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**THE BURROWING MUD SHRIMP *CALLIANASSA SUBTERRANEA* (DECAPODA)
AND BIOTURBATION IN THE NORTH SEA**

by

ASHLEY ALUN ROWDEN

A thesis submitted to The University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences
Faculty of Science

In collaboration with
The Plymouth Marine Laboratory

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**The burrowing mud shrimp *Callianassa subterranea* (Decapoda)
and bioturbation in the North Sea**

Ashley Alun Rowden

ABSTRACT

A muddy-sand site in the North Sea was studied to identify the role of the benthic macrofauna in the resuspension of sediment. The macrobenthic community contained species capable of significant bioturbation. In particular, the presence and the temporal occurrence of the brittle star *Amphiura filiformis* was correlated with seasonal geotechnical and geophysical properties of the seabed. In addition, the extensive burrowing habit of the mud shrimp, *Callianassa subterranea* (Montagu), make this species potentially the most important contributor to the degree of bioturbation experienced at the site. Mud shrimps were an abundant and stable member of the study site's macrobenthic community [mean = 11.4 indiv./0.25m²(1SD ± 2.1)]. The sexually dichotomous individuals live between 2-3 years, and reproduction and recruitment primarily occurred in the summer (though an additional late winter/early spring period was hypothesised). Resin casting of burrows constructed by *C. subterranea* in the laboratory revealed a consistent morphological pattern with particular size- and sex-specific details of dimension and design. Mud shrimps, recovered from the site, were returned to the laboratory to investigate the influence of body size and temperature upon the amount of sediment expelled. A clear relationship between these variables and the quantity of expelled sediment was identified, and a well-defined temporal pattern of expulsion activity and inactivity was demonstrated. These experimental data, together with field information on seawater temperatures and mud shrimp population dynamics from the site, allow the construction of an annual sediment turnover budget [11 kg(dry)/m²/yr] with a confidence to date unrealised. Field observations at the North Sea site show that the sediment expelled by the mud shrimp occasionally forms a multitude of unconsolidated volcano-like mounds, which significantly modify seabed surface topography. The dimensions of these surface features were measured from bottom photographs and used to determine values of boundary roughness length (Z_0) for the site (eg, September Z_0 = 0.79cm). The mud shrimps' contribution to resuspension was estimated by calculating the derived lateral sediment transport rate of 7 kg/m/month (from values of the site's near-bed current velocity, modified boundary roughness length and predicted sediment turnover rates). The links between sediment resuspension and the fluxes of trace metals, carbon and nutrients established by associated studies, demand that the bioturbatory activities of *Callianassa subterranea* must be included in any discussion of the fate of contaminants and the future modelling of associated water quality in the North Sea.

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The present study was conducted as part of an interdisciplinary project which aimed to develop an understanding of the North Sea Ecosystem. However, I should be honest and say that for me it was primarily carried out so that I might obtain a Ph.D., and thereby increase my chance of future employ in the increasingly competitive field of marine science.

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Relevant scientific seminars and conferences were regularly attended at which work was often presented; external institutions were visited for consultation purposes, and several papers prepared for publication.

Publications (or presentations of other forms of creative work):

Rowden, A.A. (1992) The life and death of the North Sea mud shrimp. *Daily Telegraph*, 30 November 1992.

Jago, C.F.; Bale, A.J.; Green, M.O.; Howarth, M.J.; Jones, S.E.; McCave, I.N.; Millward, G.E.; Morris, A.W.; Rowden, A.A. & Williams, J.J. (1993) Resuspension processes and seston dynamics. *Philosophical Transactions of the Royal Society: Physical Sciences and Engineering*, **343**, 475-491.

Rowden, A.A. & Jones, M.B. (in press) Critical evaluation of sediment turnover estimates for Callianassidae. *Journal of Experimental Marine Biology and Ecology*.

Rowden, A.A.; Jago, C.F. & Jones, S.E. (submitted) Influence of benthic macrofauna upon the geotechnical and geophysical properties of surficial sediment; North Sea. *Continental Shelf Research*.

Rowden, A.A.; Jones, M.B. & Morris, A.W. (submitted) The role of *Callianassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea. *Continental Shelf Research*.

Presentations and Conferences Attended:

North Sea Project seminars and workshops: School of Ocean Sciences, University of North Wales (1989); Dunstaffnage Marine Laboratory (1990); Proudman Oceanographic Laboratory (1991, 1992).

The Environmental Impact of Burrowing Animals and Animal Burrows Symposium: Zoological Society, London (May, 1990).

European Marine Interdisciplinary Network (EMIN) conference (1st EMINar): Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands (March, 1991).

7th Iberian Symposium of the Study of the Marine Benthos: Murcia, Spain (October 1991).

International Council for the Exploration of the Sea (ICES) Benthic Ecology Working Group meetings: Lisbon, Portugal (May, 1990); Bergen, Norway (May, 1992).

1st European Crustacean Conference, Paris, France (August, 1992).

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Signed.....*AA Rarden*.....

Date.....*11.11.93*.....

CHAPTER 1
GENERAL INTRODUCTION

The important role of organisms in altering the physical properties of the substratum in which they reside has long been identified (Darwin 1881). Dapples (1942) first identified these influences in the marine environment, where he found that "Macro-organisms which may directly affect marine sediments after their deposition are limited to benthonic forms which burrow for shelter or in search of food, and those which ingest sediments for the contained organic material". Since Dapples (1942), the influences of benthic fauna upon the geotechnical and geophysical characteristics of substrata (often termed bioturbation), and the subsequent importance of such changes, have been well reviewed (Rhoads, 1974; Richards & Parks, 1976; Lee & Swartz, 1980; Rhoads & Boyer, 1982). Laboratory and field studies have documented the importance of physical alterations in sediment shear strength, sediment water and organic content, plus changes in particle size in reducing the critical erosional velocities of seabed sediments so that they may be resuspended by low velocity currents (Postma, 1967; Gularte *et al.*, 1980). The specific relationships between the bioturbatory activity of the infauna and such physically-induced sediment erodibility have also been identified (Young & Southard, 1978; Nowell *et al.*, 1981; Grant *et al.*, 1982).

Most major phyla have representatives capable of processing and transporting large quantities of sediment (sediment reworking or turnover) via activities such as feeding and burrowing (Cadée, 1976). It is clear that the macrobenthic fauna, particularly those deposit-feeding species present in high abundance intensively reworking the upper few centimetres of the sea bottom, create the potential for sediment erosion (Rhoads & Young, 1970; Young, 1971; Myers, 1977; Yingst & Rhoads, 1978; Anderson, 1983). In the North Sea, one of the most commonly abundant benthic species is the brittle star *Amphiura filiformis* which resides in near-surface sediment in average densities ranging from 250 to 3900 individuals/m² (Duineveld *et al.*, 1987). *Amphiura filiformis* is only absent in the mobile sand of the extreme southern extent of the North Sea (Künitzer *et al.*, 1992) and elsewhere its influence upon sediment structure is presumed to be marked (Ockelmann & Muus, 1978). In addition to relatively small, high density macrobenthic infauna, certain larger species are capable of exerting significant influence upon bed properties even in moderate abundance. In particular, thalassinid crustaceans appear to be dominant sediment reworkers wherever they exist (Lee & Swartz, 1980). In the North

Sea, the mud shrimp *Callinassa subterranea* (Montagu, 1808) is one of seven thalassinid species present (Howson, 1987). The relative occurrence of *C. subterranea* was for some time poorly described, because the early use of shallow-penetrating grabs often failed to capture this deep-burrowing species. With the advent of deep-penetrating grabs and box corers, the mud shrimp was found to be the most common thalassinid member of the macrobenthic communities in the southern North Sea (ranging between 2-60 individuals/m², Künitzer *et al.*, 1992). The potential significance of bioturbation by *C. subterranea* in the North Sea has recently been identified, although a detailed appreciation of its influence upon sediment structure, turnover and possible resuspension is currently lacking (Witbaard & Duineveld, 1989). Importantly, such mobilisation and dispersal of suspended particulate matter is crucial in several chemical and biological processes that determine water quality in shelf seas (Burton *et al.*, 1993; Tett *et al.*, 1993). Thus, currently there is a pressing need to quantify the specific importance of *C. subterranea*'s contribution to the biological modification of bed properties, sediment resuspension and subsequent influence upon biogeochemical cycling in the North Sea.

The North Sea is of great socio-economic importance to the United Kingdom, and other European maritime nations, as it provides oil, gas, fish and recreational amenity, and receives natural and anthropogenic wastes. To maintain the "environmental health" of the North Sea these diverse, and potentially conflicting interests, demand careful management based on a fundamental appreciation of the physical, chemical, biological and sedimentological processes operating within the ecosystem. Following a review meeting on shelf-sea oceanography in 1985, the Natural Environment Research Council (NERC) of the United Kingdom evolved an initiative called the "North Sea Project". Subsequently, various working groups and workshops refined this initiative as a NERC Marine Science Directorate Community Research Project to run from 1987 to 1992. The North Sea Project became an interdisciplinary programme involving the joint efforts of NERC research laboratories (including The Plymouth Marine Laboratory), universities (including The University of Plymouth) and other institutions of higher education with support from NERC and government departments, especially the Department of the Environment (DoE) and the Ministry of Agriculture, Food and Fisheries (MAFF). The main aim of the North Sea Project was to produce a water quality model (as a

management tool) which would be used to isolate causal contributions, whether natural or otherwise, to observed trends and to assess the impact of specific problems (eg, contaminants) for the North Sea ecosystem (NERC, 1987). To achieve this aim, a transport model of conservative properties (eg, salinity) was to be constructed; this integrated three-dimensional numerical simulation would be a foundation for all subsequent modelling developments. Development of the transport model required details of the rates of non-conservative processes (eg, those which are involved in determining the cycling and ultimate fate of constituents such as particulate sediment) and knowledge of the seasonal cycles for a range of environmental parameters (eg, temperature).

As a contribution to the latter requirements, a Sediment Resuspension (SERE) study was established, designed to evaluate the hydrodynamic processes controlling the quantity and seasonal variability of sediment resuspension, as the degree of resuspension depends principally upon shear stresses (momentum transfer) exerted by the physical forces of tides, winds and waves on the seabed. In addition, the SERE study aimed to: (1) assess the influence of sedimentological characteristics and geotechnical/geophysical properties of the bed on sediment resuspension; (2) examine the role of benthic and pelagic organisms in sediment resuspension and deposition processes via bioturbation and biological flocculation respectively; (3) determine the impact of sediment resuspension on water quality through its influence on trace metal, nutrient and organic contaminant exchange processes (direct exchange between pore and overlying waters or subsequent alterations in the dynamic particulate/dissolved balance of a "contaminant"); and (4), develop a detailed model interrelating vertical current structure and suspended sediment concentration at a point site which could be used as a basis for constructing the fine-grid three-dimensional sediment transport model (Morris & Howarth, 1993). To achieve these aims, observations were made at two sites in the North Sea on three principal occasions in 1989. The sites chosen had contrasting water column structure (mixed and stratified), boundary layer dynamics (steady current and wave current) and seabed properties (cohesive and non-cohesive). The multidisciplinary SERE study group deployed moorings of current meters, sediment traps and transmissometers, and a bottom-lander to measure near-bottom stresses. In addition, benthic samples were taken, and water column properties assessed by conductivity, temperature and depth (CTD) (plus oxygen

and transmittance) profiling, particle counting/sizing, pumped samples and biological, trace metal and organic analyses.

The present study was conveniently conducted within the supportive framework of the interdisciplinary North Sea Project, which had the additional advantage of providing a wider ecosystem context for the study's findings. The overall aim of the thesis study, ie, to quantify the importance of macrofaunal bioturbation in the North Sea, in particular by the activities of the mud shrimp *Callianassa subterranea*, was the key to achieving the second and third aims of the North Sea Project's SERE study (as an interrelation of the influence of sediment geotechnical/geophysical properties and benthic fauna upon sediment resuspension). The present study was conducted at only one of the two SERE study sites ("North" or "B"), henceforth termed the "North Sea study site". The first aim was to describe the macrobenthic community, to establish temporal changes in faunal occurrence and abundance, and to identify bioturbatory species likely to alter seabed properties and enhance resuspension at the North Sea study site (Chapter 2). Based on these findings, the mud shrimp *Callianassa subterranea*, was identified as potentially the most important macrobenthic organism contributing to sediment mobilisation and was selected for further detailed study. The seasonal population structure and dynamics of *C. subterranea* at the study site were examined by comparing the abundance, size and sex ratio of animals recovered by box coring on separate sampling occasions (Chapter 3). The relatively unknown morphology of the mud shrimp's burrow was investigated, elucidating size- and sex- specific details of dimension/design and the means by which unwanted sediment is expelled from the burrow (Chapter 4). The pattern of sediment expulsion activity of *C. subterranea* and the quantity/unit area (sediment turnover) of material that the population transports to the sediment surface over a year was calculated (Chapter 5). The direct fate (sediment transport) and indirect influence of the expelled material (which forms discrete volcano-like mounds on the seabed thereby altering boundary properties) was also assessed (Chapter 6). Finally, the relative importance of sediment turnover by *C. subterranea* and the species' role in the resuspension of particulate material at the sediment-water interface in the North Sea was addressed (Chapter 7).

CHAPTER 2

THE BENTHIC MACROFAUNA COMMUNITY

[Aspects of this chapter are included in Rowden *et al.* "Influence of benthic macrofauna upon the geotechnical and geophysical properties of surficial sediment; North Sea." (*Continental Shelf Research*, submitted) and Jago *et al.* (1993) "Resuspension processes and seston dynamics." (*Philosophical Transactions of the Royal Society: Physical Sciences and Engineering*, **343**, 475-491).]

2.1. Introduction

Benthic macrofauna reside within or upon marine substrata and are retained on a sieve with a mesh size of between 0.5-1.0mm (Ruhomr, 1990). Members of this group of animals vary in size and morphology, and have a variety of locomotory and feeding habits (eg, Polychaeta, Fauchald & Jumars, 1979). Movement by benthic fauna will result in the physical displacement of sediment particles, whilst manipulation and ingestion of sediment for nutrition will produce faeces and pseudofaeces which affect the geotechnical/geophysical properties of the substratum (see reviews, Rhoads, 1974; Richards & Parks, 1976; Lee & Swartz, 1980; Rhoads & Boyer, 1982). The construction of tubes or burrows by infauna for habitation can both stabilize (binding by mucus or close association) and destabilize sediment (current scour/turbulence induced by isolated roughness elements) (Anderson, 1983; Meadows & Tait, 1989). At any place or time, combinations of these processes (termed bioturbation) will be experienced by the seabed, the proportions and relative importance of each depending on the composition of the fauna present and the sedimentary environment.

The seemingly unconnected multitude of species found in association with a particular seabed form a macrobenthic community; an assemblage is usually classified according to its numerical and/or biomass dominants (Petersen, 1914, 1918). Several areas in the North Sea have been investigated for their benthic macrofauna and classified according to Petersen's (1914, 1918) scheme. Most of these surveys, however, were carried out in coastal areas of the southern North Sea, and few have been conducted in the central and northern regions (see review, Kingston & Rachor, 1982). In 1986, a benthic survey, carried out by members of the International Council for the Exploration of the Sea (ICES) Benthic Ecology Working Group, allowed the relative distribution and density of macrofaunal species in the North Sea to be accurately correlated to environmental factors using sophisticated statistical ordination analysis techniques (Künitzer *et al.*, 1992). Eight major macrobenthic communities were recognised, each structured by temperature, water mass, sediment type and food supply to the benthos, and characterised by "indicator" species (Künitzer *et al.*, 1992). In the southern North Sea, where the study site was located, three distinct benthic communities are present. Two assemblages (Ia & b) are associated mainly with the coarse sediments of the coast (<30m water depth) and

contain relatively few species in low abundance. The present study site exists within the boundaries of the third macrobenthic assemblage (IIa; high species number and abundance) found to inhabit muddy-fine sand in water depths of 30-50m and characterised by three indicator species, one of which is the mud shrimp *Callinassa subterranea* (Künitzer *et al.*, 1992). The initial aim of this study was to confirm the type of macrobenthic community present, establish temporal changes in faunal occurrence and abundance, and to identify bioturbatory species likely to alter seabed properties and enhance resuspension.

2.2. Materials and Methods

2.2.1. The study site

The study site is located in the southern North Sea (54° 35'N, 04° 50'E) in 47m of water and is characterised by a seasonally-stratified water column over a seabed composed of muddy-sand ("Site B" in Morris & Howarth, 1993). The site comprised an area of one square sea mile, enclosing a twenty-five point sampling grid from which five positions were chosen randomly for the benthic sampling; the same five stations were sampled throughout (Fig. 2.1). Samples were taken during the three main cruises with R.R.S. *Challenger* (Plate 2.1) in January, May, and September 1989 with additional, opportunistic visits being made in October 1989, April and July 1990, and August 1991 principally for studies detailed in Chapter 3.

2.2.2. Shipboard sampling

A box corer, which recovers a core of undisturbed seabed with a surface area of 0.25m² to depths of 30-40cm, was used once at each visit to each of the five stations (Fig. 2.2). Several measurements were taken from each box core, including sediment temperature (at a depth of 10cm using a digital probe) and a visual assessment of surface sediment conditions (relief and consistency, faecal matter, faunal burrows/traces, the presence of living or dead fauna). Acoustic shear-wave velocity was measured in the freshly recovered box core, using piezo-electric ceramic 'bender' transducers as both shear-wave source and receiver (see Jones & Jago, 1993 for details of measurement techniques). Four such measurements, in complementary pairs, were made in each undisturbed and

water saturated box core. The shear-wave velocity (V_s) is controlled by the number of grain contacts and the strength of intergranular contact forces in the sediment. It is therefore qualitatively related to the same factors which determine sediment shear strength and is quantitatively related to sediment rigidity modulus (μ) by:

$$\mu = ds(V_s)^2 \dots \dots \dots \text{equation (1)}$$

(where ds is the bulk density of the sediment). The "rigidity modulus", a useful measure of the sediment's compactness and potential for resuspension, can thus be determined by measurement of the bulk density and shear-wave velocity. In addition, five sub-cores (10cm diameter, 30cm length) were taken from each box core to determine macrofauna abundance; each sub-core being "puddled" with seawater before being poured through a 0.5mm sieve (only two sub-cores were taken in January). The material retained on the mesh was washed gently with seawater to remove excess sediment and the residue was stored in pots containing 10% buffered formaldehyde. A further core (6.5cm diameter, 25cm length) was taken from the box core for laboratory analysis of sediment water content, organic matter content and particle size analysis [this was immediately frozen (-20°C) aboard the ship]. The remainder of the box core was examined first for signs of vertical distributions of fauna and sediment structure before being washed and sieved through a 1mm mesh, and the remaining residue stored in pots containing 10% buffered formaldehyde.

2.2.3. Laboratory sample treatment

Samples were transported by road to The Plymouth Marine Laboratory (frozen samples were stored in a box containing dry ice) and analysed as follows.

Macrofauna - A solution of Rose Bengal (a protein stain which aids the identification of organic matter) was added to the pots containing the macrofauna, and the contents washed and sieved to remove most of the sediment. Material retained was transferred to a white plastic tray and covered with freshwater. Faunal remains were hand sorted, placed in petri dishes of preservative (70% ethanol) and identified (authority for species names as per Howson, 1987), counted, measured and sexed (where possible) using a

Wild stereoscopic (x10) and Zeiss compound (x25, x40) microscopes. The sub-cores (sieved on 0.5mm mesh) were used to determine the densities of the smaller and more abundant species, whilst the remainder of the box-core sample (sieved on 1.0mm mesh) was used to enumerate the larger and rarer members of the macrofauna.

Sediment - The cores taken for sediment analysis were defrosted partially, extruded and sliced into twenty, 1cm sections. Each section was divided into three approximately equal portions and the following determinations made on each: (1) water content - the sediment was first weighed (Sartorius R200D balance) to an accuracy of 4 decimal places, dried in an oven overnight (100°C) and reweighed to constant weight (water content is assumed to be the weight loss as a percentage of the original wet weight of sediment); (2) organic content - a 4-6g portion of dried sediment (100°C overnight) was ground using a mortar and pestle, weighed and transferred to a china crucible and placed in a muffle furnace for 4h at 550°C, and reweighed to constant weight to an accuracy of 4 decimal places (organic content was assessed as the weight loss on ignition as a percentage of the original dry weight of the sediment); (3) particle size - the method utilised was the dry-sieving technique described by Buchanan (1984), using a series of sieves with mesh diameters of 1.0, 0.5, 0.25, 0.125, 0.063mm (this method allows calculation of the percentage of material in each size category, the mean particle diameter, and for sediment to be graded using the Wentworth scale).

2.2.4. Statistical analysis of benthic community data

To identify temporal changes in the macrobenthic community between the three main sampling occasions, species abundance data were subjected to multivariate statistical analysis. Differences in community structure were determined using multidimensional scaling ordination (MDS) of double square root-transformed species abundance data, using the Bray-Curtis similarity measure (Warwick & Clarke, 1991). A multivariate method, rather than univariate statistical techniques, was applied to the faunal data to allow comparison of communities on the basis of the identity of the component species as well as their abundance. The significance of any observed monthly differences in macrobenthic community structure was assessed by one-way "analysis of similarities" (ANOSIM). This programme computes a statistic reflecting the average rank

dissimilarity between replicate samples within a month, subtracted from the average dissimilarity between samples from different months (Clarke & Green, 1988). Application of the "similarity percentages program" (SIMPER) described by Warwick *et al.* (1990) identified species with the greatest contribution to differences between months observed in the ordination result.

2.3. Results

2.3.1. Macrobenthic community

The brittle star *Amphiura filiformis* was by far the most abundant species present at the site in January, May and September 1989 (mean 323/0.25m²) (Tables 2.1-2.3). Other species notable for their "indicator" presence were the cumacean *Eudorella truncatula*, the amphipods *Harpinia antennaria* and *Ampelisca tenuicornis*, the sedentary polychaete *Chaetopterus variopedatus*, and the thalassinid shrimp *Callianassa subterranea* (Künitzer *et al.*, 1992). In May and September 1989, visual observation of the box-core sample identified a number of particular sediment features which were correlated to the presence of several of the macrofauna (Plate 2.2). The near-surface sediment (approximately the top 7cm) appeared to be loosely compacted, relative to the remainder of the core, and was primarily inhabited by *A. filiformis*. Brown oxic traces (2-3mm diameter) of discrete burrows, mostly attributable to errant polychaetes (eg, *Nephtys sp.*), were most numerous in the top 10-15cm of the sediment core. Traces of larger burrows (5-10mm diameter) occurred at greater depths (20-30cm) and often contained the mud shrimp *C. subterranea*. Of the burrow holes present on the sediment surface, most were 1 or 2mm in diameter and were associated with the burrows of *A. filiformis*. Larger holes, of nearly 1cm in diameter surrounded by a funnel-shaped depression, frequently existed and were assumed to be the openings of the burrows of *C. subterranea*. Cylindrical faecal pellets (2/3mm long) which had been emitted from the tubes of the parchment worm *C. variopedatus* and the crawling traces (3/4mm wide) of the errant polychaete *Ophiodromus flexuosus* were also evident on the substratum surface. Low mounds (2/3cm height, 6/7cm diameter), produced by *C. subterranea*, were identified

occasionally on the sediment core surface. Such mounds were easily disturbed by the process of box core recovery and were possibly indiscernible at times.

A two-dimensional configuration plot of the multidimensional scaling (MDS) ordination carried out on the macrofaunal abundance data from the study site is illustrated by Figure 2.3. Such a plot is a visual representation of the dissimilarity measured by the MDS analysis between each sample (all stations, all months). Samples which are similar in macrofaunal composition will appear closer together, whilst samples which are dissimilar will be relatively further apart. Figure 2.3 clearly illustrates the "clustering" exhibited by samples from the same month. In essence, the plot suggests that the five samples taken in the same month are more similar to one another than are the samples taken from the same stations between months. A wider "cluster spread" for samples taken in January probably reflects the fact that faunal abundance was calculated from two replicate cores (rather than five) for this month. The results of the ANOSIM test (Table 2.4) show that there are indeed statistically significant differences in community structure between the three main study occasions ($P = < 0.01$). The dissimilarity in community structure is greatest between the months of January and September ($R = 0.84$), whilst the macrobenthic assemblage is the least dissimilar between September and May ($R = 0.54$). The most notable difference in the study site's macrofauna community structure, evident between January and May/September, appears to be related to changes in the abundance of *Callianassa subterranea*. However, SIMPER identified that those species most responsible (contributing to 25% of the difference) only accounted for between 2-6% of the dissimilarity observed (Table 2.5). The latter analysis indicates that the temporal changes observed in community structure at the study site result from an overall change in the balance of relative species abundances, rather than substantial differences in just a few dominants.

2.3.2. Sediment properties

In general, the vertical profiles of all measured geotechnical properties (sediment water, organic and fine fraction contents) exhibited very similar features at each station. Generally, there was an upper region of relatively high geotechnical values, and a lower region of smaller values punctuated by discrete peaks (Figs 2.4-2.6; Tables 2.6-2.8).

Differences in geotechnical profiles between May and September were relatively small. Average values of near-surface (0-5cm) water and organic contents show elevations of 24 and 11% respectively, compared with the mean values for the remaining 15cm of the core (Figs 2.4 & 2.5). This relationship (high surface, low sub-surface values) was not so obvious for the fine fraction measurements in each month (Fig. 2.6). The September near-surface fine fraction value was slightly lower (2%) than that for the deeper region, although a comparable degree of difference (12%) was observed in May. Unfortunately, the expected greater contrast between May/September and January, for all three of the geotechnical parameters, was not observable due to the loss of stored samples. Analysis of the upper 6cm of the bed shows that the geophysical properties were generally consistent in all box cores at any one time and that the most significant differences occurred between sampling periods (Table 2.9). Shear-wave velocities were very similar in May and September (26 m/s and 27 m/s, respectively) but greater in January (34 m/s); between January and May, V_s reduced by 25%. A corresponding reduction in bulk density (of 3.5%) from January to May is equivalent to a 45% reduction in bed rigidity (ie, rigidity modulus, from equation 1). The geotechnical and geophysical results indicate that the near-surface sediment at the study site in May and September has an "open" fabric, which becomes significantly more compact in January.

2.3.3. Faunal influence on bed properties

There was a highly significant ($P = <0.01$) positive correlation between the sediment water content (0-5cm) and the abundance of the burrowing brittle star *Amphiura filiformis* (Fig. 2.7). Furthermore, there was a significant ($P = <0.05$) inverse relationship between shear wave velocity (V_s), and hence bed rigidity, and *A. filiformis* abundance in the box cores from the three main sampling occasions (Fig. 2.8). Most the variability in bed rigidity was temporal and the greatest change occurred between January and May/September with corresponding changes in *A. filiformis* abundance (Table 2.9). The seabed was most rigid in January when *A. filiformis* was least abundant, and least rigid in May when *A. filiformis* was most abundant (Fig. 2.9). The implication from these correlations is that there is a biological control of the seasonal variability of bed rigidity and that *A. filiformis* is the most likely candidate. However, *Callianassa*

subterranea which produces conspicuous seabed surface features (mounds and funnels) associated with extensive burrows (which later in Chapter 4 can be shown to correlate with high geotechnical measures at depth) and plays a role in the temporal structure of the study site's macrobenthic community, is also likely to exert an influence upon seasonal changes in the geotechnical/geophysical properties of the seabed.

2.4. Discussion

The faunal composition of the study site indicates that the macrobenthic assemblage may be classified as an "*Amphiura filiformis*" community (Künitzer, 1989) or as belonging to the "muddy fine sand" (or Ila) group characterised by the presence of *Callianassa subterranea* (Künitzer *et al.*, 1992). "*Amphiura filiformis*" communities are extremely common in the North Sea, covering most of the central and northern area (Kingston & Racher, 1982). Many species of the "*Amphiura filiformis*" community have the capacity to influence the physical nature of the seabed (Schäfer, 1972). Clearly the properties of the upper few centimetres of the seabed at the study site are modulated by the presence/activities of the infauna and, in this respect, *A. filiformis* appears to dominate. *Amphiura filiformis* resides in small burrows, a few centimetres below the sediment surface, and uses its extended arms to feed on both suspended and deposited material (Ockelmann & Muus, 1978). Open burrows reduce bed rigidity and, in intertidal sediments, burrowing due to the amphipod *Corophium arenarium* produces effects of comparable magnitude to that observed at the study site (Jones & Jago, 1993). The presence of numerous *A. filiformis* burrows (also indicated by increased water content) and the production of faecal pellets (indicated by an increased percent fine fraction when sediment is analysed by dry sieving) effectively create an "open" sediment fabric. Hence, it is probable that the correlation between *A. filiformis* abundance and temporal changes to bed sediment properties is a causal relationship. Although a quantitative relationship between bed rigidity and bed erodibility was not established at the site, it can be postulated that such a reduction in rigidity probably increases potential erosion rate. Consequently, for a given bed shear stress, the bed should be more readily eroded in summer than in winter. A comparable increased potential for erosion in summer, due to bioturbation, was measured by Rhoads *et al.* (1978) at a shallow-water cohesive

sediment site. The decreased summer-time bed rigidity suggests that disruption of sediment fabric by bioturbation is greater than binding of the fabric by micro-organisms (Nowell *et al.*, 1981). *Amphiura filiformis* occurred at 70% of the stations sampled by Künitzer *et al.* (1992) during the ICES North Sea Benthos Survey, indicating that this brittle star is an important biological modifier of bed properties in the North Sea. However, despite *A. filiformis* being the only species significantly correlated with bed property measures at the present study, it is evident that the mud shrimp *Callianassa subterranea* can also modify the physical nature of the seabed (via the production of surface mounds/funnels and extensive burrows) and possibly play a major part in any observed temporal changes in seabed stability (its relative abundance was identified as a primary component of temporal changes in community structure). It is well established that callianassid shrimps can alter sediment structure via their burrowing activity (eg, Bird, 1982) and sediment expelled from their burrows forms surface mounds which are readily resuspended (Roberts *et al.*, 1981). In addition, individual mounds, on an otherwise smooth seabed, are known to cause local scour (and thus additional suspension) by deflecting fluid of relatively low momentum toward the bed (Eckman *et al.*, 1981). Present observations thus indicate that *C. subterranea* has the potential to equal (or exceed) the influence of the more abundant *A. filiformis* upon sediment mobilisation. As a result, the mud shrimp was selected for further rigorous study to determine its role in bioturbation and quantify its contribution to sediment resuspension at the North Sea study site.

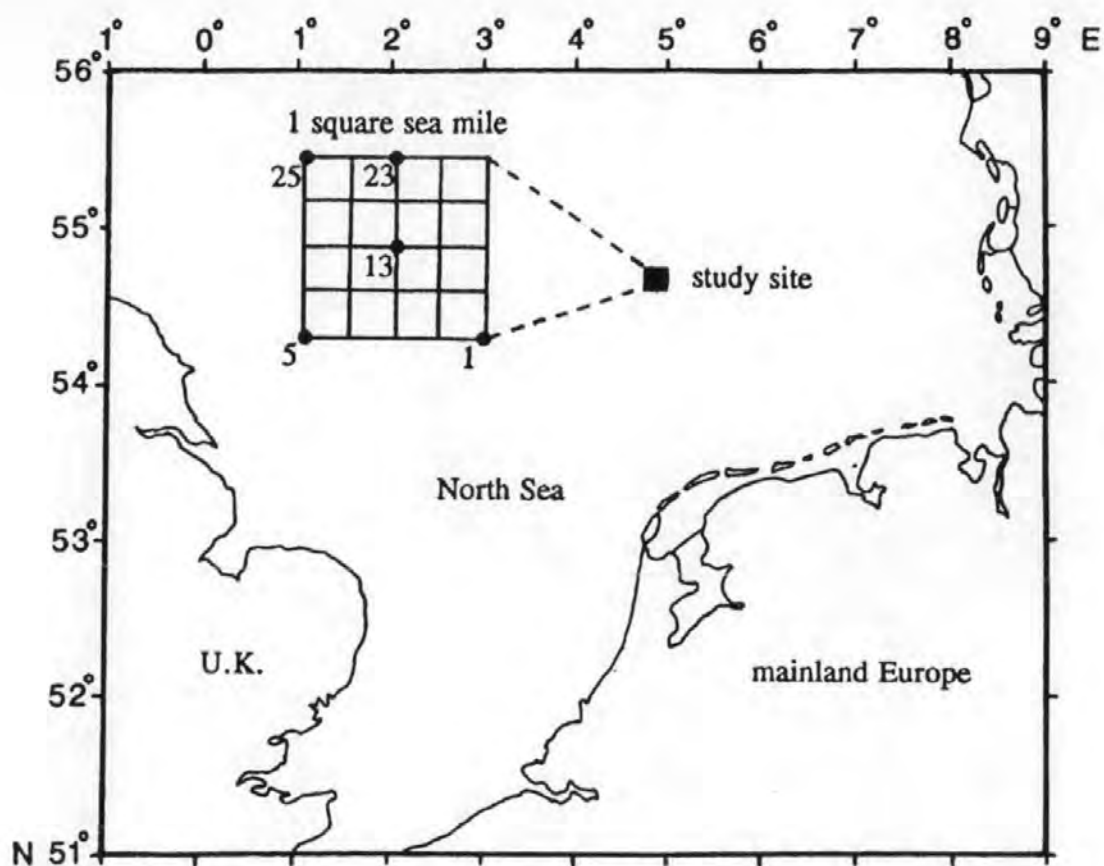


Figure 2.1. Location of study site and the five sampling stations (1, 5, 13, 23, 25) in the North Sea.

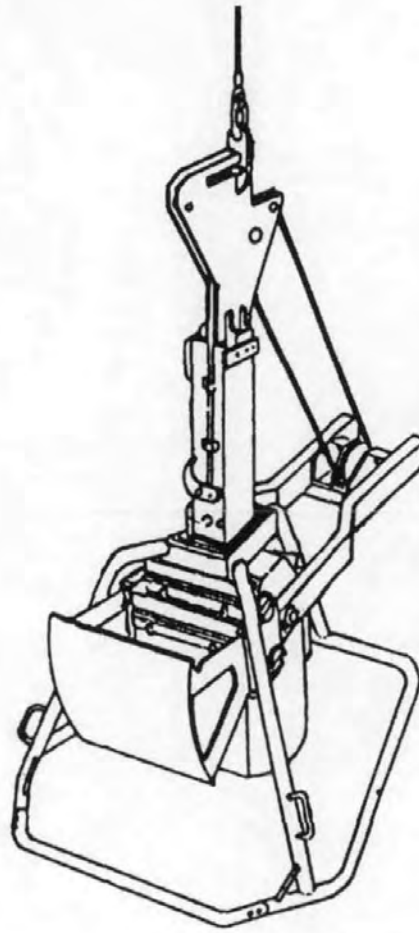


Figure 2.2. A box corer (box width = 50cm; after Gage & Tyler, 1991).

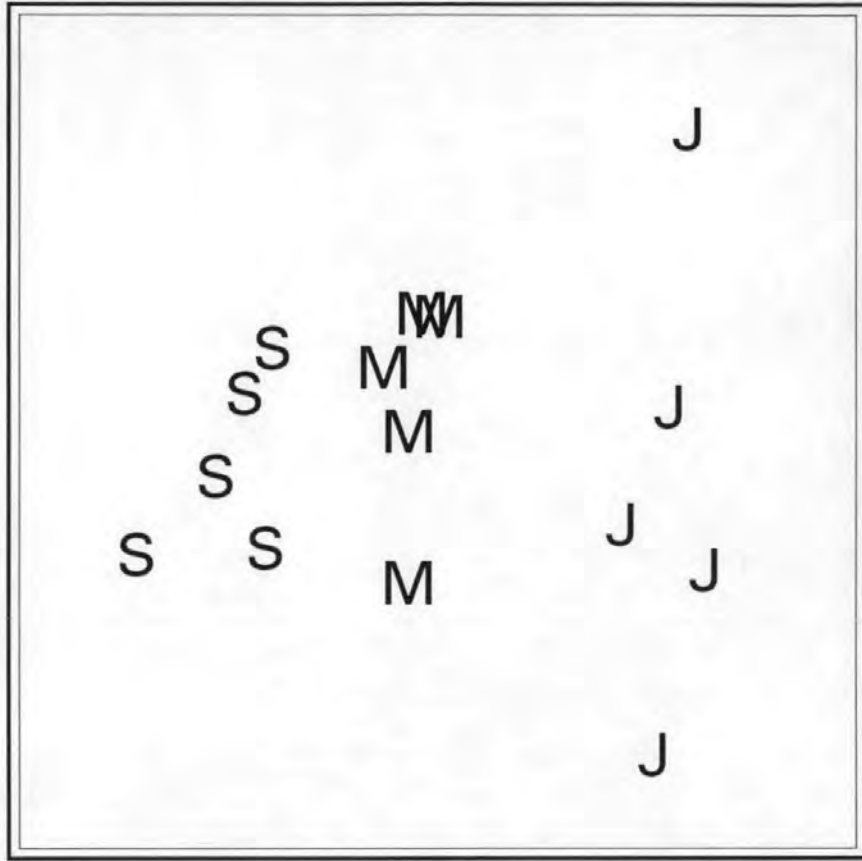


Figure 2.3. Two-dimensional plot of Multi-Dimensional Scaling (MDS) configuration for the North Sea study site macrofauna abundance (J= January, M= May, S= September 1989)(stress= 0.1; where 0.0= excellent, 0.1= good, 0.2= fair, 0.3= poor or random representation).

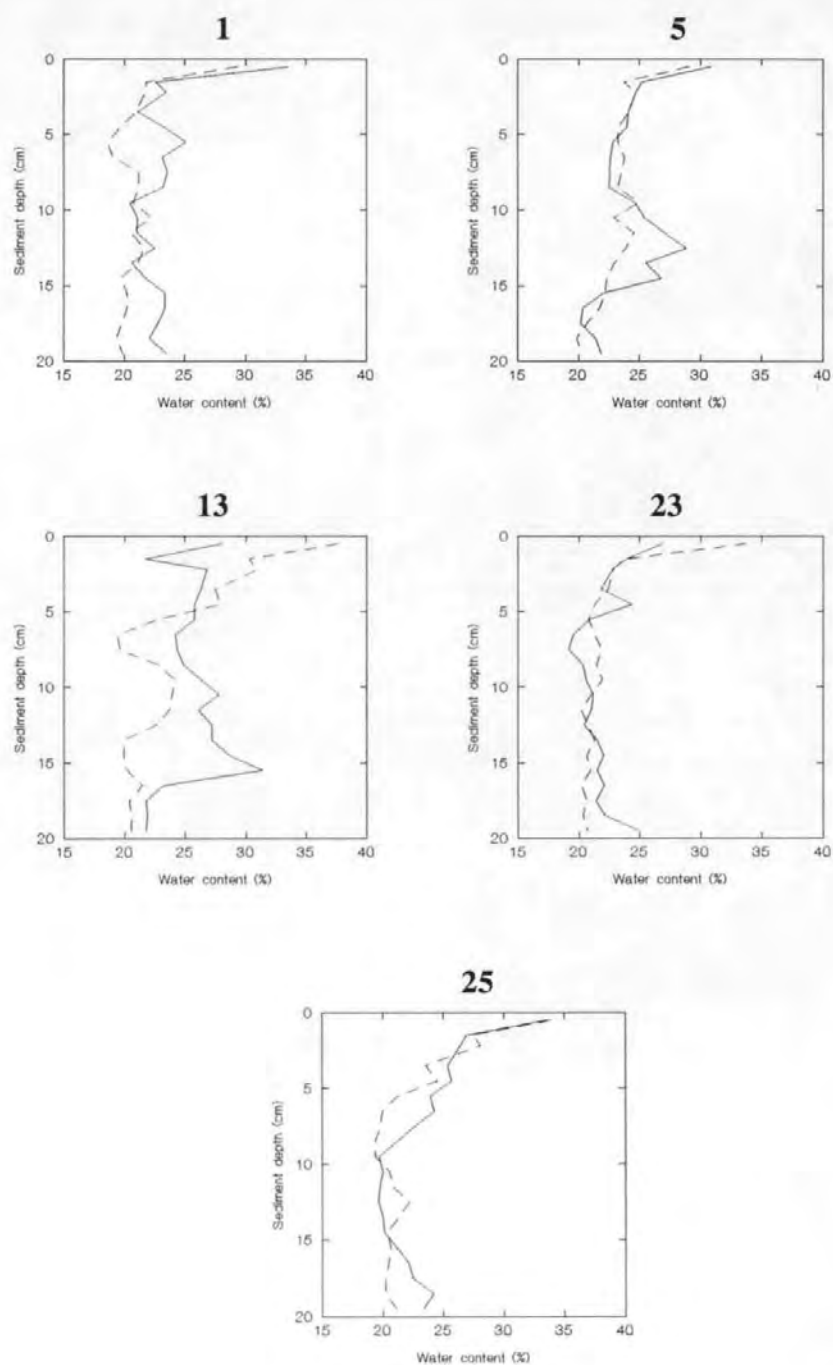


Figure 2.4. Sediment water content (% wet weight) of the sampling stations (1, 5, 13, 23, 25) at the North Sea study site in 1989 (May= solid line, September= broken line).

