera*
*Pisa gibbsi*
*Hyas corarctatus*
*Macropodia longirostris*
*Balanus porcatus*
*Balanus hameri*
Mollusca *Buccinum undatum* L.
*Calliostoma zyziphinum*
*Cappulus ungaricus*
*Pinnotheres pisum* (in *M. modiolus* mantle cavity)
*Chlamys opercularis* (L.)
*Chlamys varia* (L.)
*Chlamys distorta*
*Glycimeris glycimeris*
*Monia squama*
Echinodermata *Ophiothrix fragilis* (Abildgaard)
*Ophiopholis aculeata* (L.)
*Ophiocomina nigra* (Abildgaard)
*Asterias rubens* L.
*Crassoaster papposus*
*Henricia sanguinolenta*
*Psammechinus miliaris*
*Echinus esculentus*
*Spatangus purpureus*
Chordata (Tunicata) various particularily *Ascidia mentula*

Thorson 1957 Kattegat 25 m, Unknown
Species list from Fig. 1 (p. 462). Hardground fauna.
Cnidaria (Hydrozoa) *Tubularia* sp.
*Abetinarai*
(Anthozoa) *Alcyonium digitatum*
Polychaeta *Pomatoceros triqueter* (L.)
Mollusca *Calliostoma zyziphinum*
Echinodermata *Ophiothrix fragilis* (Abildgaard)
*Ophiopholis aculeata* (L.)
*Psolus* (Holothurian)
Chordata (Tunicata) *Botryllus*

| | |
|---|---|
| Crustaceana | *Eupagurus pubescens* |
| | *Scalpellum* |

Peer *et al.* 1980 Bay of Funday (74) 112m. Grab

| | |
|---|---|
| Mollusca | *Dentalium entale* |
| Polychaeta | *Nepthys ciliata* |
| | *Eunice pennata* |
| | *Mellinnia cristata* |
| | *Amphitrite* sp. |
| | *Ampelisca aequicornis* |
| | *Haploops fundiensis* |
| | *Unicola irrorata* |
| | *Unicola leucopis* |
| | *Leptocheirus pinguis* |
| Brachiopoda | *Terebratulina septentrionalis* (Couthouy) |

Peer *et al.* 1980 Bay of Funday (74) 46 & 64 m. Grab

| | |
|---|---|
| Mollusca | *Dentalium entale* |
| | *Isochiton alba* |
| Polychaeta | *Pomatilla neglecta* |
| | *Unicola irrorata* |
| | *Unicola leucopis* |
| | *Maera danae* |

Brown 1979 Sound of Jura 5–150 m. Various

Either living epifaunally, or semi-infaunal, bysally attached to gravel components in mud/silt areas.

| | |
|---|---|
| Cnidaria (Anthozoa) | *Alcyonium digitatum* |
| Crustaceana | *Pagurus* sp. |
| | *Macropipus* sp. |
| | *Balanus* sp. |
| Mollusca | *Buccinum undatum* |
| | *Chlamys opercularis* (L.) |
| | *Chlamys varia* (L.) |
| | *Hiatella arctica* |
| Echinodermata | *Ophiothrix fragilis* (Abildgaard) |
| | *Ophiopholis aculeata* (L.) |
| | *Ophiocomina nigra* (Abildgaard) |
| | *Asterias rubens* L. |
| | *Crassoaster papposus* |

Brun 1969 South Isle of Man sub-littoral Dredge Species associated with *O. fragilis* include *M. modiolus* and the following :-

| | |
|---|---|
| Mollusca | *Glycimeris glycimeris* |
| | *Venus casina* |
| | *Venus rhomboides* |
| Echinodermata | *Ophiopholis aculeata* (L.) |
| | *Ophiocomina nigra* (Abildgaard) |
| | *Asterias rubens* L. |
| | *Luidia ciliaris* |
| | *Leptasterias mulleri* |
| | *Crassostaster papposus* |
| | *Henricia oculata* (not *H.sanguinolenta*) |
| | *Psammechinus miliaris* |

