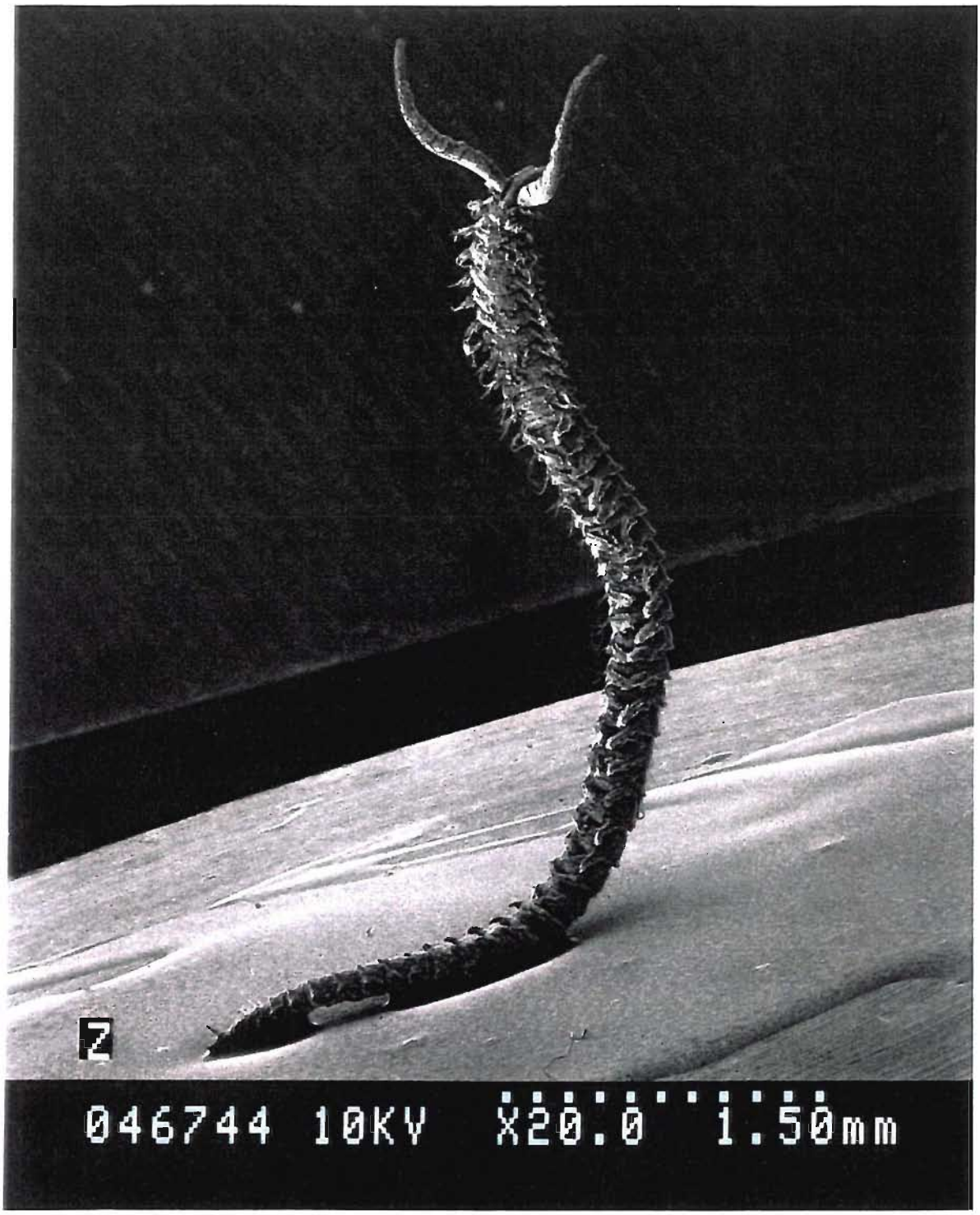
UNIVERSITY OF SOUTHAMPTON

The Formation and Dynamics of *Pygospio elegans* Tube-Beds in the Somme Bay, France.

Torin Simeon Morgan

Thesis submitted to the
University of Southampton
for the Degree of Doctor of Philosophy

Department of Oceanography
July 1997



Pygospio elegans Claparède 1863

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE
OCEANOGRAPHY

Doctor Of Philosophy

The Formation and Dynamics of *Pygospio elegans* Tube-Beds in the Somme Bay, France.

by Torin Simeon Morgan

The spionid polychaete *Pygospio elegans* Claparède 1863 is a small tube-building opportunist, commonly found in the benthic communities of organically enriched boreal estuaries. The species may reproduce both sexually and asexually; larvae may develop either planktonically or benthonically. Population densities of up to 100,000m^{-2} have been recorded.

In the macrotidal Somme Bay, N.France, the *Pygospio* population regularly exceeds densities of 100,000m^{-2}; an abundance of nearly 600,000m^{-2} was noted in December 1993. Raised sedimentary structures are formed in the presence of dense arrays of *Pygospio*-built tubes: so-called "tube-beds". A multidisciplinary study was made of these structures and the *Pygospio* population that formed them.

An extended period of sexual activity was discovered in the Somme Bay *Pygospio* population; there was no asexual activity. All larvae developed planktonically, hatching at an early stage in development. This life-history provides a massive larval availability for tube-bed foundation and an optimal spatio-temporal vantage for the re-colonisation of defaunated areas in the strongly hydrodynamic Somme Bay. Laboratory experiments suggested that this reproductive mode in the Somme Bay population was fixed. A similarly non-poecilogonous response was observed in individuals taken from Ryde Sand (Isle of Wight), which exhibited extended larval brooding. Although no morphological variation was noted among *Pygospio* specimens from populations from Europe and the USA, this apparent reproductive inflexibility within *Pygospio elegans* populations suggested the possibility of cryptic, sibling speciation.

Sampling revealed that the approximate threshold tube-bed forming *Pygospio* density in the Somme Bay was 50,000 m^{-2}. *Pygospio* had a significant effect on sediment physico-chemical characteristics and dense aggregations of the spionid stimulated the proliferation of the microbial and meiofaunal communities. *Pygospio* density affected the structure of the associated macrofaunal community: diversity peaked between *Pygospio* densities of 50,000m^{-2} and 200,000m^{-2} as tube-bed formation offered an attractive resource and refuge from erosion. Beyond *Pygospio* densities of 200,000m^{-2}, the community became more dominated by species able to tolerate the spionid's spatial monopoly.

Significant spatial variability in female reproductive success and in the proportion of un-occupied tubes was noted. Patterns of variation suggested that some benefit is derived from living at high density. Males also appeared to favour conditions of high conspecific density. *Pygospio* was randomly distributed at the scale of the individual.

Vertical profiles indicated a more heterogeneous deposit in tube-beds than in non-bed sediment. Tube-bed sediment contained discrete subsurface regions of silt and clay which non-bed sediment lacked. Such deposits were deemed an important component of a tube-bed's structural integrity, and were ascribed to the combined effects of *Pygospio*'s suspension feeding activity and the passive trapping of suspended load by a dense array of protruding tube-tips.

A conceptual model of tube-bed foundation, development, persistence and decline was considered in the light of the present findings.

Contents

Acknowledgements.

This study was funded by NERC grant GT4/93/255/A, with CASE sponsorship from the Natural History Museum. I'd like to express my gratitude to my supervisors, **DrGordon Paterson** at the Museum, and **Drs Laurence Hawkins** and **Martin Sheader** at Southampton University, for their time, advice, and spadework in the Somme.

Special thanks are due to **Dr Michel Desprez**, who helped organise my sampling trips and provided generously of his time and experience in the Somme. He also made available much of the unpublished literature on the area that has amassed since the creation of the GEMEL at the Station d'Etudes en Baie de Somme. Thanks also to **Dr Herve Rybarczyk** and all at GEMEL for their help, advice and patience during my visits. I'd like to thank **Jim Lewis**, **Ben Agboke**, and **Andy Geary** who helped out on my sampling trips at various times. Specimens were kindly lent or donated by **Dr Brian Hentschel** of the University of Washington State, **Dr Kristen Fauchald** of the Smithsonian Institute, and **Dr Danny Eibe-Jacobsen** of the Copenhagen Museum of Natural History. **Louisa Jones** at the Natural History Museum taught me to use a scanning electron microscope and **Dr Paul Wright** at the University advised on the sediment ammonium determinations. **Neil McAleece** at the Museum helped with the spatial autocorrelation theory; he also helped me begin to program a cellular automaton model. At the University's Geology Department while **Bob Jones** and **John Ford** performed the cross-sectional core resin impregnation and **Barry Marsh** helped with the x-radiography.

Thanks to the usual suspects: **Richard Acornley**, **Philippe Guyard**, **Kristen Bruhn**, **Karen Meidlinger**, **Chris Bishop**, **Grant Lawson**, **Andy Geary**, **Cathy Lucas**, **Pete Shaw**, **Leonie Dransfeld**, **Nicola Debenham**, **Rhian David**, **Gerard Bloemers** and **Adrian Clayton** for "moral guidance".

Thanks **Mum** and **Dad** for the wonderful support you've always given me, and continue to give me, in so many ways; and thankyou **Joanne** for all your love and encouragement. This is for you.

Part 1.

The *Pygospio elegans* Population of the Somme Bay

Chapter 1.
General Introduction

A population of the spionid polychaete *Pygospio elegans*, a small, opportunistic tube-builder, has proliferated to extraordinary density in the macrotidal Somme Bay, N. France. An unusual, and rarely recorded phenomenon has resulted: where *Pygospio* occurs in dense patches, distinct sedimentary structures are formed. These structures have been called "tube-beds"; their genesis, growth and impact on the environment form the focus of this thesis. The following questions are addressed: why do tube-beds form, and what is the adaptive significance of tube-bed formation by *Pygospio*? How does *Pygospio* form, and tolerate, such high conspecific densities? How do tube-beds impact the physico-chemical environment and the associated macrofaunal, meiofaunal and microbial communities? How do tube-beds grow and develop, and how do they decline?

1.1 Disturbance, and Opportunistic Life Histories

The estuarine sandy mud-flat habitat is harsh. Resident fauna are exposed to daily, cyclic fluctuations in temperature, salinity, air exposure and oxygen availability, while inhabiting a mobile, abrasive substrate which can foul feeding and respiration and hinder mobility. Estuarine-dwelling organisms usually display highly-specialised morphologies, physiologies and behaviours, all evolutionary responses to the demands placed on them by their habitat.

Estuaries are, however, often nutrient-rich and high levels of productivity are frequently encountered. In the inner and middle reaches of a large estuary, fluvial input regularly imports high levels of dissolved anthropogenic nutrient (e.g. nitrate, phosphate). Here, also, slow currents at the landward margins permit deposition of silt and clay which in turn trap fine organic particulates, becoming sites of intense microbial activity.

Estuaries are relatively dynamic habitats. Apart from the diurnal variability already mentioned, temporal and spatial variations in hydrodynamics may alter local

physico-chemical substratum conditions and radically re-structure benthic communities. Hydrodynamic disturbance has its greatest impact in macrotidal estuaries, whose "shores" are often exposed to powerful tidal scour. More occasional, severe disturbances such as storms may decimate populations, resuspending sediment and scattering infauna in the water column. Seasonal fluctuation in nutrient input can further result in periodic eutrophication and anoxia.

In this frequently disturbed habitat, a number of species have evolved opportunistic life strategies to take advantage of the "pioneer" niche: that group most likely to be among the first colonists of recently defaunated substrates (Grassle & Grassle, 1974; McCall, 1977). This first successional stage usually involves small "r-selected" polychaetes (classically *Capitella capitata* and members of the family spionidae: Zajac, 1991) able to establish dense populations swiftly and physico-chemically recondition the sediment (Rumohr, 1980; Gallagher *et. al.*, 1983; Reise, 1983b; Schmager-Noji, 1988). These species are often found dominating organic rich areas where the chemistry is hostile to other organisms (Tsutsumi, 1987).

The tube-building spionid polychaete *Pygospio elegans* is one such opportunist. It appears able to react to defaunation events, caused by physico-chemical disturbance, by forming high density populations (Anger, 1984; Noji & Noji, 1991). In the Somme Bay, N. France, *Pygospio* aggregations of extraordinary density have been found, responding to local conditions of organic enrichment and physical disturbance and forming "tube-beds" often composed of aggregations of some hundreds of thousands of individuals per square metre.

1.2 *Pygospio elegans*

Pygospio elegans is a small, sedentary, tube-building polychaete of the family Spionidae. Adults are members of the macrofauna while newly-settled juveniles verge on the meiofaunal. The species' taxonomy is addressed in **Chapter 3**, and a full taxonomic description is given in **Appendix 1.** *Pygospio elegans* has a number of interesting characteristics, including a wide tolerance of habitat conditions, a highly flexible set of feeding behaviours and an unusually wide repertoire of reproductive strategies.

1.2.1 Distribution and Habitat Preference.

Pygospio elegans is a cosmopolitan, circum-boreal species, and has been reported from the Arctic, Baltic, N. Atlantic and N. Pacific Oceans, as well as the North and Othotsk Seas, the Mediterranean and the coast of S. Africa. Although apparently widely distributed, comparatively few reports exist of *Pygospio*. Holme (1949) suggested that the comparative lack of reports of small populations of the worm was due in part to its small size.

This species can occur in huge density. In Britain, relatively high densities have been recorded from the Dovey Estuary (2,000m^{-2}: Stopford, 1951), the Blyth Estuary (1,000m^{-2}:Gudmundsson, 1985), and the Clyde Estuary (7,000m^{-2}: Meadows & Hariri, 1991) . From America, the worm has been found at densities of 60,000m^{-2}, from False Bay (Wilson, 1983) and 83,000m^{-2} from Boston Harbour (Trueblood *et. al.*, 1994). Populations from the North and Baltic Sea coasts have been found at densities of 20,000m^{-2} (Linke, 1939) and 31,000m^{-2} (Smidt, 1951), both from the Danish waddens. Hempel (1957) observed colonies on the German coast so dense that they formed "tables" in the sand. Of a greater order of magnitude still, Anger (1977) reported an asexually reproducing population from Kiel Bay whose density reached 200,000m^{-2}, and, in a review of long-term data from the Somme Bay, Noyer (1993) documented a bed-forming density peak of 200,000m^{-2} during 1986. Noji & Noji (1991) reported that bed-forming densities of small opportunist polychaetes should exceed 80,000m^{-2}.

Anger (1977) noted the highest densities of *Pygospio* coincided with areas polluted with domestic sewage, and proposed that *Pygospio* might be viewed as a pollution indicator species. Hempel (1957) found the worm in muds with a high H_2S content, indicating a tolerance of anoxic, reducing conditions. The worm's preferred substrate has been found to vary, although the majority of reports find it living in muddy sand. It has also been found in fissures (e.g. by Gudmundsson, 1985), and under rocks, providing that enough sediment is available for tube construction.

The majority of reports place *Pygospio* intertidally; Desprez (pers. comm.) has found it to maintain populations in the upper shore while Tufail *et. al.* (1989) found the worm to be approximately five times as dense at a low tide site than a high tide site. Hempel (1957), however, noted that it extended into the sublittoral; Refors (1933)

found it at a depth of 50m and Remane & Schleiper (1950) noted it at depths of 100m in the Baltic. Gerdes & Krumbein (1985) found *Pygospio* in the lower supralittoral: they proposed that *Pygospio* was able to exist so high up the shore because of microbial communities which could provide food and oxygen while reducing evaporation and sediment erosion. Hertweck (1994) found *Pygospio* thriving in the upper shore of Jade Bay tidal flats on the North Sea.

A range of salinities is tolerated; Hobson (1976) described the spionid as one occurring in both brackish and marine waters. *Pygospio* has been found in extreme brackish conditions (2‰: Hempel, 1957; 5-6‰: Refors, 1933) and in hypersaline pools (Nicol, 1935). Khlebovich (1977) observed individuals in the White Sea burying themselves deeper into the sediment in areas where fresh water was discharged, however.

1.2.2 Reproductive Strategy.

Reports of *Pygospio elegans* from around the world indicate a wide repertoire of reproductive behaviour. The species reproduces both sexually and asexually (Rasmussen, 1953). Sexually-produced larvae may develop lecithotrophically, brooded full-term within the parental tube and hatched directly into the sediment; or they may be hatched at an early stage into the water column to exist and feed in the plankton before settling (Hannerz, 1956).

1.2.2.1 Sexual Reproduction.

Rasmussen (1973) described two distinct types of egg in *Pygospio*: nurse eggs, released from the coelom when 6μm-70μm in diameter, and genuine eggs, usually around 100μm in diameter on release. Nurse eggs were found to contain very dense, orange coloured yolk and to lose their nucleus once larger than 40μm, while genuine eggs were poor in yolk and had a distinct nucleus.

After release, eggs were found to be retained externally in a capsule which was attached to the female and to the inside of her tube by single stalks. Long strings of "sling-like" egg capsules were seen to be formed. Söderström (1920) proposed that the capsules were formed by a secretion from the dorsal vents of the epitokous nephridia

which hardened in water: each capsule therefore corresponded to the total sexual products of one ripe female segment. Hempel (1957) described the individual capsules in a string as being detached from one another. Söderström (1920) found a maximum of 16 capsules in a string while Rasmussen (1973) found up to 34, anchored in the deepest part of the parent's tube. Söderström (1920) found 50-60 eggs per capsule, while others found 70 (Hannerz, 1956), and <250 (Rasmussen, 1973), although this latter figure included both nurse and genuine eggs.

Brooding is common in small-bodied taxa (Strathmann & Strathmann, 1982) and Hannerz (1956) identified members of the subfamily Spioninae (to which *Pygospio* belongs) as being specially adapted for such "parental care", with eggs lacking the usual thickened membrane, the presence in the female of the dorsal *receptacula seminalis* to accept and store spermatophores and a behavioural adaptation in the female involving the ciliary generation of a water current around the egg capsules to keep them well supplied with oxygen and nutrient.

The occurrence of two types of egg, first described in polychaetes from *Spio martinensis* by Mesnil & Caullery (1917) has great implications for the development of *Pygospio* larvae. Genuine eggs develop into embryos and consume nurse-eggs: this is termed "adelphophagia". In *Pygospio* adelphophagia is preceded by the partial cleavage of the zygote; nurse-eggs fragment into smaller "nutrient bodies" and the zygote then forms a mouth and intestine (Rasmussen, 1973). Organogenesis then stops while adelphophagia proceeds, the embryo assuming a characteristic hunchbacked appearance. Organogenesis only recommences after all the nutrient has been consumed. Chia (1974) classified adelphophagia as a form of lecithotrophy, adults depositing yolk into nurse-egg containers rather than directly into the cytoplasm of the oocyte.

Adelphophagia was first recognised in *Pygospio* by Söderström (1920) who found only 6-7 larvae developing from a capsule that had originally contained 40-50 eggs ("nurse" plus "true"). Working during the summer, he found a capsule containing larvae 16 setigers in length, and concluded that these were developing directly, feeding on stored nutrient until the moment of hatching, still in its parent's tube. Similarly, Hempel (1957) found 30 larvae at the early 4 setiger phase in a single capsule, but only

10 at the later 12 setiger stage , while Gudmundsson (1985) documented a population in which all brood capsules contained only two larvae. However, Leschke (1903) had previously proven the existence of planktonic, planktotrophically developing *Pygospio* larvae, in the spring. From this, Söderström (1920) concluded that the species had two distinct types of development: one brooded and lecithotrophic, hatching in the summer; and one planktonic and planktotrophic, hatching earlier in the winter/spring.

Thorson (1946) followed Söderström with a study in which he documented three distinct types of planktonic larva in *Pygospio*, as well as a benthonic one; such polymorphism was attributed to different types of nutrient supply. In 1951 Smidt presented data supporting this conclusion, again finding three planktonic morphological types - although no benthonic types were found. In Hannerz's 1956 study, however, only one morphological larval type was found, in both the plankton and the benthos (although benthic larvae were never seen to develop extensive larval setation). Hannerz identified Thorson's "*C*" variant and Smidt's "*i*" variant as the larvae of *Pygospio* while the other variants were reassigned to other species of spionid. Hannerz's contention that only one larval type existed was backed up by his observations and comparisons of late planktonic and brooded, benthonic larvae of similar setiger number. Hannerz hypothesised that differences in larval development were the simple result of variation in the duration of brooding time with season: in winter, larvae hatched at the three to six setiger stage, without adelphophagia; as the breeding season progressed, new batches of larvae spent protracted periods in brood capsules, with adelphophagia. Hannerz noted that the maximum time spent in the plankton by a July-hatched larva was around 24 hours. Hannerz's revision of *Pygospio* development was consolidated by Rasmussen (1973), who agreed on a single larval morphology and proposed that developmental type was not genetically determined but the qualitative result of the amount of nutrient bodies eaten while brooded.

To summarize, non-brooded larvae hatch at lengths from 3 setigers, 250-330μm (Anger *et. al.*, 1986) to 6 setigers (Hannerz, 1956) early in the season; brooded larvae hatch later, at 12 to 16 setigers (Söderström, 1920; Hannerz, 1956; Rasmussen, 1973). This size band coincides with that of planktonic larval settlement which has been put at 11+ setigers (Rasmussen, 1973), 12-14 setigers (Hannerz, 1956) and 17-20

setigers (Hempel, 1957). Anger *et. al.* (1986) put the duration of a full planktonic phase at 4-5 weeks, and noted metamorphosis at 15-16 setigers . The youngest stage found in its own tube was 27 setigers long (Hempel, 1957).

Gudmundsson (1979) found no instances of gamete production in individuals under 35 setigers in length, and found the majority of sexually mature animals to have attained at least 45 setigers.

From its distribution and reproductive seasonality, *Pygospio* can be seen to be cold adapted. Anger *et. al.* (1986) found larvae able to metamorphose at 6°C; Sautour and Cazaux (1985) observed similar temperature tolerance in the field. The species is often found to breed during the winter months and has been found surviving in frozen sediment (Hannerz, 1956). Thamdrup (1935), however, found *Pygospio* capable of withstanding quite high temperatures, up to 30°C.

1.2.2.2 Asexual Reproduction.

Pygospio has been observed reproducing asexually by architomic fragmentation. Rasmussen (1953) was first to describe *Pygospio* fragmenting, at any region along its length, "as if cut by a knife". On average, fragments were 3-4 setigers long, maximally 7 setigers. Fragments remained in the tube, wriggling, while rapidly regenerating at either end: a complete new adult was formed in eight days at 20°C. Such behaviour was in evidence all year round, though at a peak during early spring. Rasmussen (1953) made observations over two years. In 1949, the peak in asexual reproduction was short in duration (late April to early May) and almost all individuals fragmented. In 1950, the peak period of asexual reproduction lasted longer (mid March to late April), but fewer individuals fragmented. A temperature-related control was postulated, 4°-5°C being found to induce fission and regeneration in adults. In 1949 ambient temperatures rose more slowly than in 1950, and Rasmussen tentatively linked this with the period of asexuality.

Hobson and Green (1968) reported asexual fragmentation from Barnstable Harbour, Massachusetts; worms were found to divide into 2-3 fragments. Fragment length was not recorded. Wilson (1985) found in a laboratory study that fission rate was proportional to food supply and inversely proportional to density, and he noted the

implications of this for the proliferation of populations in nutrient rich areas. In an earlier study Wilson (1983) varied the density of *Pygospio* about its ambient field density (treatments were 1/3x, 1x and 3x field). Asexual reproduction was only found in the 1/3x treatment. Wilson (1985) described 4-8 fragments per worm. He also noted a temporal separation of periods of sexual and asexual reproduction in the population he studied: sexuals were present between November and December while fragmentation occurred between March and October. Similarly, Gudmundsson (1985) found fragmentation in his Cullercoats population on the North Sea coast of England to occur at the end of the breeding season, in March to April, although only in 3-20% of examined tubes: 2-3 fragments of 10-30 setiger lengths were found per worm.

1.2.3 Feeding Behaviour.

Pygospio remains in its tube to feed. It is a versatile feeder. Hempel (1957) noticed the use of the tube-tip filter net. The worm may also deposit feed, often exposing the greater part of its body to increase the reach of its palps (Brey, 1991), or using its mouth to pick up particles directly (Woodin, 1982). Small particles of detritus or algae are picked up (Thamdrup, 1935) by adhesion to sticky mucous on the palps, and are passed back by ciliary wafting along the mid-palp groove toward the mouth (Fauchald & Jumars, 1979). At the mouth, selection takes place, larger particles being discarded (Linke, 1939).

Hannerz (1956) stated that *Pygospio* was also able to suspension feed, capturing live plankters using its palps. Taghon *et. al.* (1980) experimentally demonstrated a flexibility in feeding behaviour with respect to flow conditions. At increased flow rates it ceased deposit feeding and lifted its palps into the water, actively forming them into helices for efficient food collection. This transition was noted at flow rates between 2 and 5cms^{-1}, so long as particulate matter was present suspended in the water.

Self and Jumars (1978) speculated that "palp-lashing" by *Pygospio* may act to resuspend particles of a certain range of specific gravities, creating a dense suspension of fine nutritious matter. Fauchald and Jumars (1979) described *Pygospio* as "the most

versatile of spionids" in its repertoire of feeding behaviour. Faeces are extruded at the surface in loose strings (Hertweck, 1994).

1.2.4 Tube-building Behaviour.

Hempel (1957) described tube-building behaviour: a worm deprived of its tube secreted a mucous coating which gathered available sediment, some of which was carried in the worm's mouth. Grains were observed being arranged evenly by movements of setae and parapodia. Interstices were plugged using smaller particles. Among the materials used in construction were shell shale, sponge spicules and plant material. The upper region of the vertically-placed tube was found to be more stable than the deeper region. Hempel noticed that after a while the upper end of the tube would become damaged and the worm would build a new passage from the area of the tear, sealing up the old tube. Mature tubes were found with several branches near the top. At the entrance to the tube, a "net" of hardened mucous strands was found, comprising three triangular flaps, each attached to the rim on one side. According to Hempel, these could help in food capture as a filtering device, or have a protective function, preventing entry by stray particles or other fauna which could colonise the tube or prey on the occupant. Hannerz (1956) found these flaps to spring together and form a pyramidical barrier. Taghon *et. al.* (1980) observed that *Pygospio* individuals deprived of their tubes built new ones within one hour.

1.3 The Study Area

The Somme Bay lies at 50°, 14'N 1°, 33'E in the Departement de Somme, N.France. It is a macrotidal estuary, open to north-westerly winds, with an intertidal zone 72km^2 in area, of which 12km^2 is mature salt marsh. A maximum tidal amplitude of 9-10m and a double low water enforce a highly dynamic erosional and depositional regime: the flood tide is considerably stronger than the ebb. A low freshwater input (approximately 40m^{3}s^{-1}) ensures salinity never falls below 25‰ on the mid-estuarine flats (Rybarczyk *et. al.*, 1990).

As the site of more than 60% of French national cockle (*Cerastoderma edule*) landings (1990 data), the Somme Bay is an important fishery site and has been the subject of continuous study for over 15 years, generating 13 research papers to date.

Macrobenthic surveys conducted on the intertidal flats recorded mass mortalities in 1982, '83, '85, '89 and '90. These were the attributed to anoxia promoted by phytoplanktonic and algal blooms, which were in turn the result of high summer temperatures and organic enrichment (Rybarczyk *et. al.*, 1996). The River Somme has a catchment area of 6,000km^2, much of which is agricultural land: nitrate runoff, coupled with the ammoniacal excreta of the estuary's dense bivalve populations, was cited as causing acute organic enrichment (Rybarczyk *et. al.*, 1990). A program monitoring the impact of anoxia on the commercially important *Cerastoderma* population recorded the proliferation of opportunistic *Pygospio elegans* during these periods of disturbance and reduced competition, from background levels in 1983 to $2x10^5m^{-2}$ in 1986 (Desprez *et. al.*, 1992).

Sampling was conducted between December 1993 and November 1995 on the northern mud-flats adjacent to Le Crotoy (site "LCS"; see **Figure 1.1**). An estuary-wide survey (Desprez, 1994) revealed maximal productivity and biomass at this site, and *Pygospio* densities were highest in this area during the period of sampling. Also marked on **Figure 1.1** below is site "HHS", adjacent to the southern salt-marsh, which is also referred to in this study.

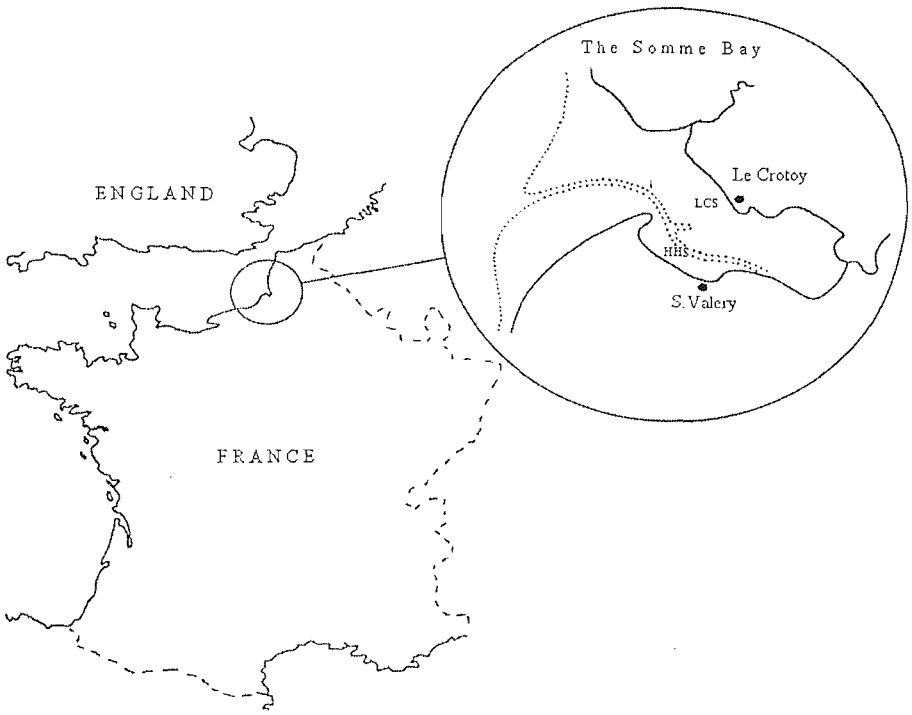


Figure 1.1: The Somme Bay, and positions of the sites LCS and HHS.