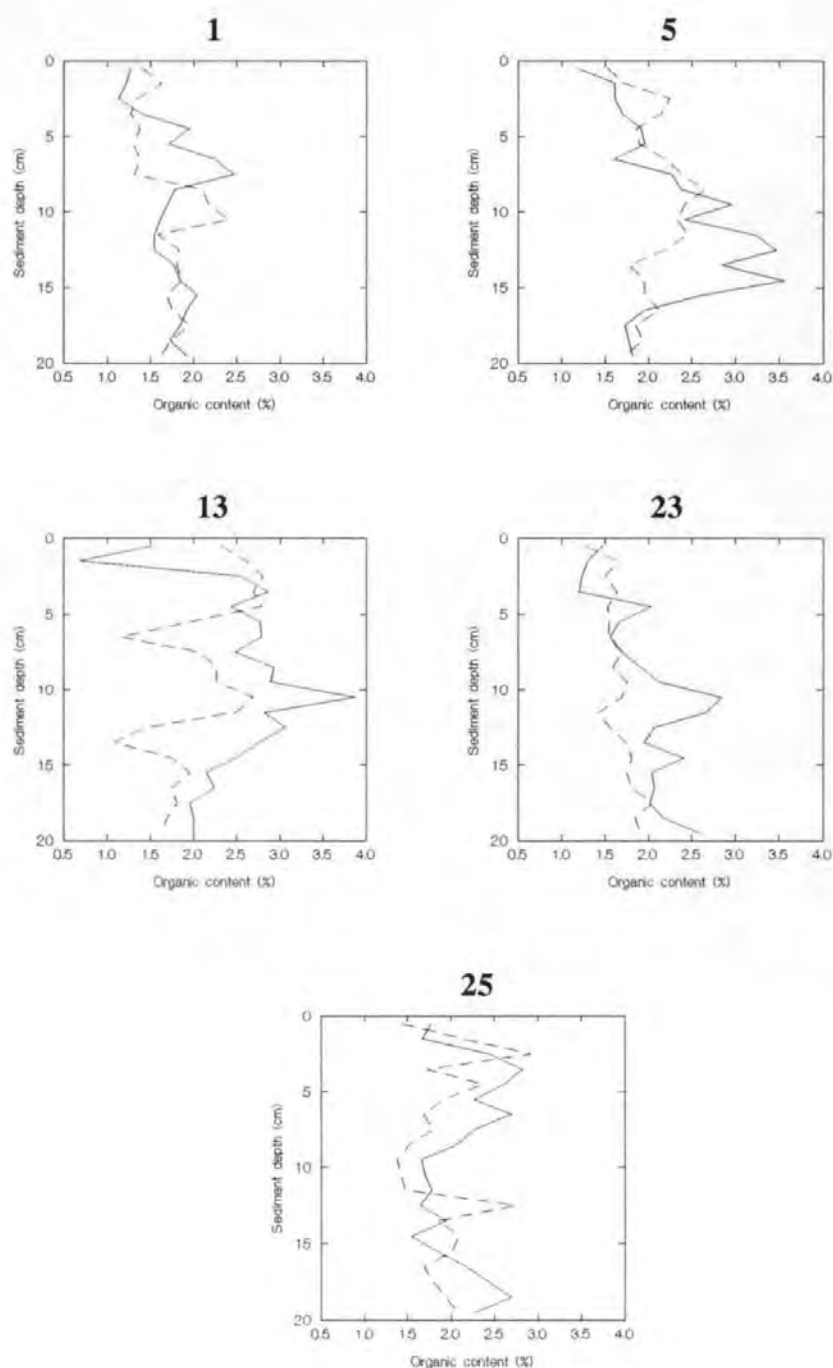


Figure 2.5. Sediment organic content (% loss on ignition) at the sampling stations (1, 5, 13, 23, 25) of the North Sea study site in 1989 (May= solid line, September= broken line).

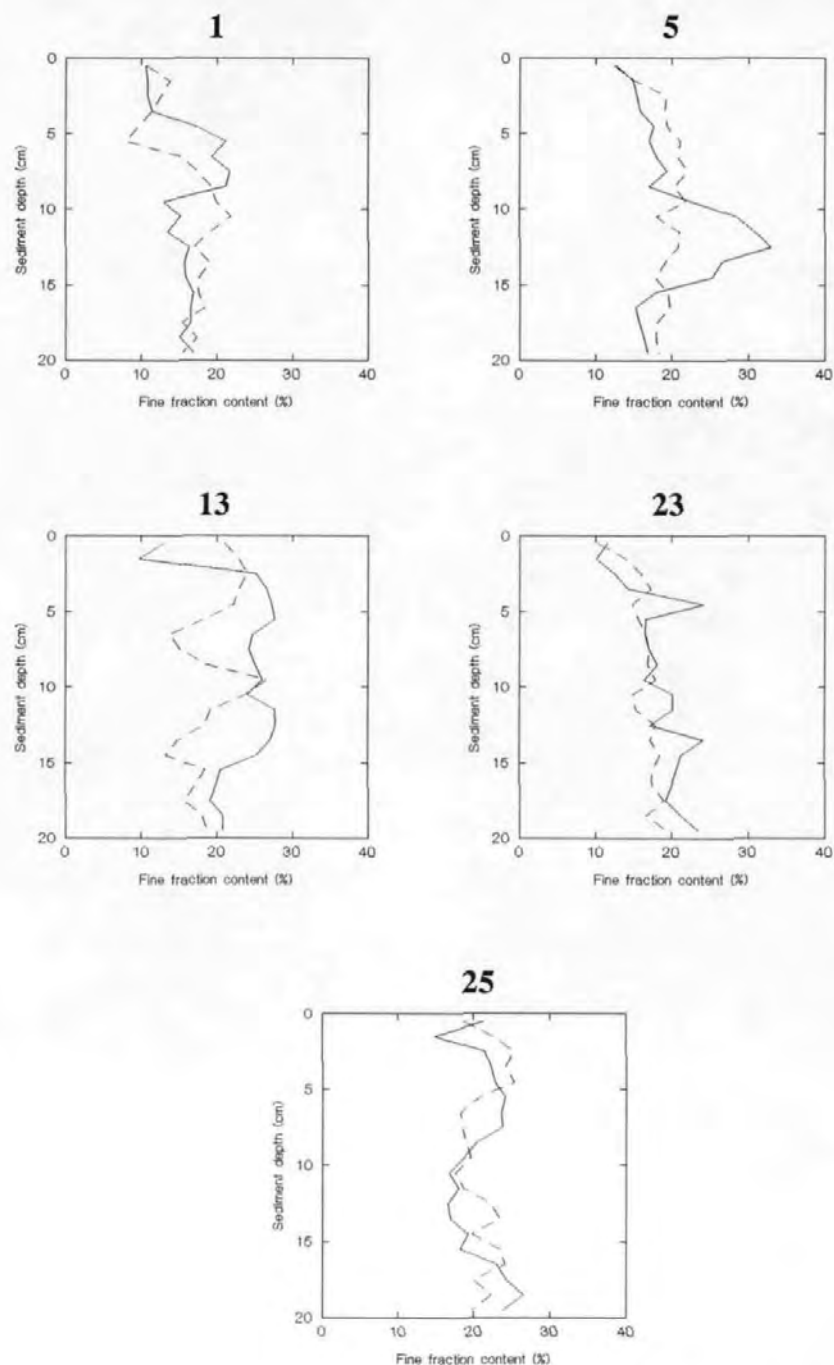


Figure 2.6. Sediment fine fraction content (% $< 63\mu\text{m}$) of sampling stations (1, 5, 13, 23, 25) at the North Sea study site in 1989 (May = solid line, September = broken line).

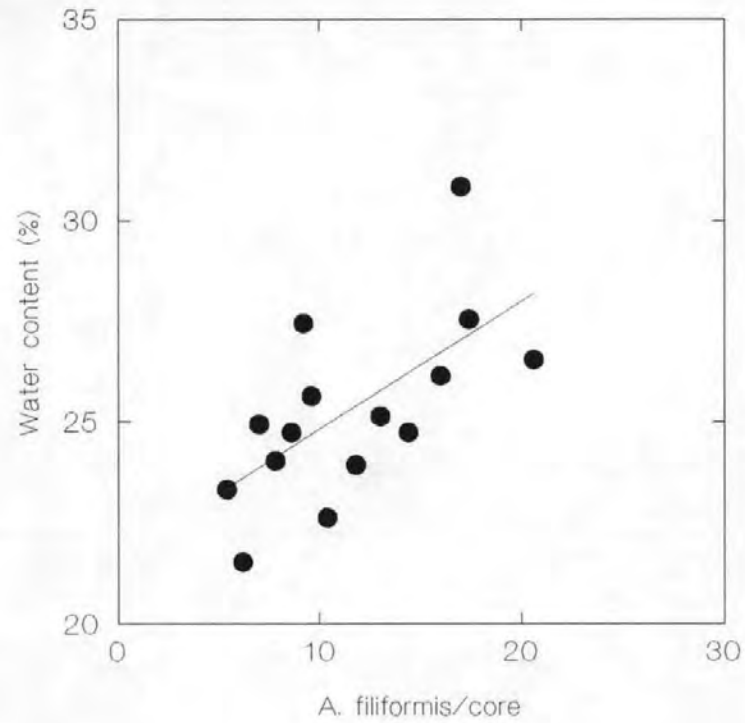


Figure 2.7. Least squares linear regression of *Amphiura filiformis* abundance (no/78.5cm² core) and the water content (% wet weight) of the upper 5cm of sediment at the study site (May, September & October 1989) ($y = 0.316x + 21.666$, $r = 0.642$, $P < 0.01$).

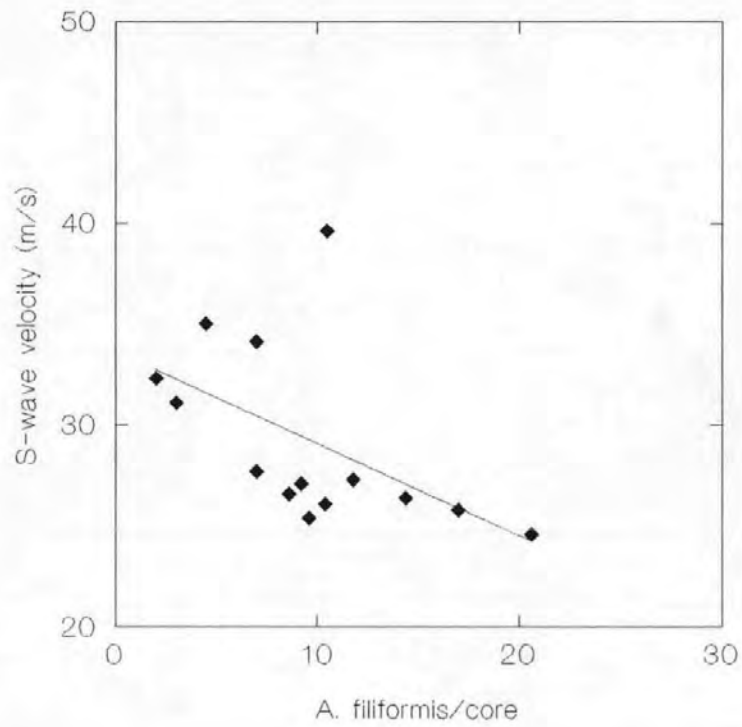


Figure 2.8. Least squares linear regression of *Amphiura filiformis* abundance (no/78.5cm² core) and surface sediment rigidity at the North Sea study site (January, May & September 1989) ($y = -0.454x + 33.621$, $r = 0.524$, $P = < 0.05$).

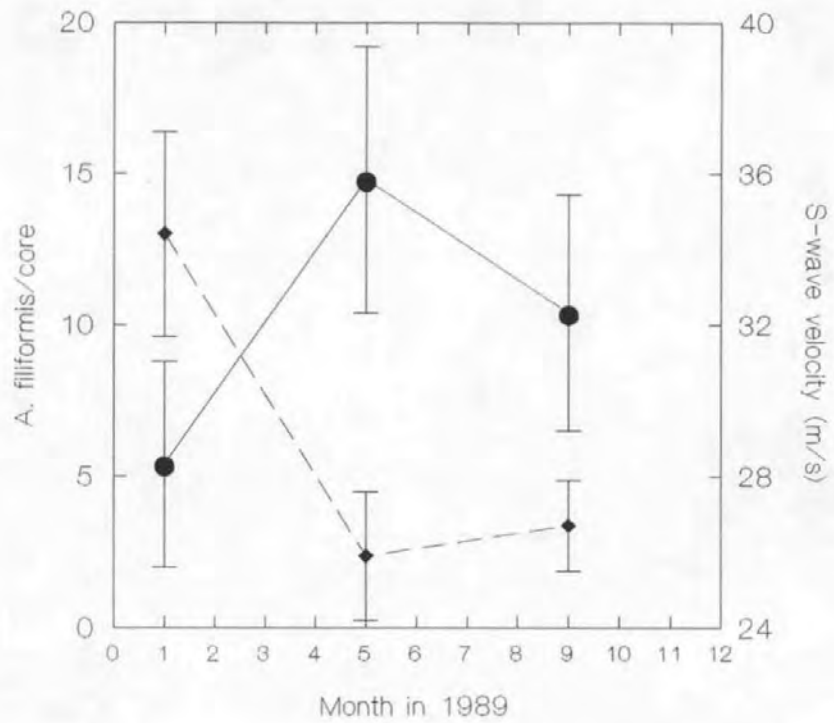


Figure 2.9. Relationship between the abundance of *Amphiura filiformis* (no/78.5cm² core) (circles) and the shear-wave velocity of surface sediment (diamonds) at the study site (January, May & September 1989) (error bars = ± 1 SD).



Plate 2.1. Photograph of Royal Research Ship *Challenger* in the North Sea.

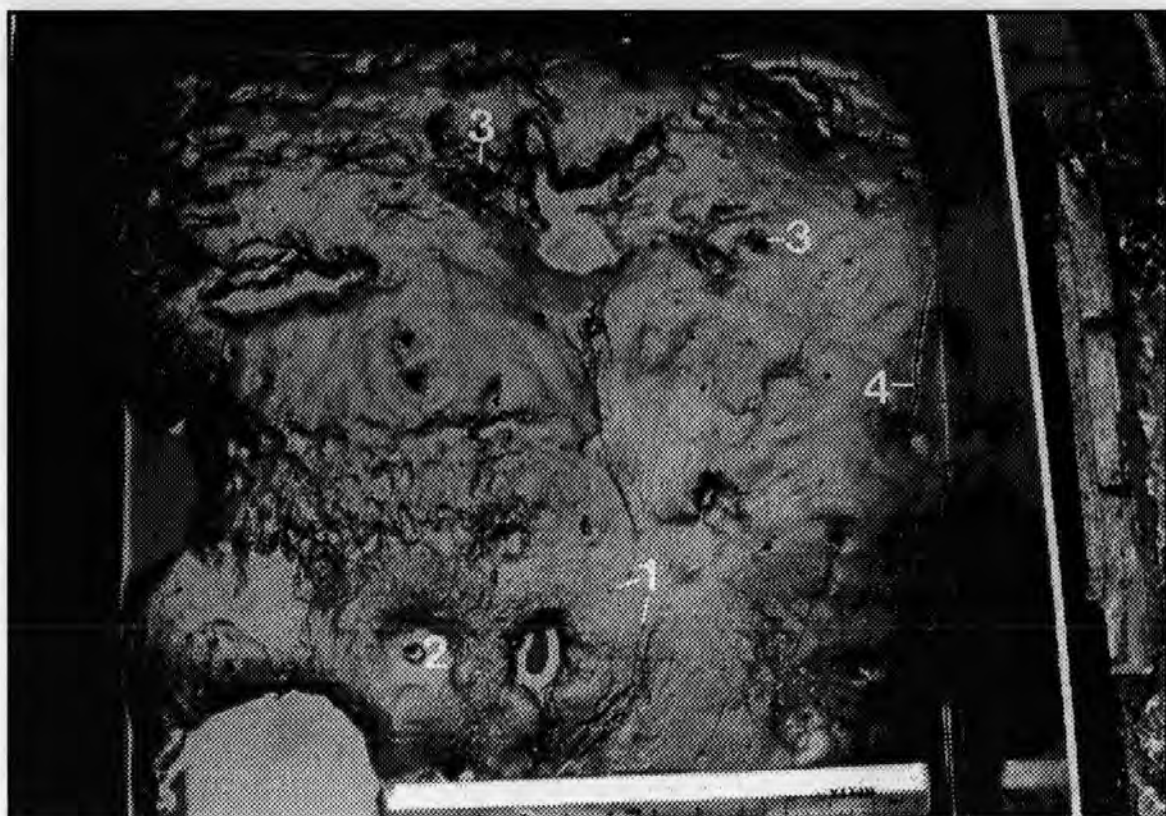


Plate 2.2. Photograph of sediment surface in a box core recovered from North Sea study site, September 1989; showing (1) the burrow holes of *Amphiura filiformis*, (2) a funnel-shaped opening to the burrow of *Callianassa subterranea*, (3) two openings to the U-shaped tube of *Chaetopterus variopedatus*, (4) and the crawling trace of *Ophiodromus flexuosus* (white rule edge = 30cm).

Species	Station Number				
	1	5	13	23	25
CNIDARIA					
<i>Edwardsia claperedii</i>	16				
Anthozoa indet.		16			
NERMERTEA					
Nermertean indet.		16			16
SIPUNCULA					
<i>Golfingia vulgaris</i>			16		
ANNELIDA					
<i>Gattyana cirrosa</i>			16		
<i>Glycera rouxi</i>		80	32	16	16
<i>Synelmis klatti</i>			16	32	
<i>Exogone hebes</i>			16	32	16
<i>Nephtys caeca</i>	32				
<i>Lumbrinereis gracilis</i>	16				48
<i>Scoloplos armiger</i>				16	
<i>Paraonis fulgens</i>	16		16	16	32
<i>Magelona alleni</i>				16	
<i>Chaetopterus variopedatus</i>		1	1	1	
<i>Cautleriella caputesocis</i>	16				
<i>Amphictene auricoma</i>					32
CRUSTACEA					
Copepoda indet.	16		16	48	32
<i>Ampelisca tenuicornis</i>	16		16	48	32
<i>Eudorella truncatula</i>	16				
<i>Upogebia stellata</i>		1			
<i>Corystes cassivelaunus</i>			1		
MOLLUSCA					
<i>Cylichna cylindracea</i>		16			16
<i>Mysella bidentata</i>	191	64	255	16	16
<i>Gouldia minimum</i>	16		16		
<i>Corbula gibba</i>			32	95	143
ECHINODERMATA					
<i>Amphiura filiformis</i>	334	223	95	143	64
<i>Ophiura albida</i>				1	
<i>Echinocardium cordatum</i>		3			
<i>Brissopsis lyrifera</i>		1			

Table 2.1. Macrofauna species composition (expressed as no/0.25m²) at the North Sea study site in January 1989.

Species	Station Number				
	1	5	13	23	25
NERMERTEA					
<i>Nermertean</i> indet.			6	19	
PLATYHELMINTHES					
<i>Turbellaria</i> indet.			1		
SIPUNCULA					
<i>Golfingia vulgaris</i>			5		1
<i>Golfingia procera</i>				1	
ANNELIDA					
<i>Gattyana cirrosa</i>		1	4		
<i>Leanira</i> juv. indet.		6			
<i>Pholoe minuta</i>	13	6	6		19
<i>Sthenelais limicola</i>			6	6	
<i>Glycera rouxi</i>		13	6		19
<i>Glycinde nordmanni</i>	6		6		6
<i>Goniada maculata</i>					13
<i>Ophiodromus flexuosus</i>		13			
<i>Synelmis klatti</i>	64	19	26	26	26
<i>Exogone hebes</i>	19	19	13	13	26
<i>Nephtys incisa</i>	6	13		6	19
<i>Lumbrinereis gracilis</i>		6			6
<i>Scoloplos armiger</i>	6	6	6	19	6
<i>Aricidea minuta</i>	38	26	26	6	32
<i>Polydora caeca</i>			32		
<i>Spiophanes bombyx</i>	6		6	6	
<i>Magelona alleni</i>	6	6			
<i>Magelona filiformis</i>		6		6	
<i>Magelona mirabilis</i>	6				
<i>Chaetopterus variopedatus</i>	1		8		3
<i>Caulleriella caputesocis</i>	19	26	6	6	19
<i>Diplocirrus glaucus</i>	6				
<i>Heteromastus filiformis</i>			6		
<i>Notomastus latericeus</i>			26		
<i>Ophelia limacina</i>				6	
<i>Ophelina acuminata</i>				6	
<i>Amphictene auricoma</i>			6		19
<i>Amphictene belgica</i>					6
<i>Ampharete baltica</i>					6
<i>Echytraeidae</i> indet.					19
CRUSTACEA					
<i>Nebalia bipes</i>			77		
Copepoda indet.	6		134	6	32
<i>Harpinia antennaria</i>	32	26	19	26	32
<i>Ampelisca tenuicornis</i>	6	6			
<i>Priambus typicus</i>			6		
<i>Ione thoracica</i>	1				
<i>Leptognathia gracilis</i>					6
<i>Eudorella emarginata</i>					6
<i>Eudorella truncatula</i>		13	13		6
<i>Euderellopsis deformis</i>		6			
<i>Diastylis laevis</i>			6		
<i>Callianassa subterranea</i>	5	7	2	2	2
<i>Corystes cassivelaunus</i>		2			

Table 2.2. Macrofauna species composition (expressed as no/0.25m²) at the North Sea study site in May 1989.

MOLLUSCA					
<i>Turritella communis</i>		1		1	
Eulimidae indet.		6			13
<i>Cylichna cylindracea</i>			6		
<i>Nuculoma (Nucula) tenuis</i>					6
<i>Mysella bidentata</i>	122	269	26	19	83
<i>Artica islandica</i>	1				
<i>Chamelea gallina</i>		1			
<i>Venus fasciata</i>			13		
<i>Gouldia minimum</i>	6				
<i>Corbula gibba</i>	26	19	38	19	45
ECHINODERMATA					
<i>Amphiura filiformis</i>	461	659	307	378	557
<i>Ophiura albida</i>					2
<i>Echinocardium cordatum</i>		1		2	1
<i>Brissopsis lyrifera</i>	1	1			

Table 2.2. (continued)

Species	Station Number				
	1	5	13	23	25
CNIDARIA					
<i>Edwardsia claperedii</i>	6				
NERMERTEA					
<i>Cerebratulus marginatus</i>					6
Nemertean indet.	6	38	26	6	13
SIPUNCULA					
<i>Golfingia elongata</i>			2		
ANNELIDA					
<i>Aphoridita aculeata</i>	1		2		
<i>Gattyana cirrosa</i>	1		1		3
<i>Pholoe minuta</i>	6		6	26	19
<i>Sthenelais limicola</i>	6	6	19		
<i>Glycera rouxi</i>			6		26
<i>Glycinde nordmanni</i>	6		6	13	
<i>Ophiodromus flexuosus</i>	13			13	6
<i>Synelmis klatti</i>	13	19	13	32	6
<i>Exogone hebes</i>	19	6	26		19
<i>Nephtys incisa</i>			6		
<i>Nephtys hombergii</i>		6	13		6
<i>Lumbrineris gracilis</i>		6			13
<i>Scoloplos armiger</i>	19				6
<i>Aricidea minuta</i>	6	6	6		6
<i>Spiophanes bombyx</i>	6	6		6	
<i>Magelona alleni</i>	6	13	6	19	
<i>Chaetopterus variopedatus</i>	1		1		4
<i>Caulleriella caputesocis</i>	6	6			6
<i>Cossura longocirrata</i>	6		6		6
<i>Diplocirrus glaucus</i>		6	6	6	
<i>Owenia fusiformis</i>			6		6
<i>Amphictene auricoma</i>	13	6	282	6	26
<i>Amphictene belgica</i>		6		6	
CRUSTACEA					
Copepoda indet.	38	6	45	32	32
<i>Periculodes longimanus</i>	13	6		38	
<i>Westwoodilla caecula</i>					6
<i>Gitanopsis inermis</i>			6		
<i>Harpinina antennaria</i>			19	13	6
<i>Ampelisca brevicornis</i>			6		6
<i>Lembos longipes</i>			13		
<i>Cirolana borealis</i>			2		1
<i>Ione thoracica</i>	1	1		1	
<i>Eudorella emarginata</i>	6		19		
<i>Diastylis bradyi</i>	6	6		6	
<i>Diastylis laevis</i>	6				
<i>Processa canaliculata</i>		6			
<i>Callianassa subterranea</i>	16	17	9	9	6
<i>Upogebia stellata</i>	1	4			1
<i>Liocarcinus pusillus</i>			6		
MOLLUSCA					
<i>Turritella communis</i>		1			
Pyramidellidae indet.	13				
Eulimidea indet.			19		

Table 2.3. Macrofauna species composition (expressed as no/0.25m²) at the North Sea study site in September 1989.

<i>Cylichna cylindracea</i>	19	6		6	
<i>Philine scabra</i>	19	6	32		6
<i>Mysella bidentata</i>	70	51	32		13
<i>Artica islandica</i>			1		
<i>Chamelea gallina</i>	1				
<i>Venus fasciata</i>	6				
<i>Gouldia minimum</i>	6				
<i>Corbula gibba</i>		6	19	6	
ECHINODERMATA					
<i>Amphiura filiformis</i>	320	224	544	288	288
<i>Ophiura albida</i>					2
<i>Echinocardium cordatum</i>	3	2	2	2	2

Table 2.3. (continued)

Sample month	<i>R</i> statistic	<i>P</i>
May - January	0.61	< 0.01
September - January	0.84	< 0.01
September - May	0.54	< 0.01

Table 2.4. Results of the one-way ANOSIM test for differences between sampling occasions on the Bray-Curtis similarity matrix using double root transformed study site abundance data.

Species	<i>a</i>	<i>a</i>	δi	$\delta i\%$	$\Sigma \delta i\%$
	May	Jan.			
<i>Callianassa subterranea</i>	1.80	0.00	3.55	5.61	5.61
<i>Harpinia antennaria</i>	0.84	0.00	2.96	4.69	10.30
<i>Aricidea minuta</i>	0.80	0.00	2.83	4.48	14.78
<i>Paraonis fulgens</i>	0.00	0.35	2.15	3.39	18.17
<i>Caulleriella caputesocis</i>	0.48	0.10	2.07	3.27	21.44
<i>Synelmis klatti</i>	1.00	0.30	2.04	3.22	24.66
	Sept.	Jan.			
<i>Callianassa subterranea</i>	3.60	0.00	4.32	6.18	6.18
<i>Ampharete</i> juv. indet.	1.96	0.00	2.48	3.54	9.72
<i>Paraonis fulgens</i>	0.00	0.50	2.22	3.18	12.90
<i>Corbula gibba</i>	0.20	1.70	2.13	3.05	15.95
<i>Pholoe minuta</i>	0.36	0.00	2.07	2.96	18.91
<i>Glycera rouxii</i>	0.20	0.90	2.00	2.87	21.78
<i>Harpinia antennaria</i>	0.28	0.00	1.92	2.75	24.53
	Sept.	May			
<i>Ampharete</i> juv. indet.	1.96	0.00	1.83	3.52	3.52
<i>Nephtys caeca</i>	0.00	0.28	1.46	2.80	6.32
<i>Philine scabra</i>	0.40	0.00	1.43	2.75	9.07
<i>Nermertean</i> indet.	0.52	0.16	1.28	2.46	11.53
<i>Mysella bidentata</i>	1.04	3.24	1.27	2.44	13.97
<i>Periculodes longimanus</i>	0.36	0.00	1.24	2.38	16.35
<i>Echinocardium cordatum</i>	0.40	0.60	1.24	2.38	18.73
<i>Corbula gibba</i>	0.20	0.92	1.22	2.34	21.07
<i>Glycera rouxii</i>	0.20	0.44	1.20	2.30	23.37

Table 2.5. Mean abundance (*a*) of the North Sea study site macrofaunal species averaged between months. Species are ranked in order of their contribution (δi) to the average Bray-Curtis dissimilarity between months, also expressed as a percentage contribution ($\delta i\%$) and a cumulative percentage ($\Sigma \delta i\%$); a cut-off to the species list is applied at 25% [calculated using "similarity percentages program" (SIMPER), of Warwick *et al.*, 1990].

Sediment depth (cm)	ST. 1	5	13	23	25	mean	SD
MAY							
0-1	33.48	30.85	27.99	26.87	33.54	30.55	3.07
1-2	22.61	25.19	21.70	23.90	26.91	24.06	2.07
2-3	23.48	24.71	26.81	22.79	26.44	24.85	1.77
3-4	21.14	24.07	26.33	21.80	25.38	23.74	2.24
4-5	23.27	23.97	25.76	24.37	25.69	24.61	1.09
5-6	25.07	22.83	25.80	20.87	23.95	23.70	1.94
6-7	23.15	22.61	24.19	19.54	24.25	22.75	1.92
7-8	23.58	22.55	24.36	19.19	22.66	22.47	1.98
8-9	23.21	22.52	24.89	20.35	21.18	22.43	1.77
9-10	20.44	24.67	26.36	20.60	19.68	22.35	2.97
10-11	21.07	25.41	27.80	21.17	20.03	23.10	3.34
11-12	21.04	27.07	26.09	21.02	19.73	22.99	3.34
12-13	22.49	28.85	27.19	20.45	19.62	23.72	4.10
13-14	20.60	25.53	27.22	21.52	20.00	22.97	3.21
14-15	21.76	26.80	28.64	22.03	20.12	23.87	3.65
15-16	23.36	22.05	31.38	21.51	21.12	23.88	4.28
16-17	23.37	20.33	23.18	22.09	22.11	22.22	1.21
17-18	22.78	20.19	21.77	21.38	22.52	21.73	1.03
18-19	22.10	21.40	21.87	22.15	24.17	22.34	1.07
19-20	23.52	21.87	21.76	24.92	23.35	23.08	1.31
SEPT.							
0-1	29.33	29.07	37.62	33.78	33.88	32.74	3.58
1-2	21.81	23.72	30.26	23.77	27.41	25.39	3.39
2-3	21.75	24.66	30.94	22.84	28.09	25.66	3.81
3-4	20.95	24.16	27.50	22.41	23.54	23.71	2.44
4-5	19.75	23.27	27.93	21.27	24.50	23.34	3.15
5-6	18.60	23.22	22.69	20.83	21.25	21.32	1.81
6-7	19.06	23.76	19.43	21.30	19.98	20.71	1.91
7-8	21.20	23.53	19.63	21.86	19.82	21.21	1.60
8-9	21.20	23.19	22.80	21.45	19.39	21.61	1.50
9-10	20.71	24.89	24.16	21.91	19.38	22.21	2.31
10-11	22.25	22.87	23.93	21.02	20.55	22.12	1.37
11-12	20.53	24.58	23.73	20.20	20.84	21.98	2.02
12-13	21.61	23.87	22.54	20.74	22.19	22.19	1.16
13-14	21.10	22.94	19.97	21.28	21.32	21.32	1.06
14-15	19.74	22.28	19.89	20.66	20.38	20.59	1.01
15-16	20.25	22.18	20.20	20.98	20.67	20.86	0.81
16-17	20.24	21.73	21.46	20.21	20.49	20.82	0.72
17-18	19.79	20.64	20.40	20.67	20.23	20.35	0.36
18-19	19.34	19.84	20.51	20.33	20.20	20.04	0.46
19-20	19.86	20.19	20.56	20.70	21.14	20.49	0.49

Table 2.6. Sediment water content (% wet weight) of the North Sea study site sample stations.

Sediment depth (cm)	ST. 1	5	13	23	25	mean	SD
MAY							
0-1	1.27	1.19	1.51	1.47	1.77	1.44	0.23
1-2	1.22	1.61	0.68	1.30	1.67	1.30	0.39
2-3	1.13	1.61	2.55	1.23	2.44	1.79	0.67
3-4	1.40	1.70	2.86	1.20	2.82	1.99	0.79
4-5	1.95	1.91	2.44	2.03	2.61	2.19	0.32
5-6	1.71	1.96	2.77	1.66	2.27	2.07	0.46
6-7	2.25	1.60	2.79	1.56	2.69	2.18	0.58
7-8	2.47	2.27	2.48	1.70	2.27	2.24	0.32
8-9	1.78	2.38	2.93	1.91	2.06	2.21	0.46
9-10	1.70	2.96	2.89	2.12	1.66	2.27	0.63
10-11	1.62	2.42	3.87	2.84	1.70	2.49	0.92
11-12	1.54	3.23	2.82	2.66	1.78	2.41	0.72
12-13	1.54	3.47	3.06	2.07	1.65	2.36	0.87
13-14	1.77	2.84	2.75	1.95	1.94	2.25	0.50
14-15	1.85	3.56	2.49	2.41	1.54	2.37	0.77
15-16	2.04	2.62	2.15	2.04	1.85	2.14	0.29
16-17	1.92	1.95	2.25	2.07	2.18	2.08	0.14
17-18	1.85	1.73	1.96	2.02	2.45	2.00	0.27
18-19	1.73	1.77	2.00	2.17	2.69	2.07	0.39
19-20	1.91	1.82	2.00	2.60	2.26	2.12	0.32
SEPT.							
0-1	1.40	1.53	2.32	1.28	1.44	1.59	0.41
1-2	1.63	1.71	2.61	1.64	2.14	1.94	0.42
2-3	1.35	2.24	2.80	1.50	2.92	2.16	0.72
3-4	1.27	2.14	2.69	1.64	1.73	1.89	0.54
4-5	1.38	1.86	2.79	1.53	2.37	1.98	0.59
5-6	1.30	1.89	1.95	1.54	1.92	1.72	0.29
6-7	1.38	2.20	1.15	1.54	1.68	1.59	0.39
7-8	1.31	2.39	2.07	1.69	1.80	1.85	0.41
8-9	2.10	2.64	2.27	1.59	1.52	2.02	0.47
9-10	2.17	2.42	2.27	1.76	1.38	2.00	0.42
10-11	2.41	2.33	2.69	1.69	1.42	2.11	0.53
11-12	1.59	2.45	2.49	1.42	1.47	1.88	0.54
12-13	1.83	2.18	1.44	1.56	2.75	1.95	0.53
13-14	1.81	1.77	1.08	1.74	1.85	1.65	0.32
14-15	1.86	1.95	1.75	1.81	2.10	1.89	0.13
15-16	1.69	1.96	1.96	1.75	2.00	1.87	0.14
16-17	1.76	2.13	1.74	1.80	1.69	1.83	0.17
17-18	1.95	1.85	1.81	2.04	1.80	1.89	0.11
18-19	1.74	1.93	1.69	1.85	1.94	1.83	0.11
19-20	1.63	1.73	1.63	1.91	2.08	1.80	0.20

Table 2.7. Sediment organic content (% loss on ignition) of the North Sea study site sample stations.

Sediment depth (cm)	ST. 1	5	13	23	25	mean	SD
MAY							
0-1	10.57	12.65	12.90	11.46	21.30	13.78	4.31
1-2	10.83	14.84	9.73	10.03	14.87	12.06	2.58
2-3	10.83	15.38	25.10	12.41	21.52	17.05	6.08
3-4	11.43	15.79	26.59	14.32	22.28	18.08	6.20
4-5	17.19	17.62	27.20	24.18	22.77	21.79	4.32
5-6	21.11	16.99	27.69	16.59	24.14	21.30	4.74
6-7	19.30	17.92	24.66	16.52	23.57	20.39	3.56
7-8	21.68	19.34	24.23	17.01	23.77	21.21	3.04
8-9	21.11	16.97	25.05	18.11	20.39	20.33	3.13
9-10	12.98	22.65	25.96	16.42	18.69	19.34	5.10
10-11	15.24	28.43	24.02	20.12	16.74	20.91	5.39
11-12	13.52	30.86	27.64	20.11	17.99	22.02	7.10
12-13	16.23	32.94	27.74	17.14	16.60	22.13	7.72
13-14	15.65	26.51	27.08	24.11	16.87	22.04	5.41
14-15	15.80	25.22	25.23	21.19	19.32	21.35	4.03
15-16	16.83	17.86	20.47	20.67	18.15	18.80	1.69
16-17	16.47	15.22	19.88	20.00	23.04	18.92	3.11
17-18	16.45	15.74	19.03	19.23	24.32	18.95	3.37
18-19	15.01	16.32	20.75	21.17	26.48	19.95	4.53
19-20	16.93	16.83	20.71	23.43	23.88	20.36	3.40
SEPT.							
0-1	10.69	12.35	20.99	10.33	18.68	14.61	4.90
1-2	13.74	15.03	22.84	13.98	22.54	17.63	4.65
2-3	12.59	19.19	23.98	15.92	25.26	19.39	5.33
3-4	11.39	19.15	22.92	17.22	24.12	18.96	5.07
4-5	9.68	19.35	22.18	14.83	25.27	18.26	6.15
5-6	7.89	21.11	18.36	15.64	20.78	16.75	5.42
6-7	15.32	20.77	13.70	16.59	18.27	16.93	2.72
7-8	17.31	22.04	15.15	16.98	18.50	18.00	2.56
8-9	19.29	20.39	18.58	16.85	19.00	18.82	1.29
9-10	19.85	21.86	26.55	17.85	19.60	21.14	3.34
10-11	21.81	18.00	23.89	14.89	17.61	19.24	3.58
11-12	19.10	21.05	19.11	15.31	18.68	18.65	2.08
12-13	16.96	20.78	18.38	17.85	22.21	19.24	2.18
13-14	19.02	19.10	14.83	17.16	23.43	18.71	3.16
14-15	17.59	17.82	13.30	18.46	19.80	17.39	2.44
15-16	17.48	19.45	18.45	17.43	23.37	19.24	2.45
16-17	18.37	19.76	17.17	17.35	24.09	19.35	2.84
17-18	15.37	17.97	15.56	18.96	19.97	17.57	2.05
18-19	17.33	17.89	18.00	16.65	22.22	18.42	2.19
19-20	15.49	18.30	18.63	19.26	19.74	18.28	1.66

Table 2.8. Sediment fine fraction content (% <63 μ m) of the North Sea study site sample stations.