*Echinus esculentus*
Chordata (Tunicata) various particularily *Ascidia mentula*

Comely (unpublished) Firth of Lorn 160 Grab sample
Mollusca *Abra alba*
*Modiolus phaseolina*
*Nucula nucleus*
*Thyasira flexuosa*
Echinodermata *Ophiothrix fragilis*
*Ophiocomina nigra*
*Amphiura chiajei*
*Thyone* sp.
Polychaeta *Nepthys incista*

Comely (unpublished) Firth of Lorn 30 Grab sample

Mollusca *Abra alba*
*Astarte sulcata*
*Nucula nucleus*
*Modiolus phaseolina*
Echinodermata *Ophiothrix fragilis*
Polychaeta *Nepthys incista*
*Lumbrinereis hibernica*

# APPENDIX III

## Composition of shallow water communities surrounding deep water Firth of Lorn Community (Comely, unpublished data)

| Site No (Comely) | 23 | 24 | 25 | 26 | 31 |
|---|---|---|---|---|---|
| % Mud | 40 | 30 | 60 | 20 | 20 |
| % Gravel | 20 | 20 | 10 | 30 | - |
| | | | Numbers (per $m^2$) | | |
| Bivalvia | | | | | |
| *Abra alba* | 10 | 20 | 203 | 27 | 190 |
| *Astarte sulcata* | 3 | | | 13 | 7 |
| *Corbula gibba* | | | | 3 | 23 |
| *Modiolus phaseolina* | | 10 | 50 | | 7 |
| *Modiolus modiolus* | | | 90 | | |
| *Nuculana minuta* | | | 7 | 3 | |
| *Nucula nucleus* | | | 17 | | |
| *Nucula sulcata* | | | | | 7 |
| *Thracia villosiuscula* | | | 7 | 7 | |
| *Thyasira flexuosa* | | | 13 | 23 | 13 |
| *Venus ovata* | | 3 | | 13 | |
| **Wet weight** | 56.83 | | 1660.32 | 8.16 | 14.33 |
| **Wet weight *M. modiolus*** | | | 476.6 | | |
| | | | Amphipoda | | |
| *Eurystheus maculata* | | 3 | 13 | 3 | |
| *Haploops tubicola* | | | 3 | | |
| *Maerella* | | | 13 | | |
| *Nototropis vedlomensis* | | | | 3 | |
| *Urothoe elegans* | | | | | 3 |
| *Ampelisca spinipes* | | | | | 3 |
| | | | Echinodermata | | |
| *Amphiura chiajei* | | | 20 | 3 | 37 |
| *Amphiura filiformis* | | | | | 20 |
| *Ophiura albida* | | | | 10 | 3 |
| *Ophiothrix fragilis* | 17 | 27 | 120 | | 10 |
| *Ophiocomina nigra* | | | 7 | | |
| *Echinocyamus pusillus* | | | 7 | 3 | |
| *Cucumaria spp.* | | | | 7 | |
| *Thyone sp.* | 3 | | 10 | 7 | |
| *Thyonidium pellucidum* | | | 17 | | |
| *Labidoplax buski* | 3 | | 177 | 30 | 40 |
| *Leptosynapta inhaerens* | | | | | 17 |
| Wet weigth | 23.0 | | 150.82 | 12.83 | 16.0 |
| Total Wet Weight | 82.5 | | 1964.8 | 38.3 | 88.7 |

# PLATES

Explanation of Plate 1

a) Two small fixed and stained post-larvae on dried surface of *M. modiolus*, from a sample collected 23/08/83, animals estimated to be approximately 8 months old (x 50)

b) Examples of destructive bioerosion of *Astarte* valves by *Cliona celata*, note the chambering effect within the robust valves of *Astarte* (x 25).

c) Characteristic micro-faceted surface produced by the boring sponge *Cliona*, internal view of chamber within *Astarte* valve (x 100).

d) External view of heavily bored and bioeroded *Astarte* fragment, with fibre from the secondary layer from *Terebratulina*, compare with fibre from sediment smear, Plate 3e. (x 2 000).