1.4 The Present Study

Dense estuarine assemblages of tubicolous polychaetes are common (Whitlach and Zajac, 1985). Among spionids, several species appear capable of mass development, including *Polydora ciliata*, *P. ligni*, *Streblospio benedictii* and *Pygospio elegans* (Noji & Noji, 1991).

This broad, multidisciplinary study approaches the phenomenon of *Pygospio* tube-beds from a number of perspectives. Many of the observations made have relevance to more than one chapter, and some cases cross-referencing between chapters was unavoidable.

Chapter 2 details the recent population dynamics of *Pygospio* in the Somme Bay and provides a background to the study. Population structure, reproductive behaviour and life cycle are examined and related to environmental conditions, and some initial conclusions about the nature of tube-beds are drawn. In **Chapter 3** the wider implications of *Pygospio* reproductive strategy are explored.

The following chapters return to the main theme of the tube-bed phenomenon and describe the results of sampling carried out between December 1993 and June

1995. A brief section appears at this point to introduce the general **Sampling Strategy** and validate the criteria used to distinguish "tube-bed" from "non-bed" areas. **Chapter 4** details the physical nature of the tube-bed environment. **Chapter 5** then examines the impact of the tube-bed on the local infaunal community, drawing on the previous chapter to interpret the patterns found. The bed-forming *Pygospio* population itself forms the topic of **Chapter 6**, while **Chapter 7** considers the tube-bed as a purely sedimentological feature. Finally, in **Chapter 8** the questions of the formation and dynamics of tube-beds are considered; evidence from previous chapters is used to build a conceptual model.

Chapter 2.
Life History Of *Pygospio elegans* In The Somme Bay

2.1 Introduction

The following chapter details the examination of archived samples and data leading to a description of the life-cycle and population history of *Pygospio elegans* in the Somme Bay. The environmental context of the area is established, and patterns of population dynamics are related to prevailing environmental conditions. Such a study sets the stage for following chapters, and provides insights into the mechanism by which the huge densities, allowing tube-bed formation, are achieved.

2.2 Population Dynamics

Figure 2.1a illustrates population fluctuations of *Pygospio* over the last 15 years. Densities are described at two contrasting sites in the Somme Bay: the exposed mud-flat on the northern coast, "LCS"; and the more quiescent site adjacent to the southern salt-marsh, "HHS" (see **Figure 1.1**). 1981 to 1990 data were supplied by J-P Ducrotoy. September 1990 to September 1992 data are taken from Batten (1994). Data collected during the present study (December 1993 to June 1995), are included. These latter may be biased towards higher densities by the restriction of sampling to areas on and around tube-beds, however. For this same reason the datum representing mean *Pygospio* density in September 1994, when a "pseudo-bed" was sampled, is omitted, as it gives what is almost certainly a misleading impression of real population fluctuations.

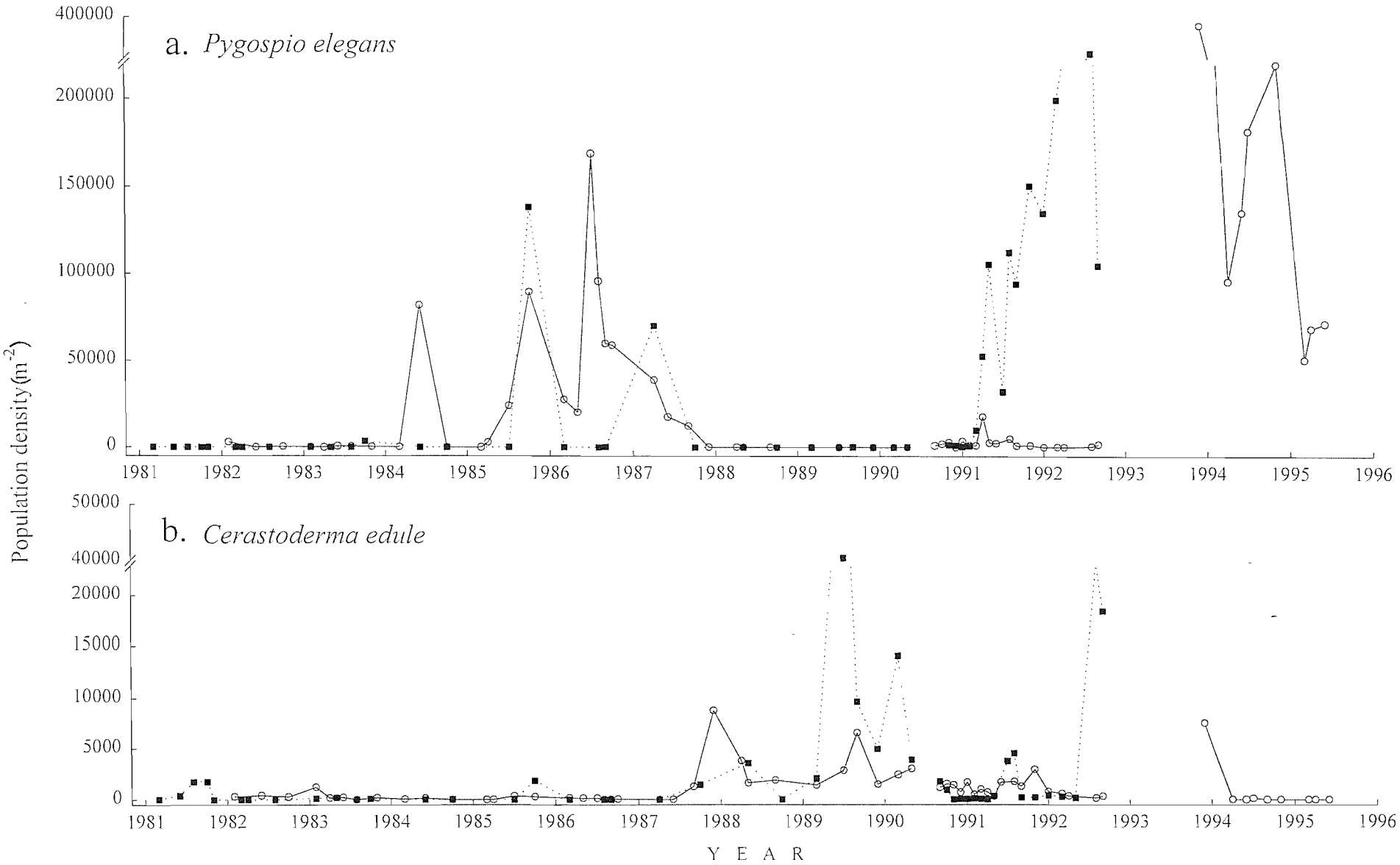


Figure 2.1: Mean population densities, 1981-1995:
—○— LCS ··■·· HHS

March 1981- May 1990 data from J-P Ducrotoy (pers. comm.);
September 1990- September 1992 data from Batten (1994);
December 1993- June 1995: LCSdata only, from present study.

Massive macrobenthic mortalities resulting from anoxia were reported in the Somme Bay in 1982, '83, '85, '87 and '92 (Rybarczyk *et. al.*, 1996). **Figure 2.1a** indicates post-disturbance, opportunistic responses by *Pygospio* at LCS in 1984, '85 and '86, when densities exceeded 170,000 individuals m^{-2}. At HHS such high population densities were less durable, short-lived population explosions occurring in late 1985 and early '87; in each case density fell to zero within a year. In all cases *Pygospio* populations peaked during the summer months. Both populations collapsed altogether during 1987, coinciding with a boom in the *Cerastoderma edule* (cockle) population: an amensalistic synergism between these two species was suggested (Ducrotoy *et. al.*, 1987; Rybarczyk, 1993). This interaction is discussed in further detail in **Chapter 5**, and illustrated here by the juxtaposition of **Figures 2.1a** and **2.1b**. The decline in *Cerastoderma* during 1990 was followed by *Pygospio* density increases in 1991, leading to a successful spring - summer recovery by the polychaete at the southern site HHS. *Pygospio* failed to re-establish at LCS at that time. *Cerastoderma* densities were low at both sites during the 1991 *Pygospio* proliferation. Sampling in summer 1993 indicated around 3,000m^{-2} *Pygospio* at LCS (Desprez, 1994). By late 1993 the *Pygospio* population at HHS had collapsed (M.Desprez, pers. comm.), and a dense, tube-bed forming population had become established at LCS. This achieved a mean density of around 400,000m^{-2} in December 1993; the actual maximum density in any one replicate was 576,000m^{-2}, the greatest recorded for this species. The peak in *Cerastoderma* density in December 1993 was caused by a massive settlement of spat, which subsequently failed to establish.

2.3 Reproductive Cycle

Archived samples of *Pygospio elegans*, taken monthly between September 1990 to September 1992 from LCS and HHS, were available from a previous study (Batten, 1994). These were examined as part of the present study to determine the reproductive cycle of the species. LCS and HHS specimens were handled and analysed separately for the purposes of comparison and replication.

2.3.1 Method.

Ten replicate samples per month had been taken at each site, sieved through a 500μm mesh and stored in 70% alcohol. Where available, fifty individuals per month and per site were randomly subsampled from the archive and measured. Specimens were stripped of their tubes using forceps and temporarily mounted in 50:50 glycerol-alcohol on slides, under coverslips. They were examined under high-power light microscopy and a record was made of sex, width of the fifth setiger, total setiger number and evidence of asexual reproduction. Total setiger number was judged to be a better measure of somatic size than length, which could vary depending on degree of contraction at death: Anger *et.al.* (1986) also suggested total setiger number is a better criterion than length for growth in *Pygospio*. A large number of specimens were broken: in these, total setiger number was estimated by regression of setiger number of whole worms on the width of their fifth setiger (r^2=0.603, $p<0.0001$, n=156), where

$$\text{total setiger number} = 9.85 + (93.6 \times \text{fifth setiger width}) \quad (1)$$

The width of the fifth setiger has found wide use as a body size correlate in previous studies of spionids (Yokoyama, 1990; Zajac, 1991; Santos, 1994). All measurements were made using a *camera lucida* and digitising tablet with "SigmaScan" image analysis software (Jandel Corporation). Males were characterised as sexually mature by the presence of a pair of branchiae on the second setiger. In females, the following reproductive characteristics were also measured:

- presence of oocytes in coelom;
- presence of oocytes and embryos in externally-borne brood capsules;
- mean diameter (across long axis) of true oocytes per individual;
- length, and number of setigers, of brooded larvae.

Oocytes were visible through the body wall. No measurements of fecundity were attempted. Nurse eggs were ignored in the consideration of oocyte diameters:

these could be distinguished by their more granular, yolk-filled appearence, and lack of a nucleus when larger than 40μm in diameter.

2.3.2 Results.

Figures 2.2 and **2.3** illustrate population size frequency distributions at LCS and HHS respectively. **Figures 2.4** and **2.5** illustrate reproductive data and accompanying environmental data at LCS and HHS. Population density data were taken from Batten (1994), and environmental data were supplied by M.Desprez.

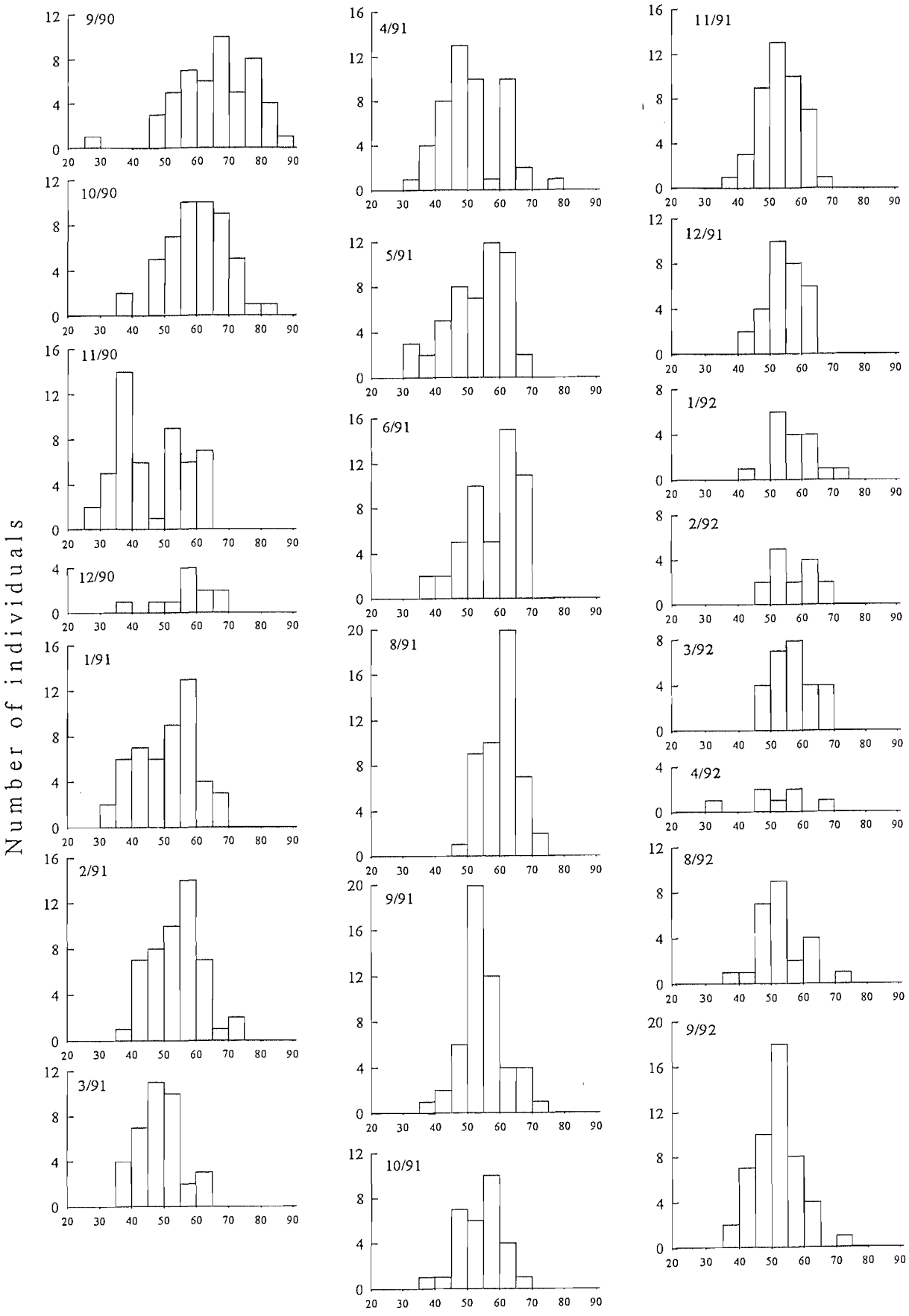


Figure 2.2: Population size frequency distributions at LCS, September 1990 - September 1992

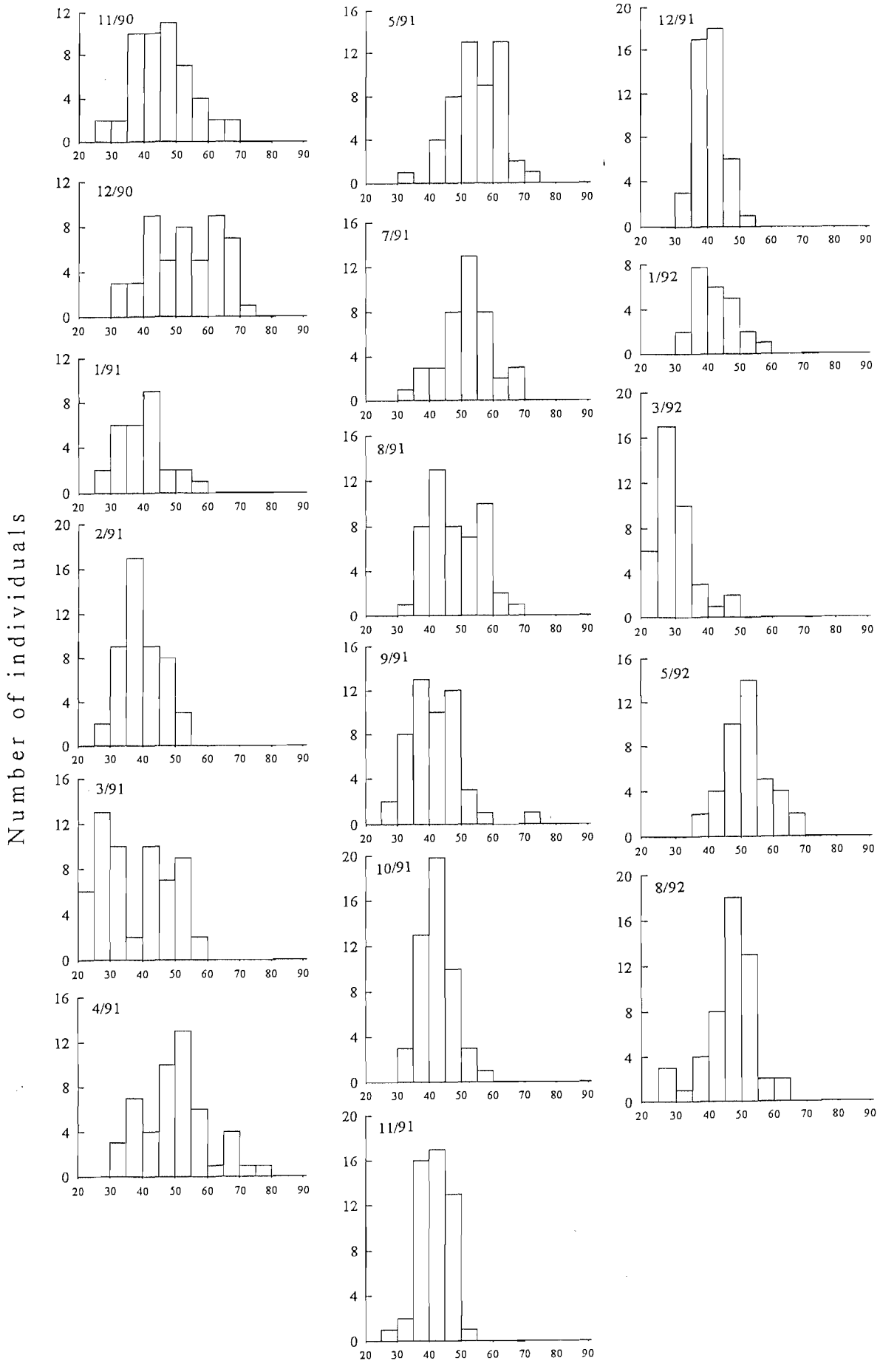


Figure 2.3: Population size frequency distributions at HHS, November 1990 - August 1992

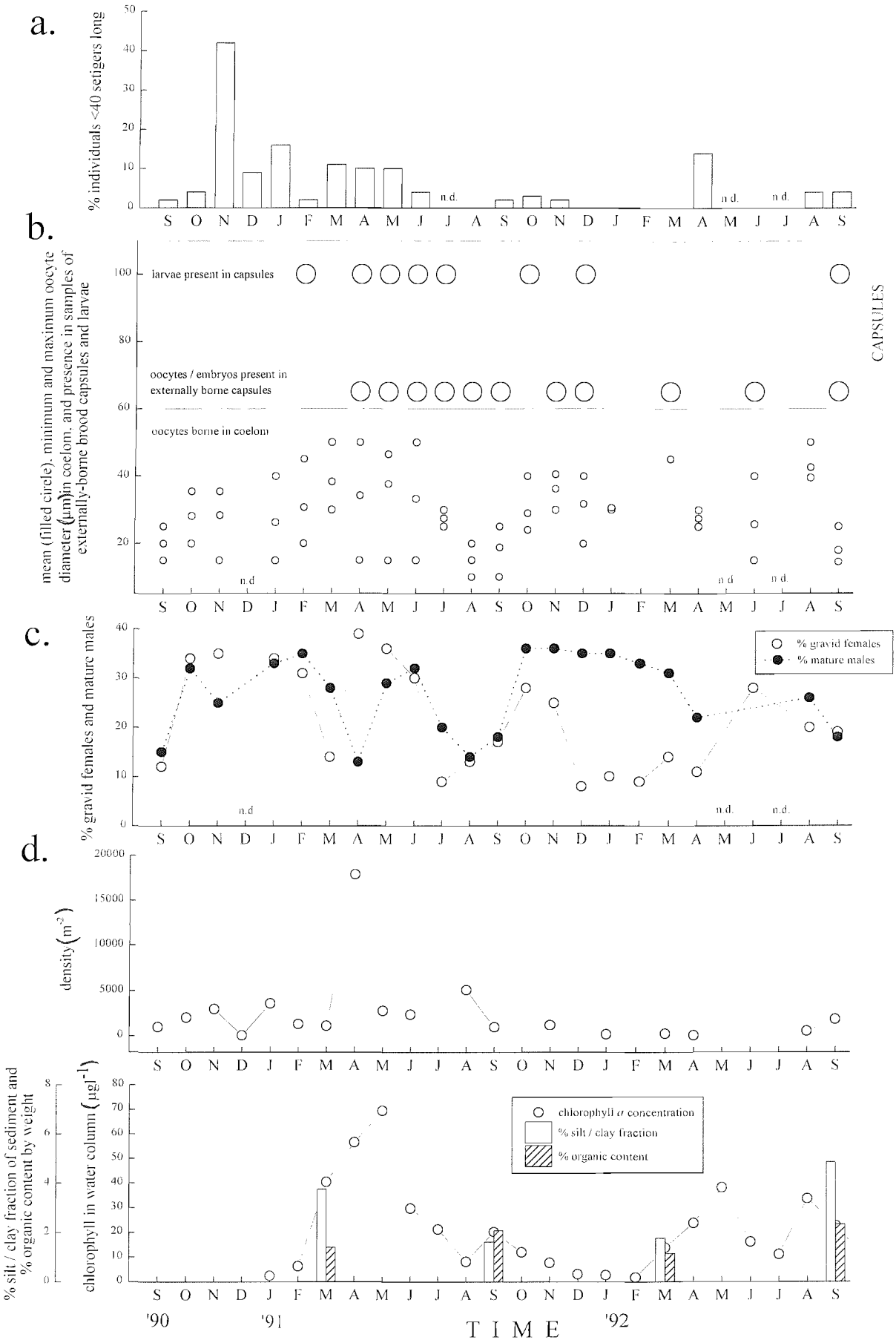


Figure 2.4: Reproductive Cycle at LCS. **a**: % individuals <40 setigers long; **b**: mean, minimum and maximum oocyte diameters per sample, and presence in sample of externally-borne brood and larvae; **c**: % females bearing gametes and % mature males; **d**: population density (data from Batten, 1994); **e**: environmental variables (data supplied by M.Desprez). n.d.: no data available

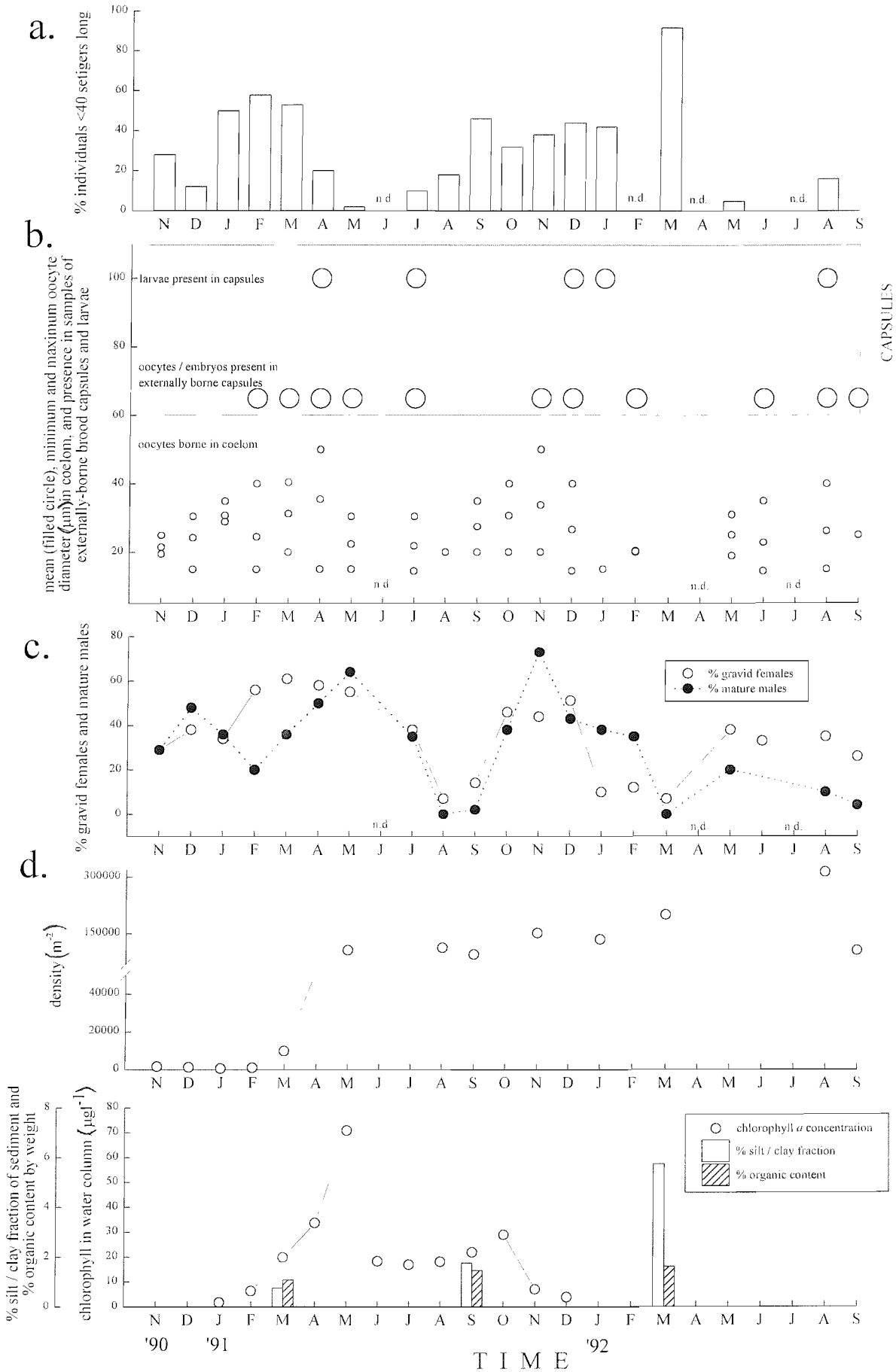


Figure 2.5: Reproductive Cycle at HHS. **a**: % individuals <40 setigers long; **b**: mean, minimum and maximum oocyte diameters per sample, and presence in sample of externally-borne brood and larvae; **c**: % females bearing gametes and % mature males; **d**: population density (data from Batten, 1994); **e**: environmental variables (data supplied by M.Desprez). n.d.: no data available.

2.3.2.1 Population Size Frequency Distributions.

Newly-settled larvae and small, non-tube dwelling juveniles would have passed a 500μm mesh: in consequence, no individuals with fewer than 20 setigers were recorded in archived samples. *Pygospio* may settle from the plankton anywhere between 11 to 20 setigers (Rasmussen, 1973; Hempel, 1957a). Metamorphosis occurs between 15 and 16 setigers (Anger *et.al.*, 1986) and tube-building begins at around 27 setigers (Hempel, 1957a).

Small, juvenile, sexually immature individuals are defined here as those less than 40 setigers long. This interpretation is based on the size at which gametes first appear (see **Chapter 6**), and on the assumption that there was no starvation-induced, and thus seasonally variable, somatic mass loss. High population densities, resulting in increased competition for food, may have accounted for the high proportion of small individuals at HHS. Pre- and post-population explosion levels of small individuals were similar, however, suggesting that these individuals were newly recruited juveniles rather than competition-stressed adults. Also, larger animals were present throughout the period of high density. At the less-densely populated LCS the proportion of small individuals only once exceeded 20%. Again, fluctuating levels of smaller individuals bore little relation to changes in population density, and all such individuals were thus assumed to be juvenile. Low levels of these were perhaps the result of poor recruitment conditions at this site.

Proportional occurrences of juvenile individuals were calculated from size frequency data and are presented in **Figures 2.4a** and **2.5a**. A seasonal pattern of recruitment was discernable at both sites, although this was more clear at HHS. The proportion of juvenile and immature individuals increased through autumn to spring, decreasing again toward the summer. Recruitment must therefore have taken place over an extended period, beginning during August - September and falling away toward the following May - June.

At LCS, immature individuals were present from September 1990 to June 1991, peaking at 42% of the population in November 1990. No similar influx of juveniles was recorded at the turn of 1991-'92, however. HHS data showed more sustained periods during which juveniles and immature individuals were present, with large

numbers of recently settled juveniles (less than 25 setigers length) appearing in March of 1991 and 1992.

2.3.2.2 Sexual Activity.

Long-term brooded larvae, with more than three setigers and with distended yolk-sacs, were not observed in any archived sample. Thus the Somme Bay *Pygospio* population would seem to sexually propagate with entirely planktonic, planktotrophic larval development.