ST.	January			May			September			October		
	<i>A</i>	<i>W</i>	<i>S</i>	<i>A</i>	<i>W</i>	<i>S</i>	<i>A</i>	<i>W</i>	<i>S</i>	<i>A</i>	<i>W</i>	<i>S</i>
1	10.5	--	39.6	14.4	24.8	26.4	10.4	22.7	26.1	13.0	25.2	--
	(6.4)	--	(1.8)	(5.3)	--	(1.6)	(2.3)	--	(0.6)	(4.1)	--	--
5	7.0	--	34.1	20.6	26.6	24.6	7.0	25.0	27.7	5.4	23.4	--
	(8.5)	--	(3.3)	(6.7)	--	(2.9)	(3.3)	--	(0.8)	(4.3)	--	--
13	3.0	--	31.1	9.6	25.7	25.4	17.0	30.9	25.8	6.2	21.6	--
	(2.8)	--	(3.6)	(2.9)	--	(2.0)	(6.7)	--	(2.6)	(4.6)	--	--
23	4.5	--	35.0	11.8	24.0	27.3	8.6	24.8	26.6	16.0	26.2	--
	(3.5)	--	(2.4)	(5.3)	--	(0.4)	(1.1)	--	(1.0)	(3.1)	--	--
25	2.0	--	32.3	17.4	27.6	--	9.2	27.5	27.1	7.8	24.1	--
	(0.0)	--	(2.4)	(6.9)	--	--	(4.0)	--	(1.1)	(5.4)	--	--
Av.	5.4	--	34.4	14.8	25.7	25.9	10.4	26.2	26.7	9.7	24.1	--
	(3.4)	--	(2.7)	(4.4)	(1.4)	(1.7)	(3.9)	(3.2)	(1.2)	(4.6)	(1.8)	--

Table 2.9. Mean ($\pm 1SD$) *Amphiura filiformis* densities (*A*) (no/78.5cm²), near surface sediment water content (*W*) (% wet weight) and shear-wave velocities (*S*) (m/s) at the study site stations (ST.) for sampling periods in 1989.

CHAPTER 3

THE POPULATION DYNAMICS OF *CALLIANASSA SUBTERRANEA*

3.1. Introduction

Members of the crustacean decapod family Callianassidae (Thalassinidea), often referred to as "mud" or "ghost" shrimps, are distributed widely in tropical and temperate waters (de St. Laurent & Bozic, 1972; Manning & Felder, 1991). Callianassids are a diverse group of shrimps whose phylogeny is uncertain; however, most have a fossorial habit, constructing a variety of permanent or semi-permanent burrows in estuarine and marine soft sediments (Griffis & Suchanek, 1991; see also Chapter 4).

The deposit-feeding mud shrimp *Callianassa subterranea* was described by Montagu (1808) as *Cancer Astacus subterraneus* based on material collected at depths of nearly 60cm in a sandbank adjacent to the town of Salcombe, Kingsbridge Estuary, south-west England. The species was renamed and assigned to the genus *Callianassa* by Leach (1814). Adult shrimps are approximately 5cm long, with a thin, smooth and almost membranous body integument; females are pink or orange whilst males have a dirty white or yellow appearance. In each sex the chelae are of unequal size, with the larger displaying a distinctive meral hook; the rostrum is small as are the eyes which are embedded in the ocular peduncle (Plate 3.1). *Callianassa subterranea* has a wide distribution around the coastal waters of northern Europe from the Mediterranean Sea to the coast of Norway (de Man, 1928; Christiansen & Greve, 1982). Early records for the British Isles are sparse, presumably as a consequence of its deep-burrowing habit and the earlier use of shallow-penetrating subtidal sampling gear (Marine Biological Association, 1957; Bruce *et al.*, 1963). By the latter half of this century however, deeper-penetrating bottom samplers were developed and a wider distribution for *C. subterranea* was established. Adema *et al.* (1982) reported that *C. subterranea* was abundant in certain areas of the North Sea. The International Council for the Exploration of the Sea (ICES) Benthic Survey of 1986 confirmed *C. subterranea* as a common member of the benthic communities of the southern North Sea, its spatial occurrence being restricted by water depth and sediment type (Kunitzer *et al.*, 1992).

The deep-burrowing nature of callianassid shrimps has meant that there are relatively few studies of their general population biology (Hailstone & Stephensen, 1961; Devine, 1966). Recent attention has focused on the specific factors which affect callianassid larval development (Thessalou-Legaki, 1990) and the relative distribution of juvenile and

adult shrimps (Tamaki & Ingole, 1993). Following the ICES Benthic Survey (Künitzer *et al.*, 1992), Witbaard & Duineveld (1989) reported the first details of the population structure of *C. subterranea* in the North Sea. In addition, these authors conducted laboratory studies which highlighted the important role of the species in local benthic community metabolism (carbon flow), and the flux of particles and dissolved compounds from the sediment to the overlying water (Witbaard & Duineveld, 1989).

To satisfy the aims of the North Sea Sediment Resuspension (SERE) study (Chapter 1), the bioturbatory role of *Callianassa subterranea* required rigorous quantification. Details of the population dynamics of *C. subterranea* in the North Sea were required to support laboratory quantification of bioturbation (see Chapter 5). The present study examines the seasonal population structure of *C. subterranea* based on mud shrimps recovered from box cores taken at the North Sea study site.

3.2. Materials and Methods

3.2.1. Field sampling

Full details of the sampling protocol for *Callianassa subterranea* are given in Chapter 2.

3.2.2. Laboratory analyses

Mud shrimps, recovered from the box core samples, were counted and identified using a diagnostic key (de Saint Laurent & Bozic, 1972). Wherever possible for each shrimp, a note was made of its sex (on the form of the 2nd pleopods which are biramous in females and vestigial or absent in males); the smallest individuals of unidentifiable sex were termed "post larvae". A note was made also of whether females were ovigerous. The carapace length (CL) (from the tip of the rostrum to the posterior margin of the carapace) of each specimen was measured ($\pm 0.5\text{mm}$) using a stereoscopic binocular microscope fitted with an eye-piece graticule. Carapace length, rather than total body length, was selected as the indicator of body size because of the inaccuracy in the measurement of flexed bodies (formalin induced). Also, shrimps were frequently damaged making the measurement of total body length impossible. The relative position of the enlarged primary chela (left or right side of the body) was also recorded; however,

sample sorting and preservation often caused the detachment of this appendage. When a primary chela could be related with certainty to an animal of identifiable sex and carapace length, its width (ChW) was measured ($\pm 0.1\text{mm}$) using a stereoscopic microscope (Fig. 3.1A). The chelar measurements were taken over a year after collection of the shrimps, by which time the number of animals with attached chelae was relatively small due to storing and handling damage. *Callinassa subterranea* is sometimes parasitised by the bopyrid isopod *Ione thoracica* (Bourdon, 1968) (Fig. 3.1B), which resides in the branchial chamber beneath the carapace of the host animal. A drastic enlargement of the thorax allows for easy identification of those individuals suffering from such parasitism. A record of all infestations was made and the side of the animal to which *I. thoracica* was attached was noted. Animals parasitised by the bopyrid were omitted from carapace length/chelar width analysis.

3.2.3. Data treatment

The distribution and density of *Callinassa subterranea* at the North Sea site was determined from the individual five box cores taken at each sampling visit. To establish population structure, however, *C. subterranea* recovered from the five box cores were pooled for each month. Each monthly population sample thus represents animals collected from a surface area of 1.25m^2 . Occasionally, it was necessary to further pool these monthly data to clarify certain aspects of the population dynamics (eg, parasitism). To calculate relative growth, one of the regression techniques described by Lovett & Felder (1989) was applied to the chelar width/carapace length measurements. These data were repetitively partitioned into two size-delimited subsets, one for animals with a carapace length less than, and the other for animals with a carapace greater than a hypothesized maturation length. A separate least squares regression was calculated for each of the two subsets after each relocation of the hypothesized maturation length. Calculations were performed interactively with sequential relocation of the hypothesized maturation length at 0.5mm intervals across the entire range of the independent variable (carapace length). Maturation length was then defined by the value at which the lowest combined sum of the squared residuals (SSR) for the regressions was achieved.

3.3. Results

3.3.1. Population distribution and density

Analysis of *Callianassa subterranea* numbers in the five box cores taken at the study site for each month (Appendix I) shows that individuals are contagiously distributed (ie, the variance is significantly greater than the mean) amongst the stations in October, April and August; in September and July the distribution is not significantly different from random (Table 3.1). A contagious relationship, between the number of individuals encountered at the sample stations, indicates that *C. subterranea* is heterogeneously (or patchily) distributed at the study site. Variation in the mean density of individuals per core between months was small, ranging from 9.4/core in April to 14.8/core in August (mean = 11.4/core, $1SD \pm 2.1$), which suggests that there is no significant difference in the seasonal abundance of *C. subterranea* (Table 3.1). Faunal density is more conventionally reported as number of individuals per square metre, thus the number of *C. subterranea* found per box core (0.25m²) was multiplied by four to give the appropriate mean unit values (Table 3.2). The mean density for the study site across all months was 46 individuals/m².

3.3.2. Population structure

Details of the population structure of *Callianassa subterranea* over the sampling period (Table 3.3) allow some consideration of the seasonality of population change (Fig. 3.2). Unfortunately, the data are limited and no obvious pattern of seasonal population change was identified. Although there are no clear cohorts on which to base an estimate of growth, combined data for all months show a bimodal population distribution (Fig. 3.3A). Separate numerical representation of male and females ($\geq 3\text{mmCL}$) more clearly highlights the two modes for each sex (1st = $\geq 4\text{mm}$, 2nd = $\geq 7/8\text{mmCL}$), and the possible existence of a third mode for males ($\geq 10\text{mmCL}$) (Fig. 3.3B). From these, admittedly limited, data it may be inferred that *C. subterranea* lives for between two or three years (if mode equals year cohort/class, eg, Hailstone & Stephenson, 1961). The existence of a possible third mode for males suggests that males generally become larger or live longer than female *C. subterranea*. This assumption is barely supported by present data which

show the maximum carapace length achieved by males was 11mm as opposed to 10mm for female shrimps.

At each sampling, the sex ratio was unequal and ranged from 1.56 (M/F) in September to 2.33 (M/F) in August, although only the latter is significant ($\chi^2 = 4.0$, $P = < 0.05$). Across all months there is nearly twice as many males as females (mean M/F ratio = 1.9, $\chi^2 = 18.5$, $P = < 0.001$) (Table 3.2). The observed significant sex ratio bias is unequally distributed amongst the size classes (total for all months), with male shrimps being significantly more abundant than females in classes ≥ 3 , ≥ 5 and ≥ 6 mmCL ($\chi^2 = 4.3$, 3.8, 5.0, all $P = < 0.05$). The sex ratio is only effectively equal ($\chi^2 = 0.03$, $P = < 0.01$) for one size class (≥ 8 mm), that which constitutes the major size distribution mode (Table 3.3, Fig. 3.3B).

3.3.3. Reproduction and recruitment

Only female *Callinassa subterranea* ≥ 7.0 mmCL were found to carry eggs (Appendix I). All, or nearly all, sexually mature females were ovigerous in July and August, 40% and 17% in April and September respectively, while no females carried eggs in October (Table 3.2). Post larvae (< 3 mmCL) were present during all months sampled, but showed a seasonal pattern with a clear peak in August and lowest numbers in October (Fig. 3.2). Based on current data a possible reproductive cycle for *C. subterranea* can be postulated (Fig. 3.4). Figure 3.4 suggests that copulation has taken place by April such that all sexually mature females carry eggs by July. From July, eggs begin to hatch and the number of ovigerous females in the population starts to decline rapidly. By September, relatively few females are berried and the remainder of mature females display evidence of having recently detached their eggs (ie, "feathery" pleopods). Approximately one month after the peak occurrence of ovigerous females, post larval abundance is highest (August), implying that newly-hatched larvae have about 4 weeks in the plankton before being recruited to the benthic population as post larvae. Based on the limited data available, the breeding period (presence of ovigerous females) extends for at least five months with a peak in July and recruitment (presence of post larvae) occurs over at least six months with a peak in August.

3.3.4. *Relative growth*

Monthly samples showed no obvious pattern of occurrence for right- or left-handed shrimps (Table 3.2). The April sample had the highest numbers of shrimps with the primary chela on the right side (L/R ratio = 0.77), whilst animals in August more often had their primary chela on the left side of the carapace (L/R ratio = 1.80). If individuals from all months are considered as a single data set representing a total site population, there appears to be a near equal ratio for primary chela occurrence (L 53: R 46, = a ratio of 1.15).

A conspicuous sexual dimorphism is apparent in the size of the primary chelae of adult *Callinassa subterranea*. The relative growth of this secondary sexual character, ascertained from regression analysis of carapace length/chela width measurements (Table 3.4), was used to establish shrimp size at maturation. The maturation lengths were found to be 6.5mmCL and 7.5mmCL for males and females respectively [ie, the carapace length when the minimum combined sum of squared residuals (SSR) is achieved (Table 3.5; Figs 3.5A & 3.5B). Note: the carapace length at maturation for females is very similar to the previously determined sexual maturation length for females (7.0mmCL)]. For both sexes, primary chelar width increases isometrically with increasing carapace length until the maturation length (Figs 3.6A & 3.6B). From maturation, the male primary chelae exhibit positive allometric growth whilst female primary chelar growth displays negative allometry (Table 3.6). Thus, female primary chelar growth is very slow, whilst male chelar width increases rapidly from the onset of maturity. The difference in relative growth results in male shrimps having larger and more massive primary chelae than females of equal carapace length (Plate 3.2).

3.3.5. *Parasitism*

Parasitism of *Callinassa subterranea* by the bopyrid isopod *Ione thoracica* occurred in all months sampled, although the degree of infestation varied from 2.0% (October) to 10.8% (August) (Table 3.2). The pattern of the level of parasitism appears to mimic the inferred reproductive cycle of *C. subterranea*, being highest at the peak (summer), and lowest at the beginning and end of the breeding season (spring and autumn). Interestingly, male shrimps have a significantly higher level of infestation by *I. thoracica*

than female shrimps (χ^2 test, $P = < 0.01$) (Table 3.7). Infestation was not apparent over the entire size range of the shrimp population, although parasitism was regularly spread ($\sigma^2 < x$) among those infested, from carapace length 2.0 to 8.5mm (Fig. 3.7). Therefore, infestation appears to be restricted to males of relatively small size, with the mean size of parasitised and non-parasitised males being 5mmCL (1SD \pm 2mm) and 7mmCL (1SD \pm 2mm) respectively.

3.4. Discussion

In 1984, a benthic survey conducted by members of the ICES Benthic Working Group in the North Sea sampled a grid of 260 stations from 61°N to 51°N, and found that *Callinassa subterranea* was restricted to water depths of between 30-50m in muddy-fine sand, and occurred at densities ranging from 2 and 60 individuals per m² (Kunitzer *et al.*, 1992). The present findings are within this relatively broad density range. However, the mean mud shrimp density (46/m²) recorded here is higher than the mean (22/m²) found by Kunitzer *et al.* (1992), but comparable to the mean densities found by Lutze (1938) (47/m²) and by Witbaard & Duineveld (1989) (65/m²) who sampled in close proximity to the present study site. The relative stability in mud shrimp numbers between monthly sampling occasions at the North Sea study site implies low mortality and consequently little predation (Buchanan, 1963); however, some predation on *C. subterranea* undoubtedly occurs as this species has been found in the stomachs of fish [including ray (Lutze, 1938) and haddock (Poulsen, 1940)] trawled from the North Sea. It may be that the population of *C. subterranea* at the North Sea study site is so large that predation is not apparent in the quantitative samples. Alternatively it may be that the burrowing habit affords a high degree of protection from predation. Witbaard & Duineveld, (1989) attributed large seasonal population differences (eg, February = 22/m², July = 56/m²) for *C. subterranea* from a nearby site in the North Sea to the animals burrowing below the depth range of the box corer at times of low temperature rather than to predation. This interpretation is supported by present findings which showed an absence of *C. subterranea* from the sub cores (30cm maximum depth) recovered from the study site in January. The spatial distribution of *C. subterranea* within the North Sea study site appears to be heterogeneous or patchy. However, more

samples are required to substantiate this interpretation. Witbaard & Duineveld (1989) took a large number ($n = 30$) of box cores and reported that *C. subterranea* was regularly (or evenly) distributed at their site in the North Sea. As the size of the box core can influence the interpretation of distributions (Elliott, 1977) and the present study used a different size (0.25m^2) from that of Witbaard & Duineveld (1989) (0.06m^2), it is possible that the *C. subterranea* population is indeed heterogeneous, but that patches are large ($>0.25\text{m}^2$) and occur in relative close proximity (in the order of the maximum diameter of the 0.06m^2 corer). Information on the spatial pattern of callianassid distribution is unfortunately rare, although Devine (1966) reported that the burrows of an intertidal species appeared to be patchy.

In the present study, two clear size modes were identified in the combined length-frequency histogram of *Callianassa subterranea*, with a possible third mode for males. If these modes represent year classes, *C. subterranea* at the North Sea study site live for between two and three years. This interpretation is consistent with reports for other callianassids. For example, *C. australiensis* lives for two years (Hailstone & Stephenson, 1961), *C. louisianensis* for between two and two and a half years (Felder & Lovett, 1989), *C. kraussi* for three years (Forbes, 1977), and *C. fiholi* for three or possibly four years (Devine, 1966). The limited monthly length-frequency data for the *C. subterranea* population at the present study site did not allow for a cohort progression estimate of growth. It may be postulated on the basis of the combined data, however, that individuals achieve a size of 6.5mmCL by the end of their first year (minima between 1st and 2nd mode). This value is similar to previous estimates of first year growth for callianassids, which include 6mmCL (Forbes, 1977), 8mmCL (Devine, 1966) and 9.5mmCL (Hailstone & Stephenson, 1961).

The sex ratio of *Callianassa subterranea* at the North Sea site was significantly biased to males (mean M/F = 1.9). Montagu (1808) observed that female *C. subterranea* were rarer than males. However, Witbaard & Duineveld (1989) found that females outnumbered males at their site in the North Sea ($53^\circ 42'\text{N}$, $4^\circ 30'\text{E}$) (mean M/F = 0.71). Although a male biased sex ratio appears to be unusual for callianassids (Hailstone & Stephenson, 1961; Devine, 1966; Felder & Lovett, 1989), Felder & Lovett (1989) stated that it is unlikely that even adjacent populations of the same species will have

similar sex ratios and population structures because of changes imposed by even small alterations in environmental conditions. Deviation from an equal sex ratio may also be related to sampling gear efficiency. For example, "yabby-pumps", which rely on suction, may sample selectively the generally lighter females, whilst corers, which achieve relatively shallow penetration, may omit the possibly deeper burrowing males. Any ecological significance of the unequal sex ratio observed at the study site is unclear. The relative growth of decapod chelae is often used as an indicator of the onset of sexual maturity (Hartnoll, 1974). Before maturity, both sexes of *Callianassa subterranea* have a similar rate of primary chelar growth. After sexual maturation, rapid growth of the primary chela was apparent in males but not in females. The production of a massive chela as a sexual dimorphic character in adult thalassinids is extremely common (see examples in Dworschak, 1988). Tucker (1930) suggested that the larger chelar size in male thalassinids is due simply to the fact that males have no drain on their energy resources for egg production. Felder & Lovett (1989), however, implied that growth of the primary chela was not simply a passive increase in size as a result of less demand for gonadal development, as a male's weight exceeds that of ovary-laden female. Changes in chelar shape have also been noted for callianassids, suggesting that the enlarged primary chela does indeed have a specific behavioural function (Dworschak & Pervesler, 1988). The relative shape of the primary chela of *C. subterranea* was not examined in the present study, but difference in coloration between sexes was apparent; males possessed white chelae whilst female chelae were more often pink. Such pigmentation differences also contribute to the suggestion that the enlarged primary chelae of decapods have a role to play in display and courtship (eg, signalling, Takeda & Murai, 1993). However, the extremely low light levels at the study site presumably preclude the usefulness of sex-specific chelar colour.

The location, timing and frequency of mating remain unknown for *Callianassa subterranea* (and all other callianassid species). Individual shrimps were never observed outside their burrows or paired within the burrow. Laboratory observations of chance and forced encounters indicate that mud shrimps are aggressive and intolerant of each other, irrespective of sex (pers. obs.). Fighting was frequent and involved the use of the primary chelae. Where escape was impossible, death usually resulted for one of the

combatants. The significance of such antagonistic behaviour for mating is unknown, but it is possible that it has a role in the regulation of population density (Tunberg, 1986).

Based on the relative growth measures of the primary chela and the size of the smallest ovigerous individual collected, female maturation appears to be at 7/7.5mmCL. Witbaard & Duineveld (1989) found that only female *Callianassa subterranea* ≥ 7 mmCL carried eggs. The major size modes exhibited by *C. subterranea* at the present study site indicate that females of 7mmCL have an estimated age of one year. Hailstone & Stephenson (1961) identified a similar correlation between maturation size and age for *Callianassa australiensis* in Australia. The relative monthly abundance of ovigerous females and post larvae at the study site suggests that *C. subterranea* has a defined summer breeding season in the North Sea. Such an inferred breeding period is supported by plankton records from the southern North Sea which specifically identify the peak occurrence (in 1989) of *C. subterranea* larvae to be August (Lindley *et al.*, 1993). Such a reproductive cycle, with a seemingly single egg laying maximum in mid summer, is simpler than the one identified for callianassid species in Australia and New Zealand, where two egg laying periods occur in an extensive breeding period of eight months (Hailstone & Stephenson, 1961; Devine, 1966). It is possible, however, that *C. subterranea* in the North Sea also has a double reproductive cycle extending over the majority of the year. Witbaard & Duineveld (1989) found that large/old females (9mmCL, 2 years old?) were ovigerous in February, whilst a large berried female has also been found in a macrofauna sample taken from the Thames estuary mouth in ^{the} same month (Rowden, unpublished data). Following an implied second late-winter egg producing period for larger/older females, post larvae were relatively abundant at the study site in April (23% of total number of individuals) which could represent the subsequent early spring recruitment. Witbaard & Duineveld (1989) also found that post larvae were extremely common in April (30% of total number of individuals). Interestingly, *C. subterranea* larvae have not been recorded in the North Sea plankton for late winter or early spring which would complete the argument for a double reproductive cycle (Rees, 1954; Lindley, 1987). It may be possible that *C. subterranea* adopts an alternative life-history strategy of direct benthic development (ie, larvae never leave the sediment) rather than planktonic larval development during this period. Indeed,

benthic larval development has been observed for *Callianassa kraussi* in South Africa, where the harsh estuarine conditions were thought to be the cause of this alternative life-cycle strategy (Forbes, 1973). It is possible that the hypothesized benthic larval development in winter is also precipitated by adverse conditions for planktonic survival, or that females do not create the current necessary to remove larvae from the burrow (*C. subterranea* are virtually inactive at low temperatures - see Chapter 5).

At the study site, parasitization levels of *Callianassa subterranea* by *Ione thoracica* were found to be of the same order of magnitude reported for other thalassinids (eg, 0.8 - 6.6%, Dworschak, 1988). Variation in the levels of infestation between sampling months may be related to a seasonal cycle, as identified for *I. thoracica* and *C. tyrrhena* in Italy (Tucker, 1930). Certainly, temporal differences in the level of bopyrid infestation are apparent for other thalassinids, although seasonality in these cases was not established due to limited data (eg, Dworschak, 1988). The observation that parasitized *C. subterranea* were nearly always male, suggests that *I. thoracica* may not occur randomly throughout the host population at the study site. Dworschak (1988) also found that male, rather than female, *Upogebia pusilla* (Thalassinidea) were more often parasitised by the bopyrid isopod *Gyge branchialis*. Tucker (1930) observed the same phenomenon of male-biased infestation despite the sex ratio of his *U. pusilla* study population being female biased. The latter author explained the excess of males amongst parasitized shrimps as simply a reflection of an effective excess of males at the period when parasitization normally takes place (when individuals are small) (Tucker, 1930). Such an explanation could possibly hold true for the observed sexual parasitization bias in *C. subterranea* at the North Sea study site, as an average of 74% of individuals (of known sex) in the smallest size class ($\geq 3\text{mmCL}$) were male. Noticeably, parasitization occurred only in a restricted size range and no *I. thoracica* infected *C. subterranea* $> 8.5\text{mmCL}$. A similar size-limited infestation has been observed for bopyrids which parasitize caridean shrimps and two explanations have been proposed. Horstead & Smidt (1956) suggested parasitization prevented the host from achieving its full size, whilst Warren (1974) reasoned that the life duration of the parasite is less than that of ^{the} host. Considering the life span of the final parasitic stage of *I. thoracica* (approximately one year), it seems

most likely that the latter rationale is responsible for the lack of parasitization in large *C. subterranea* (Bourdon, 1968).

Bopyrid infestation affects the reproductive potential of female caridean shrimps and brachyuran crabs by preventing, or reducing, the maturation of eggs (Allen, 1966; McDermott, 1991). In addition to similar potential effects on the development of the ovaries and eggs for female callianassids, bopyrid infestation has been shown to reduce the testes and slenderize the primary chelae of male shrimps (Baffoni, 1950 in Bourdon, 1968). Evidence for the slenderizing of the primary chelae of *Callianassa subterranea*, unfortunately, rests upon a single comparison. Two adult males of the same size (6.5mmCL), one parasitised the other not, had chelar widths of 3.4mm and 5.1mm respectively (equivalent to a 33% reduction in ChW). Other than the latter comparison, no measure of the physical effect on *C. subterranea* of harbouring *Ione thoracica* was undertaken in the present study.

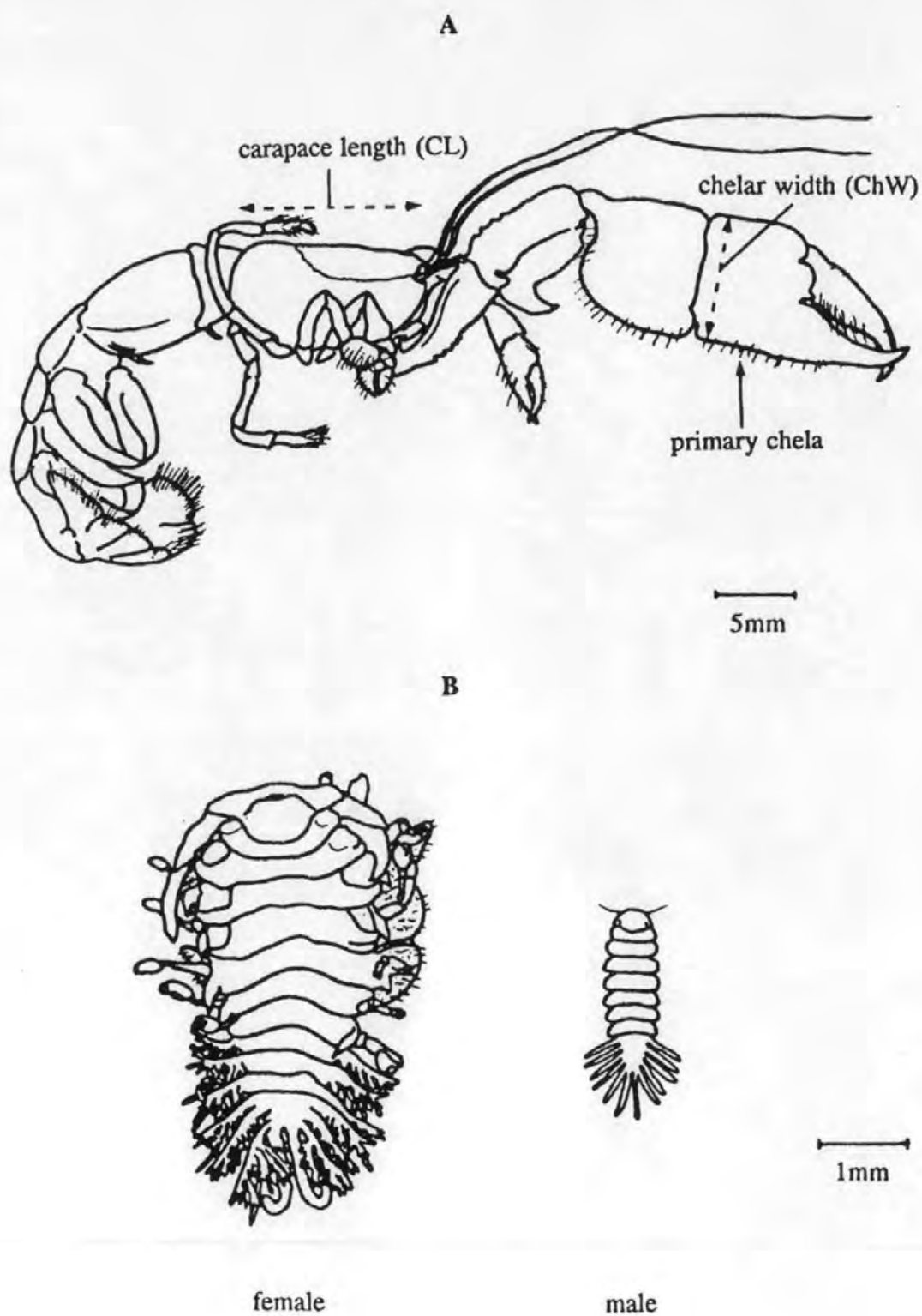


Figure 3.1. A, Lateral view of adult male *Callianassa subterranea*; B, dorsal view of parasitic isopod *Ione tharacica* (the latter after Bourdon, 1968).

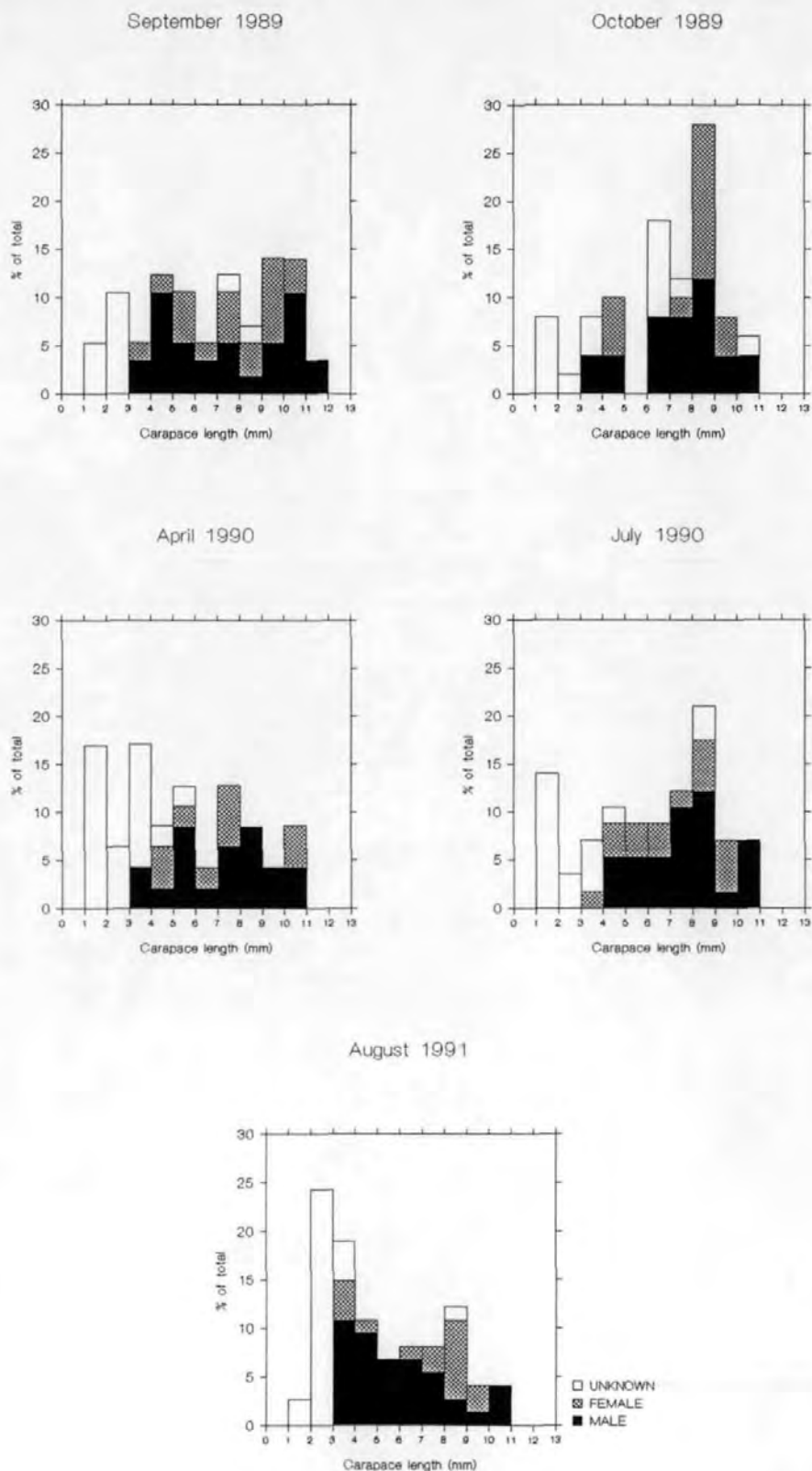


Figure 3.2. Population structure of *Callianassa subterranea* at the North Sea study site during 1989, 1990 & 1991 (n= 57, 50, 47, 57, 74 respectively) (unknown sex <3mmCL= post larvae).

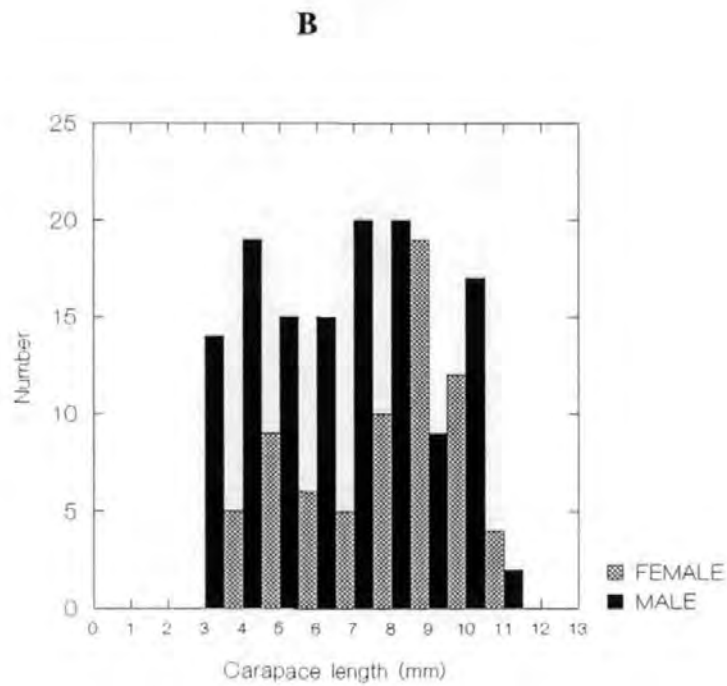
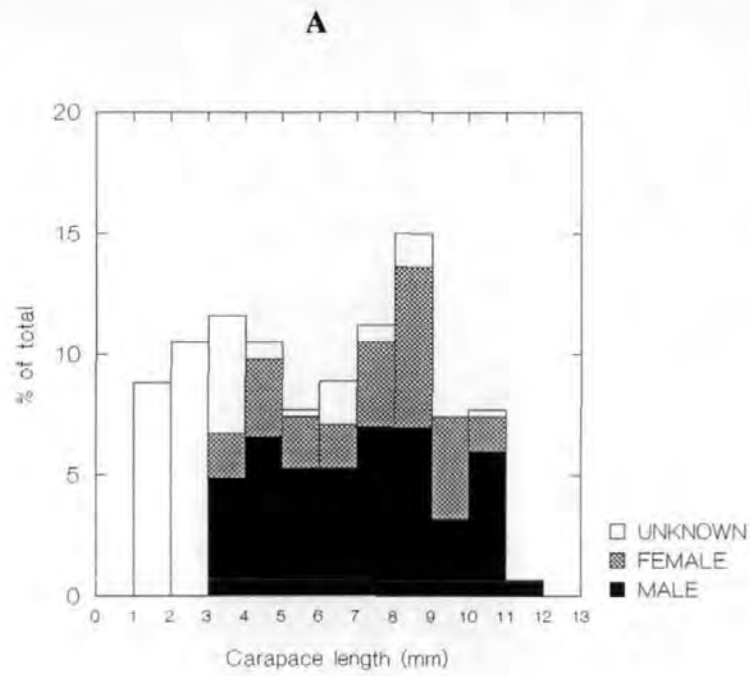


Figure 3.3. Population structure of *Callianassa subterranea* at the North Sea study site (total of all 1989, 1990 & 1991 data, n= 285); **A**, all individuals of all sizes (unknown sex <3mmCL= post larvae) **B**, only males and females >3mmCL.

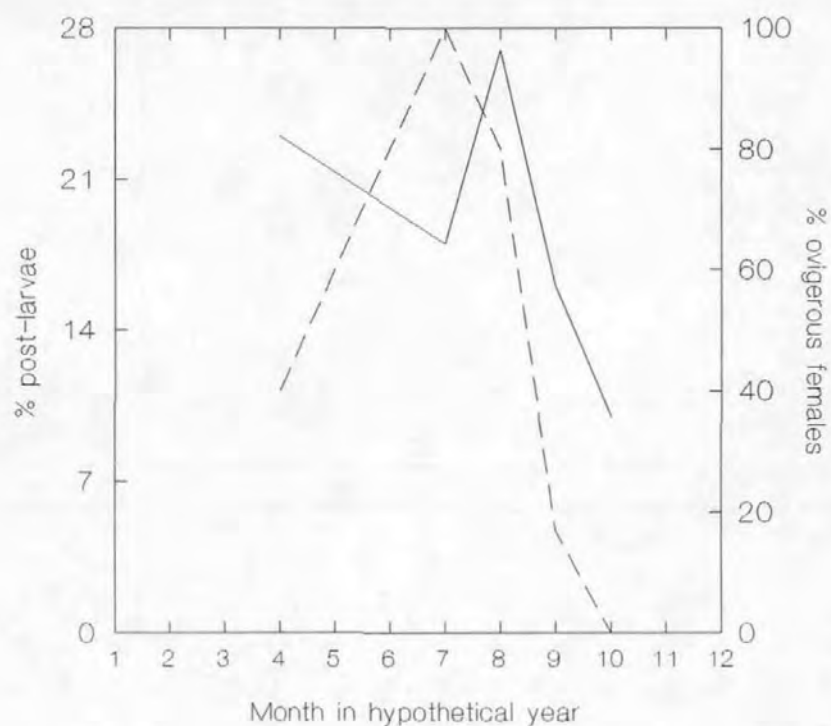


Figure 3.4. Breeding and recruitment pattern in a hypothetical year (ie, all data combined) for *Callianassa subterranea* at the North Sea study site (solid line= % post larvae of total sample; broken line= % ovigerous females of total mature females).

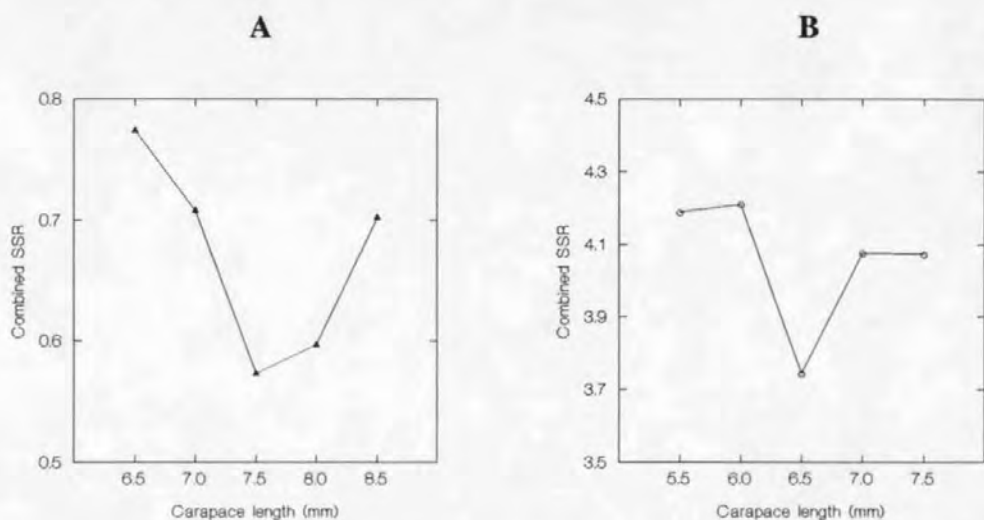


Figure 3.5. Combined sum of squared residuals (SSR) resulting from application of least squares estimate regression to carapace length/primary chelar width measurements of *Callianassa subterranea* from the North Sea study site subdivided at each hypothesized carapace length maturation point; **A**, females **B**, males.