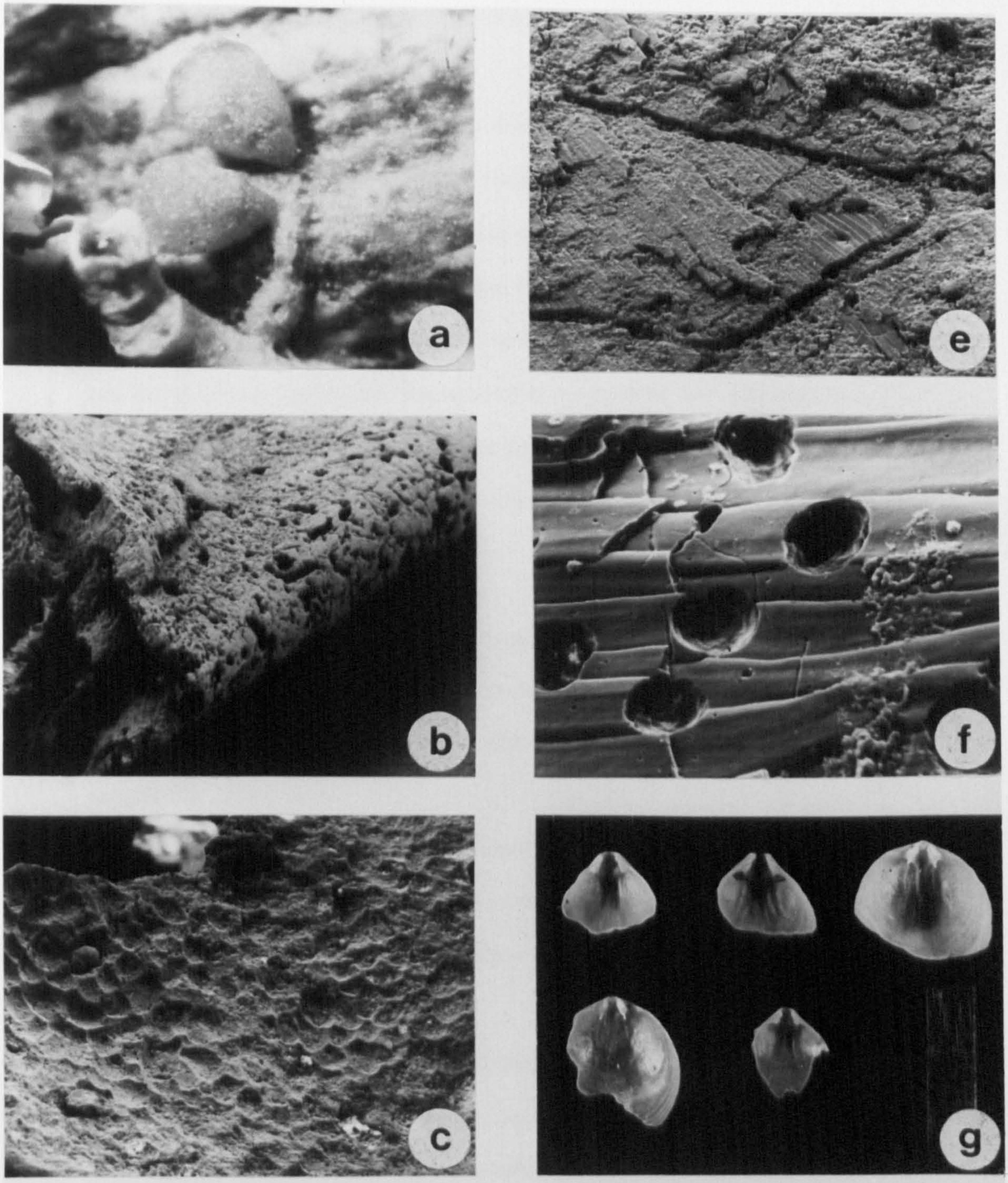
e) Eroded fragemnt of *Terebratulina* valve from within the sediment, although the fragment is heavily bored, there is no evidence of dissolution features (cf. Plate 3h) (x 200).