The study of *Pygospio* reproduction is complicated by the extrusion of more mature oocytes into externally-held capsules for the final period of embryonic and larval development. Observations of such external brood are possible only where specimens have been preserved within their tubes, with capsules intact. In some cases, 1990-'92 archive specimens were not preserved within their tubes, and the record made of externally-borne brood was certainly incomplete. It is stressed that the plots indicating presence of external brood and larvae in **Figures 2.4b** and **2.5b** form a partial record only.

No oocytes larger than 60μm were observed within the coelom, and none smaller than 60μm within capsules. Mean oocyte diameter on extrusion in Somme Bay *Pygospio* was therefore placed at 60μm. However, the size of newly extruded oocytes quoted in the literature is around 100μm (Söderström, 1920; Rasmussen, 1973). Three-setiger larvae within brood capsules did not exceed 120μm in length, suggesting their release into the plankton at that size. However, hatch-ready, planktonic *Pygospio* larvae raised in the laboratory by Anger *et.al.*(1986) had attained between 250 and 330μm in length. It would therefore seem that the benthonic period of development, from fertilised oocyte to larva, has been reduced in the Somme Bay *Pygospio* population.

The presence of morphologically mature males was monitored at both sites. Such males are ephemeral, and at times of sexual inactivity all individuals in a population appear morphologically as immature females. Male morphological characteristics may be degeneratively lost within a few days (Rasmussen, 1973). At HHS the proportion of males fluctuated widely from 0% to 80%. Males at HHS

virtually disappeared during the late summer 1991, and again in early spring 1992. At LCS the proportion of sexually mature males did not drop below 10%, nor exceed 40%. Similar differences were noted in fluctuations of the proportion of gravid females (**Figures 2.4c** and **2.5c**): these accounted for between 8% and 40% of the total at LCS and between 8% and 60% at HHS.

2.3.2.3 Asexual activity.

There was no clear evidence of asexual activity at either site. All regenerating individuals had lost one extremity only, usually the head, suggesting loss by predation or other physical damage. An asexually reproducing individual would appear to have been regenerating both head and tail from an original fragment only a few setigers in length (Rasmussen, 1953; Wilson, 1985).

2.3.2.4 Reproductive Cycle and Population Dynamics at LCS.

Archived LCS samples were available from September 1990 to September 1992.

1990-1991. Oocyte size-frequency distributions indicated the production of two batches of oocyte growth during 1990-'91, the first during autumn and winter, and the second in spring.

During September - October 1990 the proportion of mature males increased from 12% to 34% (**Figure 2.4c**) while the proportion of egg-bearing females increased from 10% to around 35%. The first batch of oocytes commenced growth sometime shortly before September 1990 (**Figure 2.4b**) and gametogenesis continued until around January - February 1991. Three-setiger larvae resulting from this batch (100-120μm in length, yolkless and ready to hatch) were observed in one sample in February 1991. Unfortunately no record of external brood was possible before March 1991.

The proportion of gravid females fell to 12% in March 1991; but rose again in April to 40%, when small (10μm diameter) coelomically-borne eggs were once again apparent, signalling the onset of a second phase of gametogenesis within the 1990-'91 season. Developmental time (oocyte to hatched larvae) during this first, winter batch was around six months (by graphical examination).

The laying period of the second batch appeared to be of shorter duration, the proportion of gravid females falling below 10% by June 1991. Oocytes larger than 60μm and extruded into capsules, were noted continuously between March and August 1991, and three-setiger larvae appeared in samples in October and December 1991. Developmental time during the warmer spring to early summer season appeared shorter, around four months (by graphical examination).

Anger *et.al.* (1986) determined the mean planktonic period of larval development in *Pygospio* larvae hatched at three setigers. This was 20-30 days at 18°C, lengthening to 60-70 days at 6°C. Therefore, new recruits might be expected to appear in the benthos between 1-2 months after hatching, depending on season. Immature and juvenile individuals were noted in samples in high numbers from November 1990, decreasing towards February 1991: these recruits were likely to be the result of the previous (1989-'90) season's sexual activity. Low levels of juveniles and immature individuals resulting from the 1990-'91 season were recorded between March and November 1991 (**Figure 2.4a**).

1991 - 1992. Newly developing oocytes were again apparent in August - September 1991 (**Figure 2.4b**); this coincided with increasing levels of mature males and gravid females (**Figure 2.4c**). This first batch of the 1991-'92 season was responsible for external brood observed between November 1991 and March 1992, and a small recruitment event in April 1992. The record of external brood and larvae at this point was probably incomplete because of small sample sizes, and the lack of tubes in archived samples.

The proportion of oocyte-bearing females fell back to the 10% level again as early as December 1991, and in February 1992 no reproductive products were found in any sample, perhaps having been resorbed by the parent. Oocyte size-frequencies suggest that first-batch gamete production ceased during October - December 1991.

A high level of mature males (peaking at 38%, the maximum for LCS during the sampling period) was maintained throughout the winter and spring, possibly in response to low levels of gravid females: *Pygospio* fertilisation is internal, preceded by a copulation (Schlötzer-Schrehardt, 1991) and the extremely low population densities at this time may have hindered the finding of mates by males in this poorly-motile

species. By June 1992, the number of gravid females rose to around 30%; and mean coelomic oocyte sizes increased through from April to August, evidence of the delayed second batch of 1991-'92. Three-setiger larvae were once more found in September 1992, having developed relatively quickly during the warmer summer months.

2.3.2.5 Reproductive Cycle and Population Dynamics at HHS.

Archived HHS samples were available from November 1990 to September 1992.

1990 - 1991. Data shown in **Figure 2.5b** suggest that the onset of 1990-'91 oocyte growth began some time before November 1990, by which time minimum oocyte diameter had increased to 20μm. This first batch was seen to grow through, and accounted for observations of larvae in April 1991.

From February to April 1991 the presence of smaller oocytes in the coelom suggested the growth of a second batch. The existence of two batches was confirmed by observations at this time of individual females carrying both small oocytes coelomically and more mature oocytes or larvae externally.

Externally borne capsules were observed in available samples from February 1991, and three-setiger larvae were observed from April 1991. A sustained period of recruitment was seen from July 1991 to March 1992, as larvae resulting from the 1990-'91 season completed their planktonic phase of development (**Figure 2.5a**).

More than 30% of all females carried eggs between December 1990 and June 1991, with a peak of 62% in March 1991 during production of the second batch of oocytes (**Figure 2.5c**). Production of the two batches of oocytes therefore overlapped more closely at HHS than at LCS. At HHS the proportion of sexually mature males fell in February 1991: this is difficult to explain as a response to high levels of gravid females, as the proportion of mature males increased again in April - May while relatively high levels (more than 50%) of females still carried oocytes. This increase was perhaps a response to the hugely increasing population density (April - May 1991: **Figure 2.5d**) and thus the greatly increased absolute numbers of unfertilised females present.

1991 - 1992. Oocyte size frequency data suggested the onset of the 1991-'92 season of gametogenesis during July - August 1991. Sexually mature males and females did not become common again until October 1992, however: gametogenesis in early summer 1991 may have resulted from fertilisation by males earlier in the year. Indeed, *Pygospio* is known to store spermatophores in dorsal *receptacula* for later fertilisation of oocytes (Hannerz, 1956). It is not recorded for how long such sperm are stored.

External capsules were observed in samples from November 1991, and three setiger larvae were observed from December 1991. By January 1992 the proportion of females carrying oocytes had dropped below 15%, and by March 1992 mature males were entirely absent from archive samples. It is notable that a similar failure in sexual activity occurred during the same period at LCS. Well-developed coelomic oocytes were absent in January and February 1992, and sexual products were altogether absent in March 1992. A second batch of oocyte growth, postponed until late spring by the winter failure, was seen in the resurgence in the proportion of gravid females in May 1992, and in oocyte growth from April 1992. External brood were noted from June to September 1992, and in August larvae were found, resulting perhaps from the previous winter's pre-failure growth.

2.4 Environmental Data

Environmental data are presented in **Figure 2.6a-c.** Meteorological data were supplied by La Station Métérologique d'Abbeville, 8 miles from the Somme Bay, and River Somme discharge rate data were provided by La Service Hydrologique Centralisateur de Lambersart. River discharge rate and rainfall data were smoothed for clarification, with damping factors of 90% and 80% respectively. Maximum windspeed data were used to plot "violent storm events", defined by The Meteorological Office as occurring at windspeeds in excess of $29ms^{-1}$ (Force 11). **Figure 2.7** provides measurements of fluvial water quality, as provided by L'Agence de l'Eau Artois Picardie.

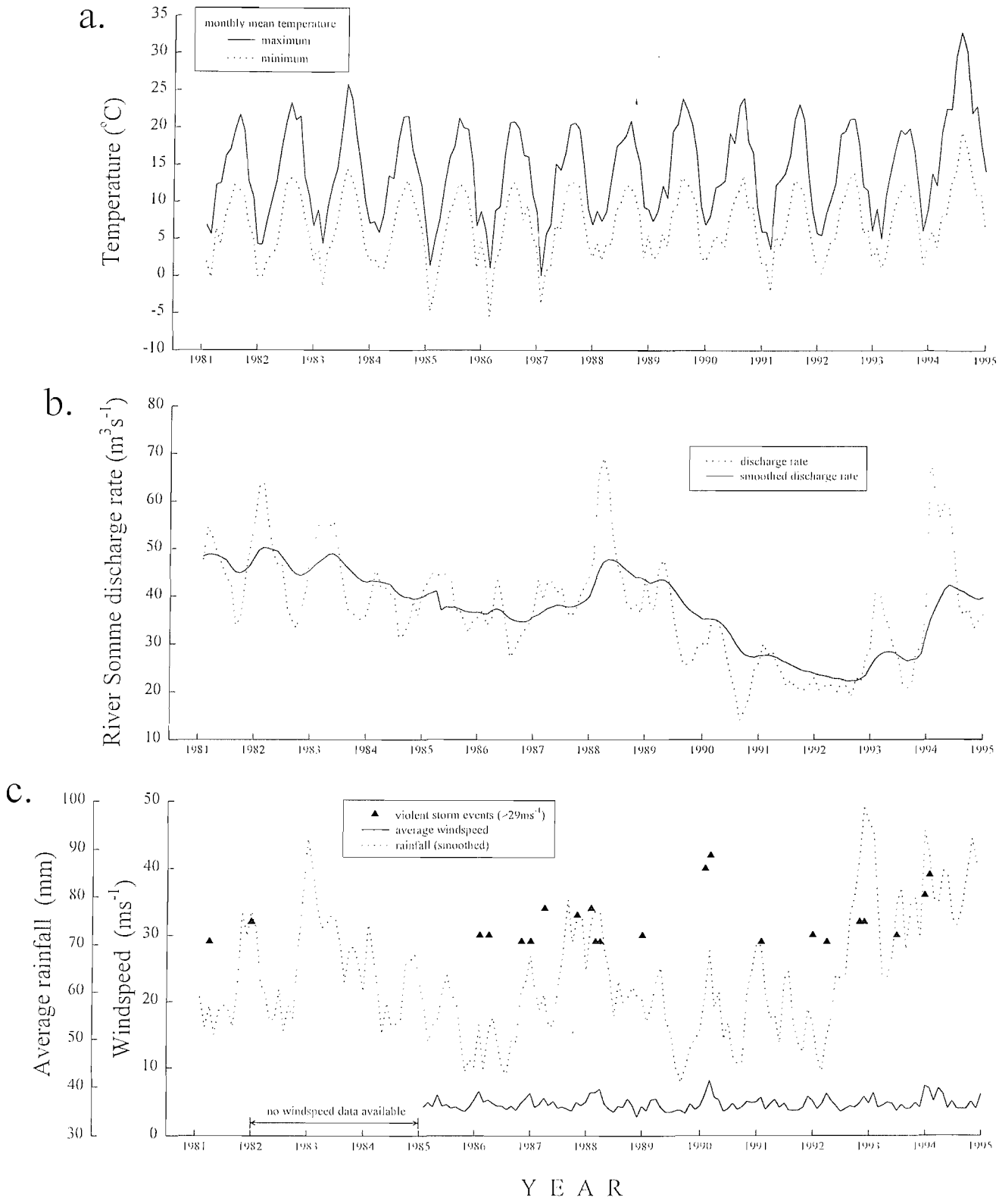


Figure 2.6: Physical environmental variables during the period 1981-1995. **a:** temperature; **b:** River Somme discharge rate; **c:** rainfall and windspeed. Meterological data supplied by La Station Meteorologique d'Abbeville.

River discharge rate data supplied by La Service Hydrologique Centralisateur de Lambersart.

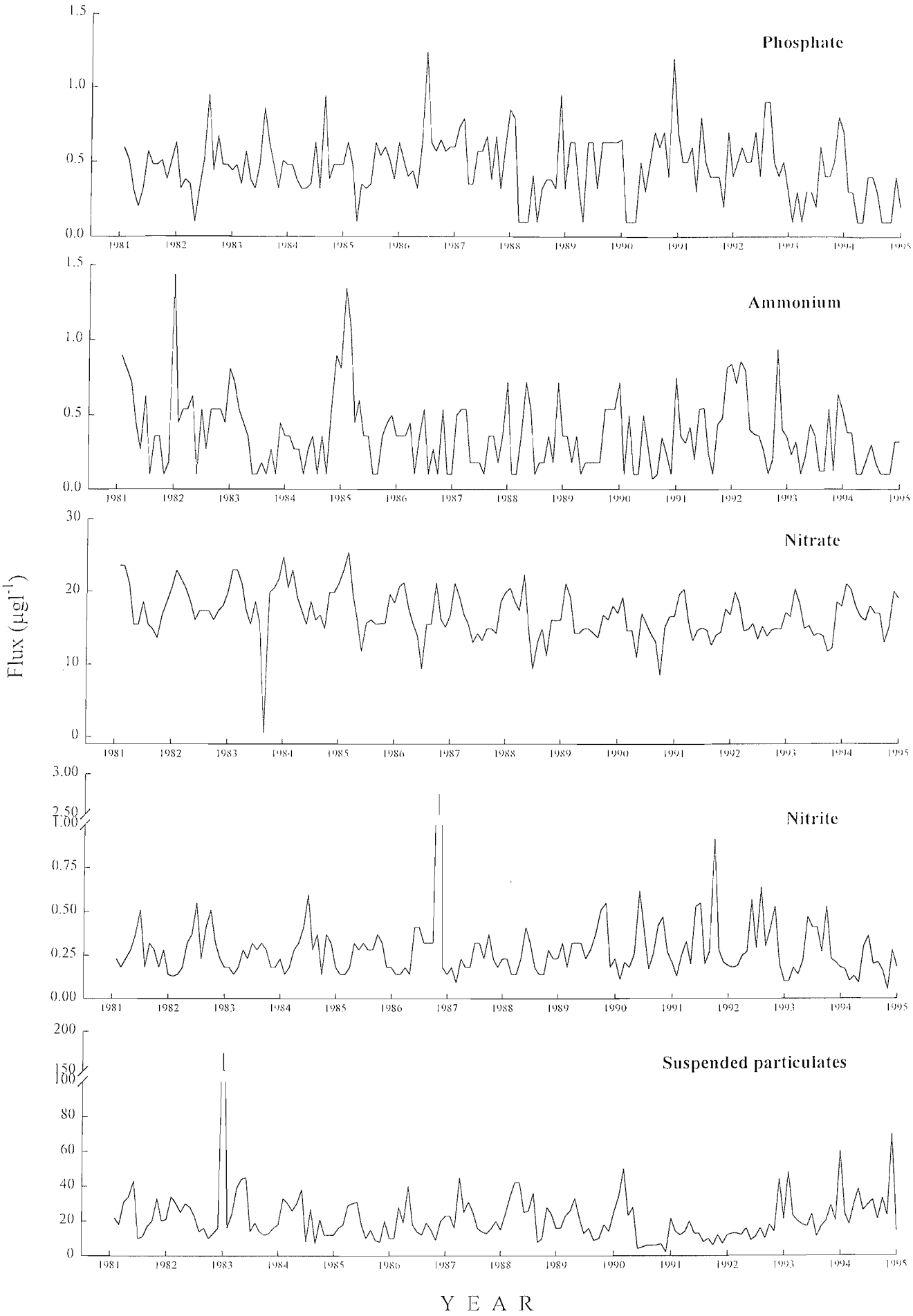


Figure 2.7: Fluxes of suspended particulate matter, and of phosphate, ammonium, nitrate and nitrite ions in The River Somme 1981-1995. Data supplied by L'Agence de l'Eau Artois-Picardie.

2.5 Discussion

2.5.1 Long-term population fluctuations.

Records of benthic macrofauna from the last 25 years indicate the periodic proliferation of *Pygospio elegans* within the mid-estuarine region of the Somme Bay.

Dupont (1975) observed that canalisation of the River Somme in 1969 enabled a massive increase in *Pygospio* densities at HHS, the population sheltering behind a newly-built seawall dyke. He monitored the formation of tube-beds by *Pygospio* populations of 10-50,000 individuals m^{-2} at both LCS and HHS. By 1978-'79, however, the population had become depleted (Dupont, 1981). The unusual warmth of the summers of 1981 and '82 (**Figure 2.6a**), coupled with elevated levels of bivalve excreta, were linked with eutrophication and macrobenthic mortalities (Rybarczyk *et. al.*, 1996). *Pygospio* increased in density again early in 1984 at LCS.

LCS *Pygospio* densities fell again during late 1984 - early 1985; cockles remained at low densities during this period, however. It is likely that the very high import concentrations of allochthonous, toxic ammonium ion ($1.3mgl^{-1}$: **Figure 2.7**), coupled with very low winter temperatures had a dire effect on all macrofauna at that time. *Pygospio* at both HHS and LCS swiftly regained a numerically dominant position in summer 1985, and remained at high densities throughout 1986 and into 1987. A dip in density at LCS and the apparent local extinction of the HHS population in early 1986 was probably the result of very low temperatures and physical damage to tube-beds by storms. Maximum windspeeds had not exceeded $25ms^{-1}$ in 1985 during *Pygospio* proliferation. Cockles failed to repopulate. *Pygospio* was clearly able to survive the two successively severe winters of 1985-'86 and 1986-'87, when minimum temperatures fell as low as -5 °C. *Pygospio* has been described as a very cold-tolerant species, active even in partially frozen sediments (Hannerz, 1956).

River discharge rates showed a tendency to decrease throughout the early 1980's, falling below $40m^3s^{-1}$ in 1984. The HHS *Pygospio* population, situated near the outflow of the river into the estuary, was therefore subjected to decreasing disturbance by hydrodynamic activity. Unsmoothed discharge rates (**Figure 2.6b**) were particularly quiescent during mid-1986, when *Pygospio* densities increased at HHS and peaked at LCS.

High density populations of opportunists are expected to crash within a relatively short time of their foundation through auto-eutrophication and unsupportable levels of competition (Whitlach & Zajac, 1985; Noji & Noji, 1991). It may have been this natural, self-induced senescence that caused the LCS *Pygospio* population crash of late 1987 and the short duration of population recovery periods at HHS. A further possible cause was the simultaneous increase in cockle density after a very successful recruitment of spat: the amensalism between *Pygospio* and *Cerastoderma* inferred from the Somme data was proven by Flach (1996) and is discussed further in **Chapter 5**. Also notable were the hurricanes (windspeeds well in excess of $32ms^{-1}$) during early 1987 and winter 1987-'88 (**Figure 2.6c**) which would have had a destructive impact on densely populated tube-beds, ripping up these drier, more raised sedimentary structures and redistributing them into the water-column.

Rising river discharge rates in 1988, and relatively frequent, violent storms during the winters 1986-'87, 1987-'88 and 1989-'90 would have conspired to hinder the redevelopment of tube-beds after the crash.

The *Cerastoderma* population flourished from late 1987 to 1989. Wide scale macrobenthic mortalities during mid 1990, again linked to high summer temperatures and eutrophication (Rybarczyk, 1996), reduced the cockle population to low levels by 1990. *Pygospio* began once more to increase in numbers at HHS in early 1991. The especially cold winter of 1990-'91 may have suppressed competition by species less able than *Pygospio* to tolerate low temperatures.

River discharge rate was once more falling during the 1990 - '91 period, to less than $25m^3s^{-1}$ by 1991-'92, creating calmer hydrodynamic conditions at HHS. The silt / clay fraction of HHS sediment in October 1992 was over 30% (M.Desprez, pers.comm.), indicating the highly depositional nature of the environment. It was at HHS that the *Pygospio* population escalated to previously unrecorded densities in 1992. *Cerastoderma* densities also increased at HHS during mid-1992, to coexist with *Pygospio*. Continuous allochthonous ammonium imports from late 1991 to late 1992 may have boosted productivity in the region and in October 1992 the organic content of the sediment at HHS was as high as 8% (by mass loss on combustion: M.Desprez,

pers.comm.). Peaking imports of nitrite ion in late 1986 and late 1991, and phosphate ion in mid-1986 and late 1990 also coincided with escalations in *Pygospio* density.

By late 1993 *Pygospio* had disappeared from HHS, (M.Desprez, pers.comm.): increased deposition of fine particulates may have become intolerable, hindering respiration and feeding. An exceptionally dense population had become established at LCS, however. This population flourished throughout the sampling period of the present study, but fluctuated considerably in density. Cockles were notably absent at LCS after failing to consolidate upon the recruitment of late 1993. LCS is more exposed to hydrodynamic conditions than HHS, and the hurricanes of winter 1993-'94 perhaps accounted for the initial drop in mean density from 400,000m^{-2} to 100,000m^{-2}. Complete environmental data were lacking for winter 1994-'95, making it difficult to explain confidently the fall in density in early 1995.

Analysis of macrofaunal abundance data from February 1982 to May 1991, and the faunal similarity index NESS (Normalised Expected Species Shared: Grassle & Smith, 1976), has revealed an approximate seven year cycle of interaction among species (Gallagher, pers.comm.). It is interesting to note the seven year periods between *Pygospio* population proliferations in 1984 and 1991, and *Cerastoderma* proliferations in 1987 and (abortively) in 1994. These observations, though speculation, appear to point to a possible cycle driving, or perhaps driven by, the *Pygospio* - cockle amensalim.

2.5.2 Reproductive cycle.

The present chapter has established a baseline cycle of reproductive activity in *Pygospio elegans* in the Somme Bay. This first step was vital for the development of a sampling strategy for the rest of the study. It also provided important perspectives for the closer study of *Pygospio* sub-populations living both in and outside of the tube-bed habitat.

Pygospio in the Somme Bay appears to have an extended period of brooding. Developing oocytes were present in all samples, except for a brief period early in 1992 when sexual activity appeared to falter. At LCS, gametogenesis occurred in two batches, beginning around August - September and continuing through to June. Gravid

females and mature males were present all year round, albeit in low numbers: the former became more common during the October - February and April - June periods, while males came into season between October and March, and again in May - June. Gametogenesis also occurred over two periods at HHS. The first began growth in July - August, the second in February, ending sometime during early summer. Mature males were absent or at very low levels during August - September and February - March; gravid females were also rare during August - September.

Pygospio was once thought to be annual, the adult dying after extrusion of eggs (Smidt, 1951; Hannerz, 1956). However, Anger *et.al.*(1986) proposed that there could be two generations per year in the natural environment on the basis of a laboratory study which quantified the species' average life-span as 9 months, maximum 45 months at 12°C. Total minimum generation time (adult-adult) was calculated as 15 -17 weeks. Gudmundsson (1985) supported this conclusion, describing *Pygospio* as "potentially polytelic" after finding individual females producing two batches of larvae during a single breeding season; the second batch appeared during the two month period between the beginning of spawning and the hatching out of the first batch of larvae.

Gudmundsson (1985) studied a population at Cullercoats (N.England): here, gamete growth began in September, with 100% mature worms by December. Oocytes were extruded into capsules from December to March. Hatching occurred from February to April, at which time the parental and new generations overlapped. A population from the nearby Blyth Estuary demonstrated similar seasonality, while lagging one month behind. Rasmussen (1973) worked on populations at Horsen's Fjord and Isefjord on the Jutland Peninsula. At the former site there was a very sudden onset of maturity in September. "Egg-laying" (*sic*; taken here to mean gametogenesis) occurred between September and early March, and larvae hatched from November to April. Gametes were almost entirely absent between May to August. At Isefjord no "egg-laying" was observed earlier than January, and laying ceased in April with larvae hatching between February and May.

These examples, and other in the literature, demonstrate the species' rather elastic seasonality. The breeding seasonalities of different *Pygospio* populations from around the world have been found to differ widely, and sexually mature worms or

brooded larvae have been encountered much of the year round (Smidt, 1951; Giere, 1968; Hernoth & Ackefors, 1979).

A four-to-six month benthic developmental period, depending on season, was inferred from the present data. Anger *et.al.* (1986) found a sexually mature adult to take a minimum three months to produce hatch-ready three-setiger larvae at 18°C in the laboratory. In the Somme Bay, the bulk of gametogenesis took place during the winter and spring months, when average temperatures were around 10°C (**Figure 2.6a**) and developmental rate slower.

Apparent periods of recruitment at both sites took place around one-to-three months after inferred periods of larval hatching. Anger *et.al.* (1986) calculated a one-to-two month planktonic period, based on laboratory observations of larvae hatched at three setigers. Hatch-ready larvae observed by Anger *et.al.* were considerably (>2x) larger than those observed in the present study, however. This suggested that Somme Bay planktonic larvae require added time in the water column to feed and grow before settlement.

The extended period of sexual reproductive activity, coupled with a long planktonic developmental period, would allow planktonic larvae to occupy the water column for nearly the whole year. Some previous studies have also described year-round occurrence of *Pygospio* larvae (Smidt, 1951; Giere, 1968; Hernoth & Ackefors, 1979). Some, for example Thorson (1946), have described *Pygospio* larvae as rare during summer months, however. Larvae were reported in the plankton from November to April on the German coast (Leschke, 1903); from February to August (Hannerz, 1956, Swedish coast); and from February to September from the German coast (Hempel, 1957).

Temperature is a significant factor in the determination of the onset and duration of gametogenesis in polychaetes (Schroeder & Hermans, 1975). Anger *et. al.* (1986) stated the ability of *Pygospio* "to reproduce during practically the whole year, even in winter", however, and related this to the species' eurythermal behaviour. They described *Pygospio* larvae settling and metamorphosing at temperatures as low as 6°C.

Hannerz (1956) worked on a population in which males were entirely absent up until gametogenesis began in females. Rasmussen (1973) described a population at

Horsen's Fjord composed of 95% morphological females between May and August: between September and April ripe females and males were found. Rasmussen dubbed the latter "winter males" and proposed a temperature-determined process of "sex-reversal". Under experimental conditions and at constant temperatures below 15°C, sexual maturation of a previously immature population occurred "explosively" within a fortnight. Furthermore, a laboratory controlled temperature increase from 6° to 18°C caused males to revert to the state of unripe females, with the degeneration of male secondary sexual characteristics (anterior branchiae) and sperm cells. The period of maturity in males could be extended by constant exposure to temperatures around 2.5°C. The onset of gametogenesis in the Somme Bay took place in the autumn, as temperatures dropped.

The apparent failure in sexual reproduction early in 1992 could not have been temperature-mediated: temperatures during the autumn / winter period 1991-'92 were seasonally normal. Ammonium ion import data showed noteworthy activity at that time, however. Concentrations exceeded $0.7mgl^{-1}$ for a continual four-to-five month period, with a peak of $0.86mgl^{-1}$ in February 1992, perhaps leading to toxically-induced disruption of gametogenesis and gamete development. Absence of gametes in samples from this period could indicate stress-induced oocyte resorption, a phenomenon known to occur in polychaetes (Olive *et. al.*, 1981).

Conditions at HHS favoured increased reproductive effort: hydrodynamically sheltered conditions, and consequently enhanced deposition rates, led to the more successful recruitment at HHS evinced by the size frequency distribution data. Also, proportions of sexually active males and oocyte bearing females were maximally very much higher than at LCS. There were very great differences in population density between HHS and LCS (**Figures 2.4d** and **2.5d**). At LCS densities remained lower than $5,000m^{-2}$ during the 1990-'92 period, often dropping as low as $250m^{-2}$ (Batten, 1994). In April 1991 LCS density peaked at $18,000m^{-2}$. HHS simultaneously experienced a population explosion, densities reaching $105,000m^{-2}$ by May 1991 and continuing to exceed $100,000m^{-2}$ for the remainder of the sampling period (Batten, 1994). Examination of archived samples revealed no increase in asexual activity at the time. A steady, population-building influx of juveniles to HHS was recorded between

November 1990 and April 1991. Further settlement between July 1991 and May 1992 appeared to stabilise high population densities. The spring 1991 phytoplankton bloom (see **Figure 2.5e**: peaking chlorophyll *a* values, >30μgl^{-1}) may have provided the stimulus for population growth and increased survival of newly recruited larvae.

2.5.3 Adaptive Significance of Sexual Reproduction and a Planktonic Larval Developmental Mode in the Somme Bay.

The existence of two larval modes in *Pygospio elegans* was initially explained as a function of seasonally varying conditions of food and temperature (Söderström, 1920; Thorson, 1946; see **Chapter 1**). Experiments by Anger (1984) showed that temperature was not involved in determination of larval developmental mode, however. Further studies described populations whose reproductive patterns could not be easily linked with seasonal stimuli (Rasmussen, 1973; Gudmundsson, 1985), and suspicions were aroused that reproductive strategy was not determined environmentally, but was genetically predetermined.