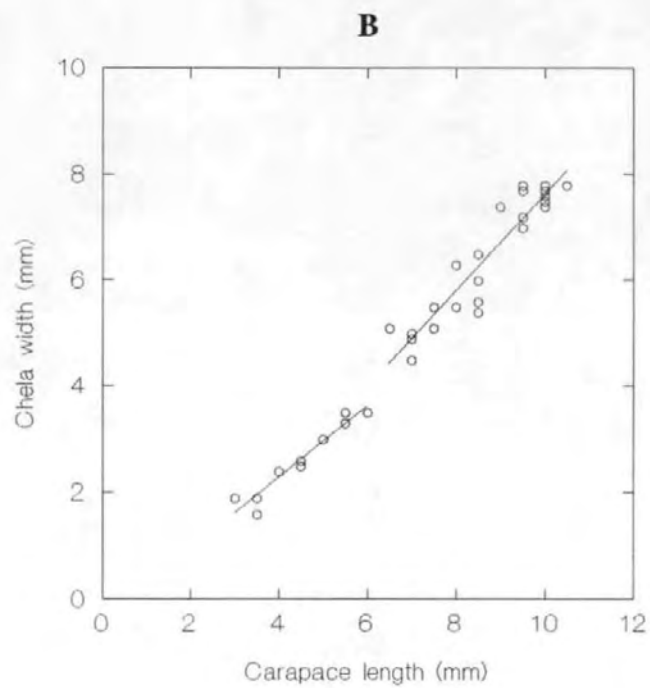
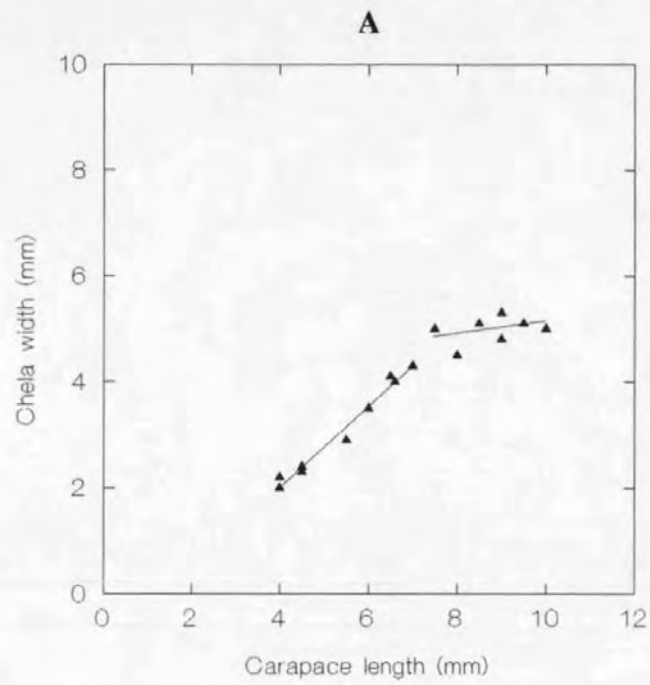


Figure 3.6. Primary chelar width (mm) in relation to carapace length (mm) of *Callianassa subterranea* from the North Sea study site; **A**, females **B**, males (see Table 3.6 for regression details).

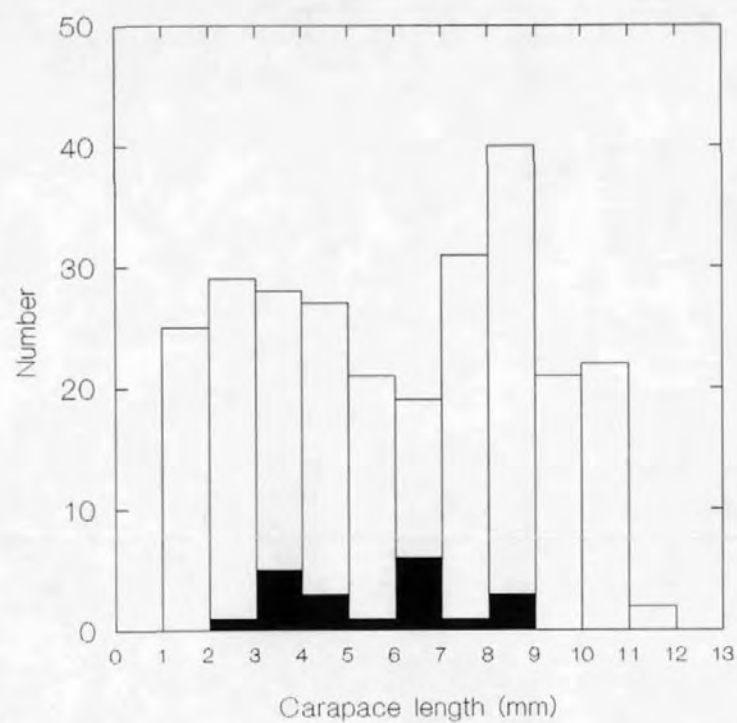


Figure 3.7. Length-frequency distribution of parasitized (bold bars) and non-parasitized (open bars) *Callianassa subterranea* from the North Sea study site (all data combined; n= 285).

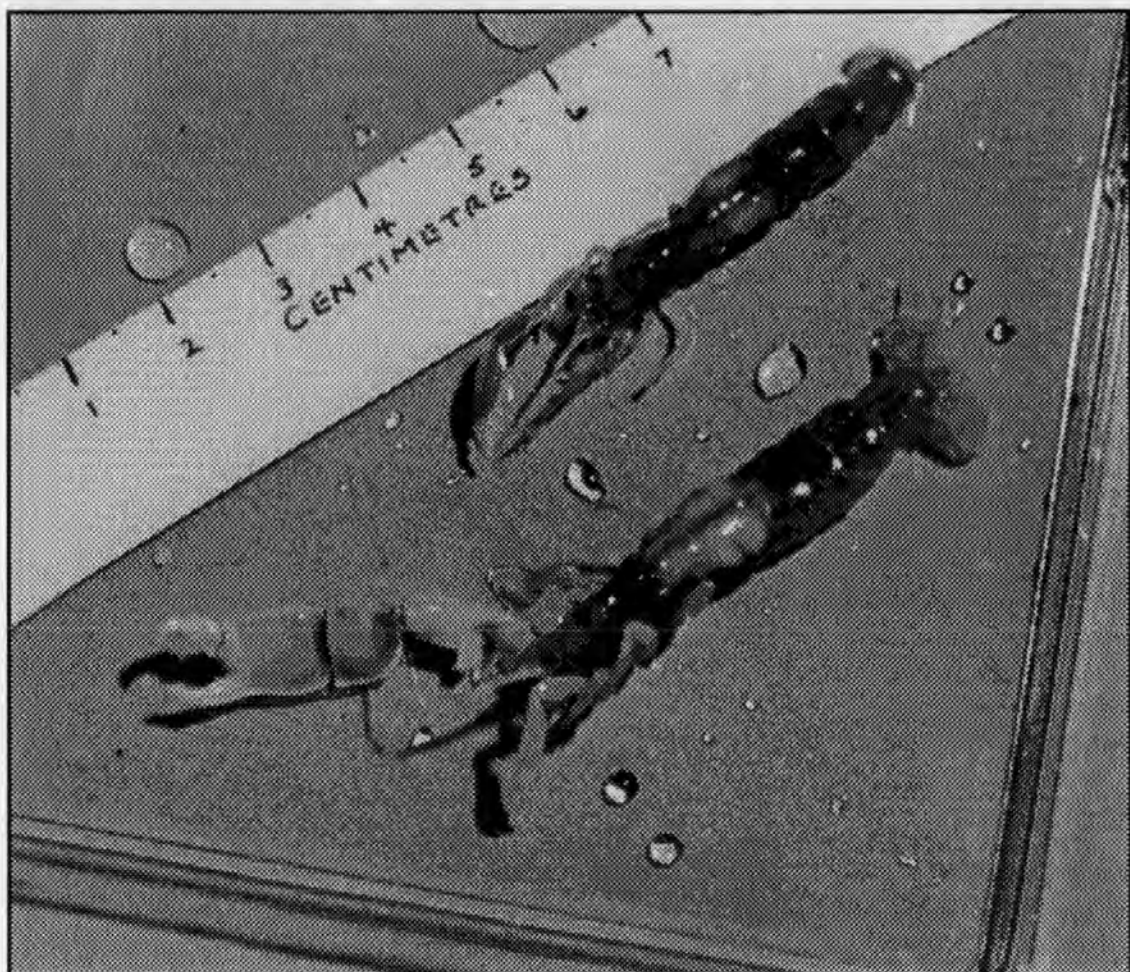


Plate 3.1. *Callianassa subterranea* collected from the North Sea study site; female above, male below (both have carapace length of approximately 10mm).

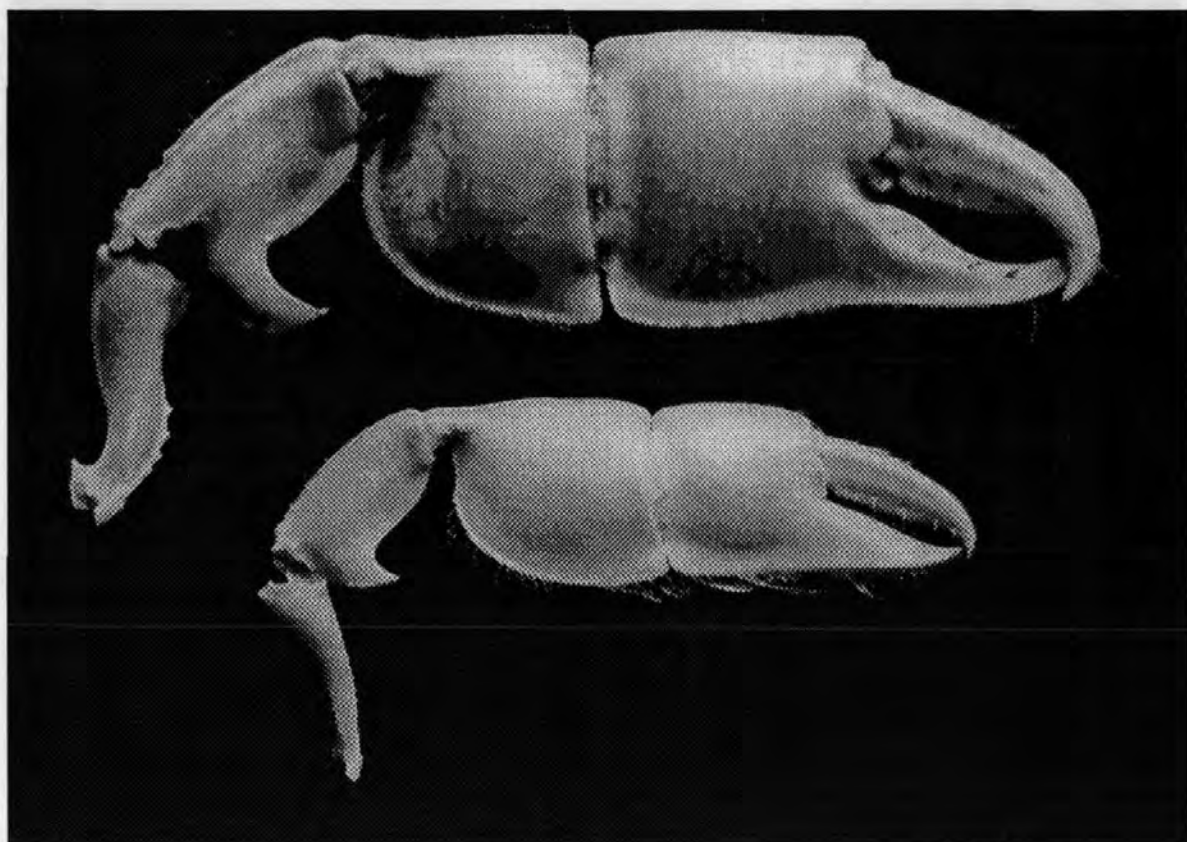


Plate 3.2. The primary chela of *Callianassa subterranea* from the North Sea study site; male above (chelar width= 7.8mm), female below (chelar width= 5.0mm) (both chelae from individuals of 10mm carapace length).

<i>Station</i>	Sep. '89	Oct. '89	Apr. '90	Jul. '90	Aug. '91
1	16	6	13	9	13
5	17	11	3	11	25
13	9	22	2	14	20
23	9	5	20	11	7
25	6	6	9	12	9
mean	11.4	10.0	9.4	11.4	14.8
σ^2	23.3	50.6	55.4	3.3	57.2
x^2	8.2	20.2	23.6	1.2	15.5
<i>P</i>	>0.05	<0.05	<0.05	>0.05	<0.05

Table 3.1. Numbers of *Callianassa subterranea* taken at the five stations of the North Sea study site.

	Sep. '89	Oct. '89	Apr. '90	Jul. '90	Aug. '91
Density (site mean) (individuals/m ²)	46	40	38	46	59
Sex Ratio (male/female)	1.56	1.57	2.11	1.93	2.33
Ovigerous Females (% of total ≥ 7 mm CL)	17	0	40	100	80
Post-larvae (% of total)	16	10	23	18	27
<i>Ione</i> parasitism (% of total)	5.3	2.0	4.3	10.5	10.8
1° Chela Ratio (left/right)	1.17	1.63	0.77	0.88	1.80

Table 3.2. Summary of population details for *Callianassa subterranea* at the North Sea study site.

Size Class (CL mm)	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10	≥11
September 1989											
unknown	3	6	0	0	0	0	1	1	0	0	0
male	0	0	2	6	3	2	3	1	3	6	2
female	0	0	1	1	3	1	3	2	5	2	0
total	3	6	3	7	6	3	7	4	8	8	2
October 1989											
unknown	4	1	2	0	0	5	1	0	0	1	0
male	0	0	2	2	0	4	4	6	2	2	0
female	0	0	0	3	0	0	1	8	2	0	0
total	4	1	4	5	0	9	6	14	4	3	0
April 1990											
unknown	8	3	6	1	1	0	0	0	0	0	0
male	0	0	2	1	4	1	3	4	2	2	0
female	0	0	0	2	1	1	3	0	0	2	0
total	8	3	8	4	6	2	6	4	2	4	0
July 1990											
unknown	8	2	3	1	0	0	0	2	0	0	0
male	0	0	0	3	3	3	6	7	1	4	0
female	0	0	1	2	2	2	1	3	3	0	0
total	8	2	4	6	5	5	7	12	4	4	0
August 1991											
unknown	2	18	3	0	0	0	0	1	0	0	0
male	0	0	8	7	5	5	4	2	1	3	0
female	0	0	3	1	0	1	2	6	2	0	0
total	2	18	14	8	5	6	6	9	3	3	0
Totals											
unknown	25	30	14	2	1	5	2	4	0	1	0
male	0	0	14	19	15	15	20	20	9	17	2
female	0	0	5	9	6	5	10	19	12	4	0
total	25	30	33	30	22	25	32	43	21	22	2

Table 3.3. Population structure of *Callinassa subterranea* at the North Sea study site (numbers from 5 pooled box cores, ie, 1.25m²)(size class, eg, ≥3 = shrimps of 3.0 and 3.5mmCL; CL= carapace length).

<i>Size</i> carapace length (mm)	<i>Male</i> 1° chela width (mm)	<i>Female</i> 1° chela width (mm)
3.0	1.9	--
3.5	1.9	--
3.5	1.6	--
4.0	2.4	2.2
4.0	--	2.0
4.5	2.6	2.4
4.5	2.5	2.3
5.0	3.0	--
5.5	3.5	2.9
5.5	3.3	--
6.0	3.5	3.5
6.5	--	4.1
6.5	5.1	4.0
7.0	4.5	4.3
7.0	4.9	--
7.0	5.0	--
7.5	5.1	5.0
7.5	5.5	--
7.5	5.1	--
8.0	6.3	4.5
8.0	5.5	--
8.5	6.0	5.1
8.5	5.6	--
8.5	5.4	--
8.5	6.5	--
9.0	7.4	4.8
9.0	--	5.3
9.0	--	5.3
9.5	7.0	5.1
9.5	7.8	--
9.5	7.2	--
9.5	7.7	--
10.0	7.6	5.0
10.0	7.4	--
10.0	7.6	--
10.0	7.7	--
10.0	7.5	--
10.0	7.8	--
10.5	7.8	--

Table 3.4. Carapace length and primary chelar width of *Callianassa subterranea* from the North Sea study site (only measures of chelae attached to unparasitized individuals of distinguishable sex).

CL(mm)	SSR	CL(mm)	SSR	Combined SSR
<i>Female</i>				
< 6.5	0.068	≥ 6.5	0.704	0.774
< 7.0	0.144	≥ 7.0	0.564	0.708
< 7.5	0.144	≥ 7.5	0.429	0.573
< 8.0	0.208	≥ 8.0	0.389	0.597
< 8.5	0.529	≥ 8.5	0.173	0.702
<i>Male</i>				
< 5.5	0.231	≥ 5.5	3.958	4.189
< 6.0	0.274	≥ 6.0	3.937	4.211
< 6.5	0.296	≥ 6.5	3.450	3.744
< 7.0	1.147	≥ 7.0	2.930	4.077
< 7.5	1.287	≥ 7.5	2.787	4.074

Table 3.5. Combined sum of squared residuals (SSR) resulting from subset linear regressions between carapace length (CL) and primary chelar width of *Callianassa subterranea* from the North Sea study site (subset divisions are hypothetical maturation lengths; subset division which produces minimum combined SSR identifies "real" maturation length).

CL(mm)	<i>N</i>	<i>r</i>	Formula	<i>P</i>
<i>Female</i>				
<7.5	9	0.99	ChW = 0.789 x CL -1.068	<0.0001
≥7.5	8	0.35	ChW = 0.116 x CL +3.990	0.4
<i>Male</i>				
<6.5	10	0.97	ChW = 0.667 x CL -0.380	<0.0001
≥6.5	25	0.94	ChW = 0.909 x CL -1.465	<0.0001

Table 3.6. Results of linear regressions between carapace length (CL) and primary chelar width (ChW) of *Callianassa subterranea* from the North Sea study site (data are subdivided at the maturation length indentified by the minimum combined sum of squared residuals, see Table 3.5).

	Males	Females	Totals
Unparasitized	112	69	181
Parasitized	19	1	20
Totals	131	70	201

Table 3.7. Level of parasitization by *Ione thoracica* of male and female *Callianassa subterranea* at the North Sea study site (all data combined).

CHAPTER 4
THE BURROW STRUCTURE OF
CALLIANASSA SUBTERRANEA

[Aspects of this chapter were presented at a meeting of the International Council for the Exploration of the Sea (ICES) Benthic Ecology Working Group, Bergen, Norway, May 1992 and are included in ICES report C.M. 1992/L:11 (section 6. Influence of macrofauna on sediment properties).]

4.1. Introduction

Many marine benthic organisms construct burrows which may be semi-permanent or permanent. Burrowing fauna vary in size from microscopic forms, such as the meiofauna (eg, nematodes; Platt & Warwick, 1980), through medium-sized macrofauna (eg, amphipods and polychaetes; Jones & Jago, 1993) to larger forms such as fish (Nash, 1980). Burrows can thus range in length from a few millimetres to several metres, may be vertical or horizontal, branched or unbranched; in general, the size and shape of a burrow is characteristic for the species which constructed it (Meadows, 1991). The burrowing mode of life is frequently adopted by relatively large decapod crustaceans (Atkinson & Nash, 1985). The burrows of decapod crustaceans fulfil a variety of functions, including concealment from predators, amelioration of adverse environmental conditions, a site for moulting, a refuge for mating, a site for egg incubation or juvenile recruitment, a territorial or display centre, a site for feeding, and access to oxygenated water (see references in Atkinson & Taylor, 1988). The complexity of decapod crustacean burrows ranges from a simple shaft or tunnel with a single surface opening (eg, *Uca pugnax*; Katz, 1980) to a complicated branching tunnel system with more than one opening to the surface (eg, *Nephrops norvegicus*; Chapman & Rice, 1971). The most complex burrows are those made by members of the Thalassinidea (eg, *Calocaris macandreae*, Nash *et al.*, 1984). Thalassinid shrimps are amongst the most common constructors of burrows in estuarine and marine sediments, and occur from the intertidal to the deep-sea, sometimes in high densities (Dworschak, 1983). They construct burrows principally for shelter, reproduction and feeding, and most thalassinids spend their entire life in their burrow, except for a larval phase which may be pelagic (Griffis & Suchanek, 1991).

Various techniques have been used to determine the burrow structure of thalassinid shrimps. Early investigations, limited to burrows which were intertidally accessible, employed digging and resulted in general information only on the extent of the subterranean passages (Allen & Todd, 1900). The use of flexible branches of willow or rubber hose run down through the entrances helped identify more precisely the course of shafts near the surface (eg, Pohl, 1946). Stevens (1929) was the first to use moulds or casts (cement and Plaster of Paris) to examine burrow structure in detail, but found that

the cement tended to pass into areas surrounding the burrow in coarse sediment, whilst Plaster of Paris often hardened before the burrow was completely cast. Such applications confined burrow casting to the shore as both methods are unsuitable for underwater use. The advent of commercial polyester and epoxy resins allowed littoral and sublittoral thalassinid burrows to be cast successfully (Shinn, 1968; Farrow, 1971). As well as suitable for use under water, resin casts have the additional advantages of being less brittle than plaster or cement and also preserve fine detail. The resins range considerably in viscosity, rate of cure and clarity, and these features determine their suitability for a particular application. The critical factor is that resins are denser than seawater and flow into the deepest regions of the burrow, displacing any water present. The resin is poured into the burrow opening(s) at the sediment surface, allowed to harden (1-48h depending on conditions) and the burrow cast is then removed by careful digging or with a suction dredge if necessary (Atkinson & Chapman, 1984). An alternative to resin casting is mapping, whereby the burrow structure is exposed by careful removal of sediment, layer by layer. This "archaeological" method permits observation of burrow wall characteristics and blocked or filled burrow passages (Vaugelas, 1984). Even so, resin casting is by far the most widely-adopted method of determining the burrow morphology of thalassinid shrimps (Suchanek, 1985). Although descriptions of burrows from resin casts have been published for the majority of British burrowing crustaceans (see reviews, Atkinson & Nash, 1985; Atkinson, 1986; Atkinson, 1988), detailed information on the burrows constructed by the thalassinid shrimp *Callinassa subterranea* is relatively limited. The first record of occurrence for *C. subterranea* did not note a burrow and attributed its presence (at depths of nearly 60cm) to the notion that it passively inhabited the subterranean passages of the burrowing bivalve *Solen marginatus* (Montagu, 1808). Lutze (1938) studied *C. subterranea* collected from the North Sea and found that individuals constructed burrows of up to 20-30cm depth in laboratory aquaria. Morphological details of the burrows constructed by *C. subterranea* have been published recently based on resin casting (Witbaard & Duineveld, 1989; Atkinson & Nash, 1990). The results of these published studies highlight the complexity of *C. subterranea* burrows and identify the potential that such structures have for bioturbatory influence.

Both sets of descriptions (Witbaard & Duineveld, 1989; Atkinson & Nash, 1990) were reported after the present study commenced and form a useful basis on which to examine the plasticity of burrow design for a single species living under different sedimentary conditions. The primary aim of the present study, however, was to quantify burrow structure in order to confirm the extent of *C. subterranea*'s physical influence upon the substratum at the North Sea study site (see Chapter 2). A second objective was to elucidate the route by which the species delivers unwanted sediment to the seabed surface to support sediment turnover/transport studies (see Chapters 5 and 6).

4.2. Materials and Methods

4.2.1. Resin casting

Initially, resin casting of the burrows of *Callianassa subterranea* was attempted on board the R.R.S. *Challenger*, using a relatively undisturbed portion of the seabed recovered by a box corer at the study site (station 13) in September 1989. Following the experience of Atkinson & Chapman (1984), a polyester resin (TRYLON SP701PA, with a 2% by weight addition of methyl ethyl ketone peroxide catalyst) was utilised. Resin was poured carefully into the burrow openings thought to belong to *C. subterranea* (Chapter 2). Plastic rings were placed around each burrow opening to prevent resin spillage and to provide a 'head' for maximising potential resin flow (Plate 4.1). Unfortunately, the core sample could not be sealed adequately and the burrows drained quickly, making complete resin penetration impossible (successful casting relies upon water displacement); no further attempts were made to cast burrows in this pseudo *in-situ* manner. Instead, resin casting was attempted on the burrows constructed by *C. subterranea* used in the laboratory experiment to determine sediment turnover rates (Chapter 5). The TRYLON resin proved to be unsuitable because its viscosity and setting time prevented complete penetration and the casting of the burrow systems. However, the epoxy resin utilised by Dworschak (1983) was successfully employed (CIBA-GEIGY Araldit GY 257, with hardener HY 830 and HY 850, 25:7:8 parts by weight). At the termination of the experiment (90 days), portions of the resin mixture were delivered to the inhalant openings of each individual burrow system (Plate 4.2) with the aid of a syringe (60ml). The resin was added in stages until the burrow system appeared to be

completely saturated with the mixture (ie, no drop in resin level at burrow opening after 1-2h). After a period of suitable hardening time (approx. 48h), the resin casts of the burrows were carefully hand excavated from the sediment microcosms, washed free of adhering sediment, and allowed to dry and harden further in air (overnight) whilst supported by retort stands.

4.2.2. Morphological measurements

Detailed information of the morphology of each burrow system constructed by *Callinassa subterranea* was obtained from the resin casts produced by the test animals used in the 15°C ($\pm 1^\circ\text{C}$) sediment turnover experiment (Chapter 5). Using digital sliding hand callipers ($\pm 0.1\text{mm}$) and a tape rule ($\pm 1\text{cm}$), measurement of the following parameters were made on each cast constructed by an individual shrimp of known size and sex: (1) mean diameter and depth of vertical shafts, (2) mean diameter and depth of lateral shafts, (3) maximum depth of burrow, (4) number and mean diameter of inhalant openings, (5) number and mean diameter of exhalant shafts, (6) number and mean diameter of turning chambers, (7) the total length of lateral shafts and turning chambers, (8) the total length of the burrow system (lateral extent and total length of vertical shafts), and (9) burrow volume. Burrow volume was calculated by dividing the cast weight by the specific weight of the resin (1.17g/cm^3). In some cases, casts were incomplete and all dimensions could not be measured.

4.3. Results

4.3.1. Burrow shape

The resin casts of the burrows constructed by test animals in the laboratory microcosms showed remarkable consistency in general morphology (eg, Plate 4.3). Several vertical "inhalant" shafts descend from the surface to a lattice of mainly horizontal or "lateral" shafts which are regularly interspersed with nodular "turning chambers" (mean = 21, $1\text{SD} \pm 2.9$) at quadri and tri-partite intersections. The vertical inhalant shafts terminate at the surface in funnel-shaped openings (Plate 4.4), whilst their base characteristically sports two "dilations" or "diverticula" where the vertical shaft joins the main network of

lateral shafts (Plate 4.5). In addition to the vertical inhalant shafts, a narrow "exhalant" shaft (a few millimetres in diameter) ascends from a tapered horizontal "expulsion nodule" in a particular fashion (Plates 4.6 & 4.7) thus, extending horizontally, or inclining downward for a short distance (5mm), before describing a turn and extending to the vertical plane. This "exhalant apparatus" ends at the surface in a mound of expelled sediment; usually one such exhalant opening is maintained by the animal but occasionally, two or even three were found. The galleried lattice is orientated to maximise the shrimp's utilisation of a given volume of sediment, the lateral shafts often crossing above or below one another (Plates 4.8 & 4.9). Blind-ending branches were observed and presumably constituted abandoned or closed off regions of the burrow system. Some burrows, however, contained an additional modified blind junction ("sump") located at the base and deepest section of the constructed system. These globular sumps had a somewhat pitted surface and may be used for the disposal of unwanted coarse material which cannot be easily expelled from the burrow (Plate 4.10). The only significant difference in burrow shape between males and females was between the number of vertical shafts, and corresponding inhalant openings maintained by the animal. Females constructed four or five openings, whilst males always possessed more, between six and eight ($t = 2.86$, $df = 8$, $P = < 0.05$).

4.3.2. Burrow dimensions

All measurements of the resin cast burrows (Table 4.1) were linearly regressed (least squares) with the carapace length of the individual which constructed them. Burrow shafts are circular in cross section, and it is not surprising to find that the mean diameters of both the lateral and vertical inhalant shafts are positively related to the size of the inhabitant ($P = < 0.0001$ and < 0.001 respectively) (Figs 4.1A & 4.1B). Burrow volume, which was found to range between 104cm³ and 404cm³ for those test animals from which a complete cast could be recovered, also appeared to be positively determined by the proportions of the constructor (Fig. 4.2A). The latter relationship, however, was not significant at the 5% probability level. There were similar trends for the relationships between the diameter of the exhalant shafts and the lateral burrow extent and shrimp size (Figs 4.2B & 4.2C), but again these were not significant ($P = > 0.05$).

No linear relationships could be established between carapace length and the remaining measures of burrow morphology (Figs 4.3A-F). Maximum burrow depths ranged between 9 and 23cm, whilst the mean depth of the lateral shafts for all the burrows cast was 13cm ($1SD \pm 3cm$).

4.4. Discussion

As revealed by laboratory resin casting, the morphology of the burrows constructed by *Callianassa subterranea* is very similar to that reported previously for this species. Lutze (1938; and redescribed in Schäfer, 1972) observed that *C. subterranea* constructed a multibranched net of burrows, mostly at the same level, which was connected to the surface by several vertical shafts, each with a funnel-shaped top. Waste material, resulting from burrow construction, was ejected to the surface to form a volcano-like mound (Lutze, 1938). Such visual observations were later confirmed and quantified by burrow resin casts of *C. subterranea* from the North Sea (Witbaard & Duineveld, 1989). Witbaard & Duineveld (1989) were the first to record that unwanted sediment and faeces were removed from the burrow to the surface via a thin, modified vertical shaft, which was also noted on burrows cast during this study. The horizontal tunnel galleries of laboratory shrimps in the present study, with their numerous nodular turning chambers (18-27), were found at a maximum depth of 23cm, which compares very favourably to the value of 25cm measured by Witbaard & Duineveld (1989). Indeed, the casts made of *C. subterranea* burrows during this study were identical in general shape, and similar in dimension, to those reported by Witbaard & Duineveld (1989) (Figs 4.4A & 4.4B). The *in-situ* burrow resin casts described by Atkinson & Nash (1990) for *C. subterranea* from the west coast of Scotland (Fig. 4.5), however, differ from those made by the same species from the North Sea. Scottish burrows are simpler and deeper than their North Sea counterparts (Table 4.2). Casts of the former comprise, with only one exception, a *single* vertical shaft which rises from the horizontal tunnels and turning chambers (depth 30-81cm, number of chambers = 5-13) to a surface opening which is mostly thistle-shaped rather than funnel-shaped. Atkinson & Nash (1990) postulated that thistle-shaped openings were partially closed funnels which constituted a surface turning chamber and

from which sediment could be expelled in the form of a bolus. Although more conventional plume expulsion of unwanted sediment from depth was observed, it was not associated with the existence of a thin exhalant shaft (Atkinson & Nash, 1990). Other features of Scottish burrow structure were generally consistent with those of the burrows cast for *C. subterranea* from the North Sea study site. All burrows possess a characteristic dilation at the base of the vertical shaft, a complex horizontal gallery with nodular turning chambers and the occasional presence of "blind ends" and "sumps".

The results of this study have shown that certain aspects of burrow morphology are related to shrimp size. Not surprisingly, the diameter of the burrow shafts were positively related to shrimp size, whilst burrow volume and lateral extent showed similar trends. The influence of size on such criteria has been demonstrated previously for other callianassids (eg, *C. bouvieri*; Dworschak & Pervesler, 1988). Present results, however, fail to confirm that the depth of the burrow produced by *Callianassa subterranea* is size-dependent as suggested by Witbaard & Duineveld (1989). This apparent contradiction may be a consequence of the restricted nature of the present data (n=13 and limited size range 6.5-10.0mmCL). It is also possible that shrimp population density may control aspects of burrow morphology (eg, volume) but there is little evidence to support this hypothesis. Nash *et al.* (1984) postulated that the burrows of *Calocaris macrandreae* were restricted in size by the high density at which they were maintained in a laboratory aquaria. The influence of population density upon burrow structure was outside the remit of the current study, however, laboratory-maintained shrimps showed self-inhibiting burrow construction (no individual utilised the full spatial extent of the microcosm). Based on this latter observation, it may be postulated that the burrows produced by *C. subterranea* at the North Sea study site are unlikely to be limited by the measured population density (the surface area of the laboratory microcosms approximated to the site's adult shrimp density; Chapter 5).

The influence of shrimp sex upon burrow structure was clearly demonstrated by shrimps from the North Sea study site. Resin casts of burrows produced by females had consistently fewer surface openings than those of males. Although the data are limited, the present observation contradicts Rice & Chapman (1971) who found that the decapod *Nephrops norvegicus* sometimes constructed a different number of burrow openings

depending on its sex (females had two or more, males only one). These authors concluded, logically, that females had more surface openings to facilitate the oxygen requirement of the developing embryos (Rice & Chapman, 1971). Why the number of burrow openings maintained by *C. subterranea* should be sex-related remains unknown. Griffis & Chavez (1988), in attempting to elucidate the effect of sediment upon the burrow structure of two callianassid shrimps, found incidentally that there was no significant effect of sex on the number of burrow openings (or burrow volume). Griffis & Chavez (1988), while investigating whether the generally accepted observation that callianassid burrows tend to be simpler when constructed in sand than in mud was true (Farrow, 1971; Dworshak, 1987), found that burrows in mud were indeed larger and had more surface openings than those constructed in sand (for both *C. gigas* & *C. californiensis*). These latter findings contradict the burrow structure of *C. subterranea*, which is relatively simple/deep in mud (Atkinson & Nash, 1990) and relatively complex/shallow in sand (Witbaard & Duineveld, 1989; this study). Griffis & Chavez (1988) attributed the difference in burrow structure in different substrata of intertidal species to draining capabilities; sand drains faster than mud, so burrows need to be deep and simple to retain water necessary for survival. Water retention is not important for survival in subtidal burrows, so an alternative explanation must be ^{sought} ~~A~~ for the apparent contradiction provided by the *C. subterranea* burrows.

The apparent differences in burrow structure between those constructed in mud (Atkinson & Nash, 1990) and sand (Witbaard & Duineveld, 1989; this study) may be related not to dissimilarities in sediment granulometry but to the associated food content of the substratum. At the North Sea study site, the sediment has a much lower organic matter content than at the Scottish site [1-2% (present) versus 7-8% (Atkinson, 1988)]. The inference is that beneath the surface of the seabed *C. subterranea* mines the organic food component of the sediment effectively and efficiently as possible. In addition, it is possible that the increased number of surface openings is an attribute related to opportunistic sediment trapping of surface-deposited detritus. Therefore, *C. subterranea* would need to construct a more complex burrow system in the North Sea than it would in the more organically rich sediments of the sea lochs of Scotland to support its energetic requirements. Interestingly, the mean size of *C. subterranea* is greater at the

Scottish site than at the North Sea sites (L. Nickell, *pers. comm.*). This observation supports the argument that individuals from the Scottish population find it relatively easier to sustain themselves and presumably utilise surplus energy to become effectively larger.

The absence of any relationship between shrimp size and vertical burrow dimensions, in particular, is contrary to expectation (Witbaard & Duineveld, 1989). The results may be somewhat misleading and the consequence of the restricted nature of the data, though it is possible that the isolated laboratory conditions could reduce the necessity for individuals to spatially partition themselves with depth. The fact that no relationship was observed between shrimp size and the diameters of burrow turning chambers and inhalant openings is perhaps not surprising. *Callianassa subterranea* use turning chambers to perform changes of direction, frequently by somersault; such actions are relatively uncontrolled and will therefore lead to the creation of a space only roughly proportional to the shrimp's size. Funnel-shaped inhalant openings are not thought to be created by the shrimp's themselves (none was observed within the funnel), rather they are most likely a product of sediment slumping around the initial surface connection of the vertical shaft. The diameter of such shafts are related to shrimp size. However, it is unlikely that such small changes ($\pm 1\text{mm}$) could be transmitted linearly to the diameter of a physically controlled feature.

The influence that a complex burrow can have upon the structural and geotechnical characteristics of the substratum in which *Callianassa subterranea* resides has been discussed to some extent in Chapter 2. In particular it should be noted that the mean depth of mud shrimp's lateral burrow shafts (13cm) often corresponds with the high geotechnical measures (sediment water, organic and fine fraction content) which punctuate the otherwise reduced values of such parameters below near-surface sediment (eg, station 5 in May, Figs 2.4-2.6). The latter finding is not surprising as the presence of water-filled burrows is frequently associated with increases in sediment water content (eg, Rowe, 1974), whilst the walls of callianassid burrows themselves are sites of high organic matter levels (Vaugelas & Buscail, 1990) and areas of preferential fine-grain sorting (Dobbs & Guckert, 1988). The transport of the sediment resulting from the

burrowing and feeding activities of *C. subterranea* may possibly have a more significant bioturbatory effect and this is discussed in the following two chapters.

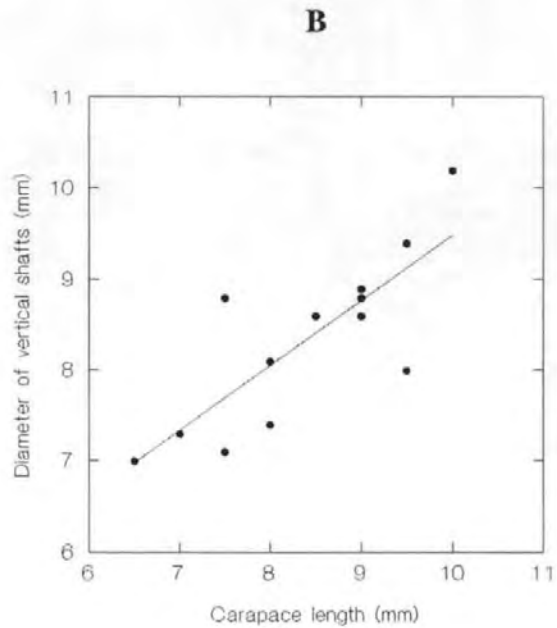
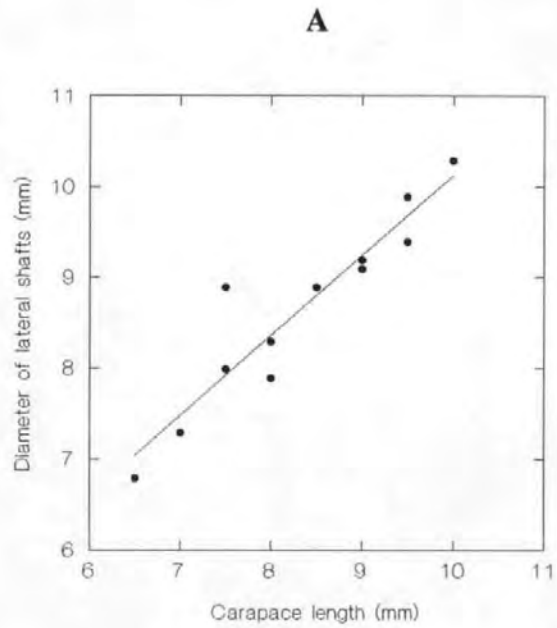


Figure 4.1. The relationship between the carapace length (mm) of *Callianassa subterranea* and **A**, diameter of lateral shafts (mm) ($y = 0.880x + 1.320$, $n = 13$, $r = 0.936$, $P = < 0.0001$); **B**, diameter of vertical shafts (mm) ($y = 0.717x + 2.311$, $n = 13$, $r = 0.799$, $P = < 0.001$).