f) Close up of unusual boring feature, which in a casual survey appeared restricted to *Terebratulina* (x 2 000).

g) Pedicle (1,2,5 ) and brachial (3,4 ) fragments of *Macandrevia cranium* recovered from box core, note the similarity of the pedicle fragments with those of *Gryphus vitreus*, (Plate 1h.).

h) Destructive sequence of *Gryphus* valves, from intact pedicle valve (upper left) to heavily bio-eroded pedicle fragment (lower right).

(Scale bar in g & h = 20 mm.)


a
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b
f
c
g
d
h

Explanation of Plate 2

a) Pedicle and brachial fragments of *T. retusa* recovered from the death assemblage in the Firth of Lorn.

b) Pedicle and brachial fragments of *T. retusa* recovered from the pulsed input experiments, although some of the fragments are similar to those in Plate 2a others are broken across the valve and are more like patterns in Plate 2c.

c) Pedicle and brachial fragments collected from a tank in which live *T. retusa* were placed with a large (carapace width, 96mm) *Carcinus maenus*. Not only are many of the fragments characterized by medinal (as opposed to longtitudinal fractures) but some are also punctured.

d) Polychaete tubes constructed within the conjoined valves of *Terebratulina* and *Gryphus*.

e) Comparative bio-erosion of pedicle (upper row) and respective brachial (lower row) valves of *Gryphus*. Note how the preferred orientation, lying on the pedicel valve, restricts the distribution of epifauna, and apparently bioerosion.