The discovery of an entirely planktonic, planktotrophic developmental mode in the Somme Bay was unexpected. Initial observations of the extreme densities of *Pygospio* in the estuary had led to predictions of a high degree of asexual proliferation, while a non-propagative larval mode had been suggested by the congregation of highly dense populations in beds. The apparent absence of both lecithotrophic larvae and asexual reproduction in Somme Bay *Pygospio* is considered at further length in **Chapter 3**.

Planktonic development entails larval risk: more than 99% of planktonic larvae die before metamorphosis (Thorson, 1946; Mileikovsky, 1971). Its benefits lie in dispersal, and in low parental investment in brooding and yolk-supply, with concomitantly higher fecundity. A planktonic mode also increases the potential number of broods: early-hatching larvae vacate the parental tube to allow the development of a second batch; parental maintenance (*e.g.* brood irrigation) is minimised. The present results suggest that *Pygospio* in the Somme Bay was polytelic, producing two batches of offspring per year and maximising fecundity. The small size

of larvae at hatching could have been an adaptation to reduce generation time, and thus increase fitness (Havenhand, 1993).

In an heterogeneous environment, a dispersive larval mode theoretically permits arithmetic increase in population growth rate, compared with the geometric growth rate theoretically associated with non-dispersive larvae (Palmer & Strathmann, 1981). In the large, physically heterogenous Somme Bay, with its widely varying range of biofacies, population growth rate is therefore perhaps maximised by planktonic development.

In view of the frequent hydrodynamic and anthropogenic disturbances experienced by the exposed LCS mud-flats, it may be that a dispersive mode was selected to avoid disturbance-induced mortality of benthic larval forms. Crisp (1974a) noted that planktonic larval dissemination was vital for species occupying transient or disturbance-prone habitats. The benthonic phase of development in the Somme Bay appeared to be telescoped, larvae hatching at a relatively small size into the plankton and this could have been a further adaption to reduce exposure to benthic disturbances. Another consideration is the possible concentration in the sediment of nitrogenous excreta at high population densities which could have a deleterious effect on the externally brooded larva. Oxygen depletion during the prolonged Somme Bay low tide, exacerbated by the concerted respiration of hundreds of thousands of neighbouring worms, may also adversely affect benthonic larval development. The HHS population showed no signs of adaptation to non-dispersion either. HHS dwelling infauna, although situated near the outflow of the River Somme and thus comparatively sheltered from harsh hydrodynamic activity, suffer stress from salinity fluctuations as well as potential suffocation under an increased deposition of fine particulates. Indeed, Batten (1994) described HHS as the more disturbed of the two sites.

Larval retention improves a species' ability to exploit areas of high nutrient availability, and it might be expected that a non-planktonic mode would be selected for in an opportunistic species, such as *Pygospio*, capable of a variety of reproductive strategies (Strathmann, 1982; Jackson, 1986). It is therefore interesting that *Pygospio* proliferates planktonically and thus dispersively in the nutrient-rich Somme Bay, an environment clearly capable of supporting hugely dense populations. Furthermore, the

maintenance of such dense populations over a period of years requires a consistently high level of recruitment. Why *Pygospio* develops planktonically, and how the population is maintained in the face of the dispersal of its propagules, are questions resolved by a theory of larval retainment. A number of studies have described mechanisms by which planktonic larvae may be retained in estuaries and coastal embayments (deWolf, 1974; Boicourt, 1982; Gaines & Bertness, 1992; Marcano & Cazaux, 1994; Thiebaut *et. al.*, 1994). Retentive mechanisms may be active, larvae migrating vertically in the water column to take advantage of the directional flows of different water bodies; or passive, related to local hydrodynamic conditions. Many crustacean and bivalve larvae have evolved vertical migration behaviour to prevent offshore transport (Cronin, 1982; Sulkin, 1984; deVries *et. al.*, 1994), while polychaete larvae appear to disperse more passively, under tidal influence (Hannan, 1984; Banse, 1986; Levin, 1986b; Belgrano & Dewarumez, 1995). Passively dispersing larvae may be retained near to their hatching ground by the hydrodynamic characteristics of their environment. Tidally-induced retainment of spionid polychaete larvae has been demonstrated in Mission Bay, California (Levin, 1986), Arcachon Bay, France (Marcano & Cazaux, 1994) and the Oosterschelde Estuary, North Sea (Belgrano & Dewarumez, 1995). In the Somme Bay a study of faecal bacterial pollution provided an insight into patterns of water circulation (Rybarczyk, 1993): water masses were shown to oscillate in and out of the bay for several tidal cycles, leading to potentially extended residence times of planktonic larvae in inshore waters. Coastal macrobenthic samples taken in summer 1993 around the mouth of the bay included few or no *Pygospio* (Desprez, 1994), evidence of low larval export to coastal waters. Low freshwater discharge rates have been linked to periods of *Pygospio* proliferation in the Somme Bay (present study): during these periods, net exports of water decrease allowing planktonic larvae to spend a longer period within estuary waters. Settlement rate of barnacle larvae was found to positively correlate significantly with flushing time in Narragansett Bay, Rhode Island (Gaines & Bertness, 1992).

Planktonic *Pygospio* larvae may thus be retained within the Somme Bay, with the benefit of the greatly increased colonisation potential afforded by a vantage in the plankton. This hypothesis was not tested in the present study as no appropriate

zooplankton samples were available. The hypothesis appears to be the most probable explanation for the observed densities in the absence of a non-dispersive reproductive mode, however.

2.6 Summary

- *Pygospio* populations in the Somme Bay at the sites LCS and HHS have achieved huge densities ($10^5 m^{-2}$) during the last 25 years. The LCS population has reached higher densities and shown a greater durability than that at HHS, suggesting the latter site is less able to support high density *Pygospio* populations over the long term. Population fluctuations were influenced by a variety of meterological and hydrographic factors. An amensalistic interaction with the cockle, *Cerastoderma edule*, was also noted.
- *Pygospio* at both sites produced two batches of larvae per year during 1990 - 1992. The period of sexual activity extended over the whole year, beginning during July - August and ending in June. Interannual variability is likely to be considerable, however, given the prevailing conditions of population density fluctuation, environmental dynamism and the opportunistic nature of the species.
- Proportions of sexually mature individuals and levels of recruitment were greater at HHS than at LCS.
- All larvae hatched at the three setiger stage to develop planktotrophically, irrespective of season. Duration of the pre-hatching, benthonic phase of development appeared to be brief when compared with reports in the literature.
- Inferred developmental time (oocyte to hatch-ready larva) during winter-spring was around 6 months, shortening to 4 months during spring-summer.
- No appreciable level of asexual reproduction was observed.
- Planktonic development is viewed as strategically beneficial in the milieu of the Somme Bay. Benthonic disturbance is avoided while reproductive output is maximised. Dispersal is limited to the short scale by the estuarine hydrodynamic regime, maintaining the population within the Bay while affording increased potential for the colonisation of newly-disturbed patches.

Chapter 3.
Reproductive Strategy of *Pygospio elegans*, and Implications for Taxonomic Status

3.1 Introduction

Among polychaetes, the widest range of reproductive strategies is found among the Order Spionida (Wilson, 1991). The variety of reproductive strategies displayed by the single species *Pygospio elegans* is unusually wide (Söderström, 1920; Rasmussen, 1953; also see **Chapter 1**). Such variability in reproductive strategy within a species is rare (Levin & Bridges, 1995) and has been termed "poecilogony" (Giard, 1905). Reports of poecilogony appear to be largely restricted to mud-flat-dwelling polychaetes and opisthobranch molluscs. This has led to the suggestion that the phenomenon involves a certain genetic predisposition, and requires for its evolution a highly dynamic environment which exerts strong selective pressures (Chia *et. al.*, 1996).

In many instances the existence of more than one reproductive mode has been re-interpreted as evidence, not of phenotypic flexibility, but of genotypic divergence, *i.e.* of sibling subspeciation (Hoagland & Robertson, 1988). Sibling species are defined as "morphologically similar or identical natural populations that are reproductively isolated" (Mayr, 1963).

In the Somme Bay, *Pygospio* appears to reproduce sexually, with planktonic, planktotrophically developing larvae; in the course of the present study neither long-term larval brooding nor evidence of asexual behaviour were discovered. The adaptive significance of such behaviour was discussed in **Chapter 2**, but certain other questions remain. Might this restricted reproductive repertoire point to non-poecilogonous behaviour and genetic divergence from other populations? Or is the species truly poecilogonous, simply adapting its reproductive strategy to suit its environmental conditions?

Simon (1968) advised that "any species which exhibits more than one reproductive or developmental mode should be examined critically to ensure that two

cryptic species are not involved". Anger (1984) suggested the possibility of cryptic, sibling speciation in *Pygospio*, and noted that further investigation must include comparisons of morphology, physiology, reproductive biology and population genetics. This chapter seeks to follow up some of these suggestions.

Reproductive flexibility in *Pygospio* was examined experimentally to see if the species exhibits true poecilogony or rather the signature of sibling species each with specific, non-flexible reproductive strategies. *Pygospio* individuals from geographically separate populations were further examined for morphological evidence of speciation.

3.2 Reproductive Strategy

3.2.1 A Qualitative Experiment.

Until recently, the reproductive response of benthic invertebrates to environmental change has been poorly understood (Levin & Creed, 1986). However, a number of studies now describe the reproductive responses of opportunistic polychaetes to such variables as nutrient, density, temperature and salinity (Grassle & Grassle, 1974; Wible, 1984; Levin & Creed, 1986; Zajac, 1986; Gremare *et. al.*, 1988; Qian, 1994). In potentially poecilogonous species such as *Pygospio*, reproductive responses to environmental quality are of increased interest as they may involve actual shifts of developmental mode. In *Pygospio*, however, such a shift has yet to be experimentally proven: Anger (1984) found no evidence of poecilogony in the species in response to varying temperature and salinity treatments.

A simple, qualitative experiment was designed to determine the previously unexamined effect of varying patch density and nutrient availability on the developmental mode of *Pygospio elegans* larvae. The aim was to test the null hypothesis that larval developmental mode would remain uninfluenced by these external factors. No quantitative measurements were made, for example of mortality, developmental rate, or fecundity.

3.2.2 Culture of *Pygospio elegans*, and Experimental Design.

Live individuals were collected during the same week from the Somme Bay and from Ryde Sand (Isle of Wight, UK). At both sites approximately $0.04m^2$ sediment were removed and immediately sieved on a 500μm mesh: all animals in each population were thus sampled from the same area. The low prevailing population density at Ryde Sand required core samples to be taken from closely adjacent areas that were judged to contain good numbers of animals. Worms were transported within their tubes; the two populations were kept separated at all times.

On return to the laboratory worms were evicted from their tubes and sorted under a dissecting microscope: small, sexually immature individuals were removed to dishes of seawater with a shallow layer of natural sediment in the bottom. These individuals, around 35 setigers in length and destined for use in the experiment, were kept in an aquarium at 15°C, in darkness, for an acclimatisation period of one month. During this time all worms were kept at ambient field densities, which were calculated to be $50,000m^{-2}$ for the Somme Bay and $4,000m^{-2}$ for Ryde Sand. Filtered, autoclaved seawater (salinity 26‰) was changed every two days and a drop of food added once every 10 days. Food was made by finely-grinding roughly 0.5g of fish food ("Phillip's Cold Water Flakes") and suspending the powder in 50ml seawater: this was left for 10 minutes before use, to allow coarser food particles to fall out of suspension. Observations of individuals showed them to actively capture and ingest this material directly from the water-column.

Pygospio culture is more successful in standing water than in through-flow systems (Anger *et. al.*, 1986), and so the experiment was designed around closed microcosms: all animals were transferred to 30ml polypropylene beakers (cross-sectional area $8cm^2$) with a thin layer of azoic sediment (particle diameter 125-250μm) in the bottom. All animals were kept in the same area for the duration of the experiment: temperature, salinity and light regime remained constant at the same levels as during acclimatisation. Water continued to be changed every two days. A simple set of treatments, involving two food regimes and three population densities, was used. The food control involved continuing the supply of food at pre-experiment levels; a higher rate of feeding (one drop of food every 4 days, x2.5 control rate) was used as a

"high food" treatment. Density controls were ambient field densities maintained from the acclimatisation period. The naturally low-density Ryde Sand population was subjected to a control and x2.5 density treatment; the more highly-dense Somme Bay population was subjected to control, x0.2 and x0.08. In this way, directly comparable densities were achieved: *e.g.* the Somme Bay x0.08 treatment yielded the same density as the Ryde Sand x2.5 treatment. On the basis of the availability of individuals from each population (a proportion of which were set aside for a separate study), the numbers of worms assigned to each treatment were as detailed in **Table 3.1**. Numbers were calculated on the basis of a microcosm of base area $8cm^2$. Replication was based on the number of individuals subjected to each treatment, rather than actual number of microcosms. Clearly, a increased chance existed that only one sex would be present in those treatments involving only three individuals per microcosm, precluding the possibility of sexual reproduction during the experimental period. Fertilisation could have occurred earlier, during the acclimatisation period, however.

Table 3.1: Numbers of Individuals per Treatment.

	Somme Bay			Ryde Sand	
equivalent density m^2	50,000 (control)	10,000 (x0.2)	4,000 (x0.08)	10,000 (x2.5)	4,000 (control)
animal density per high food treatment	40	8	3	8	3
			3		3
			3		3
			3		3
animal density per control food treatment	40	8	3	8	3
			3		3
			3		3
			3		3

At the end of each month sediment was changed and the animals were carefully examined for the presence of externally-borne egg-capsules. Non-intrusive examination was possible as tubes were usually constructed against the base of the clear-walled microcosm, through which worms and brood were visible.

3.2.3 Results and Observations.

After five months, at the end of March 1996, capsules containing larvae were noted in both populations, and the experiment was terminated.

In the Somme Bay population, of those surviving females found with brood, no instances were found of larvae with distended, yolk-filled stomachs; all had 3 setigers in size, were around 100μm length and displayed the long "parachute" swimming setae associated with a planktonic mode of development. No nurse egg material was observed. Total numbers of larvae per female were not established.

Some surviving females from Ryde Sand also successfully produced larvae: these were discovered to be of the benthonic variety, packed densely with nutrient bodies. At the time of examination, these larvae had attained 6-8 setigers and 350-400μm length. A number of Ryde Sand larvae were artificially, prematurely "hatched" by breaking open the brood sac: these were perfectly competent swimmers, and displayed positive phototropism.

Different food and density treatments did not yield any noticeable variations in larval type in either population.

3.2.4 Reproductive study: Discussion.

No previous study has reported the larval developmental mode in *Pygospio* from Ryde Sand. Thus, for the purposes of comparison with the planktonically developing Somme Bay population, it was fortuitous that the contrasting, benthonic mode was discovered. The experimental null hypothesis, that *Pygospio* would not adapt to changes in nutrient supply and population density by altering reproductive strategy, was supported by both the Ryde Sand and Somme Bay populations. As no Ryde Sand planktonic larvae were found in any treatment it was assumed that developmental mode had been conserved, although there was no prior evidence to prove that a benthonic mode was predominant in the natural population.

No signs of asexual fragmentation were discovered. This was possibly the result of low overall experimental nutrient supply, compared to nutrient availability in nature. The experiments of Wilson (1985), described in **Chapter 1**, indicated that rate

of asexual fragmentation in *Pygospio elegans* was proportional to food supply and inversely proportional to density.

Unavoidable mortality of animals during the experiment had the effect of reducing densities, but the wide variation in starting densities meant that an appreciable difference was maintained between treatments.

It should be emphasised that the animals in this experiment were not derived from laboratory culture stock but from the field. Potentially, then, individuals from the same population could have been sampled from areas with differing micro-environmental conditions. However, all animals were sampled from closely adjacent cores, so minimising environmental heterogeneity.

The conservation of reproductive strategy observed in both populations could be the result of the establishment of reproductive behavioural patterns in *Pygospio* well before maturity: that is, all animals brought into the laboratory may have previously determined their mode of reproduction in response to conditions experienced as juveniles. However, this would seem to limit the ability to respond opportunistically to changing environmental conditions, and potentially allow the development of larvae badly adapted to local hydrodynamics, food availability and levels of predation. Indeed, Eckelbarger (1986) described the opportunistic spionid *Streblospio benedictii* as able to sequester nutrient material directly from the circulatory system into eggs, and so respond to environmental conditions of food supply during gamete development. As Levin (1986a) stated, "the ability to translate elevated food supply directly into increased reproductive output may underlie opportunistic dynamics in the macrobenthos".

Rasmussen (1973) contended that *Pygospio*'s brood-period (and thus larval form) was variable, depending upon the degree of adelphophagia. What needs to be determined, therefore, is what controls the degree of adelphophagia. It seems two mechanisms are possible. **1.** The ratio of nurse-eggs to true-eggs laid into external capsules could be controlled by the female. This would involve a parental influence on larval mode. The nurse-egg to true-egg ratio may be genetically predetermined, or adaptive. **2.** Sibling embryos could compete for available nurse egg material, or cannibalise other embryos, *i.e.* a post-encapsulation, non-parentally influenced

determination of larval mode. Rasmussen's (1973) observations, of a single capsule containing both planktonic and benthonic larval forms, and of varying developmental rates of sibling larvae, led him to consider the embryo competition mechanism.

A variety of mechanisms allowing for intracapsular variation in larval developmental rate have been postulated for *Boccardia* species. Duchêne (1984; 1989) suggested the staggered onset of development among larvae in broods of *B. polybranchiata*. Guérin (1991) noted synchronous development among encapsulated embryos of *B.semibranchiata*; a marked variation in the degree of adelphophagia was observed, however. It was suggested that initial oocyte size determined the ability of the resulting embryo to compete for and ingest nurse-egg nutrient. Blake & Kudenov (1981) postulated the secretion of a substance by some embryos that inhibited feeding in others.

There were no instances in the Somme Bay population of an intra-capsular variation in larval developmental rate. Competition between sibling larvae, *i.e.* a post-encapsulation determination of larval mode is therefore seen as unlikely. Some variation in observed larval sizes would be expected were competition to occur. The absence of an adaptive response shown by the present result suggests that reproductive strategy in the experimental populations is, to some extent, genetically pre-determined during the pre-extrusion phase and that *Pygospio elegans* may consist of more than one sibling species.

Anger (1984) also suggested sibling speciation in *Pygospio*. Individuals were cultured from three geographically separate populations of *Pygospio* and it was found that reproductive mode was conserved in the face of changes in temperature and salinity. One population, sampled from a heavily organically polluted site from Kiel Bay in the Baltic, reproduced exclusively asexually, apparently having lost the ability to produce gonads. The other two populations continued to produce planktonic larvae only. Anger ventured that the non-propagative, rapid growth afforded by asexual fragmentation allowed the former population to exploit its nutrient rich environment more effectively. The loss of gonads suggests non-poecilogonous activity in this case.

Other studies of *Pygospio* have described seemingly site-specific reproductive behaviours. Such behaviour may or may not be the result of poecilogonous activity. Gudmundsson (1985) showed that the life-history at Cullercoats involved entirely benthonic larval development, all egg-sacs containing only two larvae which hatched at 14-20 setigers. This contrasted with a near-by population at Blyth producing both planktonic and benthonic larvae. Two sites on the Jutland peninsula studied by Rasmussen (1973) also yielded contrasting populations. The population at Isefjord produced no asexuals, while planktonic and benthonic larvae existed simultaneously. At Horsen's Fjord, however, the spionid produced entirely planktonic larvae, and then entirely benthonic larvae, whilst asexual fragmentation occurred throughout. Interestingly, Rasmussen (1973) noted no major differences between the two adjacent areas, the implication being that reproductive differences were not the result of adaptations to differing environmental conditions.

Sibling speciation has also been suspected in other polychaete groups, particularly opportunists (*e.g.* spionids and capitellids), exhibiting apparent poecilogony. Grassle and Grassle (1976) noticed reproductive differences in *Capitella capitata* (Capitellidae) and demonstrated the existence of at least six sibling species using enzyme electrophoresis. Niche separation and speciation were attributed to the different dispersal and colonising abilities of the larvae. *Streblospio benedictii* (Spionidae), able to produce both planktotrophic-planktonic and lecithotrophic-planktonic larvae, was constant in its reproductive mode when exposed to variations in food-levels and temperature (Levin & Creed, 1986). Although the different larval types were interfertile as adults, the F_1 and F_2 generations were intermediates in terms of egg-size, brood-size and time spent in the plankton, and thus a genetic component to larval mode was postulated (Levin, 1984b). A "network of life-history trait correlations" was proposed, defining planktotrophic *versus.* lecithotrophic "trait complexes" (Levin *et. al.*, 1991).

Among the members of the genus *Polydora* (Spionidae), *P. quadrilobata* was found to produce two morphologically different larval types (Blake, 1969) with brooded forms lacking provisional larval swimming setae: incipient speciation was suggested. Rice (1991) performed reciprocal crosses of *P.ligni* from geographically

separated populations and showed them to be reproductively incompatible. Sibling speciation has also been proposed for *P.ciliata* (Dorsett, 1961), *P.nuchalis* (Wible, 1984) and *P.giardi* (Day & Blake, 1979); and in other spionid genera, in *Spio setosa* (Simon, 1968), *Spio martinensis* (Hannerz, 1956), *Malacoceros fuliginosus* (Guérin & Kerambrun, 1984), *Pseudopolydora paucibranchiata* (Ramberg & Schram, 1982) and a number of *Boccardia* species (Read, 1975; Blake & Kudenov, 1981; Duchêne, 1984; 1989; Guérin, 1991). Of the twenty-two reported instances of polychaete poecilogony reviewed by Hoagland & Robertson (1988), only two cases (*Streblospio benedictii*: Levin, 1984; *Cirriformia tentaculata*: George, 1967) were deemed to have any merit.

The irreversibility of larval developmental mode in *Pygospio* suggested by the work of Anger (1984) and the present study may be viewed from the perspective of energetic models. Such models are based on assessments of the reproductive efficiency (in terms of investment and larval mortality) of producing many, small eggs (*c.f.* planktonic, planktotrophic *Pygospio* larvae, with little or no adelphophagia) *versus* a few, large eggs (*c.f.* brooded *Pygospio* larvae, lecithotrophic by virtue of extended adelphophagia). The models of Vance (1973a,b) and Christiansen & Fenchel (1979) predicted that selection should favour either feeding or non-feeding larvae, but not intermediate forms since the transition from a feeding to non-feeding mode would involve an energetically unsupportable, evolutionarily unstable hurdle. Indeed, a dichotomy of larval forms is apparent from recent descriptions of *Pygospio* populations (see above). However, extensions of these models by Pechenik (1979) and Gaswell (1981) involved analysis of the hypothetical trade-offs between encapsulation period, fecundity and mortality of encapsulated and planktonic larvae, and showed that the phenomenon of egg encapsulation (as found in *Pygospio*) could potentially provide the conditions for stable intermediate forms. This provided a route for the transition from feeding to non-feeding mode and thus a theoretical mechanism enabling poecilogony. The dearth of convincing accounts of poecilogony in the literature is perhaps a function of the energetic problems involved in changing larval developmental mode.

3.3 Morphological Examination

3.3.1 Method.

Specimens of mature *Pygospio elegans* from a wide variety of locations were gathered and examined using both light and scanning electron microscopy.

A number of species-diagnostic characteristics were chosen, and comparisons made of the morphologies of specimens originating from different locations. A full taxonomic description of *Pygospio elegans* is given in **Appendix 1**.

Characteristics examined were:

- shape of the prostomium;
- onset, and number, of dorsal branchiae;
- onset, and number, of neuropodial hooded hooks;
- occurrence of "spoonlike" hooded hooks;
- shape of the pygidium.

Light Microscopy. Specimens were mounted on slides beneath a coverslip in 50:50 glycerol alcohol. A compound microscope was used to view specimens under powers of x100 and x400.

Scanning Electron Microscopy. Appendix 2 details the preparation of specimens for scanning electron microscopy. Specimens were viewed using the Hitachi S2500 scanning electron microscope at The Natural History Museum, London; accelerating voltages of 10 and 15 kV were used.

3.3.2 Results of Morphological Examination.

Table 3.2 gives details of the results of the morphological examination. Data from previous taxonomic descriptions in the literature are also included.

Table 3.2: Comparison of Morphological Features of *Pygospio elegans* from Different Geographical Locations.

Location	Source	Morphological Characteristic				
		Prostomium shape	First setiger baering branchiae (♀)	Number of posterior abranchiate setigers: mean and standard deviation (♀)	Displacement of hooded hooks	Number of "spoonlike" hooks
Swale Estuary, UK	This study	incised	12 (50%) ;13 (50%)	17.4 +/- 2.9	8 to end	6
Ryde Sand, UK	This study	incised	13 (60%); 14 (40%)	24.5 +/- 3.7	8 to end	5 or 6
Plym Estuary, UK	This study	incised	12 (100%)	14.6 +/- 2.8	8 to end	5
Somme Bay, Fr.	This study	incised	12 (86%); 13 (14%)	15.0 +/- 1.5	8 to end	5
Kattegat, Den.	This study	incised	12 (100%)	*n.q.* (one replicate only)	8 to end	4 or 5
False Bay, USA	This study	incised	13 (100%)	13.7 +/- 2.3	8 to end	4 or 5
Cline Pt., USA	This study	incised	13	*n.q.*	8 to end	*n.q.*
Sagadahoo, USA	This study	incised	13	*n.q.*	8 to end	*n.q.*
Hampton Harbour, USA	This study	incised	13	*n.q.*	8 to end	*n.q.*
Barnstaple Bay, USA	This study	incised	13	*n.q.*	8 to end	*n.q.*
Bohuslän, Den.	Söderström, 1920	incised	*n.q.*	*n.q.*	8 to end	4 or 5
France	Fauvel, 1927	incised	11	7-9	8 to end	*n.d.*
S.Africa	Day, 1967	incised	11	"about 8"	8 to end	*n.d.*
Germany	Hartmann-Schröder, 1971	incised	11-13	7-9	8 to end	*n.d.*
Carribean. & Gulf of Mexico	Foster, 1971	incised	11-13	to within 7-15 setigers of end	8-9 to end	*n.q.*
British Columbia, Can.	Hobson, 1976	incised	12-13	*n.q.*	7-8 to end	*n.d.*
USA	Fauchald, 1977	"rounded"	"concentrated in short posterior region"		*n.d.*	*n.d.*
San FranciscoBay, USA	Light, 1978	incised	posterior to 10	"lacking in far posterior segments"	8 to end	2, 3 or 4

n.d.: not determined *n.q.*: not quantified

Some scanning electron-micrographs, illustrating salient features of *Pygospio elegans* morphology, are displayed in **Plates 3.1** to **3.7**. A scale bar is given in the bottom right hand corner of each electron-micrograph.

Plate 3.1: False Bay, USA x20. Whole body.

Plate 3.2: Somme Bay x50. Anterior, dorso-lateral.

Plate 3.3: Somme Bay x120. Anterior, dorsal.

Plate 3.4: False Bay, USA x150. Detail of parapodial lamellae & branchiae.

Plate 3.5: Somme Bay x400. Setigers 8-10, showing spoonlike hooded hooks.

Plate 3.6: Somme Bay x2000. Detail of spoonlike hooded hooks.

Plate 3.7: Somme Bay x220. Pygidium.

Abbreviations used:

p. palp. **nu.** nuchal organs. **cb.** dorsal ciliary band. **pro.** prostomium. **peri.** peristomium. **s.** seta. **no.** notopodial lamellum. **neu.** neuropodial lamellum. **para.** parasite. **hh.** hooded hook. **sp.** spoonlike hook. **br.** branchium. **pyg.** pygidium. **a.** anus.