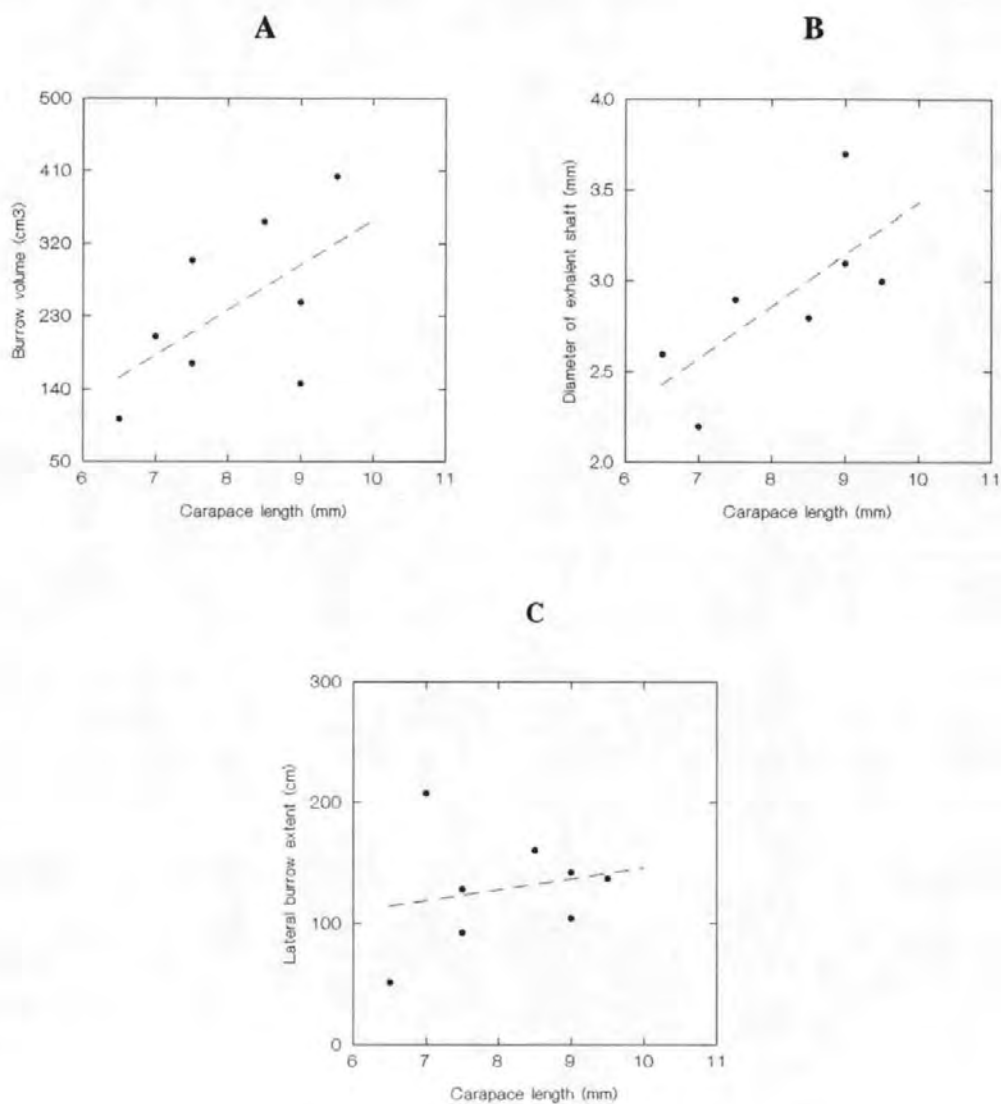


Figure 4.2. The relationship between the carapace length (mm) of *Callianassa subterranea* and **A**, burrow volume (cm³); **B**, diameter of exhalant shaft (mm); **C**, lateral burrow extent (cm) (broken lines illustrate trend only as least squares linear regression not significant, $P = > 0.05$).

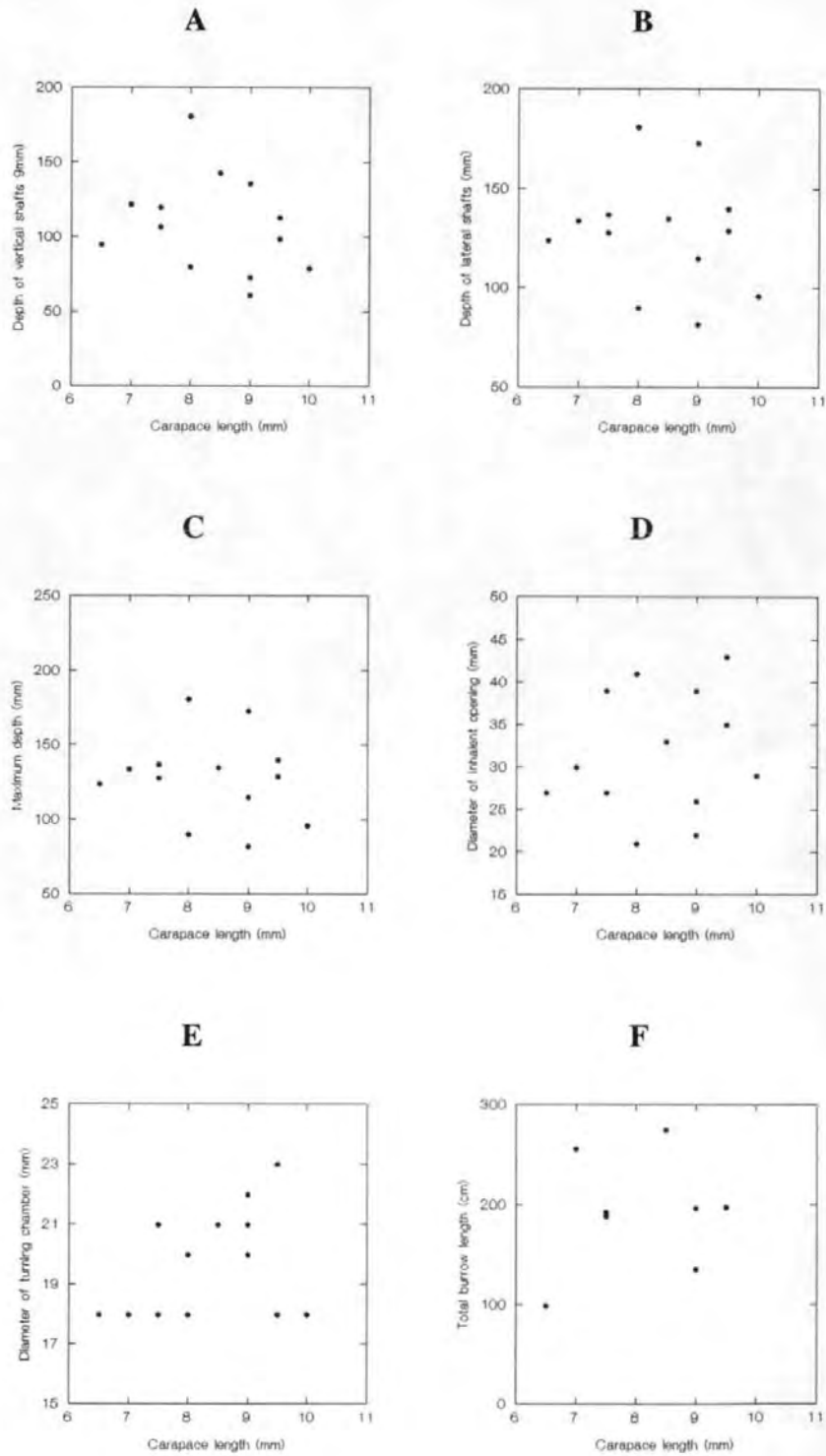


Figure 4.3. Relationship between the carapace length (mm) of *Callianassa subterranea* and **A**, depth of vertical shafts (mm); **B**, depth of lateral shafts (mm); **C**, maximum burrow depth (mm); **D**, diameter of inhalent openings (mm); **E**, diameter of turning chamber (mm); **F**, total burrow length (cm).

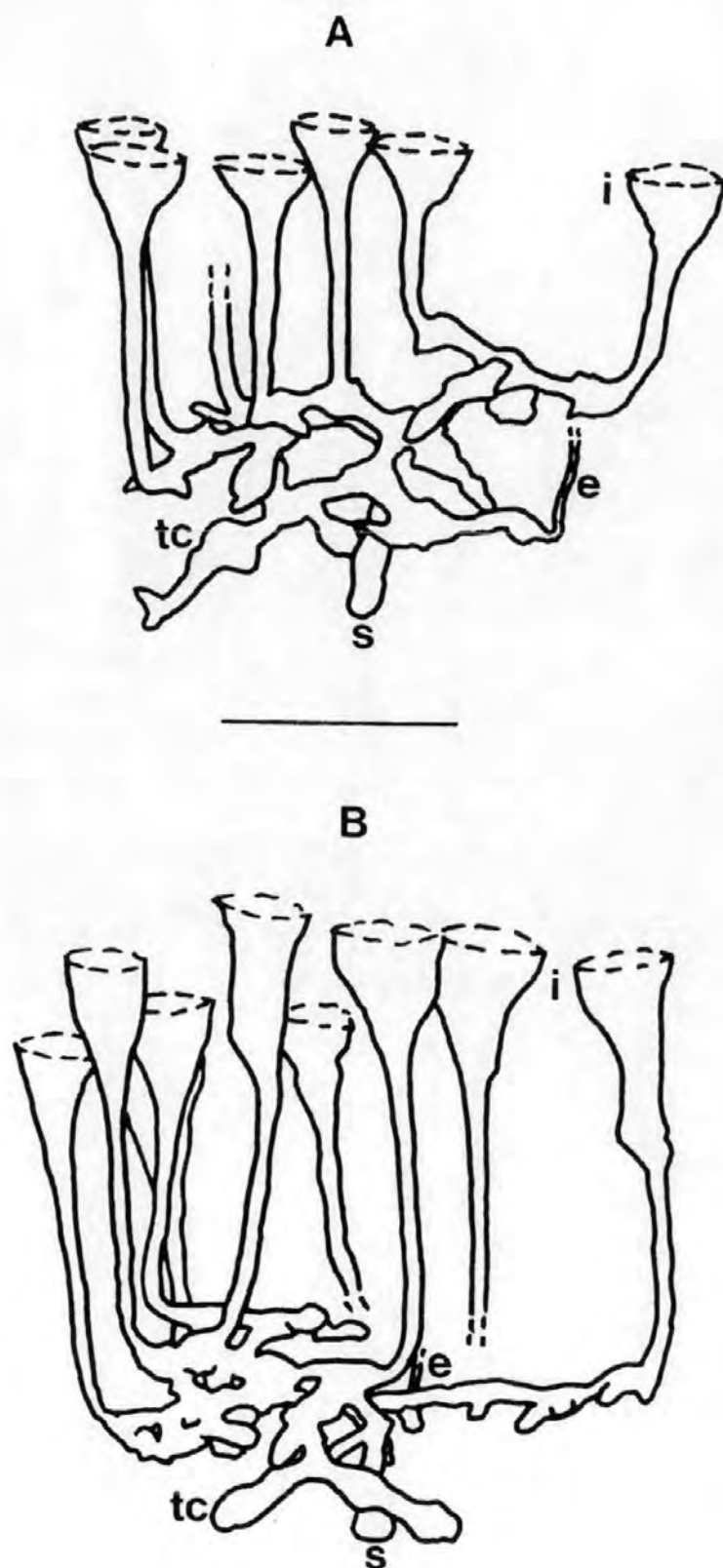


Figure 4.4. *Callianassa subterranea* burrow resin casts made in **A**, sandy sediment from the North Sea study site; **B**, redrawn from Witbaard & Duineveld (1989) (i= inhalant opening, e= exhalant shaft, s= sump, tc= turning chamber)(scale bar= 10cm).

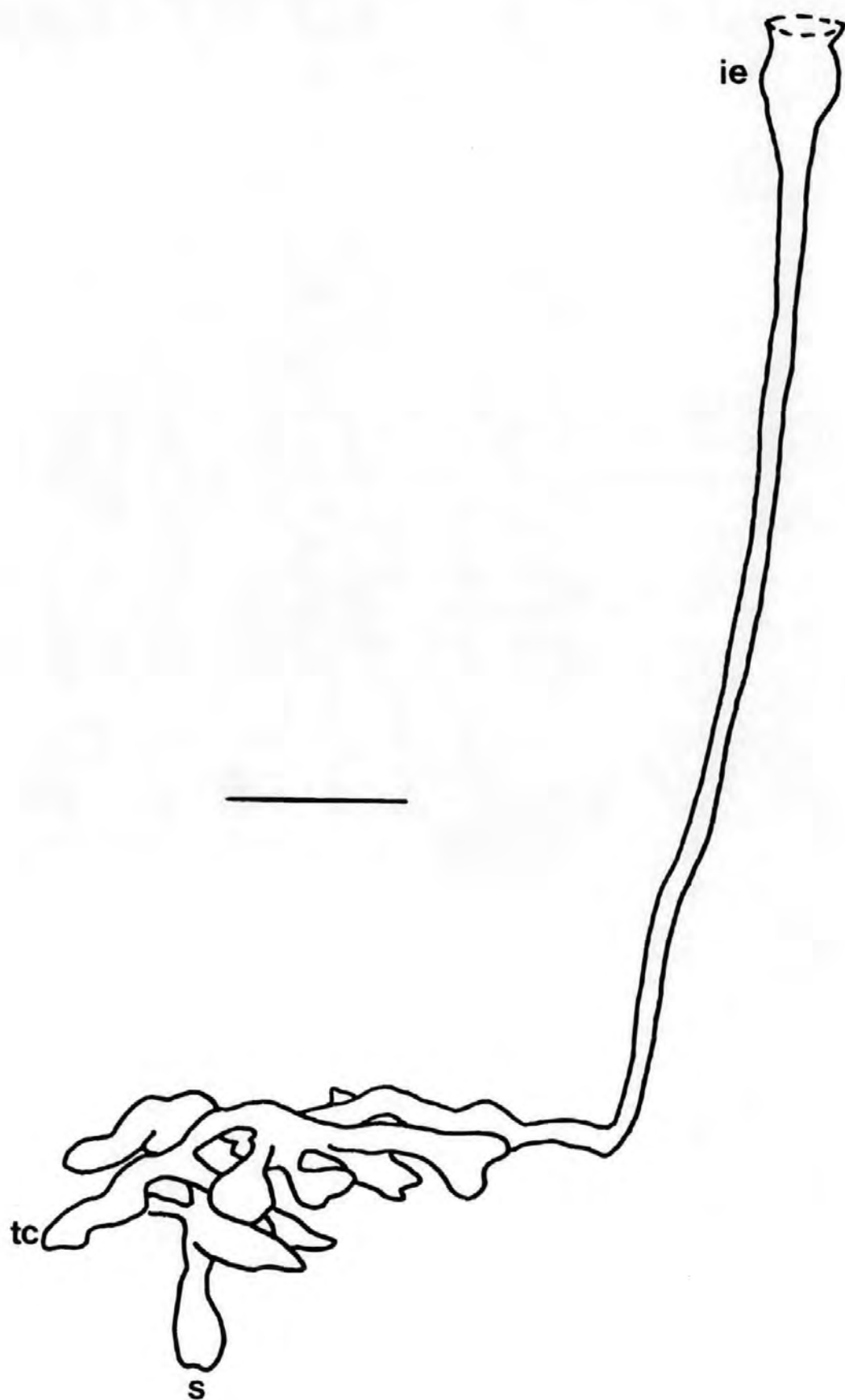


Figure 4.5. *Callianassa subterranea* burrow resin cast made in muddy sediment from a Scottish sea loch (redrawn from Atkinson & Nash, 1990) (ie= inhalant and exhalant opening, s= sump, tc= turning chamber)(scale bar= 10cm).



Plate 4.1. Epoxy resin being poured into the burrow openings (enclosed by plastic rings) of *Callianassa subterranea* aboard R.R.S. *Challenger* (box core= 0.25m²).



Plate 4.2. Photograph showing the inhalent openings (1) and exhalent opening (2) (surrounded by an expulsion mound) produced by an individual *Callianassa subterranea* (M#3, see Table 4.1) immediately prior to resin casting (scale bar marked in cm, microcosm diameter= 30cm).

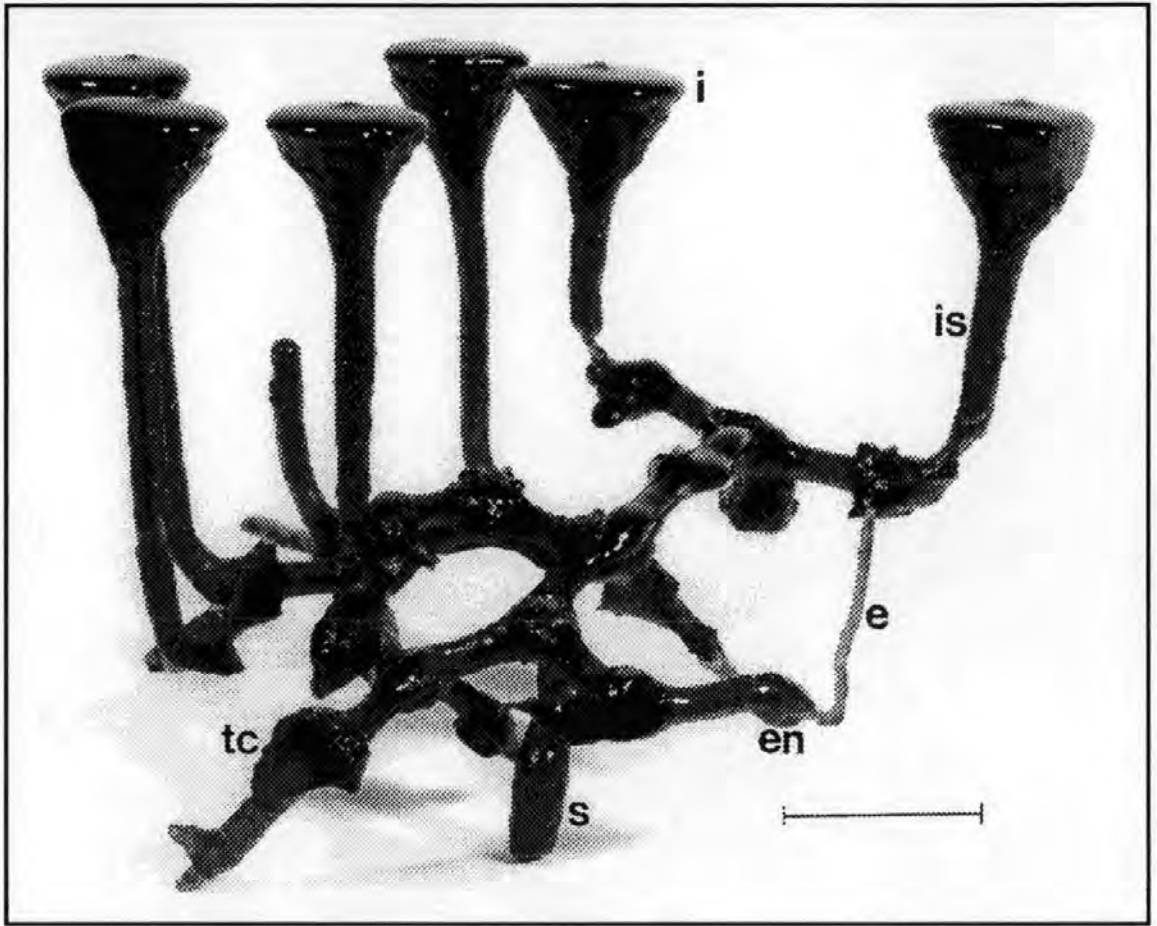


Plate 4.3. Lateral view of the resin cast of a laboratory burrow constructed by a male *Callianassa subterranea* (7.5mm carapace length; maximum depth 19.3cm, volume 300cm³) (i= inhalant opening, is= inhalant shaft, e= exhalant shaft, en= expulsion nodule, s= sump, tc= turning chamber) (scale bar= 5cm).

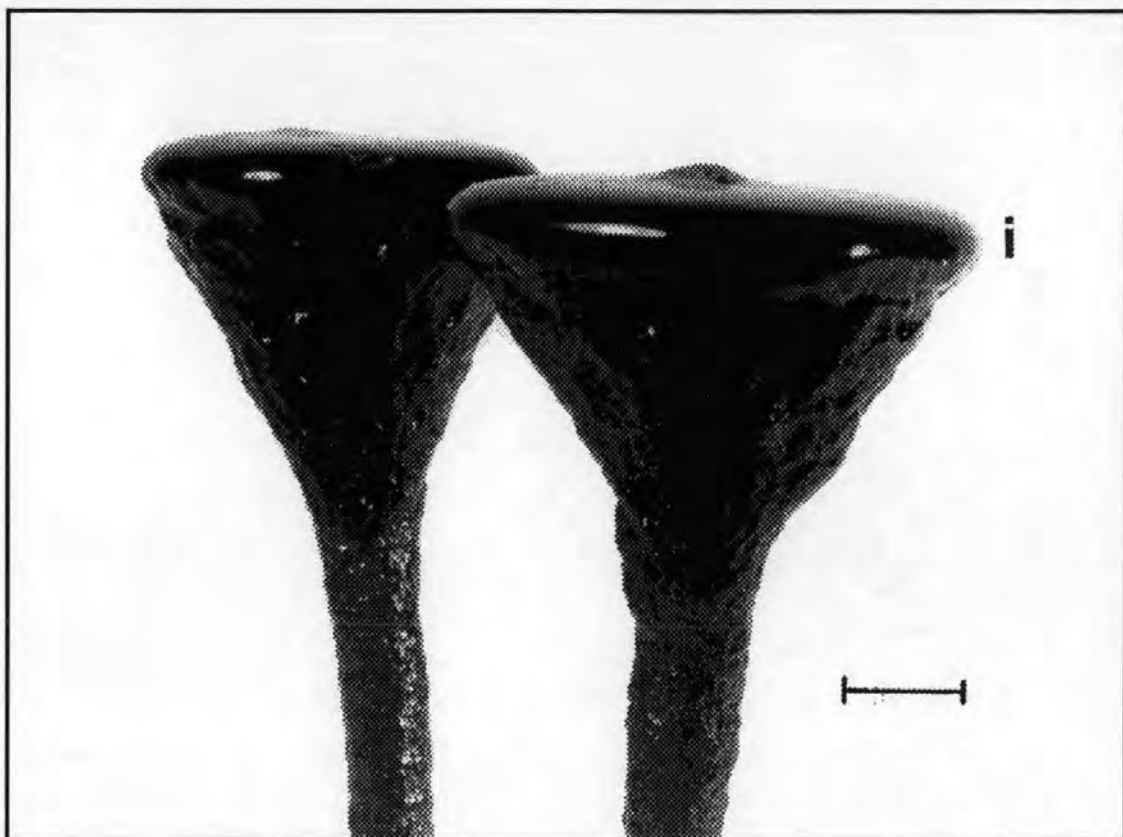


Plate 4.4. Funnel-shaped inhalant openings (i) to a burrow constructed by *Callianassa subterranea* (scale bar= 10mm).

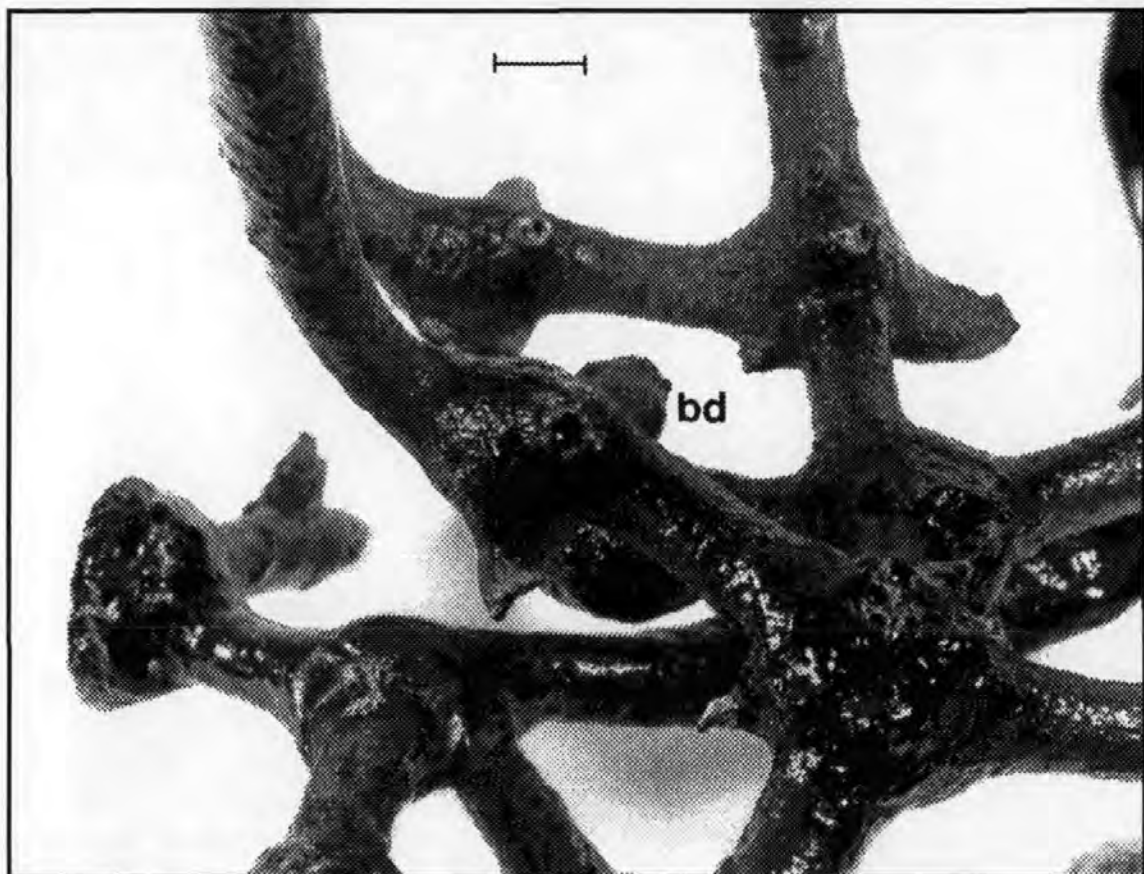


Plate 4.5. Oblique view of burrow dilation (bd) at base of vertical shaft constructed by *Callianassa subterranea* (scale bar= 5cm).

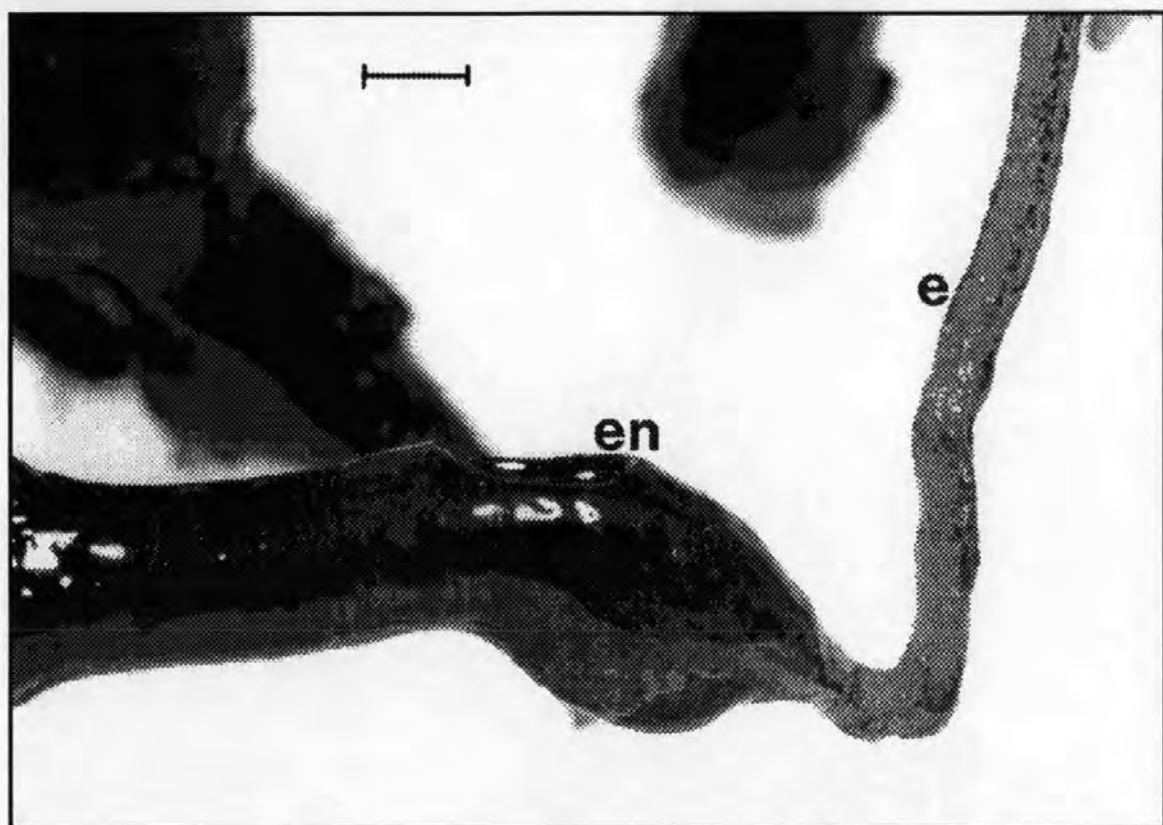


Plate 4.6. Lateral view (detail) of expulsion nodule (en) and exhalent shaft (e) constructed by *Callianassa subterranea* (scale bar= 5mm).

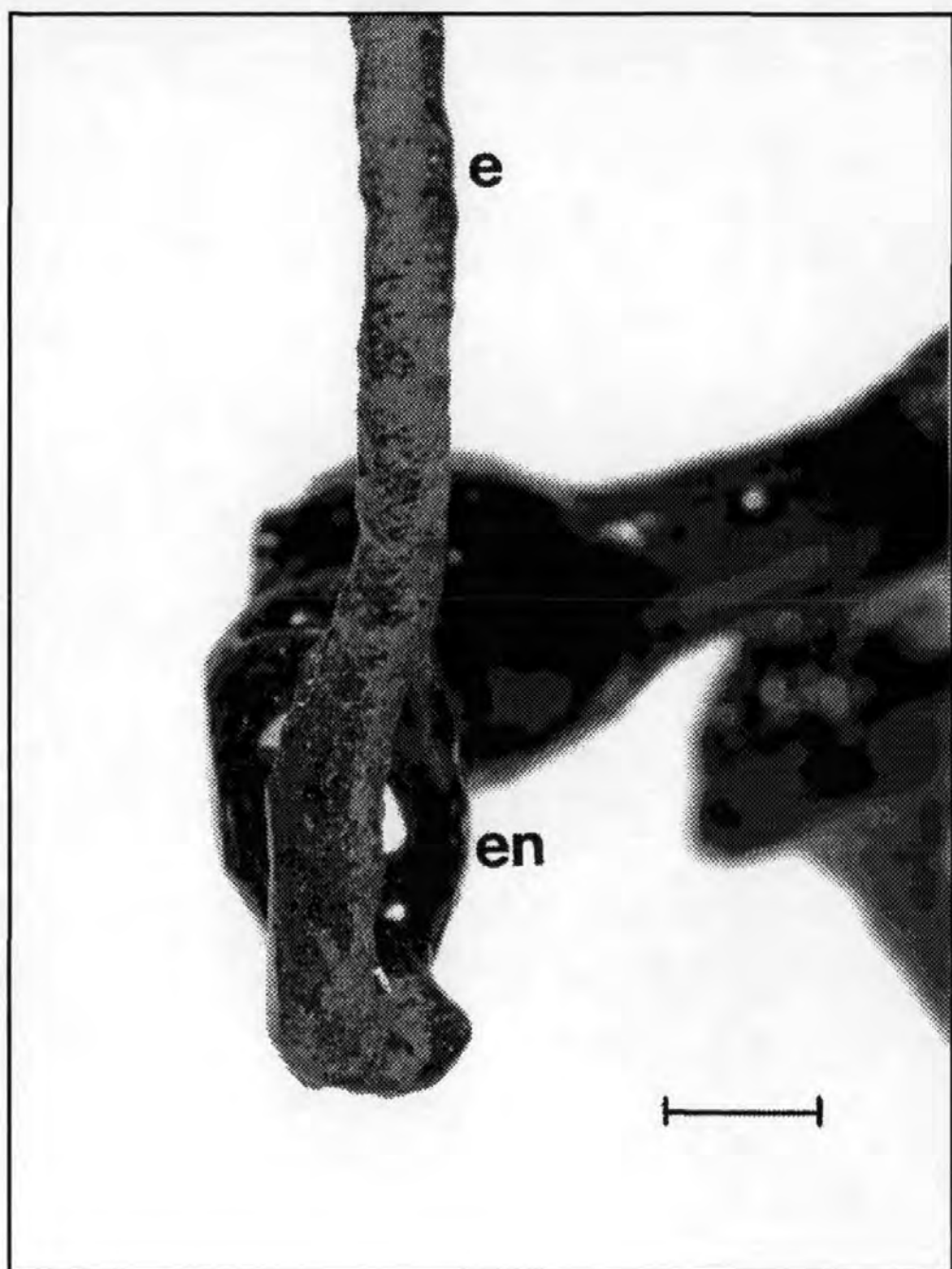


Plate 4.7. Face view (detail) of exhalent shaft (e) emerging from expulsion nodule (en) constructed by *Callianassa subterranea* (scale bar= 5mm).

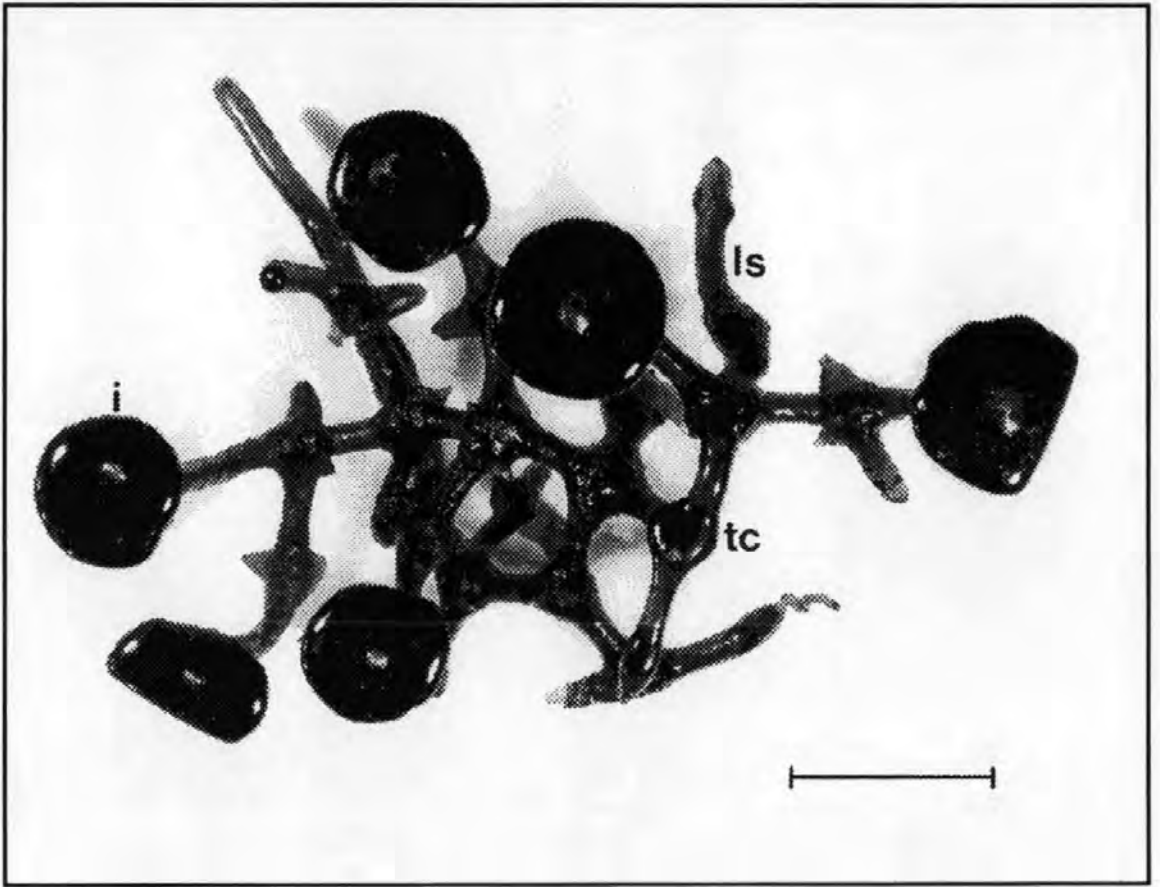


Plate 4.8. Surface view of resin cast of burrow constructed by *Callianassa subterranea* showing overlapping shafts (ls= lateral shaft, tc= turning chamber, i= inhalant opening) (scale bar= 5cm).

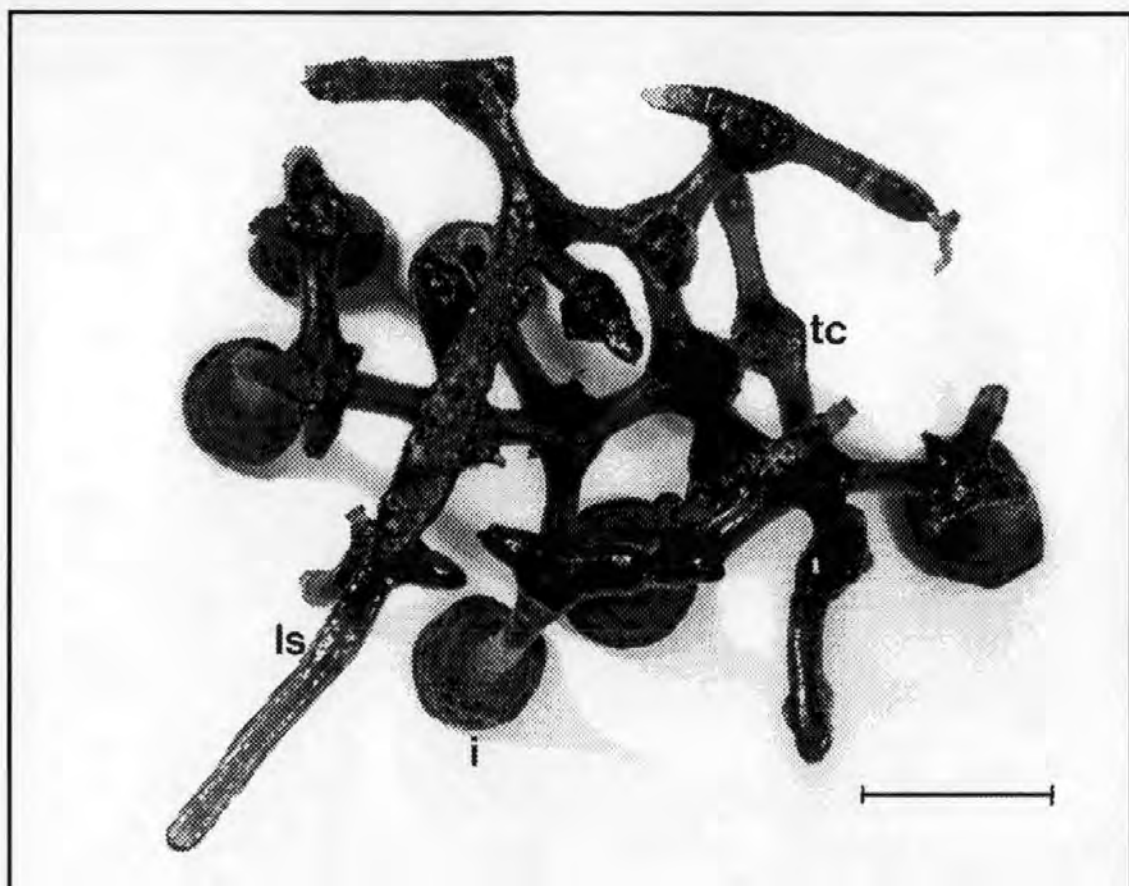


Plate 4.9. Underside view of resin cast of burrow constructed by *Callianassa subterranea* showing overlapping shafts (tc= turning chamber, i= inhalant opening, ls= lateral shaft) (scale bar= 5cm).