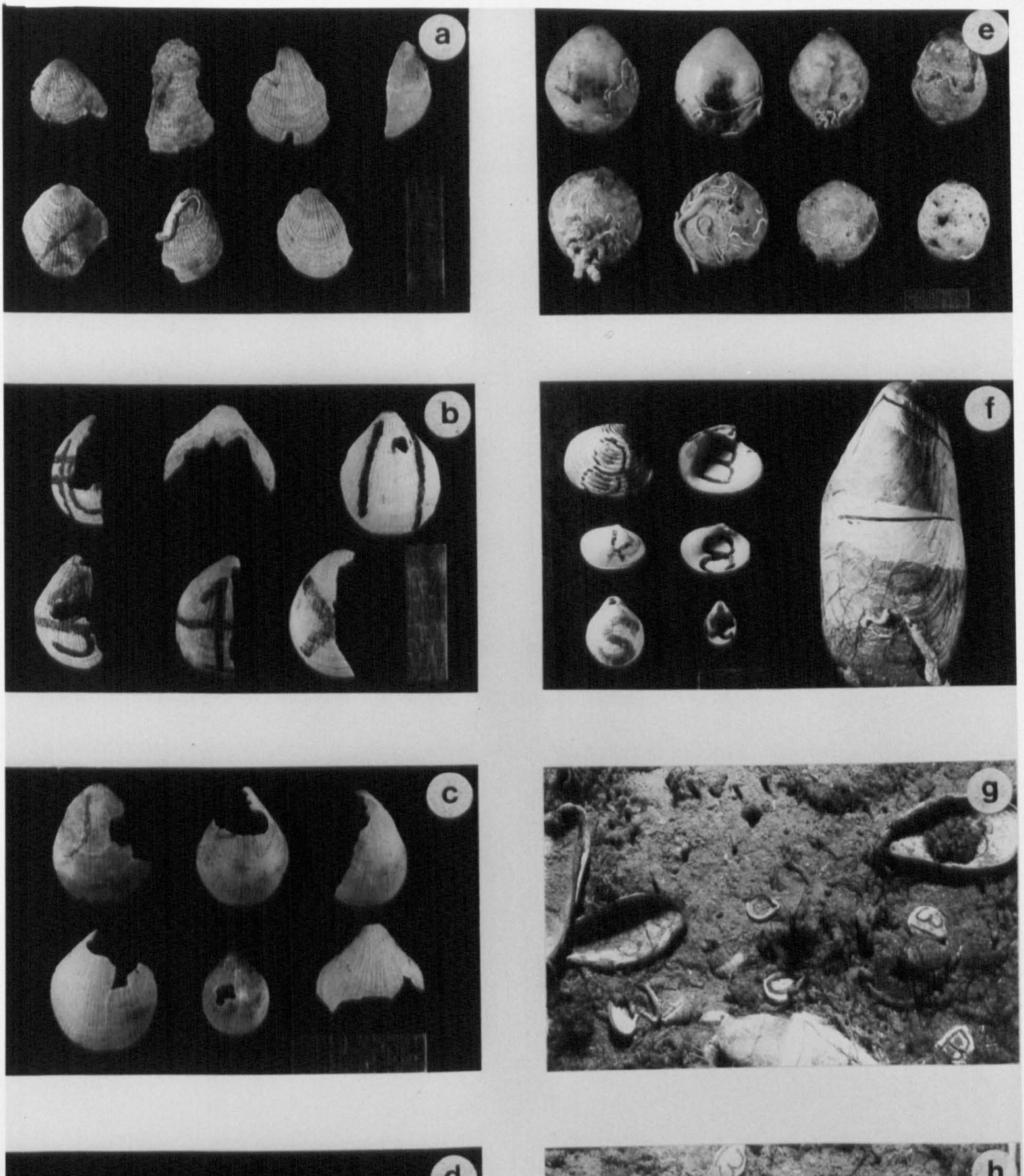
f) Carbonates used in transport experiments, or right hand side, valve of *M. modiolus*, on left hand side from top to bottom articulated and disarticulated valves of *Astarte sulcata*, *Abra alba* and *Terebratulina retusa*.

g) Stills from photographic mosaic 11/3/84, 22 days after the initiation of the experiment, most valve are lying in the hydrodynamically unstable, concave-up position, and are beginning to be infilled with sediment. The relief shadowed tubes of *Lanice concholega* can be seen in the upper part of the picture and a pagurid crab crosses the frame below *T. retusa* valve number 31.

h) Still from the photographic mosaic 11/3/84. Articulate valves of *M. modiolus* and *Astarte sulcata* project well above the sediment surface. On the left hand side of the photograph part of the frame can be seen. The valves of *A sulcata* and *M. modiolus* butterfly open upon death, unlike the valves of

*T. retusa.*

(Scale bar in a – f = 20 mm)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Explanation of Plate 3

Scanning electron micrographs of *T. retusa* shells.

a) Artificially induced fracture in a recently killed valve (x 200).

b) Artificially fractured valve from sediment (x 100)

c) Internal mosaic of a fresh shell, representing the depositional faces of the secondary layer fibres (x 500).