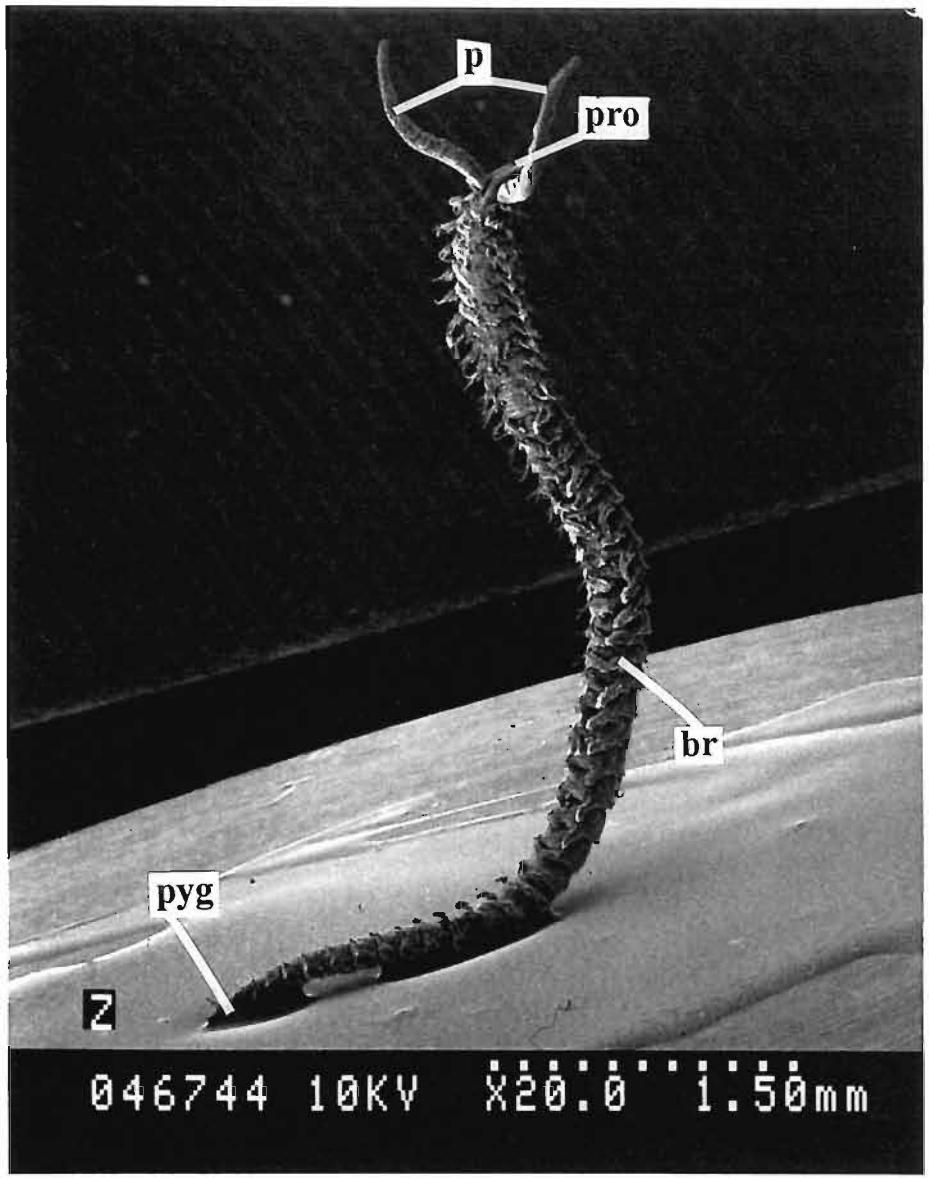


Plate 3.1: Whole body, x20. False Bay, USA

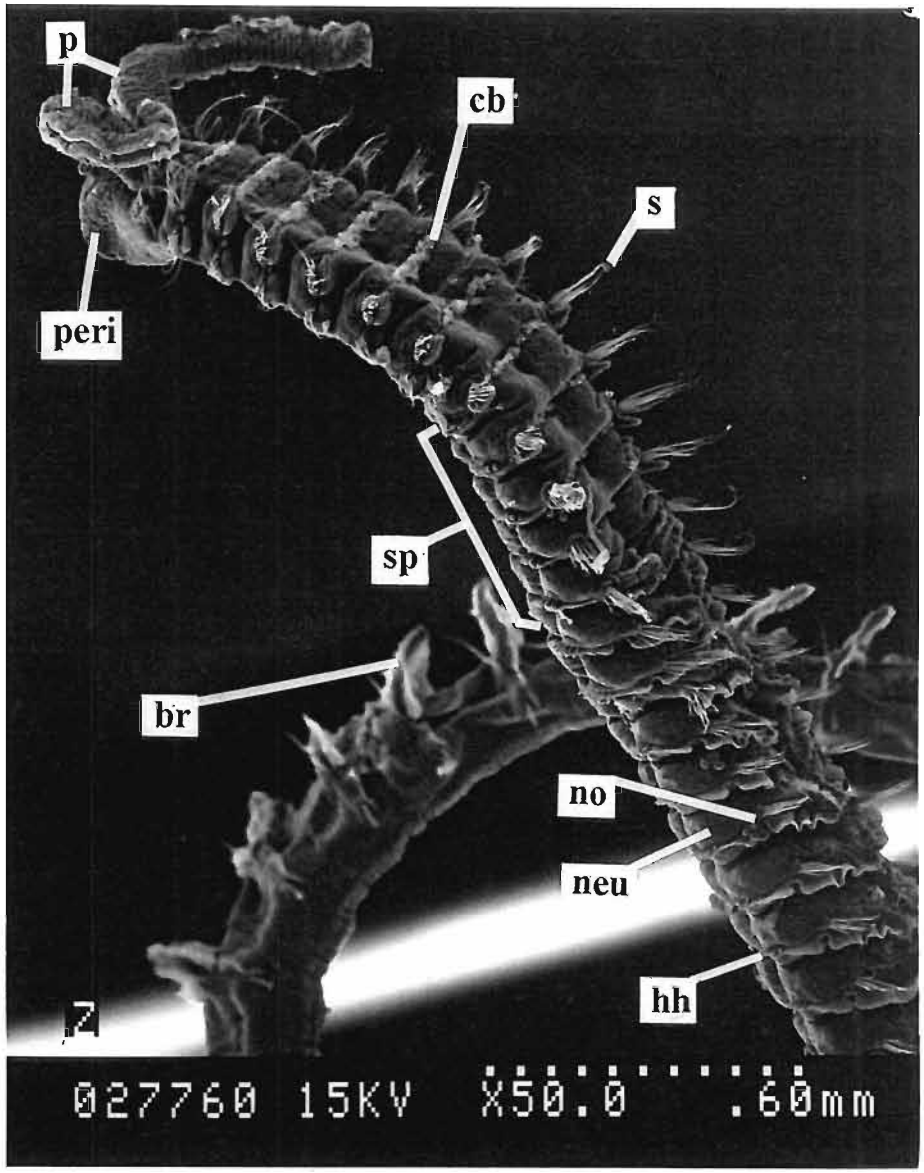


Plate 3.2: Anterior dorso-lateral view, x50. Somme Bay.

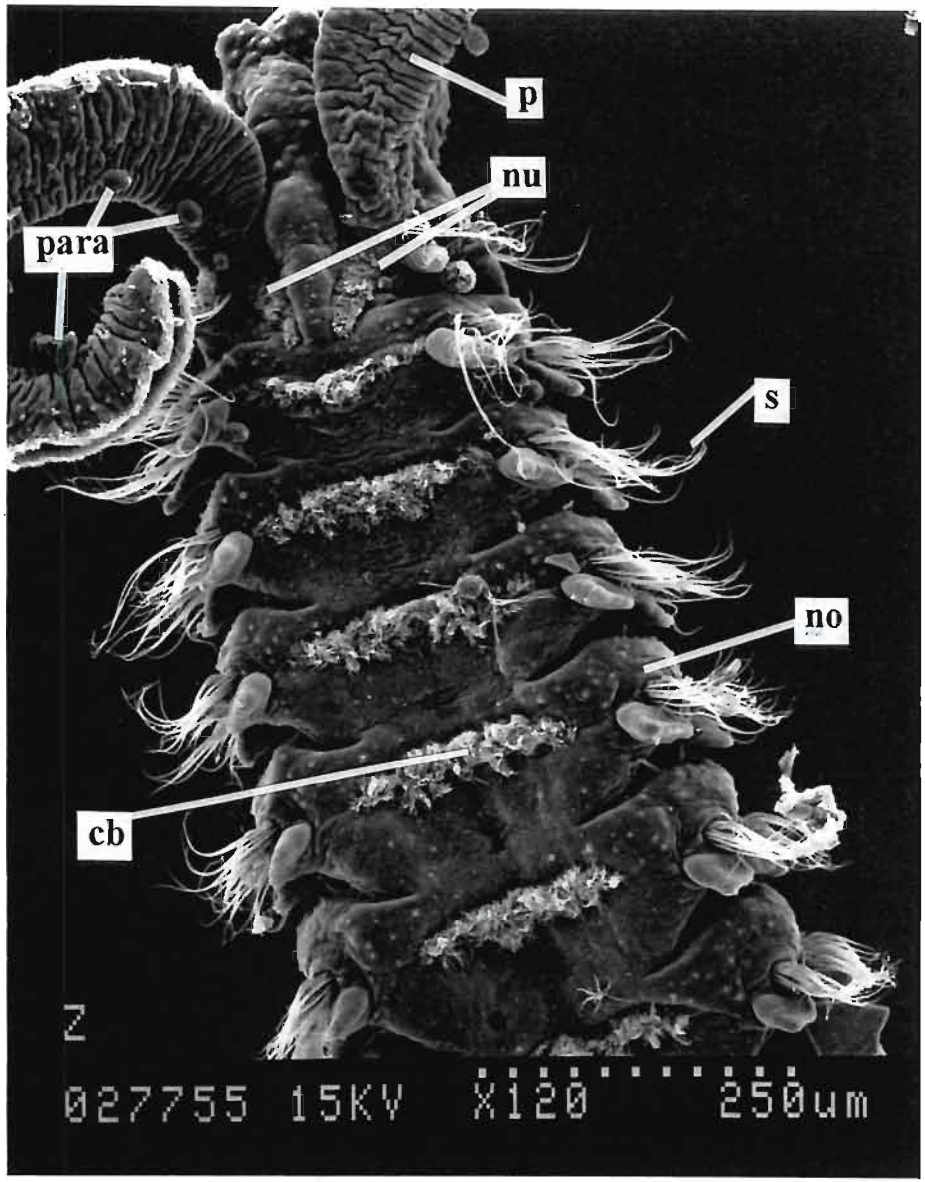


Plate 3.3: Anterior dorsal view, x120. Somme Bay.

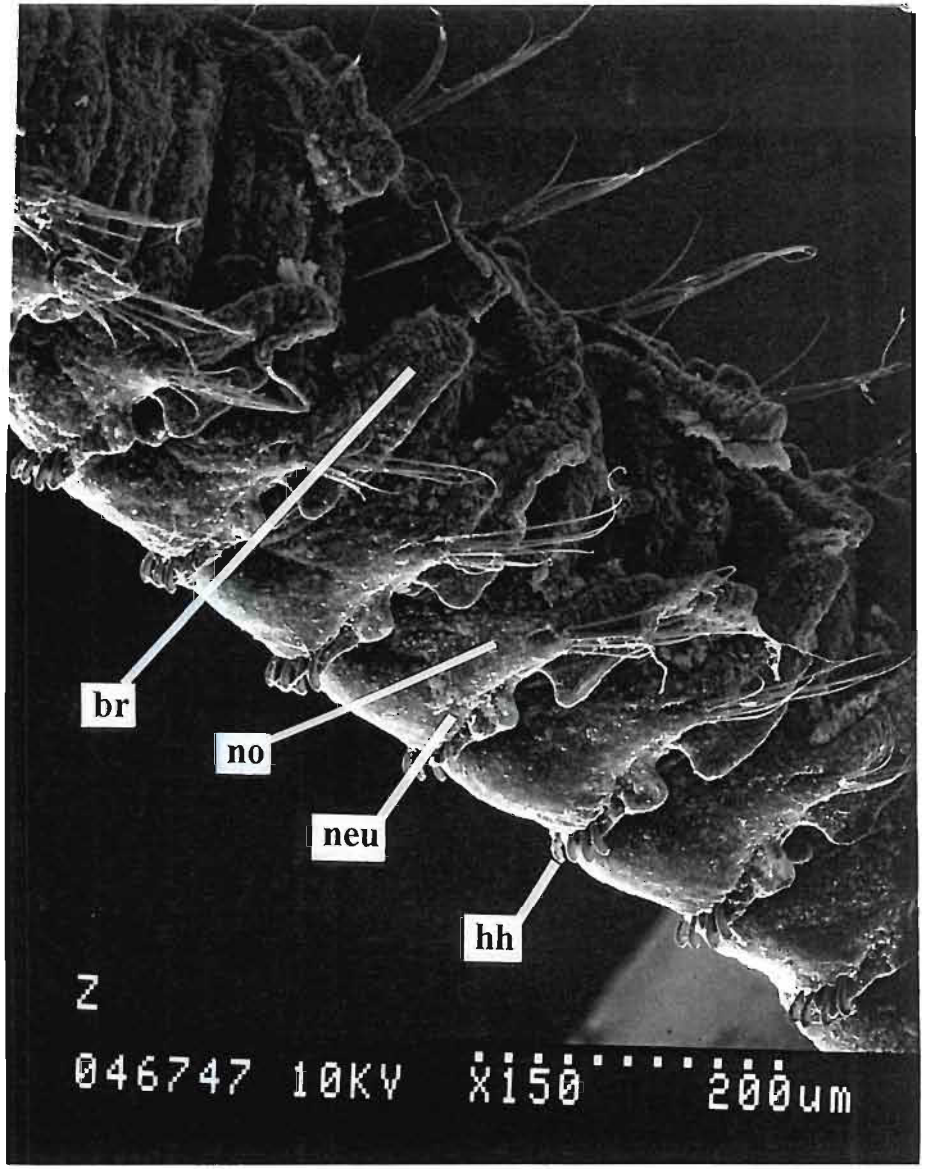


Plate 3.4: Detail of parapodial lamellae and branchiae, x150. False Bay, USA.

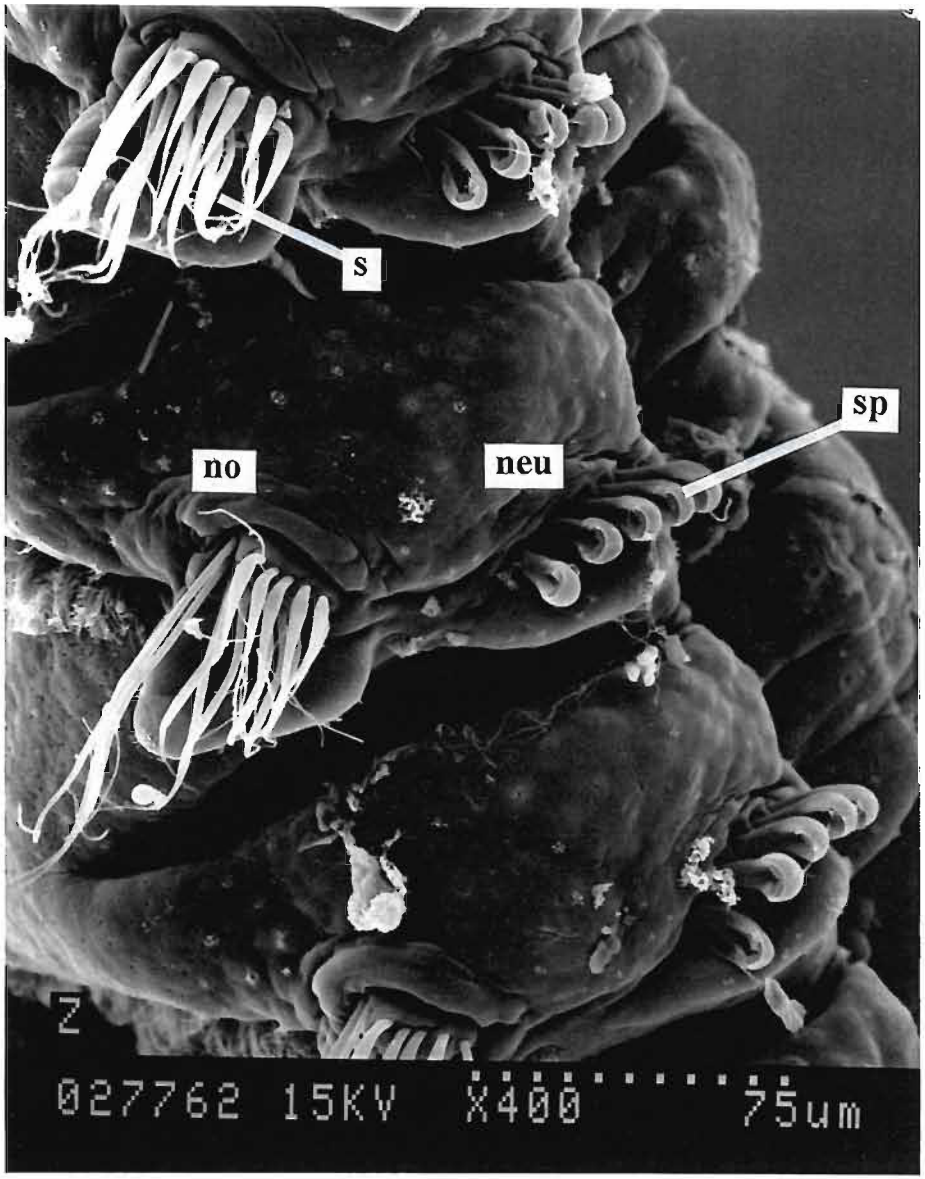


Plate 3.5: Setigers 8-10, showing spoonlike hooded hooks, x400. Somme Bay.

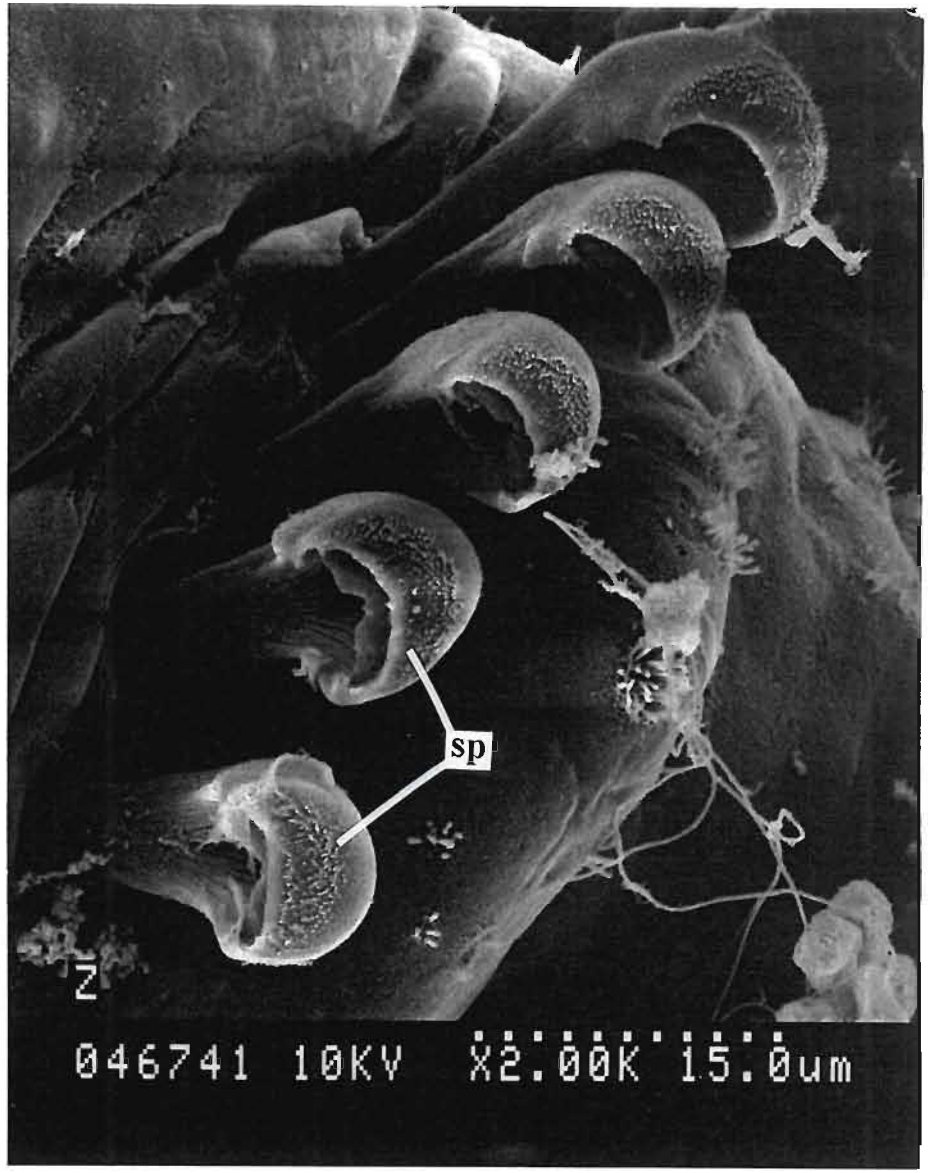


Plate 3.6: Detail of spoonlike hooded hooks, x2000. Somme Bay.

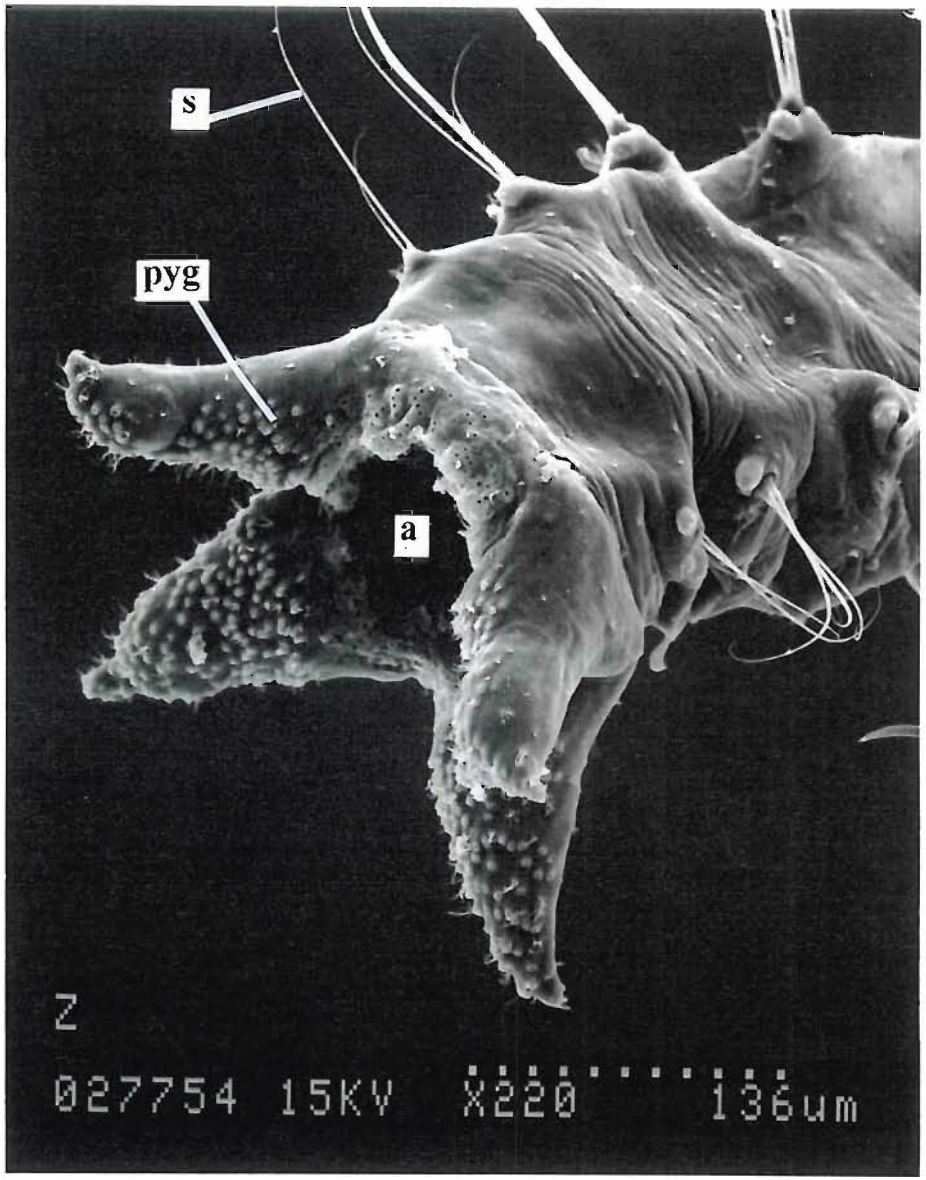


Plate 3.7: Pygidium, x220. Somme Bay.

3.3.3 Morphological Study: Discussion.

No differences were observed with respect to the shape of the prostomium or the pygidium. These characters were chosen for study because of their diagnostic status in *Pygospio elegans* (see **Appendix 1** for a taxonomic description of *Pygospio elegans*).

In Gudmundsson's study of two populations of *Pygospio* (1979) he noticed a difference in the placement of the first dorsal branchium. In one population, from Cullercoats, N.E.England. branchiae of 90% of individuals were found to appear first on setiger 13; in the second population, from near-by Blyth, branchiae of only around 20% of individuals began on setiger 13, with branchiae of over 60% of individuals first appearing on setiger 12. Similar, minor, inter-population differences in the onset of branchiae have been found in the present study and in comparisons of previous taxonomic descriptions of *Pygospio elegans* (see **Table 3.2**).

Some confusion concerning the number of branchiae in females exists in the literature. All accounts agree on the region in which the branchiae first appear anteriorly; early descriptions report branchiae continuing posteriorly for around 8 setigers in females (Fauvel, 1927; Day, 1967; Hartmann-Schröder, 1971) while others describe branchiae occurring more extensively along the body (Foster, 1971; Light, 1978). In the present study no female examined had fewer than 17 pairs of branchiae. The relationship between branchial displacement and somatic size is examined in **Figure 3.1.** This graphs the relationship between somatic size (taken as the total number of setigers) and the number of branchiate setigers among females from five populations for which replication was possible. The populations studied and compared were:

- The Swale Estuary, Kent, UK
- The Plym Estuary, Devon, UK
- Ryde Sand, Isle of Wight, UK
- The Somme Bay, France
- False Bay, USA

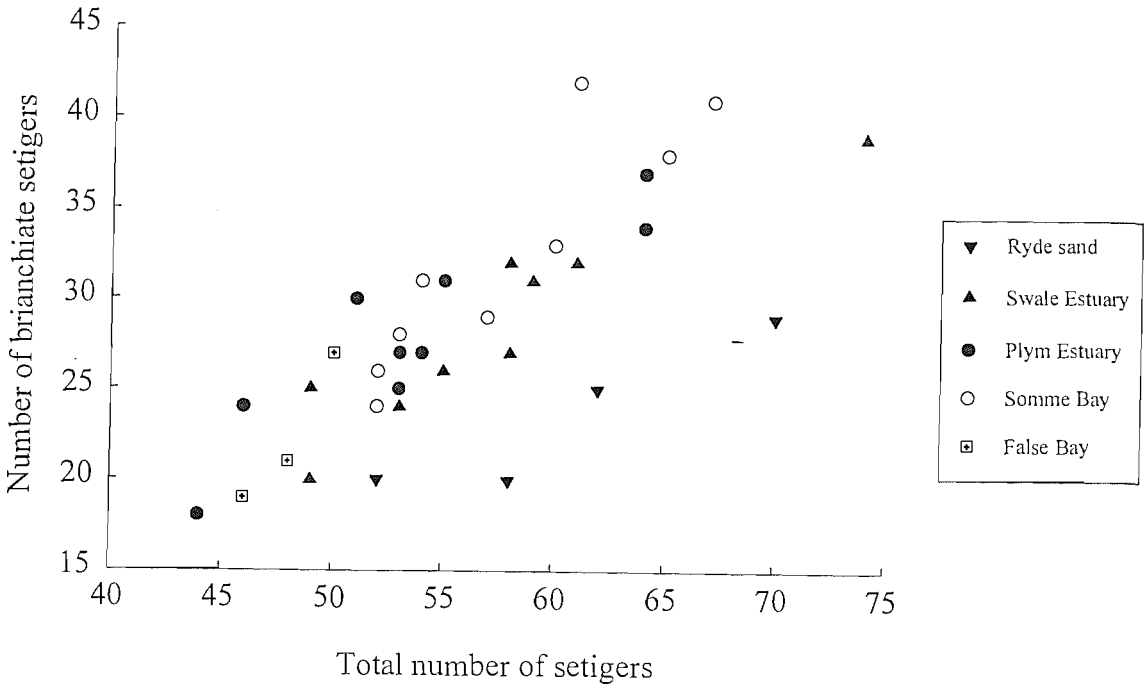


Figure 3.1: The relationship between somatic size (total number of setigers) and the number of posterior, abranchiate setigers. All individuals were female.

Figure 3.1 illustrates the allometric relationship in females between number of branchiate setigers and somatic size (n=39, r=0.856, p<0001). Inter-population differences in branchial displacement might then be an artefact, reflecting only somatic size differences. Such differences might be attributed to varying environmental conditions, or temporal variation in sampling, each population having been caught during a particular phase of its growth cycle. However, ANOVA tests between populations (not including False Bay, whose representatives were all at the small extreme) suggested that some degree of inter-population variation was present, Ryde Sand individuals having the lowest branchial to total setiger ratio. Taking the Somme Bay as a comparator site, ANOVA indicates that the two populations share a much more similar somatic size range (p=0.01) than range of branchiation (p<0.0002). Such a difference could be the result of local conditions of oxygen availability, the more

frequently immersed Ryde Sand population perhaps experiencing less chronic anoxia than the LCS flats of the Somme Bay. It should finally be noted that this character may be rendered unreliable by the species' ability to regenerate lost extremities. The extent of such regeneration among individuals is unknowable. Further work is needed to determine whether regenerated setigers restore the animal faithfully to its former state and size, or whether regenerated sections are different, for example, entirely lacking branchiae. If the latter case were true then the average ratio of branchiate setigers to total setiger number must decrease, a situation which from present data would point to an increased regenerative rate in the Ryde Sand population compared with that of the Somme Bay.

Another characteristic studied were the unusual, anterio-ventrally occurring spoonlike hooks of *Pygospio elegans*. These latter features were first described by Söderström (1920) as "löffelförmige Borsten" (spoonlike bristles) and considered by him to be normal hooks with worn-away teeth; he thus ascribed them to mature individuals, and suggested that the number of such hooks might increase with age. Clearly, were this the case, the number of such hooks could not be taken as a reliable indicator of taxonomic differences. However, observations made in the present study suggest that these "löffelförmige Borsten" are distinct structures, unrelated to the more posterior, bidentate hooded hooks - see **Plates 3.5-6**. Spoonlike hooks have a distally thickened, rounded tip and lack a central fang. Apart from the notable structural differences, no gradient of wear was observed from the row of hindmost spoonlike hooks to the row of foremost, bidentate hooded hooks: in all cases the transition of forms was abrupt from one setiger to the next. However, the very weakly significant positive correlation ($n=21$: $r=0.476$; $p=0.03$) between total number of setigers and number of spoonlike hooks potentially supports Söderström's contention that age is involved. Since growth by setiger addition occurs at the posterior end, extra spoonlike hook-bearing setigers could not be interposed during thoracic growth to produce this result, however. Hooded hooks are perhaps shed and replaced by spoonlike hooks in setigers 8 onwards as the animal grows.