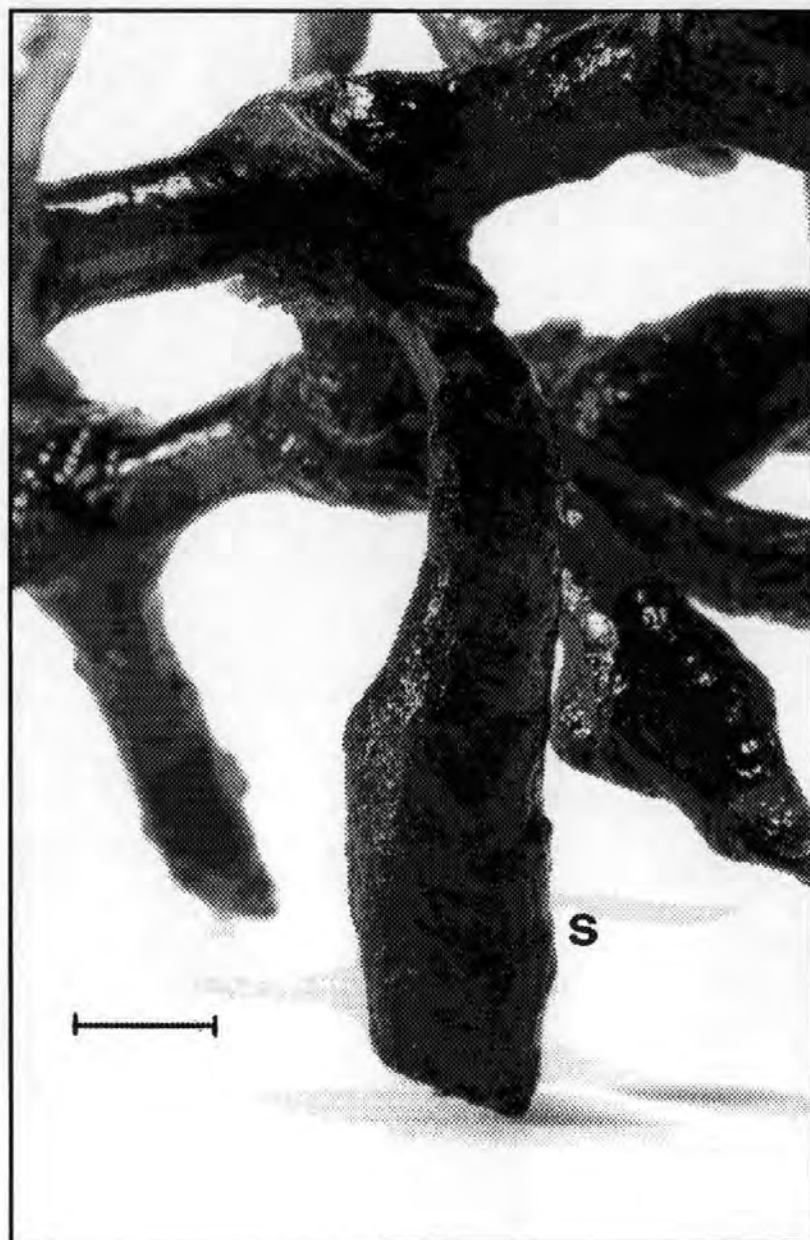


Plate 4.10. Lateral view (detail) of burrow sump (s) constructed by *Callianassa subterranea* (scale bar= 10mm).

	<i>F</i> #1	<i>F</i> #2	<i>F</i> #3	<i>F</i> #4	<i>M</i> #1	<i>M</i> #2	<i>M</i> #3	<i>M</i> #4	<i>M</i> #5	<i>M</i> #6	<i>M</i> #7	<i>M</i> #8	<i>M</i> #9
<i>CL</i> (mm)	7.0	8.0	9.0	9.5	10.0	8.0	7.5	6.5	9.0	9.5	7.5	8.5	9.0
<i>dV</i> (mm)	122	181	136	113	79	80	107	95	61	99	120	143	73
<i>dL</i> (mm)	134	181	173	129	96	90	137	124	82	140	128	135	115
<i>dmax</i> (mm)	188	194	230	150	120	90	193	132	107	208	180	220	150
<i>ØV</i> (mm)	7.3	7.4	8.6	8.0	10.2	8.1	8.8	7.0	8.9	9.4	7.1	8.6	8.8
<i>ØL</i> (mm)	7.3	7.9	9.1	9.4	10.3	8.3	8.9	6.8	9.1	9.9	8.0	8.9	9.2
<i>nIN</i>	4	5	4	4	4*	2*	6/7	7	6	6/7	8	8	2*
<i>ØIN</i> (mm)	30	41	39	35	29	21	39	27	22	43	27	33	26
<i>nC</i>	27	-	18	-	-	-	21	11+	19	21	21	21	-
<i>ØC</i> (mm)	18	18	20	18	18	20	21	18	21	23	18	21	22
<i>nEX</i>	2	-	1	-	-	2	1/2	1	3	1/2	1	2	2
<i>ØEX</i> (mm)	2.2	-	3.1	-	-	-	2.9	2.6	3.7	3.0	-	2.8	-
<i>LE</i> (cm)	208	-	143	-	-	-	129	52	105	138	93	161	-
<i>Tlen</i> (cm)	256	-	197	-	-	-	193	99	136	198	189	275	-
<i>Vol.</i> (cm ³)	206	-	248	-	-	-	300	104	148	404	173	348	-

Table 4.1. Morphological details of burrow resin casts constructed by *Callianassa subterranea* in laboratory microcosms (90 days, 15°C).

Key: M = male; F = female; CL = carapace length of shrimp; dV = mean depth of vertical shafts; dL = mean depth of lateral shafts; dmax = maximum depth of burrow; ØV = mean diameter of vertical shafts; ØL = mean diameter of lateral shafts; nIN = number of inhalent entrances; ØIN = mean diameter of inhalents; nC = number of turning chambers; ØC = mean diameter of turning chambers; nEX = number of exhalent exits; ØEX = mean diameter of exhalent shaft(s); LE - lateral extent (total length of lateral shafts and turning chambers); Tlen = total length of burrow system (lateral extent plus total length of vertical shafts); Vol. = Volume of burrow system (derived from weight of cast and density of resin).

Note: * These shrimps began to close off inhalent openings just prior to casting, possibly as a response to the detection of resin in the water. Therefore the number of inhalents cast was deemed unrepresentative and omitted from subsequent analysis.

Source	Size range of study indiv.	No. of inhalent openings	No. of turning chambers	Max. burrow depth (cm)	Burrow volume (cm ³)
Atkinson & Nash, 1990 (M)	7.6-15.5' mmCL	1.2 ± 0.8 [13]	10 ± 3 [13]	81 [13]	414 ± 237 [13]
Witbaard & Duineveld, 1989 (S)	4.1-11.5 mmCL	9.5 ± 0.7 ² [2]	23 ²	25 [?]	120 ± 165 [10]
This study (S)	6.5-10.0 mmCL	5.9 ± 1.6 [10]	21 ± 3 [7]	23 [13]	241 ± 103 [8]

Table 4.2. Burrow dimensions of *Callianassa subterranea* determined from resin casts constructed in muddy (M) and sandy sediment (S) ($\pm 1SD$, $[n]$ = number of observations).

Note: ¹ converted from shaft diameter to carapace length using the equation $y = 0.880x + 1.320$ (this study), ² taken from published photographs.

CHAPTER 5
SEDIMENT TURNOVER BY
CALLIANASSA SUBTERRANEA

[Aspects of this chapter are included in Rowden, *et al.* "The role of *Callianassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea", (*Continental Shelf Research*, submitted), were presented at the 1st European Crustacean Conference, Paris, August, 1992 and are included in Rowden & Jones "Critical evaluation of sediment turnover estimates for Callianassidae" (*Journal of Experimental Marine Biology and Ecology*, in press).]

5.1. Introduction

Unwanted sediment, produced by callianassid shrimps during the course of burrow construction/maintenance and feeding (ie, pseudofaeces and faeces), is ejected from the burrow and forms mounds on the substratum surface (Atkinson & Taylor, 1988). Large quantities of sediment [up to 12kg(wet)/m²/day] can be expelled (Branch & Pringle, 1987) and mounds often reach heights of 30cm (Riddle, 1988). Such bioturbatory activity of callianassids has important consequences for the structural and geotechnical characteristics of the substratum (Bird, 1982). For example, the selective burial of coarse sediment fragments, and the transport of finer particles to the surface to form a homogeneous upper layer, is common in coral reef lagoons inhabited by callianassid shrimps (Tudhope & Scoffin, 1984). In regions where the seabed has been contaminated by nuclear testing, the presence and activity of *Callianassa* species is linked to significant sediment and radioactive particulate resuspension (Roberts *et al.*, 1981; Colin *et al.*, 1986).

The principal method of assessing biogenic activity is to estimate sediment turnover rates (Lee & Swartz, 1980; Thayer, 1983). The most widely-used method of estimating sediment turnover rates is Direct Entrapment, which involves placing a simple trap over the site of sediment ejection (usually a mound) and collecting the expelled sediment after a given time (eg, Roberts *et al.*, 1981). The sampling is performed mostly *in situ*, although some sediment has been collected in the laboratory from shrimps recovered at sites below SCUBA-diving working depth (eg, Witbaard & Duineveld, 1989). A second method of estimating sediment turnover rates, Levelling, involves the removal of all surface sediment features from a delineated area to a recognised datum, usually a flat plane, or to a clearly marked surface horizon. Mounds of sediment which then appear after a prescribed time are assumed to result from callianassid expulsion activity and their dimensions are measured either *in situ* or they are carefully collected for laboratory weight/volume determination (Suchanek *et al.*, 1986; Swinbanks & Luternauer, 1987). A third method, the Tracer Particle method, utilises labelled sediment (usually coloured with fluorescent dye/paint) which is placed at depth(s) in the study area. Cores are taken after a prescribed time, sectioned, and the relative depth occurrence of the labelled particles is quantified; sediment turnover is estimated from the extent of the subsequent

net redistribution of the labelled particles. The latter technique has been used extensively for calculating the sediment turnover rates for bioturbators such as polychaetes (Gordon, 1966; Gerino, 1990) but has been applied rarely to callianassids (Branch & Pringle, 1987).

For callianassids, the expression of sediment turnover usually involves the three parameters of quantity, space and time. When the Direct Entrapment method is used, the quantity of sediment collected is expressed usually by weight (wet or dry) or volume (by displacement) (eg, Vaugelas *et al.*, 1986). The Levelling method also uses weight/volume when the sediment is collected directly or a volume approximation, based on the measured dimensions of height and breadth of each mound converted to a volume using the formula for a cone (Suchanek & Colin, 1986). The use of the Tracer Particle method results in the sediment turnover estimate being expressed initially in terms of sediment deposition depth (Aller & Dodge, 1974), however, conversions are sometimes made (eg, depth to weight; Branch & Pringle, 1987). The quantity of sediment determined by the Direct Entrapment method is derived generally from collections of individual mounds/shrimps. The sediment expelled (weight/volume) may be expressed per individual mound/shrimp or scaled to a surface area by taking into account population or mound density (Suchanek, 1983). The results of the Levelling method of sediment collection may be related to the surface area of the study plot or scaled to per m² (Vaugelas *et al.*, 1986). Sediment turnover estimates derived from the Tracer Particle method, expressed as depth of deposition, are independent of area and thus require no spatial unit. The length of time over which the sediment expelled is collected is the usual time unit incorporated into the final estimate of sediment turnover, although sometimes there is scaling of the temporal unit up or down (eg, week to year; Witbaard & Duineveld, 1989).

The present expulsion activity experiment adopted the Direct Entrapment method as the most practical and applicable for intensive laboratory study (see Chapter 7 for further discussion). The experiment was designed to estimate, via extrapolation of the measured expulsion rates of individuals of known size and sex at three experimental temperatures, the amount of material expelled to the sediment surface by the *Callianassa subterranea* population at the North Sea study site over a year.

5.2. Materials and Methods

5.2.1. Collection and maintenance of test animals

Experimental animals and sediment were collected using a box corer in April and July 1990 from station 13 at the North Site (see Chapter 2 for details). At each visit, ten box cores were taken to ensure sufficient animals and sediment for the laboratory study. *Callianassa subterranea* were hand sorted from the recovered cores, and placed individually into 1-l pots containing native sediment and seawater. The pots were housed in a constant temperature room, adjusted to the seawater temperature at collection, for the remainder of each cruise (April = 7°C for 14 days, July = 13°C for 7 days). Each day, moribund individuals were removed and the seawater was replaced at 48h intervals. The sediment from the box cores was bagged and frozen on board the ship. During transport to Plymouth (8h journey), the animals were packed in a container insulated with quantities of ice, whereas the sediment was uninsulated and refrozen on arrival.

5.2.2. Laboratory design, sample collection and treatment

Callianassa subterranea of known sex and size (Table 5.1) were placed individually into microcosms made from grey plastic tubing with wooden bases (Fig. 5.1A). Each microcosm measured 30cm (diameter) by 40cm (depth), approximating the natural space requirements of individual animals at the North Sea study site (site mean = 19 adult shrimps/m² = 0.05m²/individual, microcosm surface area = 0.07m², see Chapter 3 for population details). Prior to introduction of the shrimps, native defaunated sediment had been allowed to "settle" for two weeks in each microcosm. The microcosms were arranged within a large tank (approx. 3m x 1m) of circulating seawater which was maintained at a constant temperature ($\pm 1^\circ\text{C}$) (Fig. 5.1B). The experiment was conducted at three temperatures, which reflected the seawater temperatures measured at the site during the main study months of January (7°C), May (9°C) and September (15°C) 1989. Fresh shrimps were used at each temperature and these were acclimated to the experimental temperatures for two weeks prior to use.

Almost immediately after introduction to the sediment, each animal began to burrow, and records of the burrowing behaviour and surface features produced were taken at daily intervals. The day after disappearance beneath the sediment surface (deemed day

1), all pseudofaecal and faecal material expelled to the surface was collected (daily for the first seven days, twice weekly thereafter for 9 & 15 °C, and after one month for 7°C) over a 90-day period. When the exhalent opening of the burrow was conspicuous, a collector (130ml dessert pot with a hole in its base) was placed over the exit. Expelled material was easily, and accurately, removed from the collector with the aid of a large syringe (60ml). The material collected was decanted into separate pots (250ml), and vacuum filtered (Whatman GF/C 9cm), washed (to remove salt), dried (100°C overnight) and weighed (Sartorius R200D balance, $\pm 0.01\text{g}$).

5.3. Results

5.3.1. Pattern and rate of sediment expulsion

The rate at which sediment was expelled by each test animal for each experimental temperature was recorded over the duration of the laboratory study (Tables 5.2-5.4). For each shrimp, there was an initial period of intensive activity as the burrow was constructed, easily recognisable by a distinctly rapid rate of sediment expulsion (between 5-20 days). Only one test animal failed to display evidence of an initial increase in expulsion activity and this individual was omitted from subsequent analysis, on the grounds that its behaviour was possibly unrepresentative (ID #M1; Table 5.1). After the burrow construction phase, shrimps ejected sediment from their burrows in regular and discrete periods of expulsion activity, during which they were presumably feeding and maintaining the burrow structure (Fig. 5.2). Nearly all test animals displayed this general form of sediment expulsion behaviour when maintained at 15°C and 9°C (Figs 5.3 & 5.4). However, an accidental increase in experimental temperature (15°C maximum) over 10 days (the change was not acted upon during an absence from laboratory) during the 9°C study, produced an associated increase in sediment expulsion rate in the middle of the behaviour profile (this segment of data was omitted from subsequent analysis). Very little sediment was ejected by *Callinassa subterranea* kept at 7°C and the consequent low collection frequency did not allow any description of expulsion behaviour (Fig. 5.5). At 9°C and 15°C, the active phases of sediment expulsion were separated by periods of no measurable ejection of unwanted material, deemed "expulsion

inactivity". The duration and frequency of expulsion inactivity for each test animal was calculated to define sediment expulsion periodicity. Duration was simply identified as the mean number of days of inactivity for each individual shrimp (Table 5.5A). Frequency was measured as the average occurrence of inactivity in a calendar month (ie, thirty, divided by the mean number of days between each successive period of inactivity) (Table 5.5B). A significant linear relationship (least squares regression, all $P = < 0.05$) exists between *C. subterranea* size and the two parameters used to characterise expulsion inactivity (Figs 5.6A & 5.6B). With increasing body size, the periods of idleness become longer and less frequent for animals kept at 9°C and 15°C.

Mean daily expulsion rates were calculated for each individual test animal based on the periods when *Callianassa subterranea* was actively ejecting sediment. The daily rate was derived from the weight of the sediment collected on sampling, divided by the number of days over which it had been expelled (Table 5.6). The results show that the amount of material expelled to the surface as mounds was related significantly to shrimp size and the temperature at which the test animals were maintained (least squares regressions, all $P = < 0.05$, Figure 5.7). Figure 5.7 illustrates that smaller animals produce less faeces and pseudofaeces than larger ones, and animals experiencing the summer temperature (15°C) expel significantly greater quantities of sediment than those experiencing both the spring (9°C) and winter temperatures (7°C) (ANCOVA; F-ratio = 3.893, $df = 2, 12$, $P = < 0.05$).

5.3.2. Calculation of monthly sediment processing and annual sediment expulsion budget

The population structure of *Callianassa subterranea* at the study site (Chapter 3), together with the results of the expulsion activity experiment, allow an estimation of the amount of particulate material expelled to the sediment surface by the burrowing and feeding activities of these animals for the three study occasions (Table 5.7). Regression-derived values for frequency and duration of inactivity enable calculation of the number of days a *C. subterranea* of a particular size actively expels sediment. For example, in September an individual of 6.5mmCL has an inactive period of 3.53 days which occurs 2.13 times each month. By subtracting from the number of days in the month, the

duration multiplied by the frequency of inactivity, the amount of time an animal of this size actively expels sediment in a month can be estimated [eg, September, $30 - (3.53 \times 2.13) = 22.48$ days]. The individual monthly expulsion rate can be calculated by multiplying the previously-determined value by the daily expulsion rate for an animal of a corresponding size [eg, September, 6.5mmCL: $22.48 \times 3.01 = 67.66$ g/month]. This rate can be combined with the measured density of *C. subterranea* to give a value for expelled sediment per unit area [eg, September, 6.5mmCL: $67.66 \times 2.4 = 162.38$ g/m²/month]. Finally, the results of such calculations for larger shrimps can be summed to give an estimate of the amount of sediment the population is responsible for expelling to the sediment-water interface. This results in values of 2.8 kg(dry)/m²/month for September, 0.4 kg(dry)/m²/month for May and 0.06 kg(dry)/m²/month for January. Large animals (6.0-11.0mmCL) represent a significant proportion of the population's weight or biomass (94% in September) (Table 5.8; Fig. 5.8) and are also likely to account for almost all of the sediment expelled to the surface as small animals are not extensive burrowers (Witbaard & Duineveld, 1989).

From a non-linear quadratic regression of the sediment expulsion rates, calculated for each of the three study months and temperature (Fig. 5.9), it is possible to obtain estimates of sediment turnover corresponding to temperatures between 6-15°C. Combining these predicted values with the seawater temperatures measured at the site during 1989 (British Oceanographic Data Centre, 1992), it is possible to construct an annual pattern of sediment expulsion for *Callianassa subterranea* (Fig. 5.10). The model illustrates that the shrimps expel relatively negligible quantities of sediment during the months of January to April [< 0.06 kg(dry)/m²/month], before they begin to steadily increase output through the spring and early summer [eg, July = 1.3 kg(dry)/m²/month]. The maximum expulsion rate is achieved at the end of the summer [September = 2.8 kg(dry)/m²/month], then activity decreases through the autumn before sediment expulsion returns to more modest rates, corresponding to the lower temperatures experienced at the year's end [December = 0.4 kg(dry)/m²/month]. The combined monthly estimates predict a total annual sediment expulsion of 11kg(dry)/m²/yr for *Callianassa subterranea* at the study site.

5.4. Discussion

Estimates of callianassid sediment turnover are based mostly on individuals from low latitudes and testify to the prodigious amount of material transported by these shrimps. Aller & Dodge (1974) attributed the capability of reworking up to 6-7cm of sediment in one week to a Jamaican callianassid, whilst Suchanek (1983) recorded a turnover rate of 2.59 kg(dry)/m²/day for callianassid shrimps in the Virgin Islands. Murphy & Kremer (1992) studied a less dense (than Suchanek, 1983) population of callianassid shrimps in the Virgin Islands and reported that their estimate for sediment turnover [291g(dry)/m²/day] did not vary significantly from year to year. The few "comparative" data from temperate regions also demonstrate the high capacity of callianassids for moving measurable quantities of material to the sediment surface. MacGinitie (1934), who was the first person to report an estimate of sediment turnover for any member of the Callianassidae, calculated that an individual *Neotrypaea (Callianassa) californiensis* expelled from its burrow approximately 20-50 ml of wet sediment per day. Warne (1967) estimated that between 10 to 100 times more sediment is placed on the surface by burrowing animals (mainly *N. californiensis*) than is added by tidal currents and other transportational agents in a Californian lagoon. The magnitude of the *N. californiensis*'s sediment turnover rate is supported by the observations of another temperate (Mediterranean) species, *Callianassa tyrrhena* [25cm³(wet)/indiv./day; Ott *et. al.*, 1976]. When shrimp densities are high, particularly for intertidal populations, sediment turnover rates in temperate regions can be impressive, eg, *Callianassa japonica* can occur at densities up to 430/m² and effectively turnover in excess of 4-l of wet sediment per m²/day (Tamaki, 1988). The first behavioural observations of *Callianassa subterranea* reported that individuals could produce mounds from which ejections of sediment were expelled 30cm high (Lutze, 1938), however, there have been few quantitative studies of the bioturbatory activities of *C. subterranea*. Although Swift & Kershaw (1986) identified *C. subterranea* as playing a role in the redistribution of radionuclides within the sediments adjacent to the Sellafield nuclear processing plant (Irish Sea), there was no significant correlation between the calculated mixing coefficients and corresponding shrimp density. Reporting on the preliminary findings of their studies with *C. subterranea* from the North Sea, Witbaard & Duineveld (1989)

recorded the first estimate of sediment turnover for the species as 3.5 kg(dry)/m²/yr. The present study has demonstrated the influence of body size and temperature upon the amount of sediment expelled by individual *C. subterranea*. In addition, the work was conducted over sufficient time to illustrate that sediment expulsion activity was not continuous, but a complex of active and inactive periods. Combining these experimental data with field information on seawater temperatures and population dynamics (density, size frequency), it has been possible to produce an annual sediment turnover budget of 11 kg(dry)/m²/yr for a site in the North Sea. This estimate is approximately three times higher than the value reported previously for the same species at this location (Witbaard & Duineveld, 1989). Possible reasons for the discrepancy between these estimates may be that Witbaard & Duineveld (1989) extrapolated from a weekly estimate, derived from four individuals in a single experimental tank, to an annual expression of sediment turnover. Such an example illustrates the problems associated with making meaningful comparisons of sediment turnover rates for callianassids, which appear to be essentially threefold.

1. *Methodology and estimate reporting*: Each of the three measurements of the quantity of sediment turned over (weight, depth and volume) have different attributes. Weight is likely to be measured with the most accuracy (there is an accepted procedure), depth is essentially an artificial measure (there is rarely an even deposition of sediment), whilst volume is open to criticism because determinations involve the error-inducing concept of "settling time" which may be defined (eg, 1h; Suchanek & Colin, 1986) or undefined (Swinbanks & Luternauer, 1987). It is thus difficult to make meaningful comparisons between the various sediment turnover estimates for callianassids as the quantity parameter is calculated, and expressed, by three very different methods (Table 5.9). Even those estimates using the same parameters may not be compared directly as they often incorporate possible errors related to different degrees of scaling. An example of the problem is demonstrated by the results of Branch & Pringle (1987) and Suchanek (1983) for two different *Callianassa* species. The former workers estimated a sediment turnover rate of 12.14 kg/m²/day using the Tracer Particle method and compared it with the latter's estimate of 2.59 kg/m²/day based on the Direct Entrapment method. Branch & Pringle's (1987) estimate was arrived at by scaling (i) a calculated sediment depth

deposition to an approximate weight (using a density measure for wet sediment), (ii) the area of study (490cm²) to m² and (iii) from one week to a day. On the other hand, Suchanek (1983) used only one scaling factor (individual mound measurements to natural mound density/m²).

The above example illustrates two other concerns. Firstly, the validity of comparing data collected by two different sampling methods. Suchanek & Colin (1986) utilised two techniques at the same location and found that the mean sediment turnover estimate obtained by Levelling was nearly twice as much as that determined by Direct Entrapment. The second concern is that ambiguity of reporting parameters can result in unlike comparisons being made. For the estimates of sediment turnover detailed in Table 5.9, the specific quantity unit is identified as dry or wet weight. Unfortunately, clarity of reporting units is not always available from the original paper. This problem resulted in Branch & Pringle (1987) unknowingly comparing their wet with a dry weight estimate of Suchanek (1983). Another example of ambiguity which hampers meaningful comparisons is that more than one form of the sediment turnover estimate is sometimes reported. Vaugelas *et al.* (1986) reported that *Glypturus armatus* was estimated to move 1660 g/mound/wk, or 76.8 kg/100m²/wk, or the equivalent of a layer of sediment 1cm thick taking 12-16wks to pass through the burrow. MacGinitie (1934), who provided the first estimate of sediment turnover rate for a callianassid, not only expressed the value in three different ways but additionally failed to report the details of sediment collection method and the turnover calculation.

2. *Precision and accuracy of calculation:* The value of any comparison between sediment turnover estimates is reduced by differences in the degree of precision and accuracy incorporated into the final calculation. Some estimates of sediment turnover are based on a small number of single observations (eg, Ott *et al.*, 1976), whilst others are from extensive and replicated studies (eg, Swinbanks & Luternauer, 1987). Even the more extensive studies, however, sometimes fail to incorporate fundamental information into the final estimate. For example, the deep-burrowing habit of callianassids makes population density difficult to determine using normal shallow-penetrating sampling gear; density is usually inferred indirectly from the number of ejection mounds (ie, 1 mound = 1 shrimp) (Vaugelas, *et al.*, 1986). Even when attempts have been made to relate

mounds (and/or other surface openings) more precisely to actual numbers, there is a degree of error attached to the apparent ratio which will be transmitted into the extrapolation (Dworschak, 1983). In addition to the problem of an accurate measurement of population density, the size-frequency structure of the population at the study site, and its effect on sediment turnover, is frequently ignored. For example, Suchanek & Colin's (1986) Direct Entrapment estimate of sediment turnover was obtained only from mounds greater than a defined size (Table 5.9). Lack of account for the influence of population size structure imposes error on the final estimate of sediment turnover (ie, if sediment quantity is expressed per total mound density then this will result in an over estimate; if expressed per defined size mound density then this will give an under estimate). The less-frequently adopted Levelling method is likely to reflect more accurately the sediment turnover rate, as it presumes to collect all the sediment expelled by the entire shrimp population within a given area. However, the effect of the physical disturbance of levelling on the activity of the shrimps is not known. Thus, it is possible that error will be incorporated into the subsequent estimate of sediment turnover, especially as the effect of disturbance will probably be size specific (eg, smaller individuals may take longer or never recover from the disturbance).

3. *Influence of behaviour and environment*: The frequency of sediment ejection by callianassids does not appear to follow any diurnal pattern (Suchanek, 1983). Few studies have elucidated temporal changes in sediment turnover rates and those that have, fail to include any differences in their final estimate. For example, differences in sediment expulsion rates between two sampling occasions, separated by more than two months (tropical region) and a 4°C change in temperature (temperate region), have been observed by Suchanek & Colin (1986) and Swinbanks & Luternauer (1987) respectively. Although a trend was demonstrated in each case, and its possible importance recognised, the authors expressed their final estimate of sediment turnover as a *mean daily* rate. Only Vaugelas & Saint Laurent (1984) measured long-term sediment turnover rates (weekly determinations over nearly eight months) for *Glypturus laurae* and demonstrated a distinctive pattern of sediment expulsion behaviour such that the amount of material expelled was different even between successive months. Unfortunately, the differences were not incorporated into their final *weekly* estimate (Table 5.9).

At present it is impossible to make valid and straightforward comparisons because of the diversity of the collection, calculation and expression methods of sediment turnover estimates. Previous attempts to compare turnover rates converted data to a common format, but such conversions introduced error as they were neither standard, equally applied, nor verified by the original authors (eg, Vaugelas, 1985, 1990). The ability to compare sediment turnover rates with confidence requires standardization of methods and reporting. Viewed alone, however, the turnover estimate derived for the population of *Callianassa subterranea* at the North Sea study site suggests that this species is responsible for transporting a considerable amount of sediment from depth to the substratum surface. Such impressive bioturbatory behaviour identifies *C. subterranea* as a potentially significant contributor to the resuspension of sediment in the North Sea. The following chapter examines the fate of the unconsolidated mounds of expelled sediment.

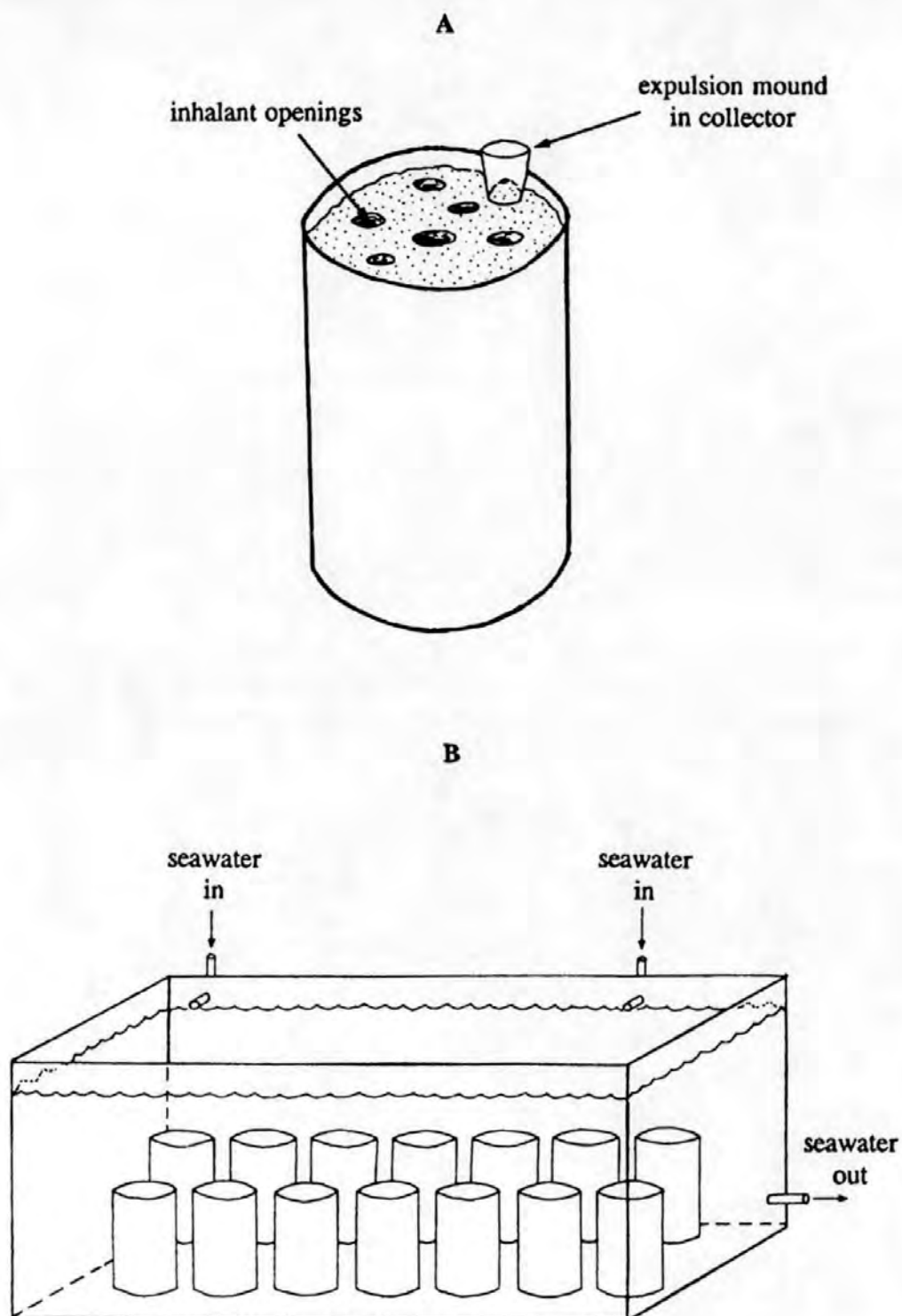


Figure 5.1. Microcosm arrangement for sediment expulsion activity experiment; **A**, individual microcosm tank (40 x 30cm) containing sediment and a burrowed *Callianassa subterranea*; **B**, main tank of circulating seawater (3 x 1m).

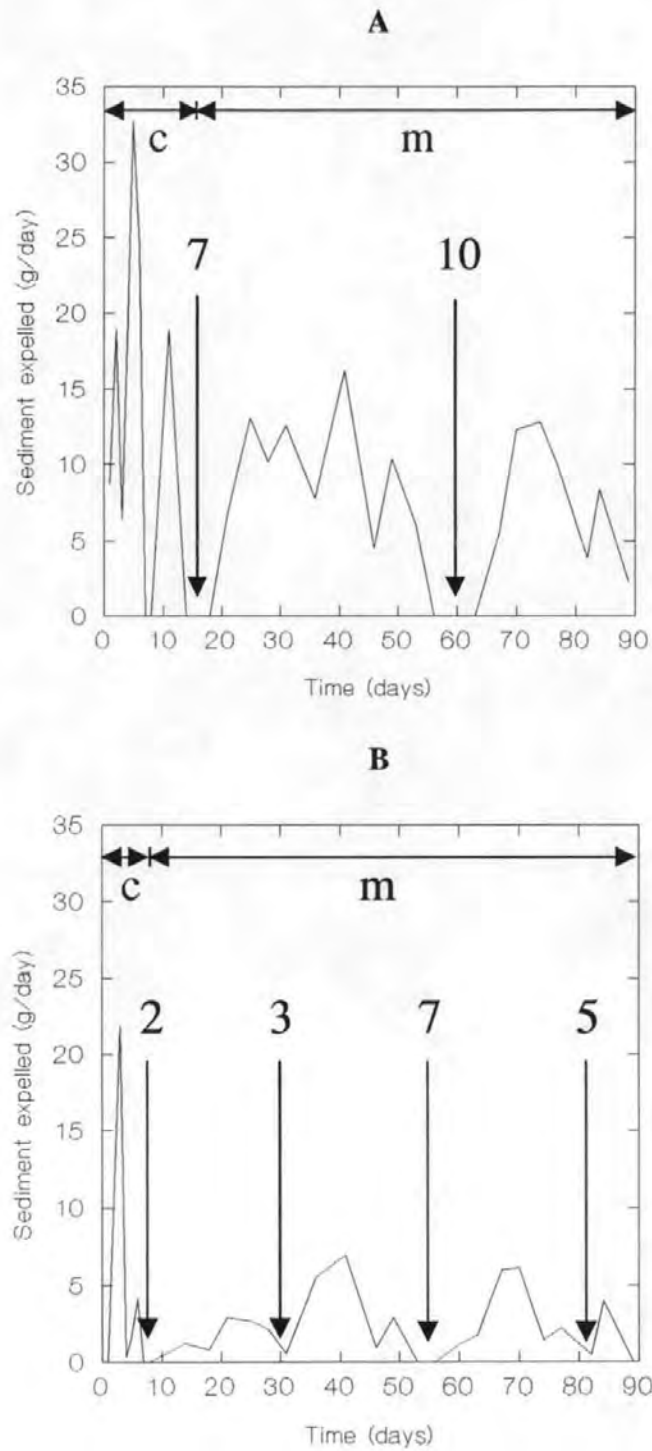


Figure 5.2. Examples of sediment expulsion behaviour by **A**, large (male, 9.5mmCL) and **B**, small (male, 6.5mmCL) *Callianassa subterranea* kept at 15°C (c= burrow construction phase, m= burrow maintenance and feeding phase; arrows indicate periods of inactivity and numbers show duration in days).

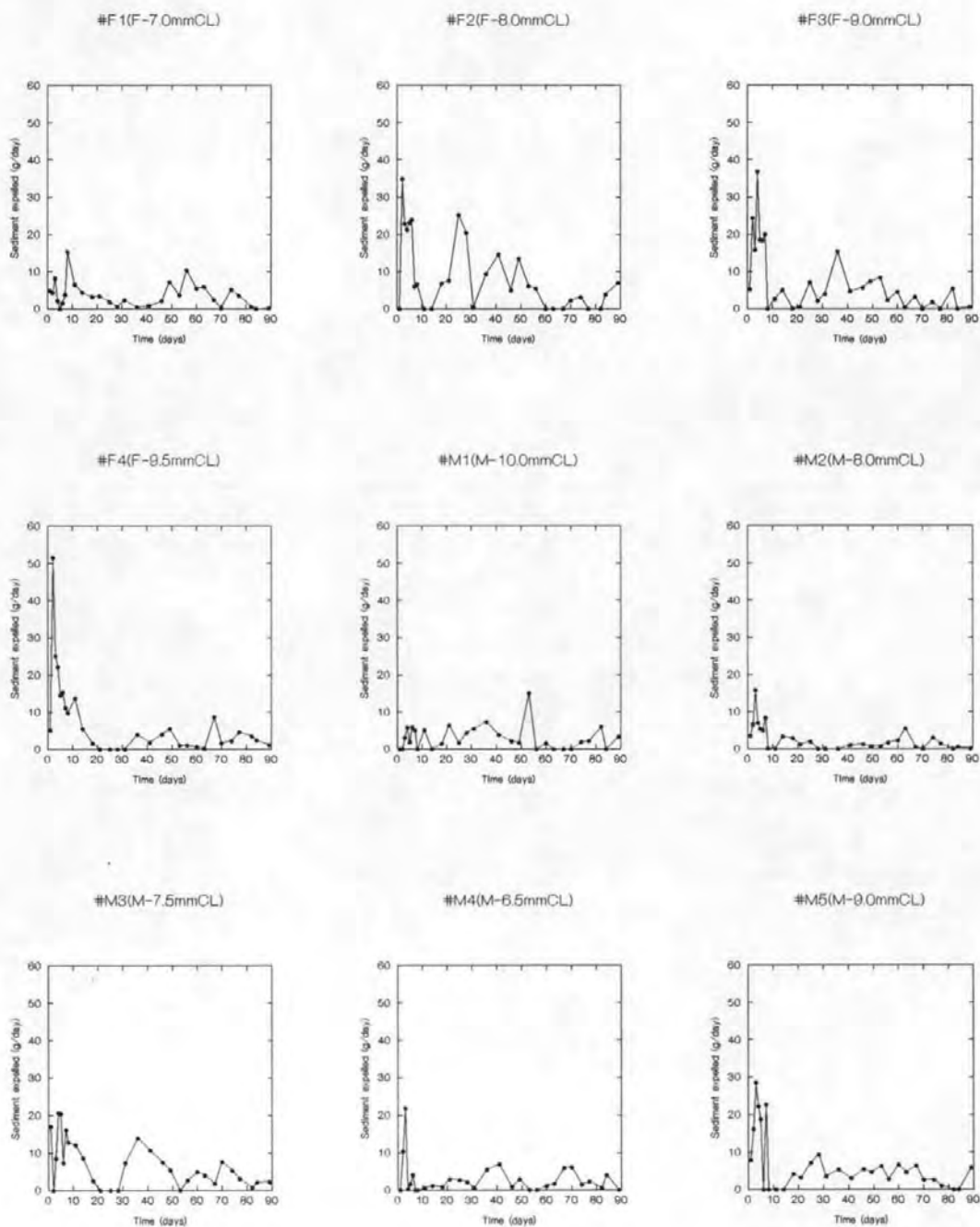


Figure 5.3. Sediment expulsion behaviour for each *Callianassa subterranea* kept at 15°C.