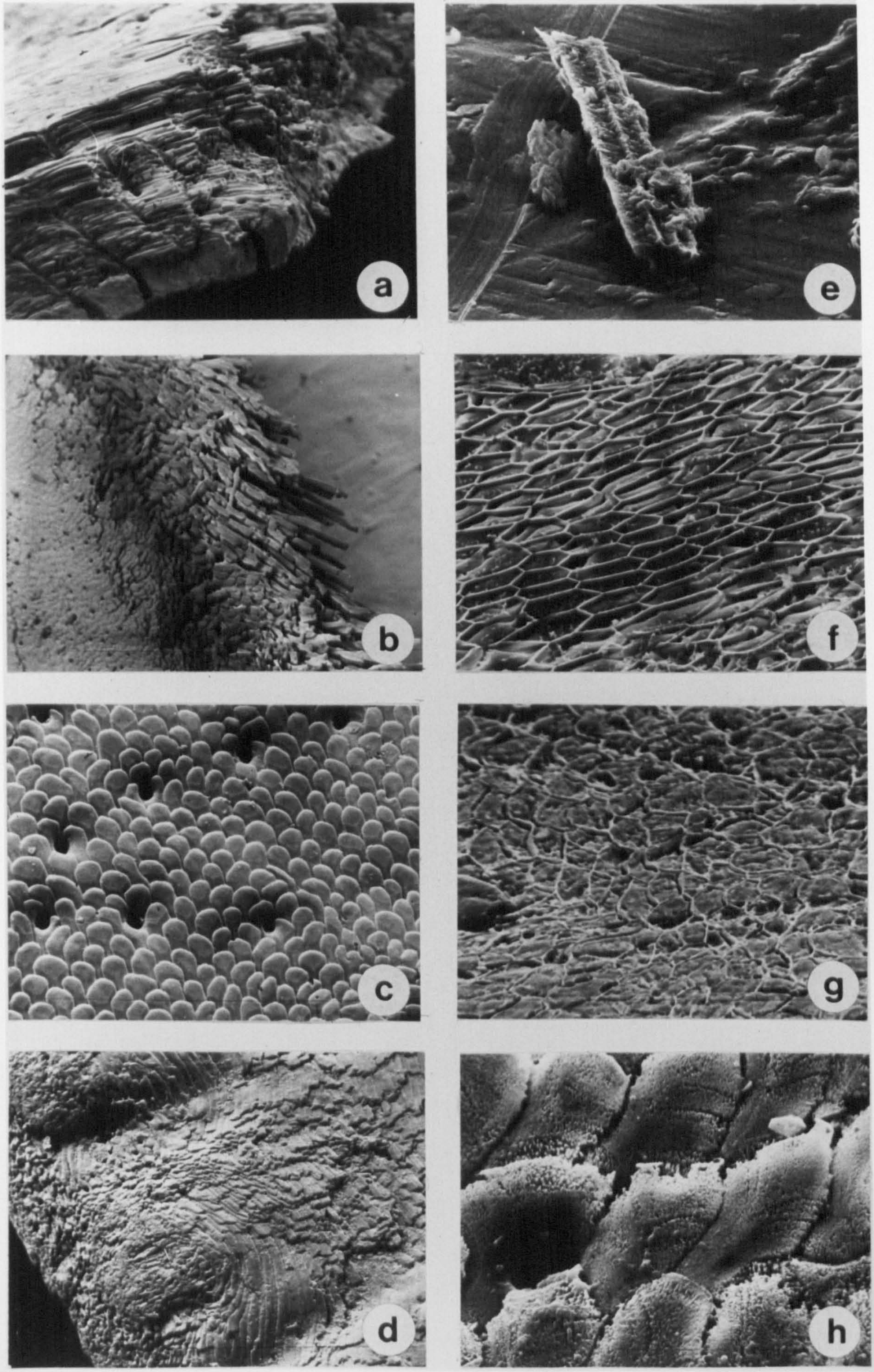
d) Internal view of anterior margin of an aged shell showing breakdown of the mosaic (x 200).

e) Secondary layer fibre from brachiopod, in sediment smear, Firth of Lorn, 200 m (x 2,000).

f) Transverse section of embedded and etched shell, from a living animal showing the organic matrix as a series of low ridges separating the secondary layer calcite fibres (x 2,000).

g) Transverse section of embedded and etched shell which had been experimentally rotted for 137 days. No organic matrix survives (x 2,000).

h) Secondary layer fibres, showing dissolution of internal mosaic, following immersion in distilled water (x 2,000).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