Rice (1991) has noted the widespread occurrence of polymorphic populations of species of the family Spionidae, finding eight of eleven characteristics to be

polymorphic among three populations of *Polydora ligni* (Spionidae). Rice and Simon (1980) had earlier compared five populations of *P. ligni* and found significant morphological divergences in the arrangement and morphology of 5th setiger setae.

The present results are conservatively interpreted as showing no significant morphological evidence for species divergence among the populations studied; rather, a natural continuous variation within characteristics is suspected. Studies which have defined new species of *Pygospio* have done so on the basis of far more dramatic morphological differences. For example, *P.californica* Hartman, 1936, has a non-incised, pointed prostomium, hooded hooks starting from setiger 23 and branchiae commencing on setiger 19. At this point it is interesting to note that Hobson (1976) described some specimens from British Columbia as "intermediate between *P.elegans* and *P.californica*" and suggested that this could be due to interbreeding between the two species. This observation clearly casts doubt on the taxonomic separation of these species. More dubious *Pygospio* congeners have been described, with occipital tentacles, cup-shaped pygidia and polydorid-like, enlarged 5th setigers (Munro, 1930; Ward, 1981).

3.4 Conclusion: Taxonomic Implications

The behavioural versatility of *Pygospio elegans* is well documented (**Chapter 1**). Distributed circum-boreally, populations have been recorded from a wide range of depths, salinities and temperatures in densities ranging from 10's to 100,000's individuals m^{-2}, and the worm has been found to exhibit a variety of feeding and reproductive behaviours (**Chapter 1**). Interest and speculation regarding the taxonomic status of the spionid has been aroused, particularly as it is a pollution indicator species (Anger, 1977). Were such an indicator species to comprise a "species complex", the physiological responses of sibling species to pollutants might vary, giving a confused and misleading result with potentially undesirable practical and economic implications (Rice & Simon, 1980). It is clearly important that such species are identified correctly.

It is further important to assess the significance of *Pygospio* as an invasive species. Larvae have been found in ballast water of trans-oceanic ships and may have

been transported from one global location to another. If *Pygospio* proves not to comprise sibling species, it must be viewed as having a highly plastic and adaptive reproductive strategy, and as a species whose settlement in new territory could have potentially grave consequences for indigenous fauna. This has clear implications for biodiversity.

Genetic evidence of speciation is now being sought in an increasing number of studies on polychaetes suspected of harbouring more than one sibling species. Such studies commonly involve analyses of inter-population allele frequencies to derive a genetic distance using cellulose acetate or starch gel electrophoresis, and have successfully detected sibling species in *Arenicola marina* (Cadman & Nelson-Smith, 1990) *Capitella capitata* (Grassle & Grassle, 1974), and the spionids *Polydora ligni* (Rice & Simon, 1980), *P.ciliata* (Mustaquim, 1988), *P.vulgaris* (Manchenko & Radashevsky, 1994) and *Marenzellaria viridis* (Bastrop *et. al.*, 1995).

Preliminary use of the technique to study geographically separated populations of *Pygospio elegans* has identified potential polymorphism in the hexokinase, and glucose-6-phosphate -isomerase and -dehydrogenase enzyme systems (C.Morgan, 1996, unpublished), suggesting a degree of physiological differentiation in response to differing environmental selective pressures.

The opportunistic life-strategies of many spionid polychaetes provide the conditions to facilitate speciation. Rapid exploitation of disturbed, often highly productive areas by these "pioneer" species leads to the foundation and proliferation of dense colonies with short life-cycles and a non-dispersive larval mode. This may lead to a high degree of inbreeding and thus genetic isolation, especially where asexual behaviour is involved. Bellan (1977) has described polychaetes as currently undergoing a "full evolutionary phase" and it is perhaps unsurprising that so many instances of sibling speciation are now being proven with the help of electrophoretic techniques. *Pygospio elegans,* like many other opportunists, is supposedly a circum-boreal species. This assumption may prove to be false if sibling species are discovered, each with narrow ranges of habitat preference and thus distribution.

The discipline of taxonomy is broadly split between those who would prefer to view minor morphological and physiological differences as intra-species polymorphism, and those who would rather argue that such differences represented the distinguishing characteristics of separate species. The following perspective was provided by Grassle & Grassle (1976): "Sibling groups of opportunistic species show little tendency to exploit different habitats or foods and a variety of life-history patterns are likely to evolve many times. The whole complex survives through evolutionary time as a unit with new adaptive modes continually being formed and becoming extinct".

3.5 Proposals for Further Research

The recent expansion of interest in the use of molecular and physiological techniques in taxonomy has revealed widespread cryptic speciation in the marine environment. The use of enzyme electrophoresis as a tool for taxonomical research was first advocated by Nair *et.al.* (1971) who stated that "phylogenetic relationships of species... based on isozyme data, parallel... taxonomic relationships, suggesting that isozyme variations could be used, with confidence, as diagnostic aids in taxonomy". It is a simple and cost-effective method, well tried and tested in taxonomic studies on many groups of invertebrates. Results can be compared with a large volume of published data (Thorpe & Solé-Cava, 1994). Furthermore, the results of enzymic work provide insights into the physiological responses of the test organism to its environment (Jollivet *et. al.*, 1995). A pilot study has targeted potentially polymorphic genetic loci in *Pygospio elegans* (C.Morgan, 1996, unpublished), and it is believed that a more comprehensive approach along these lines would considerably enhance the understanding of the taxonomic status of the species. More sophisticated, molecular procedures could then be used to provide a more detailed picture of genetic differences. RAPD Analysis (random amplification of polymorphic DNA), a simple, rapid technique based on PCR, allows the detection of species-specific DNA markers: its phylogenetic use has been advocated by Hadrys *et.al.* (1992). Use of specimens sampled from a range of global locations might perhaps reveal the existence of clines

within the species, or perhaps a series of genetically dislocated populations each having adapted to a distinctive set of localised conditions.

Ultrastructural variation in oocyte morphology, and thus vitellogenic mechanism, has been discovered between sibling species of *Capitella* (Eckelbarger & Grassle, 1983) and between populations of *Streblospio benedicti* with differing larval developmental modes (Eckelbarger & Levin, unpublished). Transmission electron microscopy would allow ultrastructural comparisons of oocyte morphology from separate *Pygospio* populations with differing larval developmental modes.

"A species is a population whose members are able to interbreed freely under natural conditions" (Wilson, 1992). This definition implies inter-species infertility. To date, no experiments involving this ultimate test of speciation on *Pygospio* from separated populations are known to have been performed - although, it must be said, such tests would contravene the definition's specification of "natural conditions". Further work should therefore also involve reciprocal crosses of *Pygospio elegans* from populations suspected of harbouring different sibling species, to determine the extent of reproductive isolation. Such work would provide definitive evidence to prove or disprove sibling speciation.

3.6 Summary

- The apparent reproductive flexibility of *Pygospio elegans* has attracted the suspicion that more than one cryptic sibling species is involved. This suspicion is partly based on laboratory and field observations of populations (such as that inhabiting the Somme Bay) that demonstrate reproductive stability.
- A basic, qualitative experiment was performed. This suggested that changes in conditions of food supply and population density do not lead *Pygospio* from either the Somme Bay or Ryde Sand to display poecilogonous behaviour and change reproductive strategy.
- No definite inter-population differences in external morphology were observed among the specimens available. Some degree of variability was noticed in the displacement of branchiae, although the use of this character is perhaps

questionable. If *Pygospio* is in the process of sub-speciating, it can only have recently begun to diverge.

- Reproductive strategy has a central role in determining a species' fitness within its environment. The study of *Pygospio elegans* may thus yield much of interest about speciation in Polychaeta.

Part 2.

The Tube-bed Study

Sampling Strategy

On each visit to the LCS site a single tube-bed was chosen at mid-shore level for sampling on the basis of its having a distinctly raised surface, at which a dense array of tube tips was just visible. It also had a discrete edge characterised by a more or less abrupt change in sediment topography and firmness, rather than a sharply eroded step. For collection of macrofaunal and organic content samples, a transect was erected to cross from the bed's centre in a seaward direction to an adjacent, "off-bed" region, and samples were taken at intervals along the transect. The spacing of such sampling stations is given in **Table SS.1**. A change in sampling strategy in 1995 allowed improved spatial sampling resolution around the tube-bed edge, the region in which sediment might be expected to show a gradation from non-bed to tube-bed conditions. This edge-bed region is seen as significant to the study of intra-tube-bed dynamics as it and its sessile inhabitants are oriented more squarely with incident tidal flows; interaction with flow is perceived to be a potentially important tube-bed structuring agent.

Sampling Date	Transect stations / metres from tube-bed edge										
8/12/1993	4	3	2	1				0		-1	
6/4/1994		3	2	1				0		-1	-2
15/6/1994			2	1				0		-1	-2
27/7/1994			2	1				0		-1	-2
13/9/1994			2	1				0		-1	-2
10/11/1994			2	1				0		-1	
8/3/1995				1	0.15	0.10	0.05	0	-0.05	-1	
10/4/1995				1	0.15	0.10	0.05	0	-0.05	-1	
8/6/1995				1	0.15	0.10	0.05	0	-0.05	-1	

Table SS.1: Sampling dates and transect stations. Stations were identified by their distance in metres from the tube-bed edge, off-bed stations taking negative values.

A variety of physical measurements were made at a station on a tube-bed and a non-bed station; in each case with the introduction of improved spatial sampling resolution in 1995, measurements were made at each transect station.

Analysis of *Pygospio* density from macrofaunal samples allowed *a posteriori* validation of tube-bed and non-bed station choice. Transect stations were assessed in the field as lying within a tube-bed or outside of one. **Figure SS.1** shows the distribution of *Pygospio* densities among such subjectively classified stations. 97% of all core samples classified as having originated from a non-tube-bed area were found to contain fewer than 50,000 *Pygospio* m^{-2}; 95% of stations apparently within tube-beds contained more than 50,000 *Pygospio* m^{-2}. The three "-1" station cores with densities exceeding 100,000m^{-2} were taken during the earliest two sampling trips; their choice as "non-bed" stations may be attributed to inexperience. On the basis of this result densities greater than 50,000m^{-2} were taken to indicate tube-bed conditions.

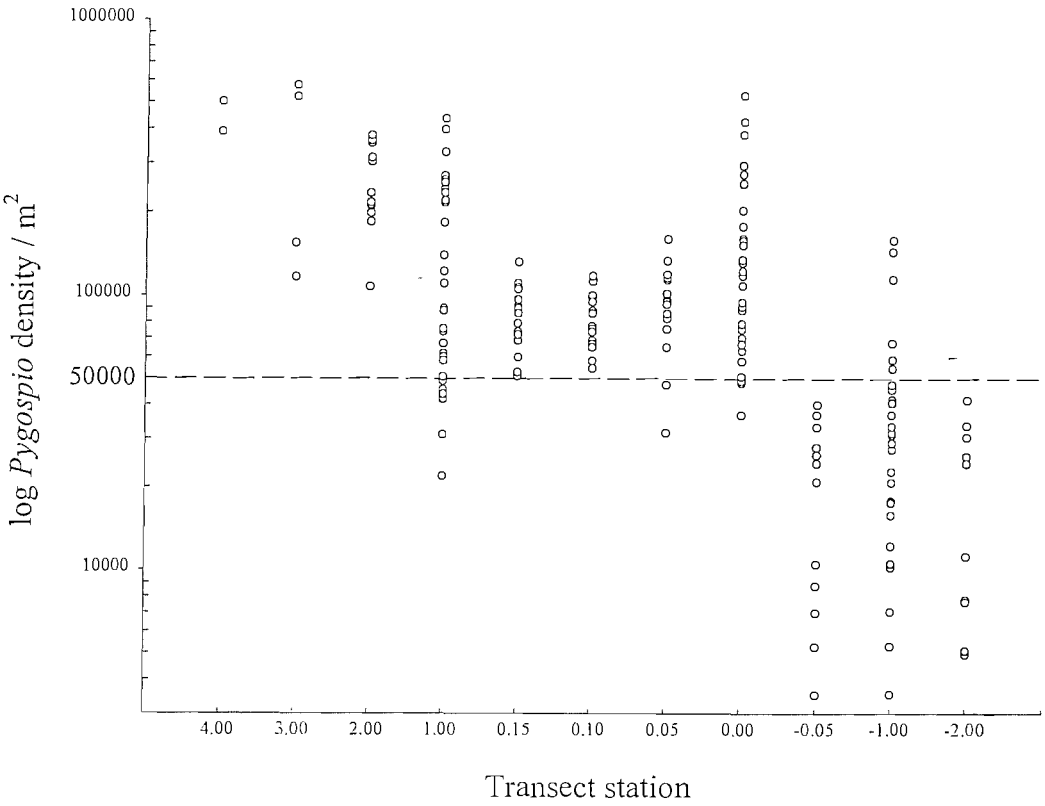


Figure SS.1: scatterplot of *Pygospio* density *versus* transect station, all data pooled (December 1993 - June 1995). A reference line is drawn at density = 50,000m^{-2}.

Chapter 4.
The Tube-Bed Physical Environment

4.1 Introduction

Dense arrays of infaunally-built tubes may alter the physico-chemistry of marine sediments. They alter sediment properties of granulometry, drainage and compaction; they increase mucous-binding, and they magnify the sediment-water interface (Aller, 1988; Meadows *et. al.*, 1990; 1991). Tube aggregations also influence sediments indirectly through their interaction with impinging boundary-layer water flows (Eckman *et. al.*, 1981; Nowell *et. al.*, 1981; 1982; Carey, 1983).

Dense populations of sessile, deposit- and suspension-feeding polychaetes such as *Pygospio* enhance the irrigation of sediments (Kristensen, 1981; 1991; Boudreau & Marinelli, 1994; Marinelli, 1994; Mayer *et. al.*, 1995). Suspension feeders sequester particulate material from the water column, egesting it at the surface: normal depositional rates are augmented and the physical nature of the sediment is altered (Frithsen & Doering, 1986). The combined rate of nitrogenous excretion of a dense population may exceed the ambient rate of waste removal, and metabolites may accumulate to toxic levels (Rybarczyk *et. al.*, 1996).

A set of measurements was made to quantify physical and chemical parameters both in tube-bed and non-bed sediments. Qualification as a tube-bed area was based on measurements of *Pygospio* density made at each sampling station. Measurements were made of sediment critical torsional shear strength, redox potential discontinuity (RPD) depth, temperature, permeability, moisture content, organic content, granulometry, gross bacterial abundance and the concentrations of photopigments and bulk sediment ammonium. Samples were taken along cross-tube-bed transects to assess spatial changes in physico-chemical parameters within the tube-bed.

4.2 Methods

4.2.1 Field Measurements.

During each sampling trip between March 1994 and November 1994 at least 6 replicate measurements of critical torsional sediment shear strength were taken at a mid-bed and an off-bed station; during 1995, 6 replicate measurements were taken at each transect station to complement the improved spatial sampling regime (see **Table SS.1**). In all cases measurements were made at 0-5cm, 5-10cm and 10-15cm depth intervals using a "Pilcon" hand-operated 33mm shear vane (Serota & Jangle, 1972). Sediment temperature and RPD depth were also measured at a tube-bed and non-bed station. Additional RPD depth measurements were made at the flood-tide-facing bed-edge during 1995 to examine variation in oxygen availability.

In the majority of cases below, sediment samples for physico-chemical analysis were taken to a depth of 5cm to concentrate on the zone inhabited by *Pygospio*.

4.2.2 *Pygospio* Population Density.

Three spatially random, replicate cores (area = $2.0 \times 10^{-3} m^2$) were taken per transect-station between December 1993 and November 1994, and six random, replicate cores (area = $5.7 \times 10^{-4} m^2$) taken per transect-station between March 1995 and June 1995. The decrease in core size in 1995 increased the speed at which samples could be processed, thus allowing improved replication. In all cases, cores were taken to a depth of 10cm, which was well below the deepest *Pygospio* tube. Macrofauna core samples were sieved in the field at 500μm, then fixed in 4% seawater-formaldehyde and stained with Phloxine B (C.I. no. 45410) immediately on return to the laboratory at St. Valery. On return to Southampton, macrofauna samples were washed again to remove any remaining sediment and stored in 70% ethanol before sorting and counting. In order to quantify abundances of *Pygospio* from the larger cores, the average of three replicate subsample counts per core was scaled by weight: the majority of *Pygospio* were obscured within their tubes and it was deemed too time consuming to count all those in a core (maximally ~1,500).

4.2.3 Granulometric Analysis.

An approximately $0.01m^{-2}$ total area of sediment was taken to 10cm depth using a trowel, and frozen until processed. Before the introduction of improved spatial sampling in 1995 only a single sample was taken at a non-bed and tube-bed area. The procedure followed that of Buchanan (1984). Sediment was thawed and chemically oxidised to remove the organic component. The hardy mucous lining of *Pygospio* tubes necessitated treatment with 1:3 water : 11% w/v hypochlorite solution in place of hydrogen peroxide. Sediment was left to oxidise for two days before further treatment. Samples were neutralised with thiosulphate, then spun down and the supernatant decanted off; samples were then resuspended in water to fully remove the oxidant.

Sodium hexametaphosphate ($6.2\ gl^{-1}$)was added to deflocculate the sediment. The silt / clay fraction could then be removed by wet sieving at 63μm; this was set aside for pipette analysis. The remaining >63μm fraction was dried for 24 hours at 70°C then sub-fractionated at 0.5ϕ intervals between 1mm and 63μm (Wentworth Scale) using stacked sieves on a shaking platform. Sediment passing the bottom 63μm sieve was added to the wet <63μm portion. This latter material was made up to 1 litre distilled water, agitated and a 20ml subsample drawn off into a tared crucible. This was dried at 70°C for 12 hours and reweighed: resulting weight of the silt / clay residue was scaled x50 to give the total mass of the <63μm fraction. Resulting sediment fraction masses were calculated as cumulative percentages of the whole.

The standard descriptive characteristics, median ϕ; inclusive graphic standard deviation; inclusive graphic skewness; graphic kurtosis; and percentage silt / clay, were calculated as follows:

- *Median phi* represents the median grain size; it equals the ϕ value at 50%.

- *Inclusive graphic standard deviation* represents the spread of data about the median, and equals

$$\frac{\phi 84\% - \phi 16\%}{4} + \frac{\phi 95\% - \phi 5\%}{6.6} \qquad (2)$$

- *Inclusive graphic skewness* measures the asymmetry of the spread of data about the median, and equals

$$\frac{\phi 16\% + \phi 84\% - 2\phi 50\%}{2(\phi 84\% - \phi 16\%)} + \frac{\phi 5\% + \phi 95\% - 2\phi 50\%}{2(\phi 95\% - \phi 5\%)} \qquad (3)$$

- *Graphic kurtosis* measures the peakedness or flatness of the distribution, as is found as

$$\frac{\phi 95\% - \phi 5\%}{2.44(\phi 75\% - \phi 25\%)} \qquad (4)$$

- *Percentage silt / clay* was found as the percentage by mass of the total sample represented by the <63μm fraction.

Verbal interpretations of these statistics are included on the relevant figures.

An assessment was also made of the specific granulometries of tube-bound and non-tube-bound sediment from December 1993. Tubes were isolated from the surrounding sediment and analysed separately.

4.2.4 Determination of Sediment Permeability.

The permeability of bed and off-bed sediment was investigated using the "falling head" method (Allen, 1985). 15cm long corers were used to take 3 replicate 5cm depth cores from a mid-tube-bed and an off-bed area in July 1994. Sediment was transported back to the laboratory within its coring tube, sealed at either end with plastic bags to minimise dessication. In the laboratory, each core was uncapped and suspended upright with its base submerged in a bucket of seawater. A 300μm mesh gauze was fitted across the core's base to prevent sediment collapsing out of the core tube. Water was slowly introduced into the space above the sediment surface to a known height. Core permeability was expressed as the rate of fall of the head of water to move through two consecutive 3cm distances marked on the inside of the core tube.

4.2.5 Determination of Sediment Moisture Content.

At least 6 replicate 5cm depth sediment cores were taken per transect station. These were extruded into pre-weighed glass jars in the field, and immediately capped so that they were airtight. All samples were taken during low tide. These sealed, wet samples were weighed in their jars immediately on return to the laboratory. Caps were then removed from the jars and each sample dried in its jar at 80°C to constant weight. Jars were recapped and sample dry weight found. Moisture content was represented as the ratio of moisture to dry sediment, expressed as a percentage.

4.2.6 Determination of Organic Matter.

Three replicate 5cm cores per transect station were taken for quantification of sediment organic matter. These were kept frozen until processed. Approximately 5g sediment from each core was picked clean of macrofauna and tubes and dried down to constant mass at 70°C. Dry mass was recorded and the sediment placed in a muffle furnace at 550°C for 12 hours. Samples were allowed to cool in a dessicator and their weight was recorded once more. Weight loss signified the oxidation of organic matter, and this was expressed as a percentage of the original dry weight of sediment.

4.2.7 Determination of Sediment Bacterial Abundance.

Three replicate sediment samples were taken during July 1995 using a narrow bore corer (mouth area $=7.9 \times 10^{-5} m^{-2}$) to 10cm depth at a mid-bed and non-bed station. Cores were sectioned in the field into 0-1cm, 1-5cm and 5-10cm horizons, fixed immediately in 4% formalin and stored in capped, acid-washed vials.

Gross bacterial numbers were estimated in the laboratory by epifluorescence microscopy. Prior to analysis all sediment subsamples were homogenised using a sterilised glass rod. An approximately 0.1g portion of sediment was taken from each horizon and placed in a watch glass to air-dry; dry mass was then noted. A single drop of filter-sterilised $0.1 mg ml^{-1}$ Primulin dye solution was added and mixed with the sediment to form a slurry; this was then used to make a temporary smear preparation of known area on a sterilised glass slide. Ten randomly-chosen fields were viewed under

high power light microscopy and the number of bacteria per field counted. Counts were scaled by area and expressed as numbers of bacteria per unit dry mass of sediment.

4.2.8 Determination of Sediment Photopigment and Ammonium Concentration.

Cores were taken in June 1995 to determine the concentrations of photopigments, and ammonium ion, in tube-bed and non-bed sediments. 3 replicate cores were taken at each station to 5cm depth using cut-off, acid-washed 5ml syringes.

A second set of such samples was taken every 2 hours between 1000h and 1800h inclusive during a single low spring tide, to measure temporal fluctuation of sediment ammonium levels during exposure.

Cores were taken with the syringe plunger kept flush to the sediment surface to avoid entrapment of air. Sediment was retained in the corer, sealed at one end by the syringe plunger; a plastic bag was taped across the open end immediately upon drawing the core to prevent atmospheric oxidation of reduced chemical species. Transparent syringe barrels were wrapped in tape to protect the sediment from light. All cores were placed immediately into a closed ice-box and frozen at -20°C on return to the laboratory. All analyses took place within two weeks of sampling.

In the laboratory sealed cores were placed in a glove bag and opened under nitrogen to prevent oxidation. Sediment was allowed partially to thaw in the dark. Semi-frozen cores were then halved longitudinally and both halves sectioned horizontally into 1cm depth horizons using an acid-washed blade. Each resulting sediment portion weighed approximately 0.5g when wet. Halving the cores allowed measurements both of chlorophyll *a* and ammonium from closely adjacent portions of sediment.

Sediment photopigment.

Core horizon halves were placed into glass vials and freeze-dried in the dark. Samples were then removed under low light to tared polypropylene tubes, and weighed. Samples were sonicated in an iced water bath for 30 minutes in the presence of 5ml 90% acetone neutralised with magnesium carbonate, then allowed to stand in a refrigerator for 24 hours to complete the extraction of photopigments. Samples were centrifuged at 3000rpm for 5 minutes and the supernatant analysed

spectrophotometrically at 665nm and 750nm wavelengths; samples were then acidified with a drop of 1M hydrochloric acid and re-analysed at these same wavelengths. This set of measurements allowed correction to be made for the presence of phaeopigments, *i.e.* inactive and detrital pigments.

The equations of Lorenzen (1967) were employed:

$$\text{chlorophyll } a \text{ / } \mu g\ g^{-1} = \frac{26.7\ (665_0 - 665_A)\ V}{m \times l} \qquad (5)$$

$$\text{phaeopigments / } \mu g\ g^{-1} = \frac{26.7\ (1.7\ (665_A) - 665_0)\ V}{m \times l} \qquad (6)$$

26.7 = constant;

665_O = adsorption at 665nm before acidification minus that at 750nm;

665_A = adsorption at 665nm after acidification minus that at 750nm;

V = volume of extractant used (= 5ml);

m = sediment dry mass;

l = spectrophotometer path length (in this case = 1cm).

Sediment ammonium ion.

Core horizon halves were placed into tared, acid-washed, screw-cap polypropylene tubes and wet-weighed. Ultracentrifugation to isolate pore-waters yielded little because of the relative coarseness of the sediment and the period of tidal exposure prior to sampling: total sediment ammonium (dissolved + adsorped) was therefore initially extracted using 5ml 2N potassium chloride solution in "MilliQ" deionised water (Mackin & Aller, 1984). Extraction was completed by sonication in an ice bath for 1 hour. Ammonium standards were made up to 1μM, 5μM, 10μM, 50μM, 100μM, 200μM and 500μM concentrations using ammonium chloride in 5ml 2N potassium chloride. All samples, blanks and standards were centrifuged at 3000rpm for 20 minutes. Supernatant was drawn off into a clean set of acid-washed tubes for Solorzano's (1969) ammonium analysis. Residual sediment was drained and allowed to air dry for 48 hours before weighing to assess original moisture content.

The following Solorzano's reagents were added, in order, ensuring good mixing between each step:

- 200µl phenol solution (10g phenol in 100ml 95% v/v ethanol);
- 200µl nitroprusside solution (1g sodium nitroprusside in 200ml MilliQ water);
- 500µl freshly-made oxidising solution
  (100g trisodium citrate + 5g sodium hydroxide in 500ml MilliQ water, to which added 25ml hypochlorite solution).

Tubes were capped and left to stand for 2 hours in the dark before spectrophotometric analysis at 640nm. Ammonium standards were used to construct a calibration curve from which sample ammonium concentrations could be read. Sediment ammonium ion concentration was expressed as µM ammonium g^{-1} wet wt. sediment.

4.3 Results

Correlations were used to determine the degree of influence of local *Pygospio* density and tube-bed relative position (rendered as distance from the bed edge; see **Table SS.1** for distances) on the physico-chemistry of a tube-bed. Apart from percentage organic content, for which samples were taken at each transect station throughout the sampling period, such analyses were only attempted using data collected during 1995, when the spatial resolution of sampling and replication were improved and data pairs of *Pygospio* density and physical character were available.

Where calculated, levels of statistical significance are represented by the symbols: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; n.s., not significant.

4.3.1 Granulometry.

The granulometric differences between tube-bed and non-bed sediment are illustrated in **Figure 4.1** overleaf. The figure also shows how these characteristics varied in time. Values in 1995 represent means of tube-bed and non-bed stations. Verbal interpretations of the statistics are included on the figure.

Coefficients of correlation were calculated between station granulometric characteristics and both station mean *Pygospio* density and transect station position. These are displayed in **Table 4.1**, where $p \leq 0.1$.

Table 4.1: Correlations of granulometric character with position and *Pygospio* density.

Date	Coefficient of correlation									
	median ϕ		sorting		skewness		kurtosis		%<63μm	
	Pygospio	Station	*Pygospio*	Station	*Pygospio*	Station	*Pygospio*	Station	*Pygospio*	Station
March 1995	+0.92 **	+0.68 n.s.	+0.68 n.s.	n.s.	+0.75 *	n.s.	n.s.	n.s.	+0.85 *	n.s.
April 1995	n.s.	n.s.	+0.85 *	n.s.	+0.80 *	n.s.	+0.87 *	n.s.	+0.69 n.s.	n.s.
June 1995	+0.82 *	n.s.	+0.77 *	n.s.	+0.84 *	n.s.	n.s.	n.s.	+0.78 *	n.s.