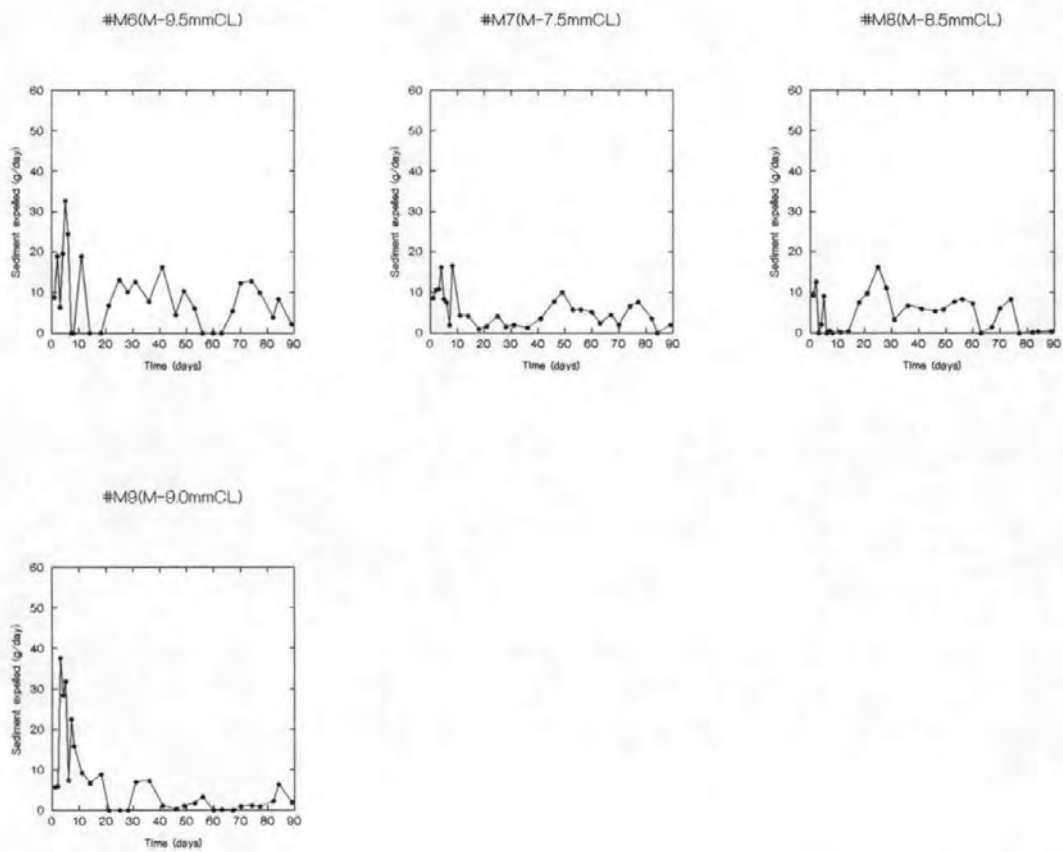


Figure 5.3. (continued)

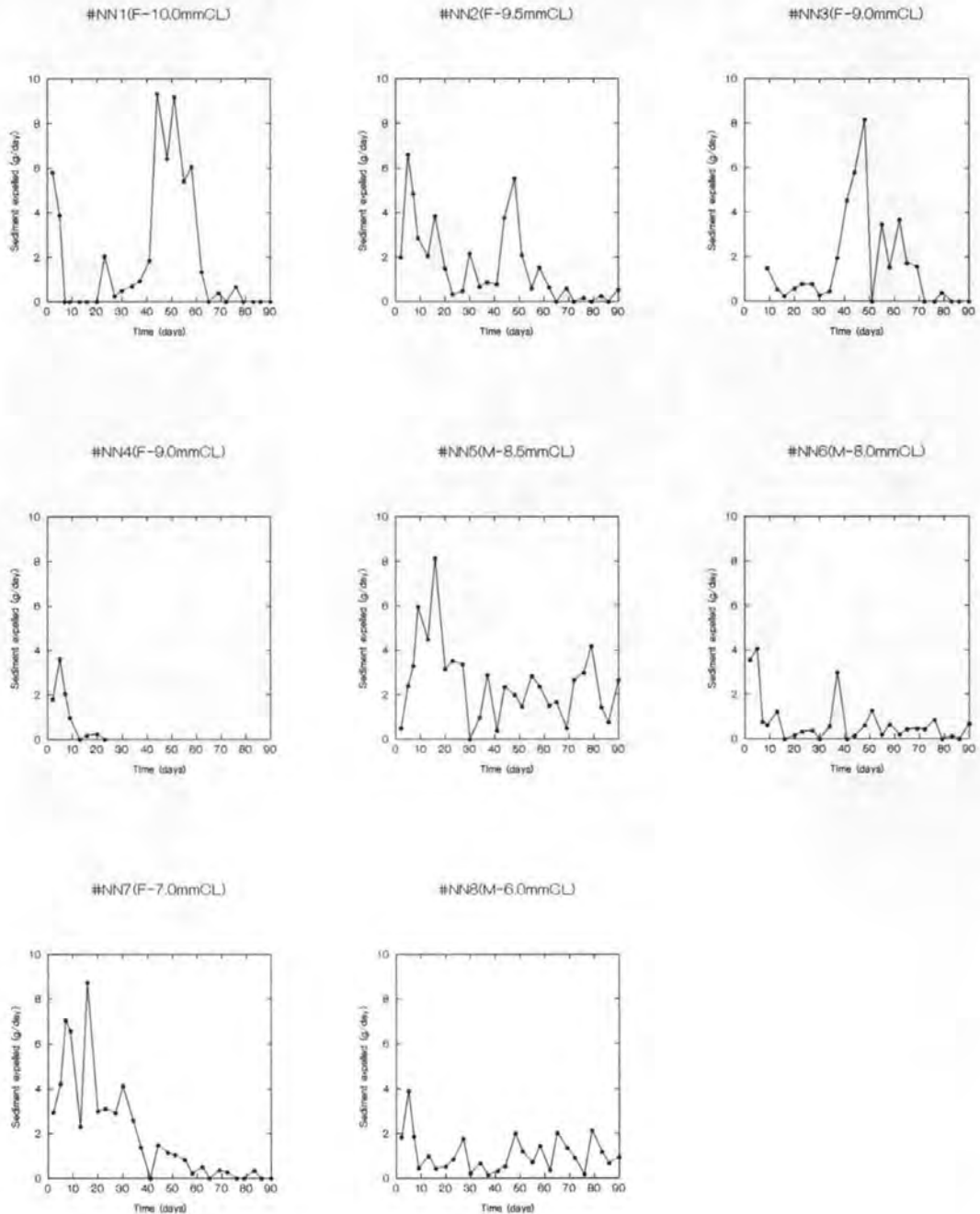


Figure 5.4. Sediment expulsion behaviour for each *Callianassa subterranea* kept at 9°C [Note: accidental increase in experimental temperature (to 15°C) during days 41-51 caused increase in expulsion rate; data from this period was omitted from subsequent analysis].

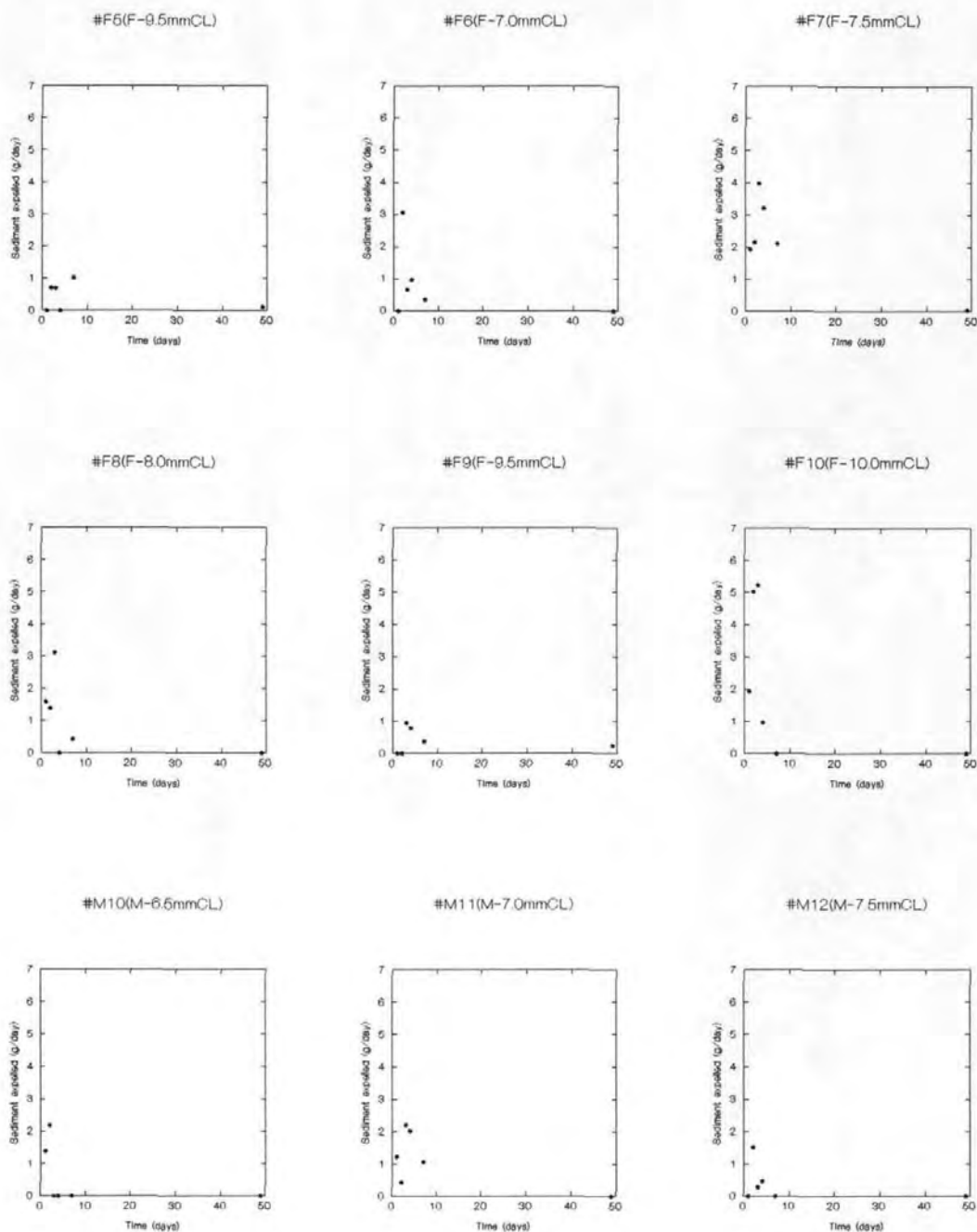


Figure 5.5. Sediment expulsion behaviour for each *Callianassa subterranea* kept at 7°C.

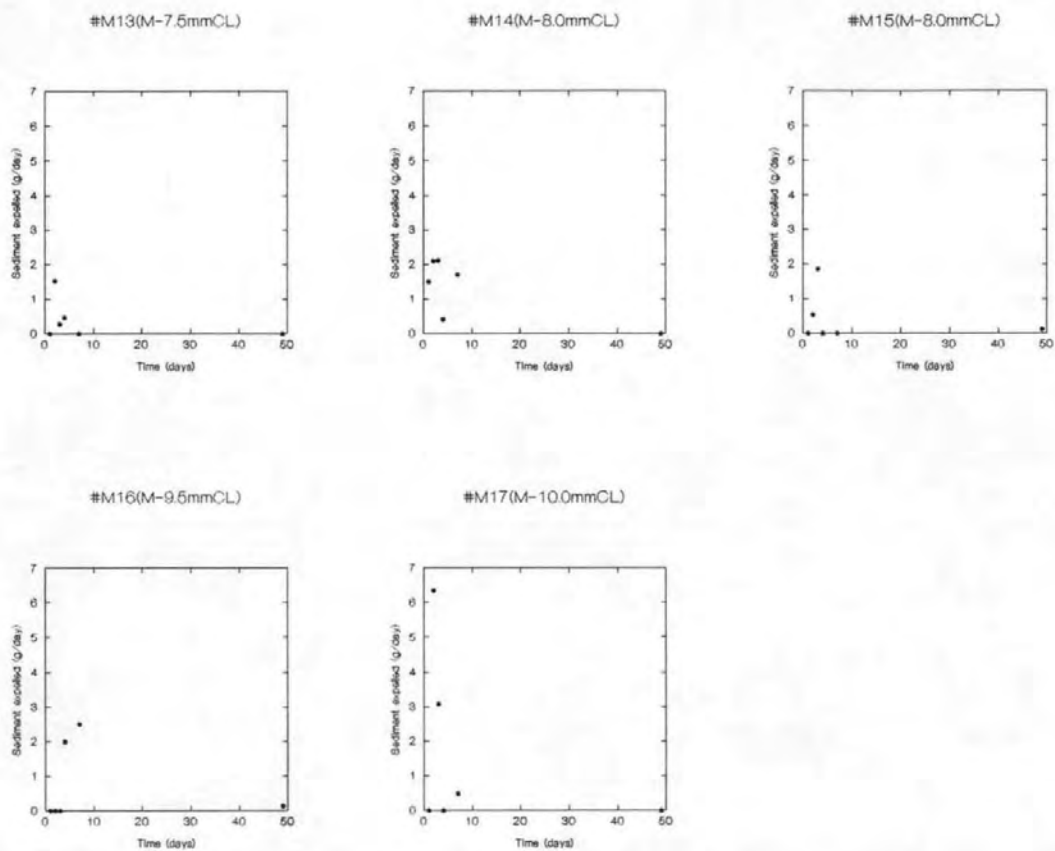


Figure 5.5. (continued)

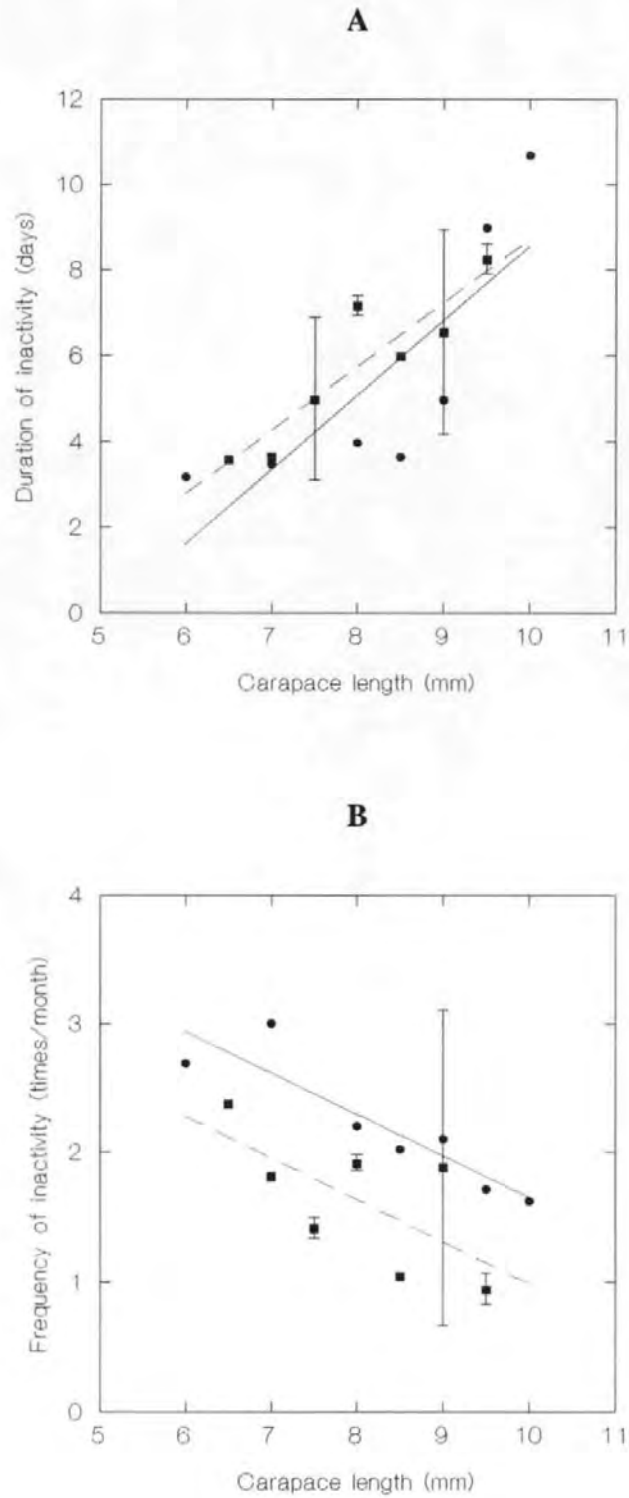


Figure 5.6. The relationship between size of *Callianassa subterranea* and sediment expulsion inactivity; **A**, duration; **B**, frequency (9°C =circles and solid line; $y = -8.778 + 1.733x$, $y = 4.874 + -0.323x$, $r = 0.812$, $r = 0.910$, $P = <0.05$, $P = <0.01$ respectively. 15°C =squares and broken line; $y = -6.096 + 1.481x$, $y = 4.216 + -0.323x$, $r = 0.911$, $r = 0.690$, $P = <0.01$, $P = <0.05$, respectively) (error bars = $\pm 1\text{SD}$).

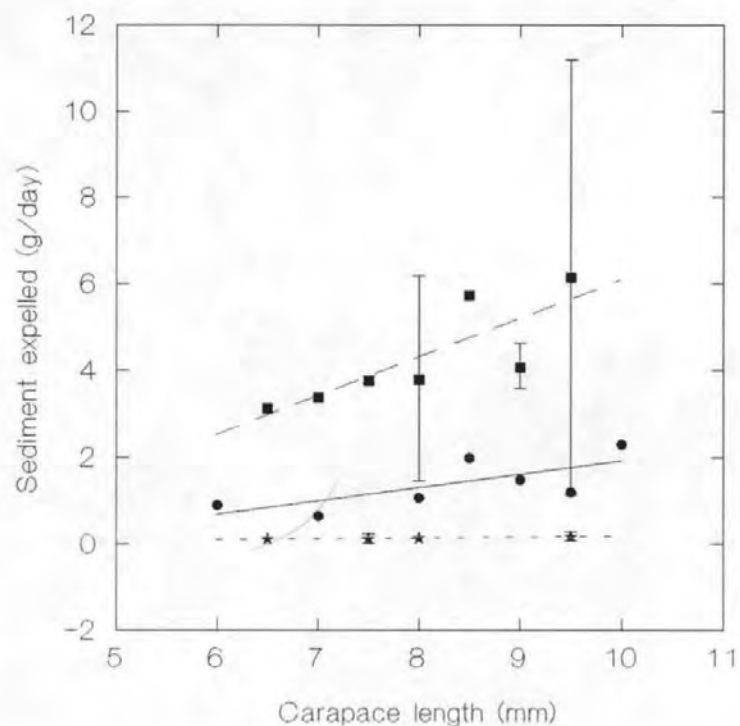


Figure 5.7. The relationship between size of *Callianassa subterranea* and sediment expulsion rate for 7°C (stars and dashed line; $y = -0.019 + 0.021x$, $r = 0.976$, $P = < 0.05$), 9°C (circles and solid line; $y = -1.163 + 0.310x$, $r = 0.734$, $P = < 0.05$) and 15°C (squares and broken line; $y = -2.786 + 0.887x$, $r = 0.817$, $P = < 0.05$) (error bars = $\pm 1SD$).

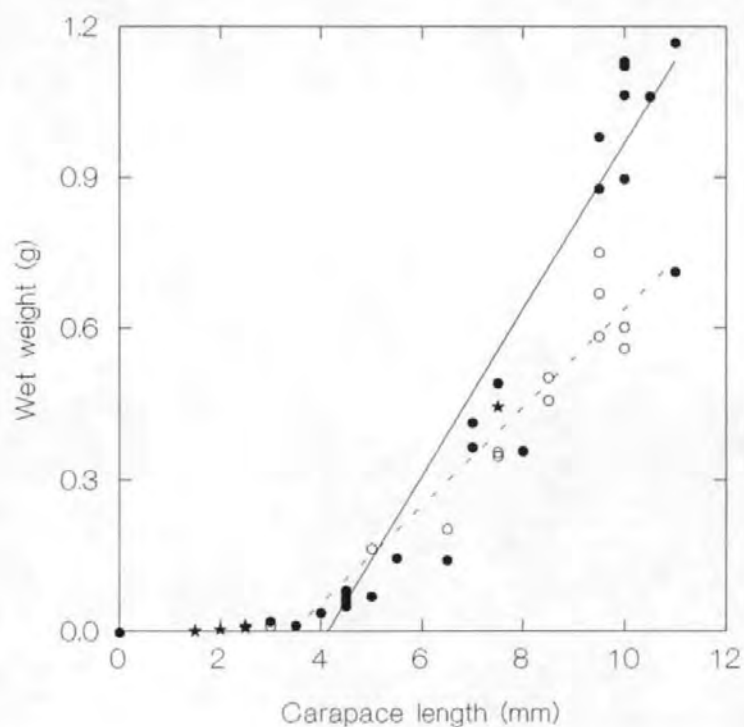


Figure 5.8. The relationship between the size and weight of *Callianassa subterranea* ($\geq 4\text{mmCL}$) in September 1989 (Males= solid circles and solid line; $y = -0.682 + 0.165x$, $r = 0.965$, $P = < 0.001$. Females= open circles and dashed line; $y = -0.333 + 0.097x$, $r = 0.947$, $P = < 0.001$. Unknown sex = stars, excluded from regressions).

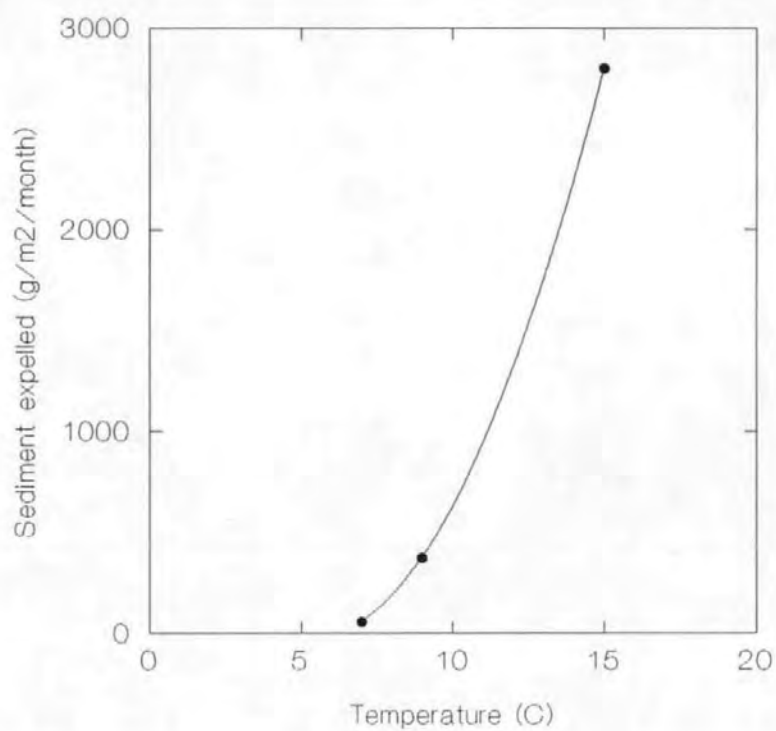


Figure 5.9. Relationship between the estimated amount of sediment expelled by *Callianassa subterranea* during the three study months and temperature (non-linear quadratic, $y = 30.73x^2 + -333.18x + 888.45$).

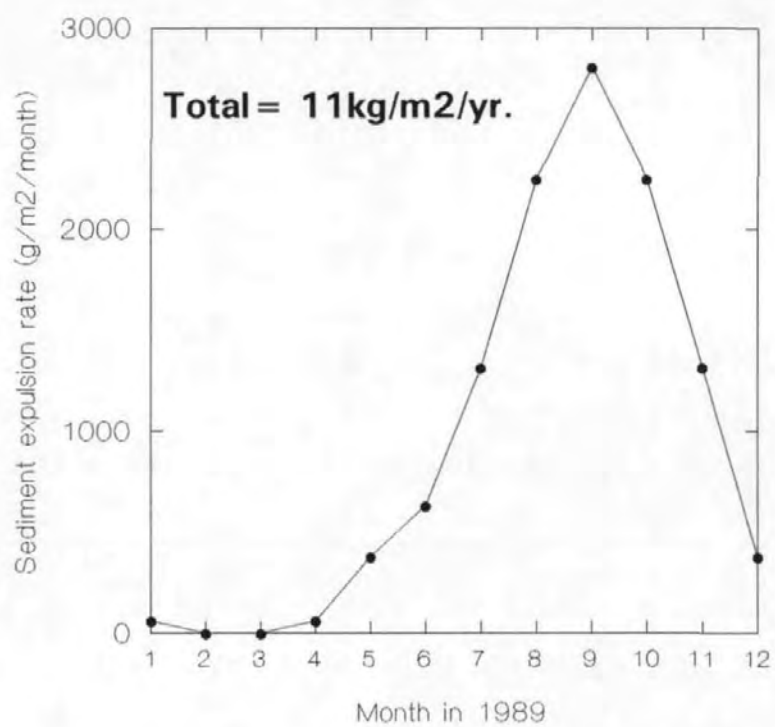


Figure 5.10. The predicted annual sediment turnover budget for *Callianassa subterranea* at the North Sea study site in 1989.

7°C (=January)			9°C (=May)			15°C (=September)		
ID	Size (mmCL)	Sex	ID	Size (mmCL)	Sex	ID	Size (mmCL)	Sex
#F5	9.5	F	#NN1	10.0	F	#F1	7.0	F
#F6	7.0	F	#NN2	9.5	F	#F2	8.0	F
#F7	7.5	F	#NN3	9.0	F	#F3	9.0	F
#F8	8.0	F	#NN4	9.0	F	#F4	9.5	F
#F9	9.5	F	#NN5	8.5	M	#M1	10.0	M
#F10	10.0	F	#NN6	8.0	M	#M2	8.0	M
#M10	6.5	M	#NN7	7.0	F	#M3	7.5	M
#M11	7.0	M	#NN8	6.0	M	#M4	6.5	M
#M12	7.5	M				#M5	9.0	M
#M13	7.5	M				#M6	9.5	M
#M14	8.0	M				#M7	7.5	M
#M15	8.0	M				#M8	8.5	M
#M16	9.5	M				#M9	9.0	M
#M17	10.0	M						

Table 5.1. Details of individual *Callianassa subterranea* used in laboratory sediment expulsion determinations conducted at three experimental temperatures (ID= identity number, mmCL= carapace length in mm, F= female, M= male).

ID	#F1	#F2	#F3	#F4	#M1	#M2	#M3	#M4	#M5	#M6	#M7	#M8	#M9
S/S	F/7.0	F/8.0	F/9.0	F/9.5	M/10.0	M/8.0	M/7.5	M/6.5	M/9.0	M/9.5	M/7.5	M/8.5	M/9.0
D													
1	4.85	0.00	5.24	5.16	0.00	3.50	17.14	0.00	7.92	8.74	8.62	9.21	5.79
2	4.28	34.94	24.48	51.62	0.00	6.64	0.00	10.44	16.19	18.93	10.58	12.64	5.95
3	8.29	22.98	15.98	25.19	3.09	15.85	8.61	21.88	28.58	6.39	10.80	0.00	37.73
4	2.14	21.33	36.93	22.16	5.93	7.04	20.72	0.30	22.30	19.58	16.16	2.14	28.50
5	0.00	23.25	18.55	14.63	1.92	5.44	20.49	1.58	18.79	32.72	8.38	9.05	32.02
6	1.56	23.98	18.52	15.43	6.00	4.98	7.38	4.11	0.00	24.47	7.53	0.00	7.51
7	3.81	6.00	20.13	11.23	5.18	8.40	16.26	0.00	22.70	0.00	1.95	0.57	22.58
8	15.42	6.61	0.00	9.85	0.00	0.15	12.65	0.00	0.00	0.00	16.63	0.00	15.86
11	6.48	0.00	2.65	13.79	5.16	0.07	12.19	0.60	0.00	18.92	4.34	0.19	9.26
14	4.38	0.00	5.07	5.52	0.00	3.37	8.69	1.23	0.00	0.00	4.21	0.36	6.70
18	3.17	6.80	0.07	1.68	1.50	2.86	2.54	0.83	4.26	0.00	0.96	7.48	8.95
21	3.44	7.58	0.53	0.00	6.51	1.21	0.00	2.90	3.19	6.80	1.62	9.80	0.01
25	1.83	25.25	7.14	0.00	1.73	2.00	0.00	2.73	7.24	13.09	4.19	16.25	0.00
28	0.59	20.50	2.17	0.00	4.42	0.00	0.00	2.14	9.41	10.13	1.52	11.10	0.00
31	2.35	0.42	4.01	0.00	5.54	0.00	7.39	0.58	3.55	12.62	2.02	3.32	7.05
36	0.46	9.37	15.48	4.03	7.43	0.00	14.00	5.50	5.38	7.74	1.27	6.70	7.35
41	0.81	14.61	4.74	1.78	3.88	1.08	10.77	6.96	3.02	16.22	3.62	5.90	1.16
46	2.08	4.94	5.64	4.07	2.18	1.25	7.51	0.91	5.42	4.50	7.75	5.39	0.31
49	7.20	13.58	7.39	5.55	1.77	0.68	5.43	2.91	4.71	10.37	10.10	5.79	1.17
53	3.65	6.11	8.39	1.09	15.17	0.74	0.00	0.00	6.31	6.03	5.72	7.75	1.82
56	10.42	5.46	2.38	1.11	0.00	1.70	2.70	0.00	2.81	0.00	5.74	8.29	3.33
60	5.49	0.00	4.57	0.70	1.58	2.29	5.02	1.15	6.67	0.00	5.14	7.26	0.00
63	5.86	0.00	0.45	0.19	0.00	5.54	4.08	1.72	4.64	0.00	2.40	0.00	0.20
67	2.40	0.00	3.24	8.75	0.00	0.49	1.82	6.00	6.37	5.49	4.48	1.42	0.00
70	0.20	2.25	0.00	1.65	0.00	0.00	7.69	6.11	2.64	12.29	2.03	6.04	1.03
74	5.21	3.08	1.81	2.28	1.91	3.02	5.34	1.46	2.65	12.79	6.64	8.29	1.21
77	3.54	0.00	0.00	4.65	2.21	1.42	3.15	2.25	1.00	9.98	7.62	0.00	0.95
82	0.58	0.00	5.46	3.55	6.03	0.00	0.71	0.50	0.00	3.87	3.52	0.25	2.25
84	0.00	3.85	0.00	2.46	0.00	0.49	2.17	4.00	0.00	8.37	0.00	0.34	6.45
89	0.18	6.99	0.54	1.23	3.34	0.13	2.25	0.00	5.87	2.23	2.04	0.44	1.99

Table 5.2. Daily sediment expulsion rates [g(dry)/day] for *Callianassa subterranea* at 15°C [ID= identity number; S/S= sex/size (F= female, M= male, size measured as carapace length in mm); D= day number].

ID	#NN1	#NN2	#NN3	#NN4	#NN5	#NN6	#NN7	#NN8
S/S	F/10.0	F/9.5	F/9.0	F/9.0	M/8.5	M/8.0	F/7.0	M/6.0
D								
2	5.82	2.00	-	1.80	0.50	3.56	2.96	1.83
5	3.89	6.62	-	3.62	2.40	4.07	4.23	3.91
7	0.00	4.85	-	2.05	3.30	0.77	7.06	1.86
9	0.00	2.86	1.49	0.98	5.97	0.63	6.58	0.47
13	0.00	2.05	0.55	0.00	4.50	1.23	2.31	0.99
16	0.00	3.85	0.23	0.17	8.16	0.00	8.75	0.43
20	0.00	1.50	0.57	0.24	3.16	0.16	2.99	0.53
23	2.05	0.32	0.77	0.00	3.52	0.33	3.11	0.87
27	0.24	0.48	0.27	*	3.37	0.38	2.92	1.77
30	0.50	2.18	0.45		0.00	0.00	4.13	0.22
34	0.70	0.67	1.95		0.98	0.57	2.59	0.68
37	0.93	0.87	4.55		2.90	3.01	1.39	0.14
41	1.83	0.77	5.82		0.38	0.00	0.00	0.33
44	9.34	3.77	8.20		2.35	0.15	1.48	0.54
48	6.43	5.55	0.00		1.99	0.61	1.15	2.00
51	9.20	2.10	3.48		1.47	1.29	1.05	1.20
55	5.41	0.59	1.54		2.84	0.19	0.84	0.72
58	6.06	1.54	3.68		2.38	0.65	0.23	1.44
62	1.34	0.64	1.74		1.51	0.20	0.52	0.35
65	0.00	0.00	1.58		1.67	0.44	0.00	2.02
69	0.38	0.60	0.00		0.50	0.47	0.37	1.35
72	0.00	0.00	0.00		2.67	0.44	0.28	0.91
76	0.66	0.17	0.39		2.98	0.86	0.00	0.18
79	0.00	0.00	0.00		4.19	0.00	0.00	2.14
83	0.00	0.25	0.00		1.43	0.13	0.36	1.18
86	0.00	0.00	0.00		0.77	0.00	0.00	0.67
90	0.00	0.55	0.00		2.67	0.68	0.00	0.94

Table 5.3. Daily sediment expulsion rates [g(dry)/day] for *Callinassa subterranea* at 9°C [ID= identity number; S/S= sex/size (F= female, M= male, size measured as carapace length in mm); D= day number; *= shrimp died].

ID	#F5	#F6	#F7	#F8	#F9	#F10	#M10	#M11	#M12	#M13	#M14	#M15	#M16	#M17
S/S	F/9.5	F/7.0	F/7.5	F/8.0	F/9.5	F/10.0	M/6.5	M/7.0	M/7.5	M/7.5	M/8.0	M/8.0	M/9.5	M/10.0
D														
1	0.00	0.00	1.94	1.59	0.00	1.95	1.40	1.23	0.00	0.00	1.50	0.00	0.00	0.00
2	0.71	3.07	2.16	1.39	0.00	5.04	2.19	0.43	0.71	1.52	2.10	0.54	0.00	6.36
3	0.70	0.67	3.98	3.12	0.95	5.24	0.00	2.21	1.44	0.28	2.12	1.86	0.00	3.09
4	0.00	0.98	3.22	0.00	0.79	0.97	0.00	2.03	0.49	0.47	0.42	0.00	2.00	0.00
7	1.02	0.36	2.12	0.43	0.37	0.00	0.00	1.07	0.53	0.00	1.71	0.00	2.51	0.49
49	0.11	*	0.05	*	0.25	*	*	*	0.20	*	*	0.12	0.14	*

Table 5.4. Daily sediment expulsion rates [g(dry)/day] for *Callinassa subterranea* at 7°C [ID= identity number; S/S= sex/size (F= female, M= male, size measured as carapace length in mm); D= day number; *= shrimp died].

Size (mmCL)	9°C (= May)	15°C (= September)
A		
6.0	3.20	-
6.5	-	3.60
7.0	3.50	3.67
7.5	-	5.00 (± 1.89)
8.0	4.00	7.17 (± 0.23)
8.5	3.67	6.00
9.0	5.00	6.56 (± 2.37)
9.5	9.00	8.25 (± 0.35)
10.0	10.70	-
B		
6.0	2.70	-
6.5	-	2.38
7.0	3.01	1.82
7.5	-	1.42 (± 0.08)
8.0	2.21	1.92 (± 0.06)
8.5	2.03	1.05
9.0	2.11	1.89 (± 1.22)
9.5	1.72	0.95 (± 0.12)
10.0	1.63	-

Table 5.5. A, Duration (days) and B, frequency (times/month) of sediment expulsion inactivity by *Callianassa subterranea* at two experimental temperatures ($\pm 1SD$).

Size (mmCL)	7°C (=January)	9°C (=May)	15°C (=September)
6.0	-	0.93	-
6.5	0.12	-	3.15
7.0	-	0.68	3.40
7.5	0.13 (± 0.11)	-	3.79 (± 0.08)
8.0	0.14	1.10	3.82 (± 2.35)
8.5	-	2.02	5.75
9.0	-	1.52	4.10 (± 0.52)
9.5	0.18 (± 0.10)	1.23	6.17 (± 5.02)
10.0	-	2.33	-

Table 5.6. Sediment expulsion rate [g(dry)/day] by *Callianassa subterranea* at three experimental temperatures (± 1 SD).

Size (mmCL)	Sed. Exp. (g/day)	Dur. Inact. (days)	Freq. Inact. (times/mo.)	Exp. Act. ¹ (days)	Sed. Exp. (g/mo.)	Density ^{1 2} (no./m ²)	Sed. Exp. (g/m ² /mo.)
Jan. (7°C)							
6.0	0.11	--	--	24.94	2.67	0.40	1.07
6.5	0.12	--	--	23.29	2.75	0.40	1.10
7.0	0.13	--	--	21.94	2.81	2.40	6.74
7.5	0.14	--	--	20.84	2.90	2.80	8.11
8.0	0.15	--	--	20.02	2.98	1.60	4.77
8.5	0.16	--	--	19.47	3.12	1.60	4.98
9.0	0.17	--	--	19.17	3.26	0.40	1.30
9.5	0.18	--	--	19.14	3.46	3.60	12.47
10.0	0.19	--	--	19.38	3.70	4.40	16.29
10.5	0.20	--	--	19.93	4.03	0.40	1.61
11.0	0.21	--	--	20.70	4.39	0.80	3.51
						Total =	61.96
May (9°C)							
6.0	0.70	1.62	2.94	26.24	18.29	0.80	14.63
6.5	0.85	2.49	2.78	24.09	20.52	0.80	16.42
7.0	1.01	3.35	2.61	22.24	22.40	2.40	53.75
7.5	1.16	4.22	2.45	20.65	24.00	2.40	57.59
8.0	1.32	5.09	2.29	19.35	25.48	2.40	61.16
8.5	1.47	5.95	2.13	18.33	26.98	0.80	21.59
9.0	1.63	6.82	1.97	17.59	28.62	0.00	0.00
9.5	1.78	7.69	1.81	17.12	30.51	1.60	48.81
10.0	1.94	8.55	1.64	16.94	32.81	3.20	105.00
10.5	2.09	9.42	1.48	17.03	35.63	0.00	0.00
11.0	2.25	10.29	1.32	17.41	39.12	0.00	0.00
						Total =	378.95
Sep. (15°C)							
6.0	2.56	2.77	2.30	23.63	60.49	0.00	0.00
6.5	3.01	3.53	2.13	22.48	67.66	2.40	162.40
7.0	3.45	4.27	1.96	21.63	74.62	2.40	179.10
7.5	3.89	5.01	1.79	21.03	81.81	3.20	261.78
8.0	4.35	5.75	1.62	20.68	89.96	0.80	71.97
8.5	4.78	6.48	1.45	20.60	98.47	2.40	236.32
9.0	5.22	7.22	1.28	20.76	108.37	0.80	86.69
9.5	5.67	7.96	1.11	21.16	119.98	5.60	671.87
10.0	6.11	8.70	0.94	21.82	133.32	5.60	746.59
10.5	6.55	9.44	0.76	22.83	149.54	0.80	119.63
11.0	7.00	10.18	0.59	23.99	167.93	1.60	268.69
						Total =	2805.04

Table 5.7. Estimates of sediment expulsion rate for *Callinassa subterranea* at the North Sea study site during the three main sampling months (derived from regression of experimental data together with field population density data).

Key: Size = Size of *C. subterranea* measured as carapace length (mmCL); Sed. Exp. = Sediment Expulsion; Dur. Inact. = Duration of Inactivity; Freq. Inact. = Frequency of Inactivity; Exp. Act. = Expulsion Activity; mo. = month. **Note:** ¹= January's expulsion activity and density values are an average of those calculated for May and September, ²= May's density value is that of a sampling visit a year later in 1990 (-2 weeks).