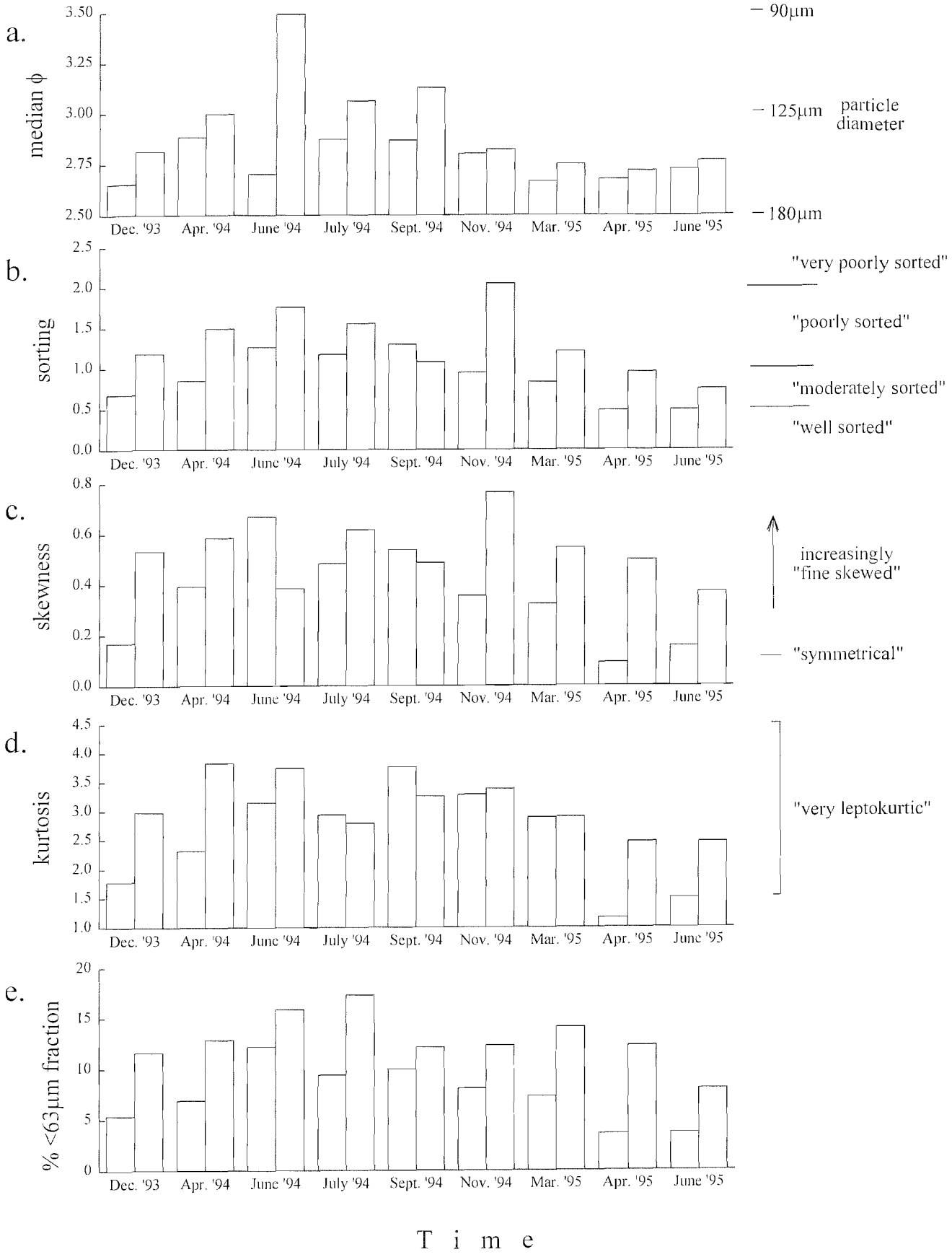


Figure 4.1: Sediment granulometry: non-bed sediment and tube-bed intertubular sediment (definitions in text). **a**: median ϕ; **b**: inclusive graphic standard deviation, a measure of sorting; **c:** inclusive graphic skewness; **d:** graphic kurtosis; **e:** percentage by mass of the <63μm fraction. Verbal interpretations of statistics from Buchanan, 1984.

non-bed sediment

tube-bed intertubular sediment

The granulometric characteristics of isolated tubes are displayed in **Table 4.2**. They are compared with those of the remaining, intertubular tube-bed sediment (see **Figure 4.1** for interpretation of the values). Sediment was taken from a mid-bed area in December 1993.

Table 4.2: Granulometric characteristics of *Pygospio* tubes.

	Tube-bound sediment	**Intertubular sediment**
median ϕ	2.83	2.81
sorting	0.54	1.18
skewness	0.16	0.53
kurtosis	1.30	2.96
%<63µm	3.73	11.66

4.3.2 Sediment Permeability and Moisture Content.

Detailed results of the permeability study carried out in July 1994 are shown in **Table 4.3**. Three replicate cores from a tube-bed and a non-bed area were tested; the tube-beds cores were significantly more permeable ($p<0.001$; one-way analysis of variance).

Table 4.3: Results of the permeability study.

Sample	**Falling rate of water head / cm.hour^{-1}**		
	through first 3cm	through second 3cm	mean and st.dev.
tube-bed core #1	15.62	14.90	15.42 ± 1.11
tube-bed core #2	15.08	14.76	
tube-bed core #3	17.56	14.69	
non-bed core #1	2.95	2.81	2.99 ± 0.58
non-bed core #2	3.77	3.58	
non-bed core #3	2.50	2.34	

The mean moisture contents of tube-bed and non-bed areas are shown by **Figure 4.2** below. Significance of the difference in moisture content is shown on the graph (one-way analysis of variance). A significant difference was observed in 5 of 7 sample sets; non-bed areas were wetter than tube-bed areas in all but one case.

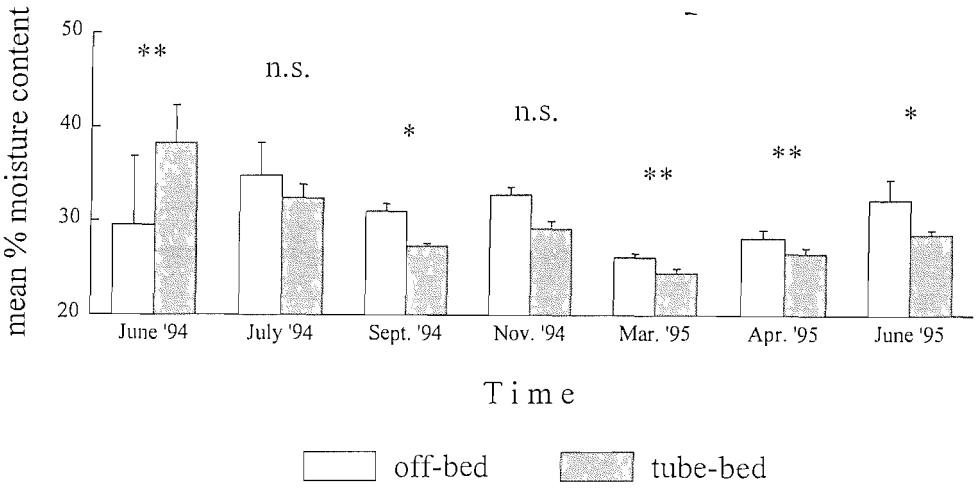


Figure 4.2: Mean percentage moisture content (0-5cm depth) by mass + one standard deviation: tube-bed and non-bed areas; June 1994 to June 1995.

Coefficients of correlation were calculated between station mean percentage moisture content and both station mean *Pygospio* density and transect station position: the results are shown below in **Table 4.4**, where $p \leq 0.1$.

Table 4.4: Correlations of moisture content with position and *Pygospio* density.

Date	Coefficient of correlation	
	Pygospio	Station
March 1995	-0.73, n.s.	n.s.
April 1995	n.s.	-0.88**
June 1995	-0.77*	n.s.

4.3.3 Organic Content.

Mean sediment organic contents of tube-bed and non-bed areas are illustrated in **Figure 4.3** below. Significance of the difference in organic content is again shown on the graph (one-way analysis of variation). Tube-beds contained significantly more organic matter per unit weight of sediment than non-bed areas in all sample sets. Percentage content of organic matter at LCS varied between approximately 0.5% and 2.5% by weight.

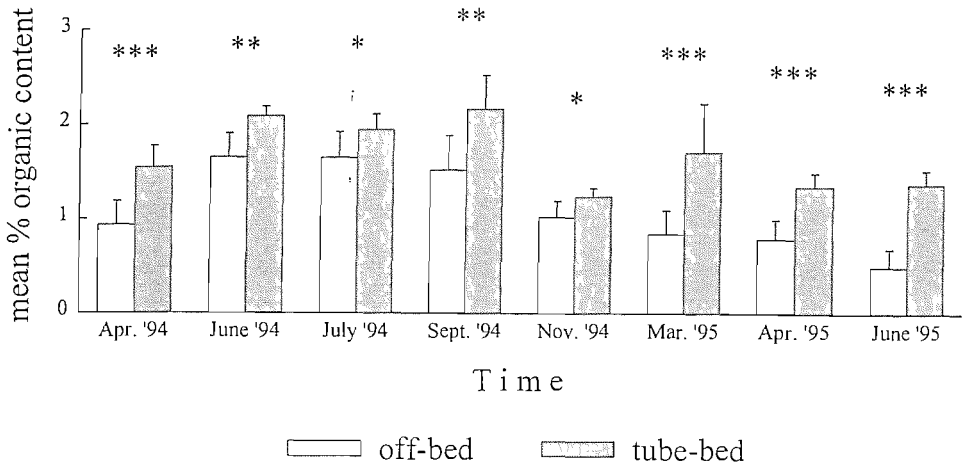


Figure 4.3: Mean percentage organic content by mass + one standard deviation: tube-bed and non-bed areas; April 1994 to June 1995.

Coefficients of correlation were calculated between station mean percentage organic content and both station mean *Pygospio* density and transect station position: the results are given in **Table 4.5** below, where $p \leq 0.1$.

Table 4.5: Correlations of organic content with position and *Pygospio* density.

Date	Coefficient of correlation	
	Pygospio	Station
March 1995	+0.84*	n.s.
April 1995	+0.79*	n.s.
June 1995	+0.83*	+0.77*

4.3.4 RPD Depth and Sediment Temperature.

Field measurements were made of the depth of the redox potential discontinuity, and of sediment temperature at 5cm depth. **Table 4.6** shows the results:

Table 4.6: Field measurements of RPD depth and sediment temperature.

Date	RPD depth / cm			Temperature / °C	
	mid-bed	edge-bed	non-bed	tube-bed	non-bed
June 1994	3	-	4	23	23
July 1994	2	-	5	22	22
Sept. 1994	4	-	6	19	19
Nov. 1994	4	-	12	4	4
March 1995	3	3	20	7.5	8
April 1995	5	3	9	10	10
June 1995	3	3	5	20	20

Sediment temperatures fluctuated between 4 °C and 23 °C, showing a clear seasonal response. The depth of the RPD ranged from 2cm to 20cm, tending to be deeper in non-bed sediment. Observations of RPD depth at the tube-bed's seaward, flood-facing edge were similar to those made in mid-bed areas.

4.3.5 Critical Torsional Shear Strength.

The variation in mean sediment shear strength with depth on and off tube-beds is illustrated by **Figure 4.4** overleaf. Significance of the difference in surficial shear strength (0-5cm) is indicated on the graph (one-way analysis of variation).

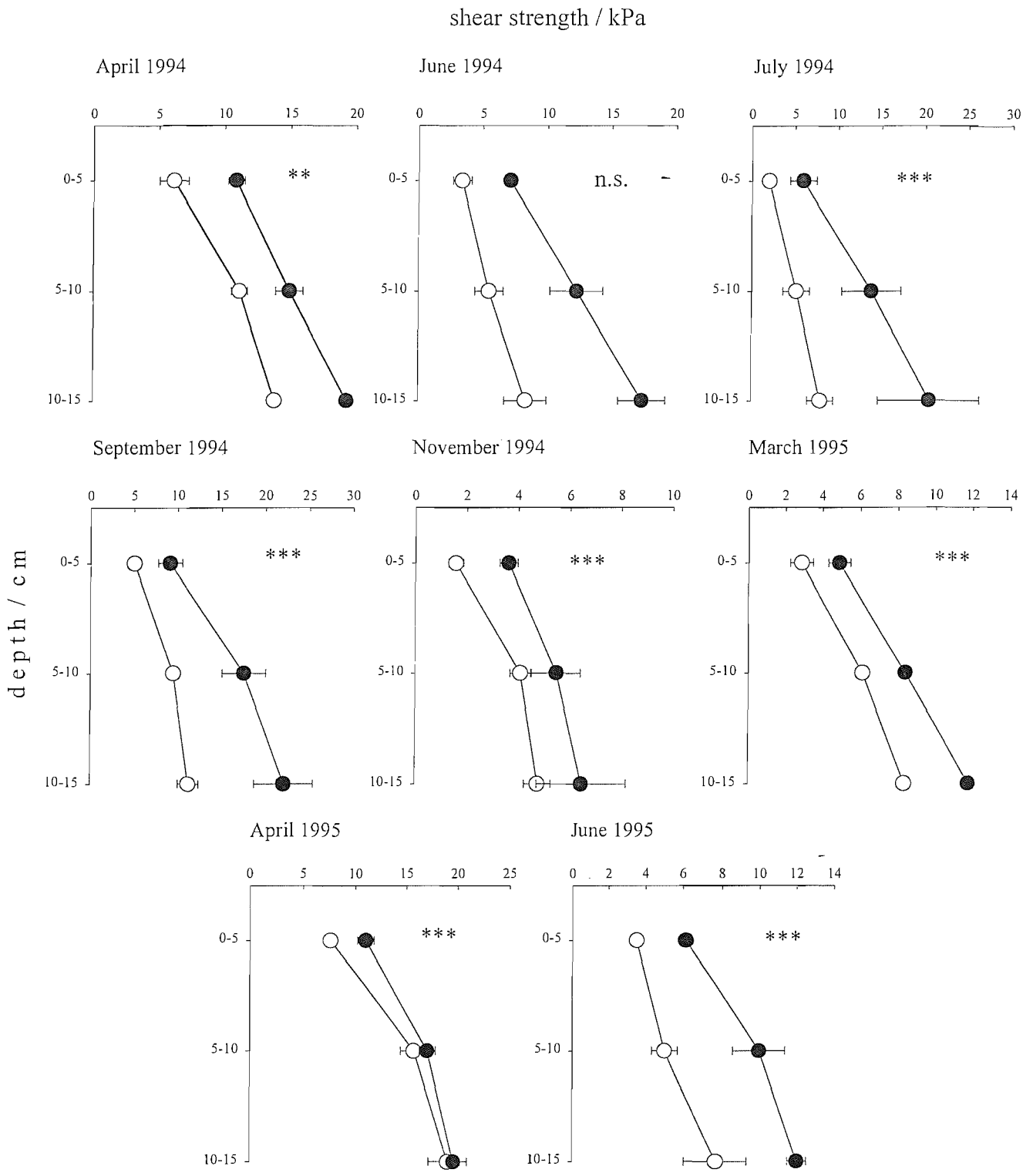


Figure 4.4: Mean sediment critical torsional shear strength with depth, +/- 1 standard deviation; April 1994 - June 1995.

—○— non-bed sediment —●— tube-bed sediment

Coefficients of correlation were calculated between station mean shear strength (at 0-5cm depth) and both station mean *Pygospio* density and transect station position, and the results are given below in **Table 4.7**, where $p \leq 0.1$.

Table 4.7: Correlations of station mean shear strength with position and *Pygospio* density.

Date	coefficient of correlation	
	Pygospio	Station
March 1995	+0.84*	+0.79*
April 1995	n.s.	+0.70, n.s.
June 1995	+0.79*	+0.71, n.s.

4.3.6 Bacterial Abundance.

Mean bacterial abundances per gram dry sediment, and the significance of the difference between tube-bed and non-bed abundances, are shown by **Table 4.8**. The significance of the difference in bacterial abundances between tube-bed and non-bed areas was found to decrease with depth.

Table 4.8: Total bacterial counts.

Depth / cm	Bacterial abundance/ 10^6 g^{-1} mean and standard deviation		Significance level
	tube-bed	non-bed	
0-1	978±691	188±108	**
1-5	1188±456	608±476	*
5-10	578±345	484±266	n.s.

4.3.7 Sediment Photopigment Concentrations.

Results of photopigment analysis of samples taken in June 1995 are displayed graphically in **Figure 4.5**, overleaf.

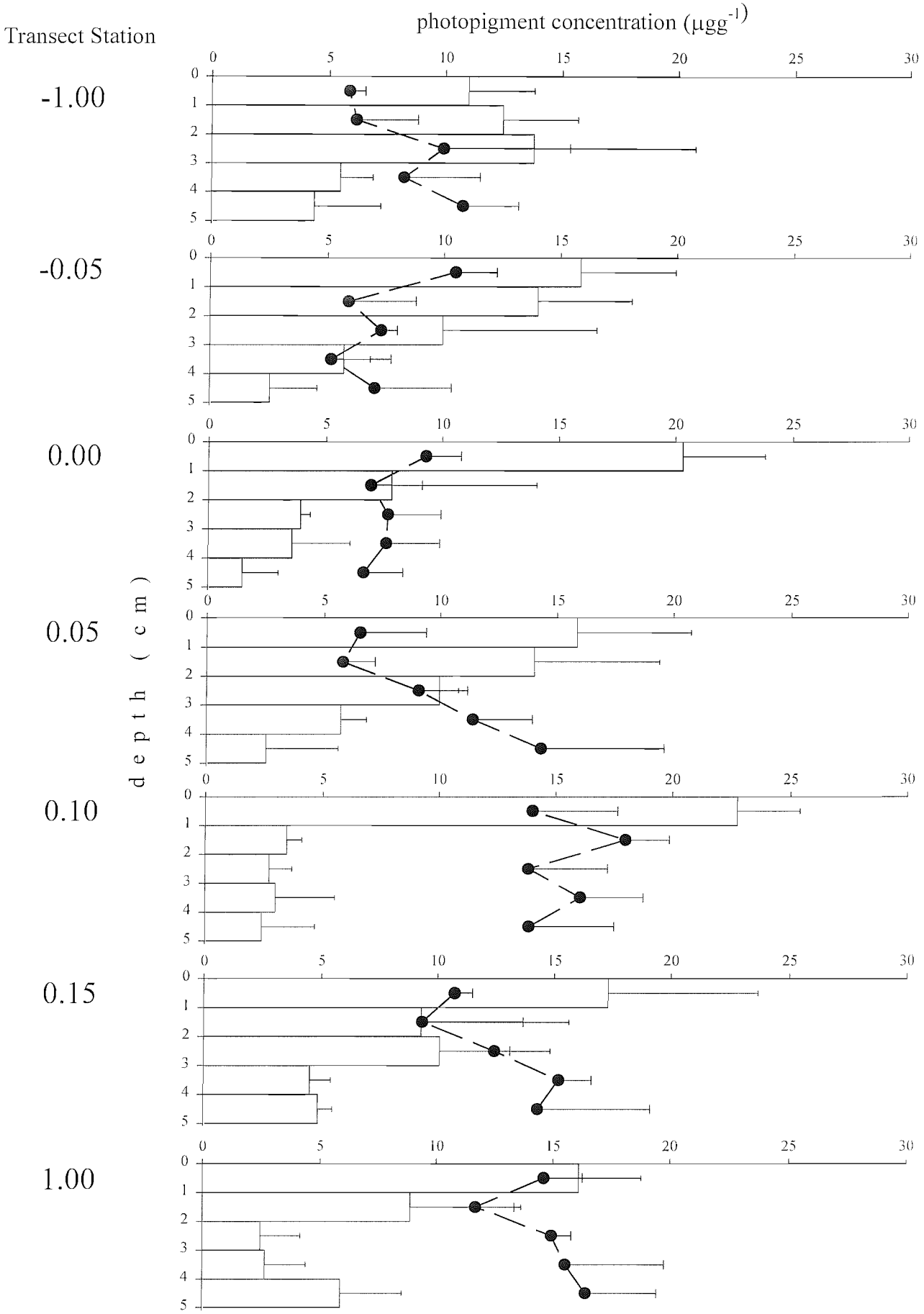


Figure 4.5: Mean photopigment concentration with depth at each transect station, +1 standard deviation. June 1995.

chlorophyll *a* — phaeopigments

A number of significant differences were found in chlorophyll *a* and phaeopigment concentrations with relation to both tube-bed position and depth. **Tables 4.9** and **4.10** display results of analyses of variation:

Table 4.9: Spatial variation:
chlorophyll *a* and phaeopigment data compared by station, at each depth.

Depth / cm	**significance level**			
	comparison of all transect stations		comparison of pooled tube-bed *versus* non-bed stations	
	chl. *a*	phaeo.	chl. *a*	phaeo.
0-1	n.s.	***	***	***
1-2	n.s.	***	n.s.	***
2-3	*	*	n.s.	***
3-4	n.s.	**	n.s.	***
4-5	n.s.	*	n.s	***
pooled (0-5)	n.s.	***	*	***

Table 4.10: Depth variation:
chlorophyll *a* and phaeopigment data compared by depth, at each station.

Transect station	**significance level**	
	chlorophyll *a*	phaeopigments
-1.00	*	n.s.
-0.05	*	n.s.
0	***	n.s.
0.05	***	*
0.10	***	n.s.
0.15	*	n.s.
1.00	***	n.s.

Correlations were calculated between station mean *Pygospio* density and station mean photopigment concentration at depths of 0-1cm and 0-5cm; the results are shown in **Table 4.11** below, where $p \leq 0.1$.

Table 4.11: Correlations of photopigment concentration with position and *Pygospio* density.

depth	coefficient of correlation			
	chlorophyll *a*		phaeopigments	
	Pygospio	Station	*Pygospio*	Station
0-1cm	+0.76*	n.s.	n.s.	+0.77*
0-5cm	-0.79*	n.s.	n.s.	n.s.

Phaeopigment concentrations were found to increase with depth; this was more pronounced in tube-bed sediment, as seen more clearly in **Figure 4.6**, which plots the change in the ratio of active and inactive photopigments with depth.

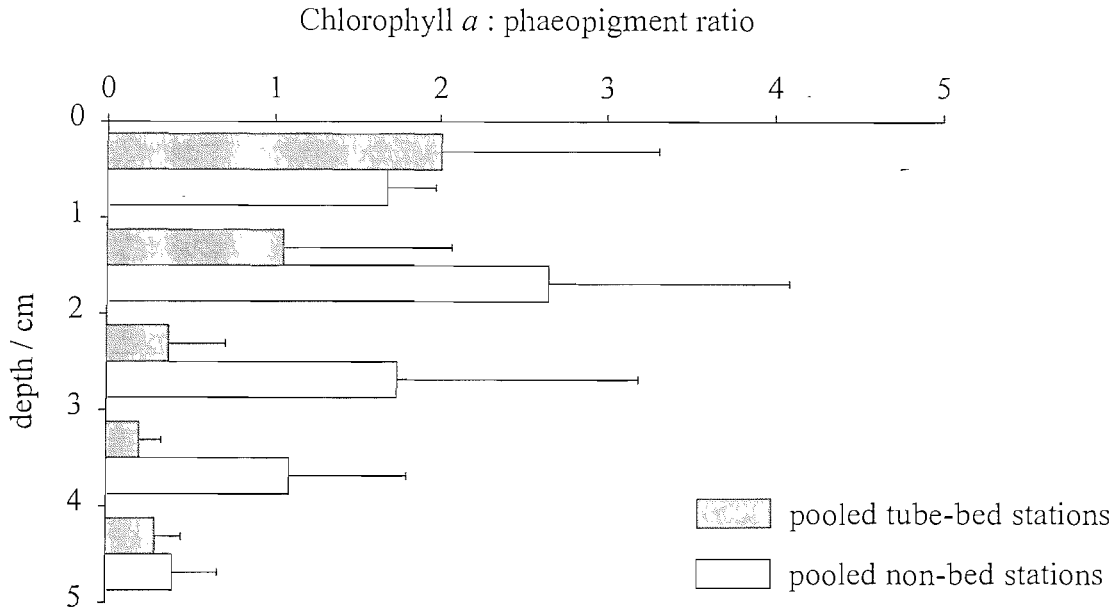


Figure 4.6: tube-bed and non-bed mean chlorophyll *a* : phaeopigment ratio + one standard deviation, with respect to depth.

4.3.8 Sediment Ammonia Concentrations.

Analyses of variation of sediment ammonium concentration with relation to tube-bed depth and position were performed. No significant interaction with depth was found at any station. **Table 4.12** shows how ammonia concentration varied with tube-bed relative position:

Table 4.12: ammonium concentration data compared by station, at each depth.

Depth / cm	Significance level	
	comparison of all transect stations	comparison of pooled tube-bed *versus* non-bed stations
0-1	n.s.	***
1-2	n.s.	*
2-3	n.s.	*
3-4	n.s.	*
4-5	n.s.	n.s.
pooled (0-5)	n.s.	***

Correlations were calculated between station mean ammonium concentration and station mean *Pygospio* density and transect station position at depths of 0-1cm and 0-5cm. No significant interactions were found, although correlations with transect station position were moderately positive ($r = +0.50$ at 0-1cm; $r = +0.66$ at 0-5cm).

Figure 4.7 overleaf illustrates spatial trends in ammonium concentration. **Figure 4.8** following after shows the temporal change in ammonium levels in a mid-bed area of sediment during a tidal cycle. There was no significant variation with time in levels of ammonium in the top 5cm of sediment ($p = 0.16$; n.s.).

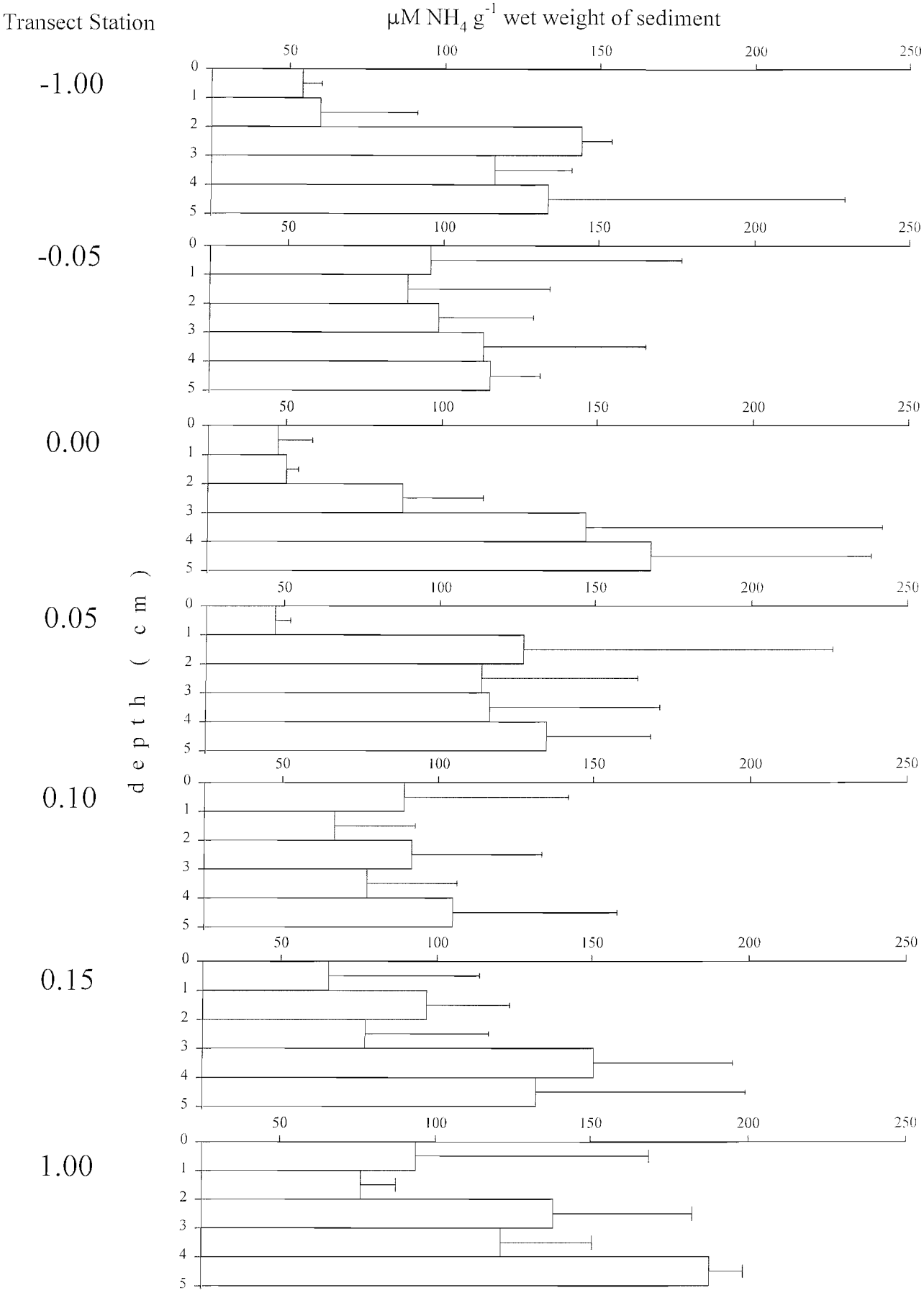


Figure 4.7: Mean ammonium concentration with depth at each transect station, +1 standard deviation. June 1995.