Size (mmCL)	Sex	Wet weight (g)	Size (mmCL)	Sex	Wet weight (g)
1.5	U	0.0004	7.0	M	0.3665
1.5	U	0.0011	7.0	F	<i>0.3460</i>
1.5	U	0.0006	7.5	U	0.4445
2.0	U	0.0043	7.5	F	0.3567
2.0	U	0.0038	7.5	M	0.4924
2.5	U	0.0070	7.5	F	0.3494
2.5	U	0.0066	8.0	M	0.3594
2.5	U	0.0118	8.5	F	0.5039
2.5	U	0.0072	8.5	F	0.4590
3.0	F	0.0128	8.5	U	<i>0.6060</i> ¹
3.0	M	0.0217	9.0	M	<i>0.8030</i>
3.5	U	0.0137	9.5	F	0.7522
4.0	F	<i>0.0350</i>	9.5	F	0.6706
4.0	M	0.0387	9.5	M	0.9822
4.5	M	0.0517	9.5	M	0.8784
4.5	M	0.0774	9.5	F	0.5854
4.5	M	0.0832	9.5	F	<i>0.5885</i>
4.5	M	0.0656	9.5	F	<i>0.5885</i>
4.5	M	0.0628	10.0	M	1.1235
5.0	M	0.0715	10.0	F	0.6036
5.0	F	0.1657	10.0	F	0.5614
5.0	F	<i>0.1520</i>	10.0	M	0.8981
5.5	M	0.1470	10.0	M	1.1330
5.5	M	<i>0.2255</i>	10.0	M	1.0657
5.5	F	<i>0.2005</i>	10.0	M	<i>0.9680</i>
6.5	M	0.1432	10.5	M	1.0626
6.5	F	0.2049	11.0	M	1.1698
6.5	M	<i>0.3905</i>	11.0	M	0.7133 ²
7.0	M	0.4150			<i>= 1.1330</i>

Total weight (biomass) of population = 23.0207g
 $\geq 6\text{mmCL} = 21.5331\text{g}$ (94%), $< 6\text{mmCL} = 1.4876\text{g}$ (6%)

Table 5.8. Size, sex and weight of *Callinassa subterranea* population (57 indiv./1.25m²) at North Sea study site in September 1989 (mmCL= carapace length in mm; F= female; M= male; U= unknown sex; missing values in *italics* calculated from linear regression of remainder of data; ¹= mean of male and female regression derived value; ²= omitted from regression as missing primary chela: see also Fig. 5.8).

Species	Sediment turnover rate	°Scaling	Method	Source
<i>Neotrypaea californiensis</i>	20-50 ml(wet)/indiv./day	?	?, ?	MacGinitie, 1934
<i>Callianassa sp.</i>	6-7 cm/week	?	L. & T., i	Aller & Dodge, 1974
<i>Callianassa sp.</i>	0.1-0.2 cm/week	?	L. & T., i	"
<i>Callianassa tyrrenna</i>	25 cm ³ (wet)/indiv./day	?	?, ?	Ott <i>et al.</i> , 1976
<i>Callianassa sp.</i>	3.395 kg(dry)/m ² /day	1	D., i	Roberts <i>et al.</i> , 1981
<i>Callianassa sp.</i>	0.819 kg(dry)/m ² /day	1	D., i	"
<i>Callianassa sp.</i>	0.004 kg(dry)/m ² /day	1	D., i	Suchanek, 1983
<i>Neocallichirus rathbunae</i>	2.59 kg(dry)/m ² /day	1	D., i	"
<i>Glypturus laurae</i>	3.0 kg(dry)/mound/week	0	?, i	Vaugelas & Saint Laurent, 1984
<i>Glypturus laurae</i>	1.5 kg(dry)/mound/week	0	?, i	"
<i>Callianassa sp.</i>	240.1 cc(wet)/m ² /day	1	L., i	Suchanek <i>et al.</i> , 1986
<i>Callianassa sp.</i>	56.0 cc(wet)/m ² /day	1	L., i	"
<i>Callianassa sp.</i>	800 cc(wet)/m ² /day	1	D. & L., i	Suchanek & Colin, 1986
<i>Glypturus armatus</i>	1660 g(dry)/mound/week	0	D., i	Vaugelas <i>et al.</i> , 1986
<i>Glypturus armatus</i>	500 g(dry)/mound/week	0	D., i	"
<i>Neotrypaea californiensis</i>	18 ml(wet)/indiv./day	0	L., i	Swinbanks & Luternauer, 1987
<i>Callianassa kraussi</i>	12.14 kg(wet)/m ² /day	3	T., i	Branch & Pringle, 1987
<i>Callianassa subterranea</i>	3.5 kg(dry)/m ² /yr.	2	D., l.	Witbaard & Duineveld, 1989
<i>Callianassa subterranea</i>	11 kg(dry)/m ² /yr.	2	D., l.	Rowden, this study

Table 5.9. Comparison of sediment turnover rates for Callianassidae.

N.B. This table is intended to be illustrative and not exhaustive.

(Key: ? = unknown, D = Direct Entrapment, L = Leveling, T = Tracer Particles, i = *insitu*, l = laboratory).

CHAPTER 6
SEDIMENT TRANSPORT BY
CALLIANASSA SUBTERRANEA

[Aspects of this chapter are included in Rowden, *et al.* "The role of *Callianassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea," (*Continental Shelf Research*, submitted) and in Jago *et al.* (1993) "Resuspension processes and seston dynamics," (*Philosophical Transactions of the Royal Society: Physical Sciences and Engineering*, **343**, 475-491).]

6.1. Introduction

Macrobenthic organisms are capable of producing a variety of features from their feeding or burrowing activities which alter the topography of seabed sediments (Frey, 1973). The scaling of these surface features ranges from metres (eg, ray pits; Grant, 1983), centimetres (eg, echiuran mounds; Smith *et al.*, 1986) to millimetres (eg, worm faecal casts; Cadée, 1979). Depending on their shape, size, orientation and density, the surface features may cause sediment erosion or deposition (Jumars & Nowell, 1984), with the mass of evidence indicating that biogenically-produced seabed topography results in a hydrodynamically rough surface which facilitates the resuspension of bottom sediments by currents (Rhoads, 1970; Young, 1971; Young & Southard, 1978). In particular, mounds enhance surface sediment mobility, and aid the erosion and resuspension processes (Anderson & McLusky, 1981).

The activities of the benthic macrofauna influence sediment transport (resuspension) both indirectly and directly. Biological reworking can increase bottom boundary roughness to effect destabilisation and subsequent erosion (indirect), whilst sediment particles can be elevated into the water flow above the sediment-water interface (direct) (Rhoads *et al.*, 1978; Nowell *et al.*, 1981). For example, the high turbidity above the mounds produced by a burrowing holothurian was attributed to increased turbulent stress from tidal currents acting on a rough easily erodible bottom (Rhoads & Young, 1970). In addition to the larger sediment particles, which are deposited to form a mound, some finer-grained material is carried sometimes by the stream of water issuing from the mound apex to heights of many centimetres into the water column. Colin *et al.* (1986) found that a portion of the material ejected from the mounds produced by callianassid shrimps is suspended only very temporarily, whilst finer fractions can become suspended and transported for some time and distance.

Resuspended sediment influences nutrient budgets and pelagic/benthic production (eg, McLachlan, 1980; Walker, 1981; Simon, 1989) in marine environments, and links between these ecosystem functions and the activity of benthic fauna have been established. Roman & Tenore (1978) reported that tidal resuspension can result in >50% increases in particulate carbon, primary productivity and chlorophyll *a* per m² in Buzzards Bay (U.S.A.). This resuspension was found previously to be expedited by the

erodability of the seabed induced by the presence of deposit-feeding macrofauna (Rhoads & Young, 1970). Floderus & Hakanson (1989) found that the presence of "mud blankets" (which underwent a seasonal cycle of resuspension and redeposition - by wind/wave induced currents) controlled the nitrogen budget and water quality of a bay in the Kattegat Sea. The principal component of the "blanket" was pelletized organic material derived from the faecal matter of two sediment-dwelling macrofauna species.

It is also possible that a single species is capable of making a significant contribution to sediment transport. For example, the feeding activities of the bivalve *Yoldia limatula* result in both direct and indirect sediment resuspension through expulsion of loose pseudofaeces directly into the water column and destabilisation of the sediment-water interface respectively (Bender & Davis, 1984). More commonly, the mounds produced by bioturbatory species are responsible for a significant proportion of biologically-mediated sediment resuspension (see review, Lee & Swartz, 1980). In particular, the amount of material discarded by members of the Callianassidae is relatively high because it includes a large proportion of pseudofaeces in addition to faeces alone (Cadee, 1976). Mounds produced by callianassid shrimps are relatively large features, often up to 30cm (Riddle, 1988) or occasionally bigger (50cm, Murphy & Kremer, 1992). Callianassid mounds are easily dispersed and resuspended by wave action (Aller & Dodge, 1974), whilst material ejected from the mound can clearly elevate suspended sediment levels (Murphy, 1985).

A combination of the previously-determined sediment turnover rates (Chapter 5) for *Callianassa subterranea* and a quantification of the physical influence of the shrimp's mounds upon near-bed flow, will allow an estimate for the *C. subterranea*-derived sediment transport (resuspension) at the North Sea study site.

6.2. Materials and Methods

6.2.1. Seabed photography and calculation of mound size

In January, May and September 1989, a seabed photographic survey of the North Sea study site was completed using a "cage-type" UMEL (Underwater and Marine Equipment Ltd.) underwater camera assembly. The equipment consisted of a separate

waterproof-housed 35mm camera and flash-unit obliquely mounted within a tubular metal frame (Plate 6.1). A photograph is taken when the operating switch is triggered by contact of a suspended weight with the seabed. The instrument was deployed from a hydrographic winch (mid-ship). At each station, the camera was "fired" (at 25cm above the seabed) five times by small (2-3m) successive raising and lowering of the whole assembly. The survey was conducted at times of lowest tidal current speed to ensure maximum potential imaging. To confirm the successful operation of the camera assembly, the photographic film was developed immediately on completion of the survey in the darkroom of the R.R.S. *Challenger*.

Calibration trials in a swimming pool with the camera assembly arranged as per field deployment, allowed the total area and depth of field of view to be calculated, plus the relationship between an object's imaged and real height/width [conducted by J. Humphrey, Proudman Oceanographic Laboratory] (Figs 6.1A & 6.1B). To obtain the real dimensions of a mound on the seabed from the photographic negative the following measures of height/width and procedures were undertaken. Height: (1) the height of the mound on the negative (H) in mm, (2) the distance from the bottom edge of the negative to the centre of the mound ($D1$) in mm, (3) substitution of the value of $D1$ into the equation ($Mh = 39.168 + -0.459D1 + 0.190D1^2$) to find the value of multiplier (Mh), (4) multiplication of $H \times Mh$ to obtain the real height of mound in mm; width: (1) The base width of the mound on the negative (W) in mm, (2) the distance from the bottom edge of the negative to the base of the mound ($D2$) in mm, (3) substitution of the value of $D2$ into the equation ($Mw = 32.122 + 0.245D2 + 0.044D2^2$) to find the value of multiplier (Mw), (4) multiplication of $W \times Mw$ to obtain the real width of the mound in mm. Measurements H , W , $D1$ and $D2$ on the negatives were made with the aid of sliding callipers ($\pm 0.1\text{mm}$) and a stereoscopic microscope (x20).

6.3. Results

6.3.1. Estimation of bottom boundary roughness

From the seabed photographs (area of view = 2.75m^2 , depth of field = 1.64m) taken on each of the three main sampling occasions, an attempt was made to evaluate a measure of

bottom boundary roughness (Z_o). In January, the seabed appeared essentially smooth and it was not possible to discern any discrete mounds attributable to *Callianassa subterranea* (Plate 6.2). In instances where no biogenic features are measurable, bottom boundary roughness is simply a function of the mean grain size of seabed sediment, thus using a formula after Kamphuis [see Dyer, (1986); $Z_o = D/15$, where D = mean diameter of sediment grain size (0.01cm)], the Z_o in January was 0.0007cm. In May, suspended sediment load near the bed was so high as to obscure any clear image of the bottom, preventing any estimate of Z_o for this month. *Callianassa subterranea* mounds were clearly visible in September (Plate 6.3), and ten individual mound measurements on each replicate image for each of the five stations were made and the real mound size calculated as detailed previously. A mean site value for mound height and base width was then calculated for September (Table 6.1). Mounds had a mean height of 5.4cm (1SD= ± 0.1) and a mean base width of 11.7cm (1SD= ± 0.9). Using the formula $Z_o = 0.5HS/\zeta$ [Lettau, (1969), applicable for roughness elements larger than individual grains (ie, a mound), where H = vertical extent (5.4cm), S = cross-sectional area (31.59cm²) and ζ = horizontal area (107.5cm²)], the bottom boundary roughness (Z_o) measure for September was estimated as 0.79cm.

6.3.2. Estimation of derived lateral sediment transport

An estimate of the amount of lateral sediment transport, derived from *Callianassa subterranea*'s activity at the study site, was calculated by multiplying values for ejected particle settling time (PST), transport velocity (TV) and expelled sediment rate (ESR) (Roberts *et al.*, 1981).

Firstly, particle settling velocity (V) was calculated from Stokes Law (see Holme & McIntyre, 1984):

$$V = \frac{(p_1 - p_2)gd}{18n} \dots\dots\dots \text{equation (1)}$$

Where, p_1 = density of ejected sediment (1.16g/cm³), p_2 = density of seawater (1.025g/cm³), g = acceleration due to gravity (980cm/sec), d = mean particle diameter (0.01cm), and n = viscosity of seawater (0.0122 g/cm/sec). This calculation resulted in a

value of 0.06 cm/sec for all occasions the site was visited. The first principal component (*PST*) can then be established by dividing the height to which sediment was variously ejected, ie, mound height plus 3cm (latter value from laboratory observation), by the value of *V*. In January, when there were no obvious mounds present, particles from the middle of the ejection plume would only have to fall 1.5cm, giving them a settling time of 25sec. Whilst in September at the other extreme, sediment would be ejected to a mean height of 6.9cm and take 115sec to reach the substratum surface.

The second principal component (*TV*) is defined as a depth-averaged velocity over the height of ejected sediment, which is an integration over the logarithmic profile of near-bed flow (*U_z*), described by the von Karman-Prandtl equation (see Sternberg, 1972):

$$U_z = \frac{U^*}{\gamma} \ln \left(\frac{z - Z_1}{Z_0} \right) \dots\dots\dots \text{equation (2)}$$

Where *U_z*= near-bed flow, *U**= shear velocity, *γ*= von Karman's constant, *z*= height above seabed, *Z₁*= ambient bed roughness, *Z₀*= bottom boundary roughness. Firstly, shear velocity (*U**) has to be calculated from the equation:

$$U^* = \frac{\gamma \times U_z}{\ln (z - Z_1/Z_0)} \dots\dots\dots \text{equation (3)}$$

Where, *γ* = 0.4, *U_z* = 5cm/sec, *z* = 41cm, *Z₁* = 0.01cm (ie, mean particle diameter in January) and 5.4cm (ie, mean mound height in September), *Z₀* (as calculated previously) = 0.0007cm (January) and 0.79cm (September). Shear velocities (*U**) were estimated as 0.17cm/sec for January and 0.52cm/sec for September. At the North Sea study site, mean near-bed current speed (*U_z*) measured by the bottom landing device STABLE (Sediment Transport and Boundary Layer Equipment) at 41cm above the seabed (Williams *et. al.*, 1993), was 5cm/sec for both January and September (no corresponding data available for May). The average transport velocities (*TV*) through the sediment ejection plumes produced by *Callianassa subterranea* were then calculated, after substitution and integration of equation (2), to be 3.0cm/sec for January and 2.2cm/sec for September.

The third principal component of derived sediment transport (*ESR*) was 0.06 kg(dry)/m²/month in January and 2.8 kg(dry)/m²/month in September (calculated in Chapter 5). Thus, lateral sediment transport (*PST* x *TV* x *ESR*), as an indirect and direct result of *Callianassa subterranea* activity, was estimated as 0.045 kg(dry)/m/month for January (25 x 0.03 x 0.06) and 7 kg(dry)/m/month for September (115 x 0.022 x 2.8). No value can be ascribed to May, because, as already stated, no measure of *Zo* and near-bed current velocity could be confidently determined.

6.4. Discussion

The effective influence of any species in altering bed topography is best evaluated by a change in the measure of bottom boundary roughness (*Zo*) (Nowell *et al.*, 1981). At the North Sea study site, values of *Zo* increased from 0.0007cm (January - when the shrimps were relatively inactive) to 0.79cm (September - when shrimp expulsion activity is apparently at its peak). Values of *Zo* for January of 0.00025cm and 1cm for September modelled by Howarth (1993) at the same study site agree very closely with the bottom boundary roughness measures calculated via the photographic evidence. The present data illustrate that (for a portion of the year at least) the mounds of *Callianassa subterranea* exert a significant influence upon the topography of the seabed and its potential for mobilisation. In addition to an indirect contribution to sediment resuspension, the material ejected by the shrimps has the capacity to go into direct suspension and to be laterally advected and redeposited by near-bed currents.

A population of a *Callianassa* species inhabiting a lagoon in the Marshall Islands (Pacific Ocean) contributed approximately 5mg/l to the 6-11mg/l of the suspended sediment load observed 10cm above the bed (Colin *et al.*, 1986). Furthermore, Roberts *et al.* (1981) demonstrated that the expulsion activity of callianassid shrimps made a significant and substantial contribution to sediment transport in a Caribbean lagoon. The present estimate of lateral sediment transport for the North Sea study site in September [7 kg(dry)/m/month] is comparable with the Caribbean value of 8 kg(dry)/m/month [reported as 0.27 kg(dry)/m/day; Roberts *et al.*, 1981]. The transport rate for the study site testifies to the potential influence of *Callianassa subterranea* upon the resuspension

of sediment in the North Sea; however, such a capacity varies temporally. There was a negligible contribution of lateral sediment transport estimated for January. Also, at times of increased near-bed currents velocities (storms, peak tides etc.), it is likely that quantities of sediment even greater than those attributed to the month of September will be suspended (evidenced by the failure to observe the seabed in May's bottom photographs). *Callianassa subterranea* is thus thought to be the most effective agent of bed sediment resuspension at this site. Tidal currents only resuspended recently deposited organic detritus following phytoplankton blooms (Jones *et al.*, 1993).

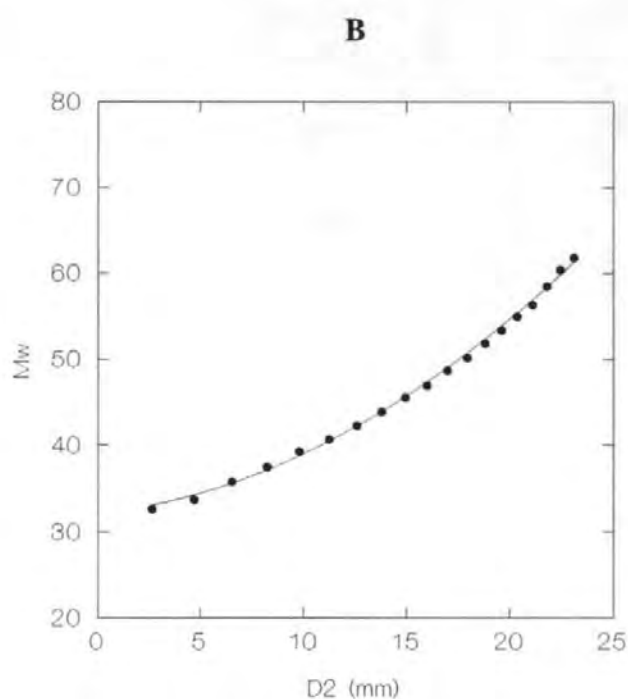
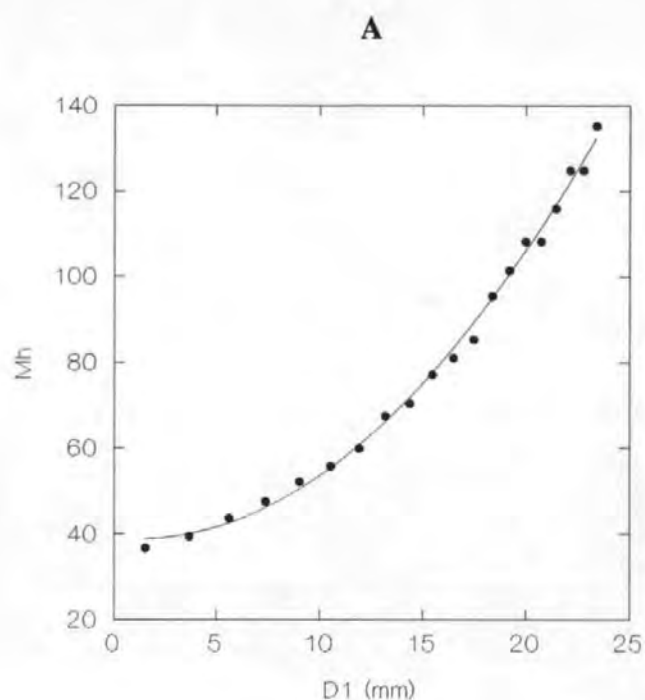


Figure 6.1. Conversion curves for calculating the dimension of a mound measured on a photographic negative taken by UMEL camera assembly at 25cm above the seabed. **A**, Height conversion ($D1$ = distance from negative edge to centre of mound in mm, Mh = multiplication factor, $Mh = 39.168 + -0.459D1 + 0.190D1^2$); **B**, Width conversion ($D2$ = distance from negative edge to base of mound in mm, Mw = multiplication factor, $Mw = 32.122 + 0.245D2 + 0.044D2^2$).



Plate 6.1. "Cage-type" camera assembly used to take seabed photographs at the North Sea study site; (1) camera, (2) flash unit, (3) switch, (4) trigger weight.



Plate 6.2. Photograph of the seabed at the North Sea study site in January 1989, depicting a "smooth" topography devoid of biogenic features (area of view= 2.75m^2 , depth of field= 1.64m).



Plate 6.3. Photograph of the seabed at the North Sea study site in September 1989, depicting a "rough" topography produced by the volcano-like mounds of *Callianassa subterranea* (area of view= 2.75m^2 , depth of field= 1.64m).

	Rep.	St. 1	St. 5	St. 13	St. 23	St. 25	Site mean
<i>Mound height</i> (mm)	1	55.6	46.2	59.0	40.6	47.6	
	2	53.4	56.2	49.2	56.0	58.2	
	3	41.6	54.0	48.3	53.0	55.1	
	4	58.0	56.3	59.2	55.6	57.4	
	5	55.6	52.8	57.6	55.5	58.0	
	mean	52.8	53.1	53.9	52.1	55.3	53.5
<i>Mound width</i> (mm)	1	100.1	82.3	110.2	73.8	88.1	
	2	105.6	111.4	93.2	112.1	139.2	
	3	83.2	97.2	106.3	110.1	134.2	
	4	139.2	146.4	148.0	156.2	162.2	
	5	122.3	115.1	115.2	126.5	141.9	
	mean	110.1	111.3	114.6	115.7	133.1	117.0

Table 6.1. Converted measurements of *Callianassa subterranea* mound height and width taken from photographs of the seabed at the North Sea study site in September 1989 (Rep. = replicate photographic image, St. *n* = station sample number).

CHAPTER 7

GENERAL DISCUSSION

[Aspects of this chapter were presented at the 1st European Crustacean Conference, Paris, August, 1992 and are included in Rowden & Jones "Critical evaluation of sediment turnover estimates for Callianassidae" (*Journal of Experimental Marine Biology and Ecology*, in press).]

7.1. Discussion

The identified need to investigate the mode and magnitude of bioturbation by specific members of a macrobenthic community in the North Sea, to establish the significance of biological control upon marine sediment dynamics, has been confirmed by the present study.

Intensive reworking of the upper few centimetres of the sea bottom by deposit-feeding infauna produces an "open" surface that is easily resuspended by low-velocity tidal currents (Rhoads & Young, 1970). The temporal variation in the stability of such an "open" seabed (Yingst & Rhoads, 1978) and overlying turbidity (Young, 1971) has been qualitatively related to changes in the occurrence of the macrobenthic fauna. At the North Sea study site, high values of sediment water content and shear-wave velocity in the near-surface region correlate most notably with the occurrence and temporal abundance of the brittle star *Amphiura filiformis*. Most variability in seabed rigidity, and hence susceptibility to mobilisation by bottom currents, occurred between January and May/September, when *A. filiformis* was least and most abundant, respectively. The study findings show also that the mud shrimp *Callianassa subterranea* alters the stratigraphy of the seabed deposits and the physical properties of the sediment. Elevations in the sediment water and organic contents, plus the silt/clay fraction at depth, correlate with the location of the shrimp's burrow shafts. The feeding and burrow maintenance activities of these shrimps produce faeces and unwanted sediment which are periodically expelled via a thin exhalant shaft to form unconsolidated volcano-like mounds on the seafloor. Field (core sampling/ photography) and laboratory evidence indicates that mud shrimps are relatively inactive during winter months, which suggests that bioturbation by *C. subterranea* contributes to the strongly seasonally modified erodability of the North Sea study site seabed. The *Callianassa subterranea* population at the North Sea study site is relatively dense (site mean = 46/m²; compared with North Sea mean = 22/m², Künitzer *et al.*, 1992) and the species' bioturbatory influence demands detailed consideration.

The present study confirmed that in the southern North Sea, the mud shrimp *Callianassa subterranea* constructs a complex burrow of several vertical shafts which descend from the surface and connect to a maze of horizontal galleries at depth (Witbaard &

Duineveld, 1989). The comparative architecture of thalassinid burrows, as revealed by resin casting, has been used recently to interpret the life habits and the burrow use of different callianassids (eg, feeding), and their interaction with the surrounding environment (eg, food obtained from within or outside the burrow). Such an interspecific, functional morphological approach to the study of thalassinid burrows was initially presented by Suchanek (1985) and expanded by Griffis & Suchanek (1991), who proposed a model of thalassinid burrow architecture and trophic mode from a review of 44 species. Griffis & Suchanek (1991) identified six basic types of burrow morphology associated with three basic methods of feeding. The burrows constructed by *C. subterranea* were assigned by Griffis & Suchanek (1991) to "type 2" of the morphotype model (burrows of simple branches which contain no seagrass, made by species which produce sediment mounds via deposit-feeding activities). Griffis & Suchanek (1991) found that the burrow form most commonly associated with the genus *Callianassa* is type 2 (72% of the species reviewed). Although the *C. subterranea* burrow resin casts from the present study comply with the majority of the criteria associated with type 2 burrow morphology, they also possess features of another morphology type. *Callianassa subterranea* burrows from the North Sea have a narrow exhalent shaft (or "chimney"), long vertical shafts (not helical) and deep, reticulate branching. These latter details contribute to the classification of a "type 4" burrow (Griffis & Suchanek, 1991). Griffis & Suchanek's (1991) burrow model predicts that type 4 burrows belong to suspension feeding thalassinid species as associative mounds (indicative of deposit-feeding) are not produced.

It is clear from these observations that species-specific models of burrow morphology are open to criticism, despite the fact that it is widely recognised that members of the Callianassidae (at least) appear to construct burrows of different morphology (see review, Dworschak, 1983). Reasons for the difficulty in successfully categorising burrow morphology may relate to the observed variability of callianassid burrows in relation to population and environmental factors. The plastic nature of *C. subterranea*'s burrow constructing ability is clearly demonstrated by the differences in morphology associated with those burrows constructed in sandy (this study, see Chapter 4; Witbaard & Duineveld, 1989) and muddy sediments (Atkinson & Nash, 1990). Clearly, therefore,

the present study illustrates that it is wise to treat with caution any model of thalassinid burrow morphology which aims to predict trophic mode and thereafter infer ecological significance/influence for or upon a soft-sediment environment.

The burrows of callianassids are sites for biogeochemical processes which involve important elements such as trace metals and carbon, which in particular can be associated with the organic lining of the burrow wall (Abu-Hilal *et al.*, 1988; Vaugelas & Buscail, 1990). In addition, the redistribution of sediment, associated with burrow construction and maintenance, can control the indigenous plant (eg, by physical smothering and photosynthetic light reduction; Suchanek, 1983) and animal populations (eg, by sediment granulometry alteration and physical disturbance; Alongi, 1986). The flux of nutrients associated with burrow venting by callianassids may be substantial and contribute significantly to the nutrient demand for primary production (Koike & Mukai, 1983; Murphy & Kremer, 1992). The influence of callianassids upon ecosystem functions is most frequently assessed by measures of sediment turnover rates (Lee & Swartz, 1980). At the North Sea study site, *Callianassa subterranea* was estimated to have a sediment turnover rate of 11kg(dry)/m²/yr. Assessing the significance of such a sediment turnover rate relative to that of other callianassids is difficult and requires standardization of methods and reporting (see Chapter 5). As a first step towards this goal, the following recommendations are made:

1. Whenever possible, the Direct Entrapment method should be adopted as the most accurate and practical method for collecting expelled sediment.
2. Dry weight, rather than volume or depth, should be used as the most exact and appropriate unit for expressing the quantity of sediment turned over.
3. The remaining two units of the turnover expression (space and time) should be constrained by the confidence of their measurement.

As an illustration of the importance and significance of ^{the} last recommendation, the present study of *Callianassa subterranea* demonstrated the influence of body size and temperature upon the amount of sediment expelled by individuals. In addition, the experiments were conducted over sufficient time to illustrate that sediment expulsion activity was not continuous, but a complex of active and inactive periods. Combining these experimental data with field information on seawater temperatures and population

dynamics (density, size frequency), it has been possible to produce an annual sediment turnover budget for the North Sea study site, with a confidence unrealised to date. The present estimate is approximately three times higher than the value reported previously for the same species at this location (Witbaard & Duineveld, 1989). Although the latter authors acknowledged that their findings were preliminary, their estimate has, nonetheless, been used for comparative purposes (Vaugelas, 1990).

Thus, to reduce possible error, and to allow comparison of reported estimates [if there is little, or no, information on population dynamics or total mound (including small density)], only the unit of individual shrimp, or mound, should be utilised in the final expression of sediment turnover. In addition, a similar constraint should be applied to the temporal unit of the estimate. The actual length of time over which expelled sediment was collected should be the standard reported unit, with alternative values being utilised only if account has been taken of possible variability with time (eg, influence of expulsion behaviour and of changes in productivity and temperature in tropical and temperate regions respectively). So, whilst it is often preferable to have a final value of sediment turnover expressed as quantity per m^2/year , extrapolation to these, or other units, should not be undertaken unless the estimate incorporates sufficient confidence in the spatial or temporal unit quoted. In addition, all the original values and calculations used to obtain the sediment turnover estimate by extrapolation must be reported. Sediment turnover rates, expressed as suggested, would enable direct comparison of estimates of bioturbatory activity for callianassids. Until such standardization, the *relative* importance of callianassids in sediment dynamics and ecosystem function will not be identified accurately.

In this study, it was possible to assess the significance of the sediment turnover by *Callianassa subterranea* on sediment resuspension relative to physical forces at the North Sea study site. At the study site, *C. subterranea* occurs in relatively high densities and seabed photographs show that numerous surface mounds can be produced by mud shrimps. These mounds have a significant influence upon the physical dynamics of the bed, in addition to being the source of direct lateral sediment transport [maximum = $7\text{kg(dry)}/\text{m}/\text{month}$]. Biological modifications of bed properties and bed roughness between January and September at the study site would have increased the susceptibility

of the bed to resuspension. However, none of the modifications sufficiently lowered the threshold of movement for substantial and prolonged resuspension of the bed to occur at the study site (Morris & Howarth, 1993). Nevertheless, these biological effects must become important when wave/current interaction (eg, summer storms) boosts the bed stress (Jago *et al.*, 1993). Since the seabed at this site is important to biogeochemical and metal fluxes in spring and summer, especially after plankton blooms (Jones *et al.*, 1993), summer storms may produce significant effects in these respects. In particular, dissolved and particulate Fe and Mn were released across the sediment-water interface by the resuspension of degraded organic-rich particles (Millward *et al.*, 1993). Unfortunately, the total influence of mud shrimps upon the resuspension of sediment in the whole of the North Sea is difficult to predict because of the identified variability in sediment turnover/transport correlated with current strength, temperature, population density, and possibly even small differences in bottom sediment characteristics. *Callianassa subterranea*, however, must have the potential to contribute significantly to the process of sediment resuspension considering its geographical range (Künitzer *et al.*, 1992). Therefore, the bioturbatory activities of *C. subterranea* must be included in any discussion of the fate of contaminants and the future modelling of associated water quality in the North Sea.

7.2. Conclusions

1. Components of the macrobenthic fauna, particularly the brittle star *Amphiura filiformis* and the mud shrimp *Callianassa subterranea*, significantly modify, via bioturbation, the physical properties of the seabed at a muddy-sand site in the North Sea.
2. Despite the abundance of *C. subterranea* in the macrobenthic communities of the North Sea, the relative bioturbatory significance of the mud shrimp has to date been thinly described and underestimated.
3. Burrows produced by *C. subterranea* in the southern North Sea are extensive and complex; their structure is size-, sex- and sedimentary environment-specific.

4. The burrowing activities of the mud shrimp population at the study site result in a significant annual sediment turnover, the magnitude and pattern of which is influenced by shrimp size and environmental temperature.
5. *Callianassa subterranea* contributes directly (via sediment expulsion) and indirectly (via modification of bed properties) to sediment resuspension at the North Sea study site, though its influence is only periodically significant (ie, at times of summer storms).

7.3. Recommendations

1. The apparent environmental plasticity of *C. subterranea* burrows has an important consequence for the validity of the use of thalassinid burrow models as tools to predict the relative influence of shrimps upon their environment; therefore, such use should proceed with caution.
2. To identify the relative importance of thalassinid bioturbation upon ecosystem function, strictly comparable methods of making and reporting sediment turnover estimates should be adopted.
3. A thorough investigation of the mode and magnitude of bioturbation by the macrobenthic fauna is essential to establish the significance and a realistic measure of the biological control exerted upon marine sediment dynamics.
4. The notable contribution of *Callianassa subterranea* to sediment resuspension, and its potential influence upon biogeochemical cycling plus the local and geographic abundance of this and similar species, illustrates the need to incorporate a measure of thalassinid bioturbation in any critical evaluation of shelf-sea ecosystems (eg, the production of a water quality model for the North Sea).

APPENDIX

September '89				October '89				April '90				July '90				August '91			
CL	S	C ¹	I	CL	S	C ¹	I	CL	S	C ¹	I	CL	S	C ¹	I	CL	S	C ¹	I
1.5				1.5				1.5				1.0				1.0			
1.5				1.5				1.5				1.0				1.5			
1.5				1.5				1.5				1.0				2.0			
2.0				1.5				1.5				1.0				2.0			
2.0				2.5				1.5		r		1.0				2.0			
2.5				3.0	M	r		1.5		l		1.5				2.0			
2.5				3.0		r		1.5		l		1.5				2.0			
2.5				3.5	M			1.5		r		1.5				2.0			
2.5				3.5				2.5				2.0				2.0			
3.0	M			4.0	M	l		2.5		l		2.5				2.0			
3.0	F			4.0	F			2.5				3.0				2.0			
3.5	M	l		4.5	F			3.0				3.5				2.0			
4.0	M			4.5	M			3.0				3.5				2.0			
4.0	F			4.5	F			3.0				3.5	F			2.0			
4.5	M		l	6.0	M	l	l	3.0				4.0	M			2.0			r
4.5	M			6.0				3.0		r		4.0				2.0		r	
4.5	M			6.0				3.0	M	r		4.0	F			2.5		r	
4.5	M			6.0	M	l		3.5		r		4.0	M			2.5			
4.5	M			6.0		l		3.5	M	r		4.5	M		r	2.5			
5.0	F			6.5				4.0	M			4.5	F			2.5			
5.0	F	r		6.5				4.0	F			5.0	M			3.0			
5.0	M			6.5	M			4.5				5.0	M			3.0			
5.5	M			6.5	M			4.5	F			5.5	F			3.0			
5.5	M			7.0	M	l		5.0	F			5.5	M		l	3.0	F		
5.5	F			7.0				5.0	M			5.5	F			3.0	M	l	l/r
6.5	M	l	r	7.0	M	l		5.0		l		6.0	M			3.0	M		l
6.5	M			7.0	F			5.0	M	l		6.0	M		l	3.0	M		
6.5	F	r	l	7.5	M			5.5	M			6.0	M			3.0	M		r
7.0	F	r		7.5	M			5.5	M	l		6.0	F			3.0	M		
7.0	M	l		8.0	M			6.0	M	r	l	6.5	F	l		3.5	M		l
7.0	M	l		8.0	F			6.5	F			7.0	Fo			3.5	M		
7.5		r		8.0	F	r		7.0	F	r		7.0	M			3.5	F		
7.5	Fo			8.0	M			7.0	F			7.0	M			3.5	M		r
7.5	Fo	l		8.0	M	l		7.0	F	l		7.0	M	r	r	3.5	F		
7.5	M	l		8.0	F	l		7.5	M			7.5	M			4.0	M		r
8.0	M	r		8.0	F	l		7.5	M			7.5	M	l		4.0	M		
8.5	Ff	r		8.0	F	r		7.5	M	l		7.5	M	r		4.0	F		
8.5	Ff	l		8.5	M	l		8.0	M	r	l	8.0	M			4.0	M	r	
8.5				8.5	M			8.0	M	r		8.0	M	r		4.0	M		
9.0	M			8.5	F	r		8.0	M	l		8.0	Fo	r		4.5	M		
9.5	Ff	l		8.5	F	r		8.5	M			8.0	Fo	r		4.5	M	r	
9.5	Ff			8.5	M	l		9.5	M			8.0	M	l		4.5	M		
9.5	Ff	r		8.5	F	l		9.5	M	r		8.0				5.0	M		
9.5	Ff			9.0	M			10.0	Fo	r		8.0	M	r		5.0	M	r	

Appendix I. Population details for *Callinassa subterranea* from the North Sea study site.

Key: CL = Carapace length (mm); S = Sex (M= male, F= female, Fo= female in ovigerous condition, Ff= female with "feathery" pleopods ie. eggs recently released); C¹= Primary Chela (r= right, l= left); I= *Ione thoracica* parasitism (r= right, l= left - side of carapace).

9.5	M	l		9.0	M			10.0	Fo			8.0		l	l	5.0	M		
9.5	Ff	l		9.5	F			10.0	M	r		8.5	M			5.0	M		
9.5	M	r		9.5	M			10.0	M	l		8.5	Fo	l		5.5	M	l	
10.0	M	l		10.0	M	r						8.5	M	r		6.0	M	l	
10.0	M			10.0	M	r						8.5	M	l	r	6.0	M		
10.0	Ff	l		10.0		l						9.0	Fo			6.0	F		
10.0	Ff	l										9.0	Fo	l		6.0	M		l
10.0	M	l										9.5	Fo			6.5	M		
10.0	M	r										9.5	M	r		6.5	M		
10.0	M	r										10.0	M			7.5	M		
10.5	M	r										10.0	M			7.5	M		
11.0	M	r										10.5	M			7.5	F		
11.0	M											10.5	M			7.5	M	l	
																7.5	M		
																7.5	F		
																8.0	Fo		
																8.0	Fo	l	
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Appendix I. (continued)

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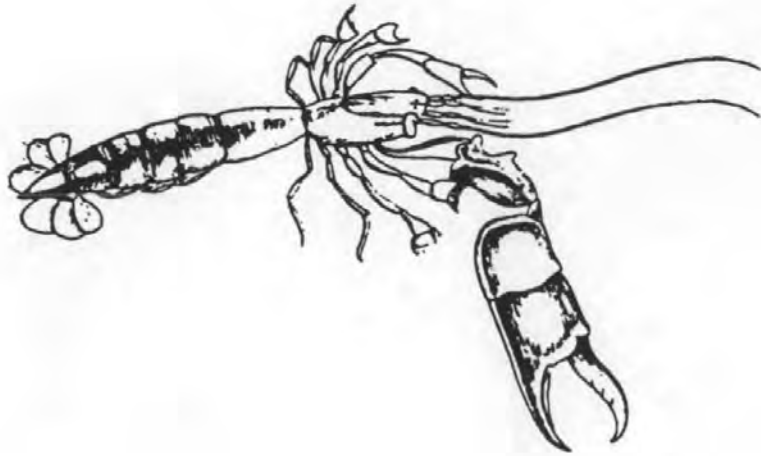
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(Montagu, 1808)

"Now the word *Callinassa* I presume, is made up from two Greek words (Kalli, anassa), signifying Beautiful Queen; but I fancy that if a female monarch had one of her hands normal and the other bigger than her chest and head combined, none but courtiers would flatter her by declaring she was beautiful, and possibly they might be partly actuated thereby through a wholesome fear of that big hand."

(By the Deep Sea - *The Natural History of the Seashore* by Edward Step, 1896)

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