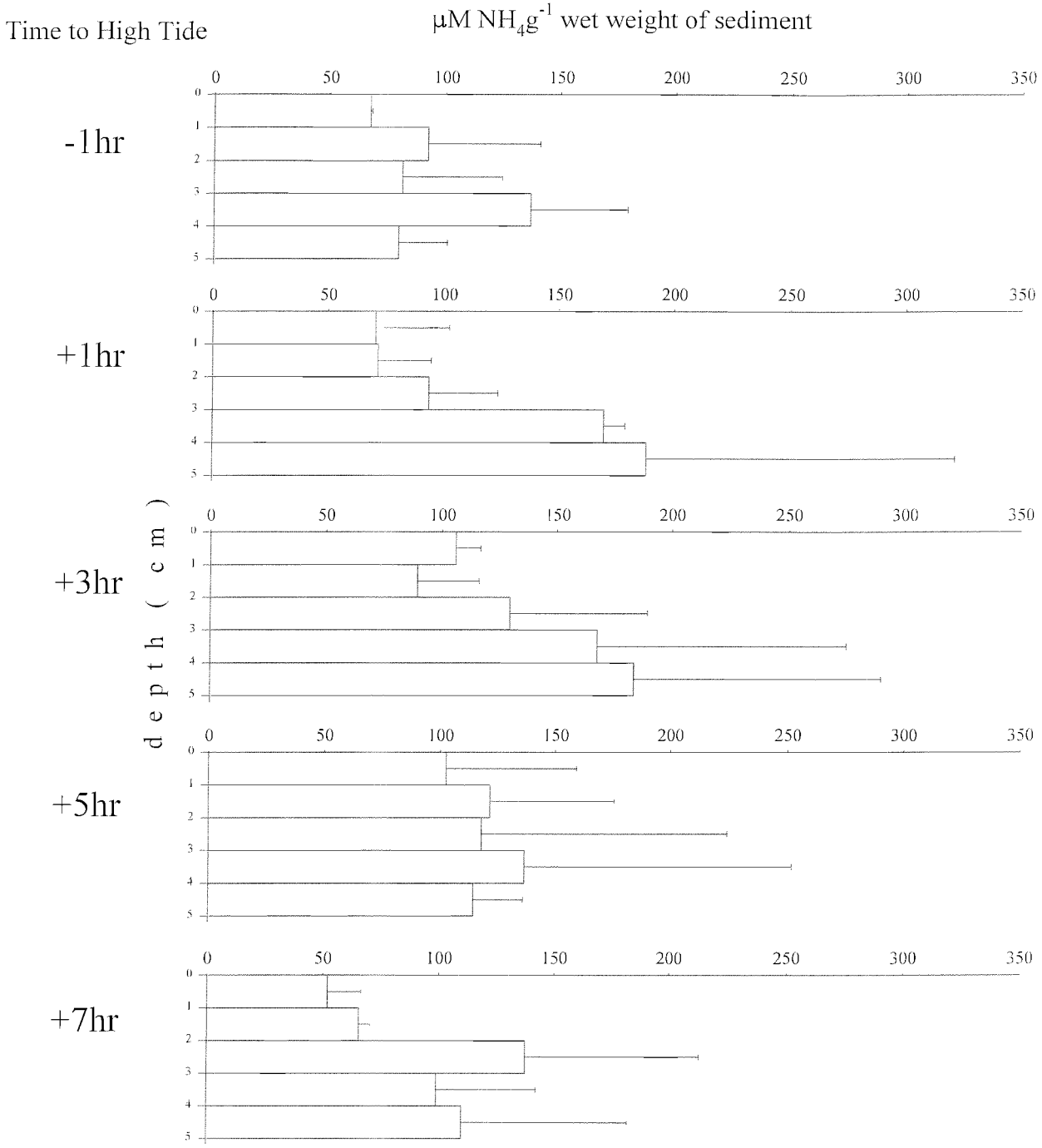


Figure 4.8: Mean ammonium concentration with depth during tidal exposure, +1 standard deviation. June 1995.

4.4 Physical Environment

4.4.1. Granulometry.

During the period of sampling median ϕ values indicated a median grain size of around 125μm in the mid-to-upper tidal flats of the LCS site. This value may have been biased towards higher median ϕ values because of preferential sampling on or adjacent to tube-beds, which are seen to contain higher levels of silt and clay.

Sediments in estuaries tend to grade from coarse to fine particles as one proceeds upshore towards HWST (Dyer, 1979; Reineck & Singh, 1980). Lafite (1986) demonstrated such a gradient in the Somme Bay, on a transect running north through LCS: median grain diameter was greater than 270μm at LWST, while at HWST it was less than 160μm. Finer particles, with slower settling rates, move in suspension and follow residual waterflow, flocculating and depositing higher on the shore. Here they resist total re-erosion by the weak ebb currents circulating at estuarine margins, and muddier, upper-tidal flats become established. It was on such mid- to upper-tidal flats that the extensive *Pygospio* populations of LCS were found.

A tendency for mean grain size to increase was noted from summer 1994 and throughout 1995, especially in the non-bed areas. This may have pointed to increasing hydrodynamism at the relatively exposed LCS site, encouraging resuspension of finer material into the water column. It may equally have represented the return of an equilibrium grain size distribution after an earlier influx of fine particulates to the area. Between 1975 and 1985, two power stations were constructed along the coast from the Somme Bay, and this is known to have released fine silt into the area (Rybarczyk *et.al.*, 1990).

LCS sediment data were characteristically "very leptokurtic", indicating a broader, flatter distribution of grain sizes; this distribution tended to be finely skewed, although again the potential bias resulting from tube-bed sampling may have been involved.

The proportion of silt and clay was greater in tube-beds than in off-bed stations. Tube-bed sediment was correspondingly more finely skewed in distribution and also less well sorted, a consequence of increased silt accretion. Granulometric character was more strongly correlated with *Pygospio* density than transect station position,

suggesting that granulometry is influenced by *Pygospio* at the local scale. The mechanisms by which *Pygospio*, and thus tube-beds, attract increased deposition of fine material are discussed below in sections **4.4.2** and **4.4.3**. The higher-resolution spatial sampling performed in 1995 revealed no significant differences in granulometric character at the tube-bed edge.

Dupont (1975) described the structure of a Somme Bay *Pygospio* tube in cross-section: grains were arranged "methodically" and "concentrically". The average tube-wall was similar in thickness to the radius of its lumen. When separated from extra-tubular sediment, the granulometric character of tubes was found to closely approximate to that of well-sorted estuarine muddy-sand. In the present study, isolated *Pygospio* tubes proved to contain nearly a third less silt and clay compared with the tube-bed sediment from which they had been taken; tube-bound sediment was also better sorted. Dupont (1975) found tube-component sediment was not finer than 25μm, while 10-15% of inter-tubular material was finer than this. He also noted that more than 55% of the tube material was bioclastically-derived carbonate, suggesting that the worm was making a qualitative choice with respect to the mineralogy of particles: adjacent, off-bed sediment contained only 20-30% carbonate.

There are two potential areas in which *Pygospio* tube-beds may impact sedimentology: flow-related effects and biodeposition. A short review of each of these processes in given below.

4.4.2 Flow-related effects.

The presence of projecting tubes - technically "roughness elements" - complicate the hydrodynamic forces acting at the sediment / water interface. Size, geometry and spatial density of roughness elements all determine the properties of near-bed flow, including rate of fluid transport and the magnitude of the shear stress exerted on the substrate (Eckman, 1983).

Tubes may theoretically cause increased erosion of adjacent sediment. An isolated "roughness element", *e.g.* a tube-tip, increases overall boundary skin friction by directing high momentum fluid downwards along its upstream face towards the

substratum: in the lee of the tube, fluid "rolls up" forming an horseshoe vortex. Erosion velocity is increased towards the bed, encouraging particle resuspension. The induced erosive force is proportional to the relative protrusion of the tube. Tubes may also facilitate deposition, however: if the shear stress is sufficiently low and there is no scouring in the vortex region, particles travelling as suspended load may be deposited in the wake of a tube (Eckman & Nowell, 1984). Isolated tubes produce complex patterns of fluid circulation, sediment scour and local deposition (Eckman, 1979a; 1982). Even a single, isolated tube may facilitate deposition on a small scale, while low density arrays create patchwork patterns of deposition; high densities can bring about more uniform patterns (Eckman, 1979b).

Rhoads *et. al.* (1978) reported bed "stabilisation", *i.e.* decreased erosion, by the shielding effects of dense tube arrays. The transition from "destabilisation" to "stabilisation" appears to occur at around 8% cover by roughness elements (Wooding *et. al.*, 1973; Nowell & Church, 1979). Investigating this effect further, Eckman *et. al.* (1981) found that reports of tube-induced sediment stablisation often involved percentage tube coverages well below 8%, and emphasised the importance of mucous-binding.

Figure 4.9, redrawn from Eckman *et.al.* (1981), illustrates this effect. It is based on data collected during flume studies on non-cohesive sediments, and thus represents an idealised situation. The relationship is also dependent on flow rate and the relative protrusion of the tube-tip above the sediment surface. It should therefore not be construed as predictive of actual, field conditions, but rather as a simple model. The range of conditions generated by *Pygospio* tube-beds in the Somme Bay is superimposed for reference.

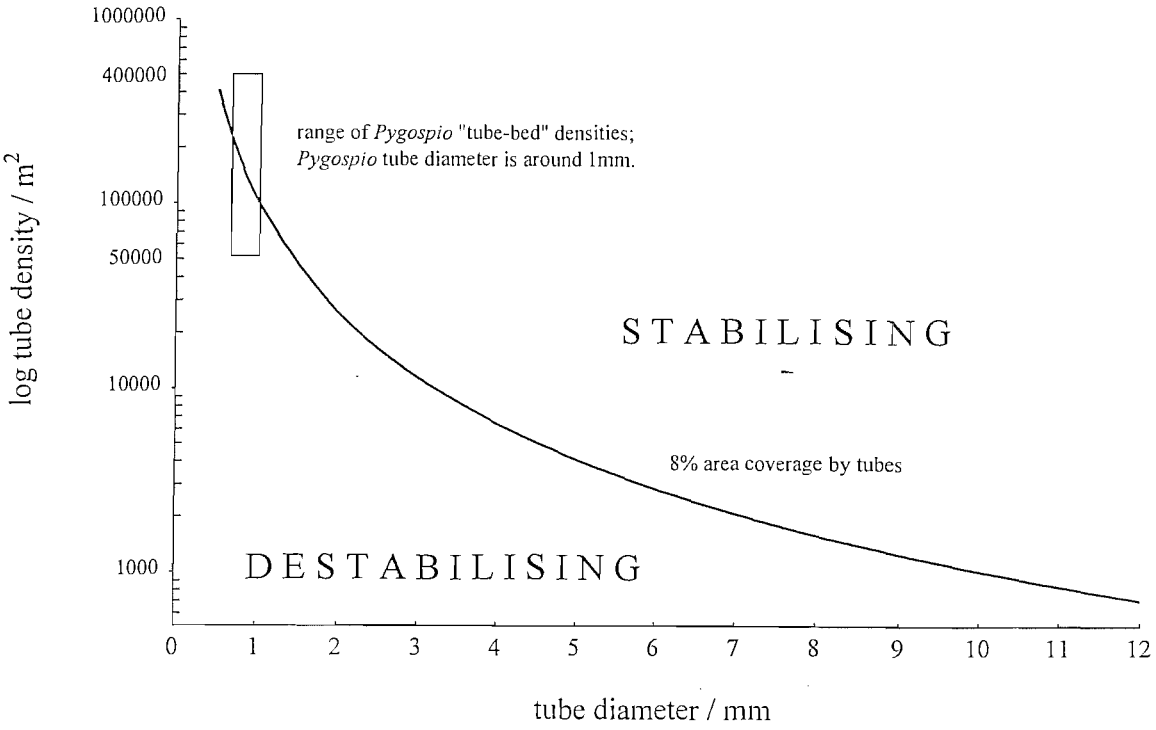


Figure 4.9: Minimum tube density required to stabilise sediments as a function of tube diameter: after Eckman *et.al* (1981). *Pygospio* data from the present study.

The theoretical 8% coverage criterion is met by a *Pygospio* population density of 100,000m^{-2} (where mean tube diameter = 1mm). The threshold density of 50,000m^{-2} found empirically to separate tube-bed from non-bed (see **Sampling Strategy**) corresponds to a coverage of only 4%.

Eckman (1983) performed flume experiments with high (**H**), medium (**M**) and low (**L**) density tube arrays. In the **L** treatment increases in turbulence were noted near the sediment surface, resulting in above-ambient shear stresses. In the **H** and **M** treatments a net reduction in boundary shear stress was observed. Jumars *et. al.* (1981) presented an analogy comparing such tube densities to a shag-pile carpet, which "protects the floor below from shear forces and allows dirt to escape the lifting and shearing forces of the broom". Treatment **H** eventually attained the highest densities of deposited material, through enhanced deposition rates and decreased shear stress and erosion. By influencing shear stress, roughness elements thus help determine adjacent sediment granulometry.

Eckman *et. al.* (1981) noted that tubes may reach such densities as to stabilise sediment purely by the obstruction of near-bed flow. This "skimming flow" (*sensu* Morris, 1955) is produced where the region of maximum turbulent kinetic energy occurs away from the bed.

4.4.3 Biodeposition.

Suspension feeding and defecation also enhance deposition. Such "biodeposition" by suspension feeders can double local sedimentation rates (Rhoads, 1974). Frithsen & Doering (1986) noted increased rates of removal of suspended particles to the bottom by the spionids *Streblospio benedictii* and *Polydora ligni*. In an experiment using microspheres, deposition increased by a factor of x3 in the worms' presence; 25% of this increase was attributed to active filtration and defecation, the remainder to passive, trapping effects by the tubes. Daro & Polk (1973) observed a very dense *Polydora ciliata* population causing deposition rates of up to 50cm $year^{-1}$. Exopolymers such as mucous secreted during feeding also effect the "stickiness coefficient" of sediment - *i.e.* the degree by which deposition is increased by adhesive mucous on the surface (Jumars & Nowell, 1984a).

Egestion of fine particulate matter occurs at the sediment surface. Such egesta are bound by mucous into tiny pellets, which may persist until broken down by microbial action. Pelletisation influences surficial sediment granulometry and susceptibility to erosion (Nowell *et. al.*, 1981). Long-chain exopolymers, shed near the surface during feeding, decrease drag by increasing boundary viscosity and protect against erosion (Dade *et.al.*, 1990).

4.4.4 Sediment Permeability and Moisture Content.

The permeability of the surficial 5cm was measured; this represented the region in which *Pygospio* tubes lie. Tube-bed sediment in July 1994 (mean *Pygospio* density = $2.5 \times 10^5 m^{-2}$) containing 24x *Pygospio* than non-bed sediment (mean *Pygospio* density = $1.4 \times 10^4 m^{-2}$) was significantly more permeable ($p<0.001$): rate of flow of water through tube-bed cores was approximately 5x that of non-bed cores. The granulometric evidence showed that the uppermost 10cm of tube-beds were less well sorted; poor permeability

would be expected in poorly sorted sediment because of the filling-in of interstitial spaces with silt and clay and microscopic detritus. Tubes must therefore play an important role in facilitating the passage of water. Meadows & Hariri (1991) noted significantly increased sediment permeability in high density *Pygospio* aggregations, and found that even low densities of *Pygospio* (2,300m^{-2}) increased sediment permeability. In Noji's (1994) experiments on *Polydora ciliata*, pore-water content was 10-20% lower among tube-aggregations than in control sediment.

The intertidal position of LCS *Pygospio* tube-beds complicates the study of moisture content. The state of the tide must have a big influence on this variable. Moisture contents of samples collected during a tidal cycle in June 1995 for ammonium analysis were used to construct a graph to reveal this influence.

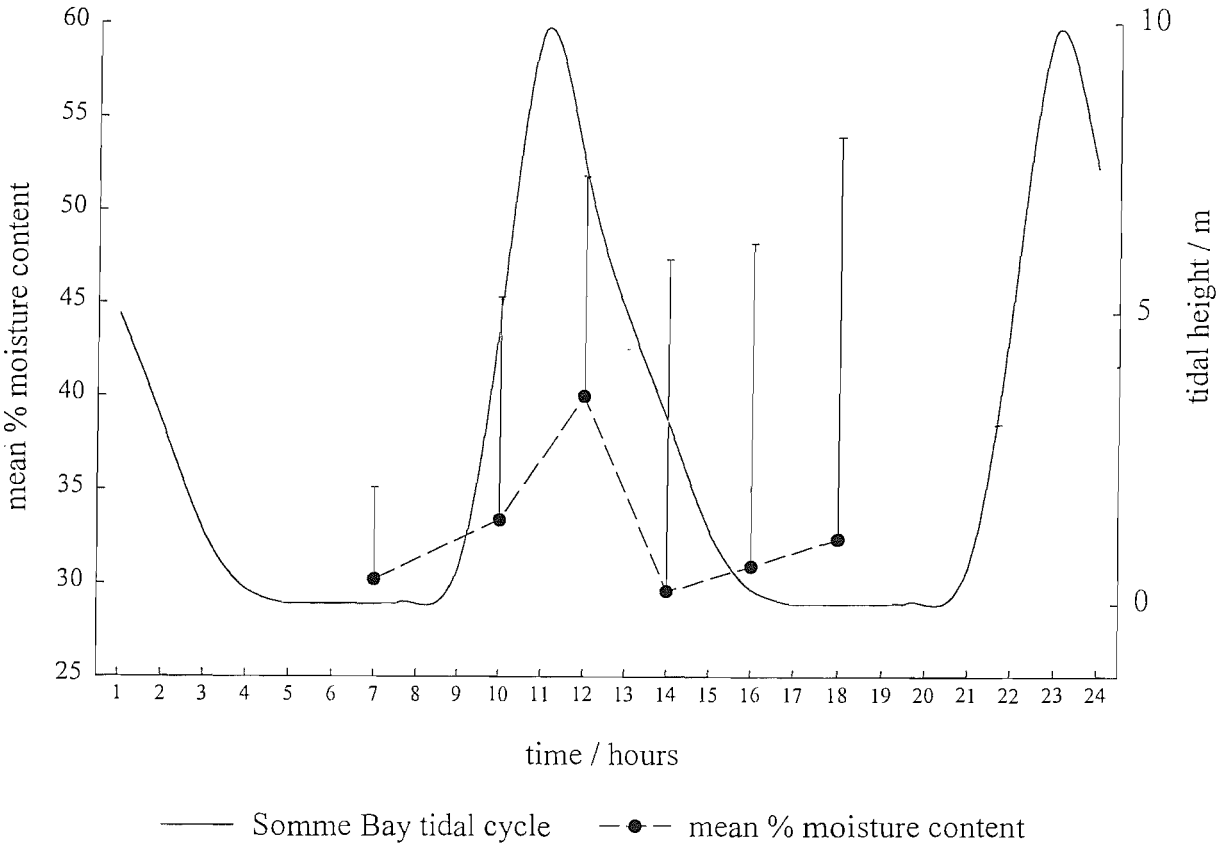


Figure 4.10: LCS tidal cycle, and variation in mean sediment percentage moisture content (+ one standard deviation) with time in a mid-upper shore tube-bed; June 1995.

Consulting **Figure 4.10**, percentage moisture content can be seen broadly to follow the tidal cycle. 30 minutes before high tide, soon before the sampled tube-bed was submerged, mean moisture content was 33% by mass; minutes after emersion sediment contained 40% moisture. Three hours after high tide moisture content was down to 30%.

The first measurement of percentage moisture content, made in June 1994, was unusual in showing the tube-bed to contain significantly more water than the non-bed area ($p<0.01$). However, samples had been taken within an hour of emersion, and the tube-bed had retained more moisture than surrounding non-bed sediment. At all other times sampling was conducted nearer to the middle of the low-tide period. Tube-beds then contained less water than their non-bed comparators, although this was not a significant difference in either July or November 1994. No special conditions of moisture content were encountered at the bed edge.

The permeability data suggests that tube-bed sediment was drier as a result of better drainage. Reduction in sediment moisture content may also have been brought about through lateral compaction of sediment grains during tube-wall construction (Meadows & Tait, 1989).

Moisture content was correlated negatively with both *Pygospio* density and transect position. This interaction was variable in time: it was apparently stronger with *Pygospio* density in March and June 1995 and stronger with transect station position in April 1995. This reflects the variablity of other environmental variables which may affect moisture content of sediment.

4.4.5 Organic Content.

Overall percentage organic contents of LCS sediment were in the region of 1-2%. Sediment organic content was significantly greater in tube-beds that in non-bed areas throughout the sampling period. Increased organic content cannot have been accounted for by tube-wall material as all samples were picked clean of tubes and other macrofauna. Such increases in organic content were consistent with the granulometry of tube-beds: poorly sorted sediment with increased levels of fine particulates traps organic detritus more effectively than coarse, well sorted sediment.

Correlation of organic content with *Pygospio* tended to be strongly positive ($r \geq +0.75$); strength of correlation with station transect position was widely variable, from $r = +0.95^{**}$ in July 1994 to $r = +0.04$ (n.s.) in November 1994. Again, a number of variables, including local rates of detrital input and microbial activity, are involved in determination of organic matter content. Like granulometry and moisture content, organic content did not show any clear pattern of variation from the tube-bed edge inwards.

4.4.6 Sediment Critical Torsional Shear Strength.

The use of the torsional shear vane device to quantify sediment erosion resisance represented a compromise. In each measurement the vane integrated the response of 5cm depth of sediment to torsional shear about a vertical axis. The true agent of shear stress in the natural environment, tidal current, acts on the sediment with a force varying at depth and with topography. However, use of the shear vane was consistent and resulting measurements were therefore inter-comparable, and could be used to show relative differences between stations. The apparatus also allowed a large number of replicate measurements to be quickly and easily taken in the field; furthermore, it was a relatively non-invasive technique, allowing measurements to be made at different depths in the same position.

Tube-beds were stronger than non-beds in their resistance to torsional shear throughout the sampling period. At the sediment surface this difference was highly significant in nearly all cases, although non-significant in June 1994. In all cases shear strength increased with depth, suggesting increasing compaction or an increased proportion of silt and clay at depth. Surficial shear strength correlated strongly positively with transect station position, although only significantly so in March 1995; correlation with *Pygospio* density was strongly and significantly positive in March and June 1995 but weak in April 1995. Shear strengths at tube-bed edges were not significantly different.

The stabilisation of sediment by *Pygospio* has been investigated by Meadows & Hariri (1991) in the laboratory using the falling cone method (Hansbo, 1957). Shear strength equalled 2.2kPa at a tube density of $21{,}000 m^{-2}$, while the shear strength of

defaunated sediment was 1.3kPa. Unfortunately it is impossible to compare these findings directly with the present data; apart from the differences in method of measurement, other physical factors are involved in the determination of shear strength. Sediment shear strength increases are often associated with a reduction in water content and an increased proportion of silt and clay (Trask & Rolston, 1950). Tufail *et.al.* (1989) observed that raised patches of sediment had a greater shear strength than adjacent areas; this was perhaps because of the increased drainage of the raised area. A feature of tube-beds is that they are raised above the mean sediment surface level.

The present study did not examine the relationship between shear strength and other physical data. Such a correlative approach must rely on high resolution sampling, closely spatially corresponding samples being taken with each shear strength measurement. As no such small-scale sampling of physical parameters was attempted, it was decided that no such statistical examination of the present physical data would be sufficiently robust.

Temperature has an effect on shear strength (Muskananfola, 1994). There were no significant differences in temperature between tube-bed and non-bed areas that could have played an effect, however.

Shear strength is further affected by the activity and abundance of the community of mucous-secreting biota. Mucopolysaccharide binding material is secreted by macrofauna during construction of tube dwellings (Meadows & Tufail, 1986; 1989; 1990; 1991), and by associated microbial communities (Coles, 1979; Frostick & McCave, 1979; Risk & Yeo, 1980; Grant, 1988; Tufail *et. al.*, 1989; Underwood & Paterson, 1993). Paterson *et. al.* (1990) suggested that the degree of biostabilisation by microbial biofilms may be related to microbial biomass. The thread-like microburrows of nematodes contain mucous for structural maintenance (Cullen, 1973), and nematode "mucous-trap" production has been related to sediment texture (Riemann & Schrage, 1978). Secretion of microbial exopolymers is stimulated by chemical or fluid stresses (Nickels *et. al.*, 1981).

Boer (1981) applied biocide to a patch of estuarine sediment and observed a dramatic reduction in local shear strength compared to controls.

A comprehensive set of experiments conducted by Dade *et.al.* (1990) demonstrated the positive correlation between the degree of erosion resistance (critical boundary shear strength) and the concentration of of exopolymer-component uronic acids (acid polysaccharides) secreted by the benthic bacterium *Alteromonas atlantica.* Uronic acid was in turn positively correlated with relative nitrogen content of the growth medium. Using quartz sand (125-177μm in diameter) a doubling of flume velocity was required to initiate particle transport with every 100nmol of exopolymer per gram dry sediment.

Tube dwellers that have been reported to stabilise sediment include *Owenia fusiformis* (Fager, 1964); ampeliscid crustacea (Mills, 1967); *Euchone incolor* (Young & Rhoads, 1971); *Polydora ciliata* (Daro & Polk, 1973); *Spiophanes wigleyi* (Featherstone & Risk, 1977); *Chaetopterus* spp. (Bailey-Brock, 1979); tubificid oligochaetes (McCall & Fischer, 1980); *Pygospio elegans* (Bick & Gosselk, 1985; Meadows & Hariri, 1991); *Corophium volutator* and *Nereis diversicolor* (Meadows & Tait, 1989) and *Fabricia sabella* (Meadows & Hariri, 1991).

The present examination of sediment shear strength is complemented in **Chapter 7** by the study of the potential effect of *Pygospio* tube aggregations on the shear stresses induced by tidal currents.

4.5 Sediment conditioning

4.5.1 The Sediment - Water Interface.

In an examination of the irrigation of sediment by tube-dwellers, Aller (1978) described sediment containing extensive burrow galleries as a "large sponge" in its interaction with the overlying water. During immersion, water in tubes is generally held at ionic concentrations close to those of the overlying water, and the consequent supply (at all tube depths) of electron acceptors (oxygen, nitrate and sulphate) aids bacterial growth (Aller, 1978).

The area of the sediment - water interface determines the rate of diffusion of solutions across it. Rates of waste removal and oxygen replenishment are crucial in determining the ability of a sediment to support a diverse and abundant biotic community.

Figure 4.11 illustrates how, for a given area coverage, many smaller tubes provide a far greater sediment-water interface magnification effect than do a few larger tubes.

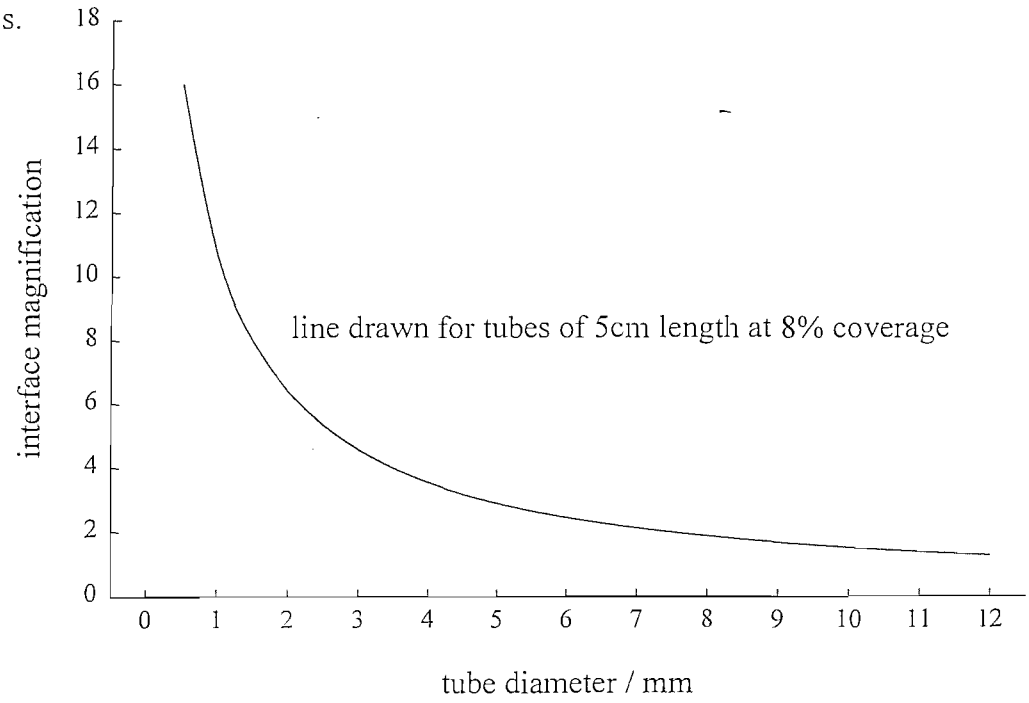


Figure 4.11: Sediment - water interface area magnification as a function of tube diameter, length and density.

Pygospio (mean tube-length 5cm) tube-beds of density 100,000m^{-2} (8% area coverage) magnify the sediment-water interface area by a factor of around x16, leading to proportionally greater overall diffusion rates.

Sedentary, tube-dwelling macroinfauna typically irrigate their tubes. Ciliary action, coupled with muscular undulations of the body, produce currents which import nutrient material and oxygen while removing waste metabolites. Marinelli (1994) demonstrated the threefold reduction of sediment ammonium concentration by burrow ventilation in the terebellid polychaete *Eupolymnia heterobranchia*; ventilation rate was increased in the presence of increased ammonium (Woodin & Marinelli, 1991), suggesting a toxin removal response by the worm. Burrow ventilation is a non-continuous process, however, which results in a high degree of microspatio-temporal variability in redox potentials in the vicinity of the burrow wall. Distributions of

ammonium can be quite sensitive to the duration of irrigation, leading to concentration fluctuations near to the tube-wall (Boudreau & Marinelli, 1994 475).

Irrigation power varies considerably among invertebrate species. Foster-Smith (1978) compared six species, including three polychaetes: *Arenicola marina* which produced $5.5x10^{-6}Js^{-1}$ pumping power; *Nereis diversicolor,* producing $3.1x10^{-6}Js^{-1}$ and *Malacoceros fuliginosa* (Spionidae) producing $1.1x10^{-8}Js^{-1}$. Evidently *Nereis* and *Arenicola* produced a greater irrigation effect than the spionid. At up to 6cm in length and 2mm in width, *M.fuliginosa* has a surface area approximately one order of magnitude greater than that of *Pygospio*; the smaller confamilial, measuring around 1cm in length and 1mm in width and possessing similar musculature and ciliation, is estimated to generate a pumping power of $9.2x10^{-10}Js^{-1}$ (by scaling).

Davey & Watson (1995) noted 100x normal solute fluxes across the sediment-water interface in a population of $5000m^{-2}$ *Nereis diversicolor* compared to control sediment. Such a density represents a coverage of nearly 40% by area and an interface magnification of around x31.5 (mean tube diameter = 1cm, depth = 20cm). Taking Forster-Smith's (1978) calculations into account, this *Nereis* population therefore produced a pumping power across the sediment-water interface of $9.4x10^{-5}Js^{-1}m^{-2}$. This is three orders of magnitude greater than that produced by a *Pygospio* population of density $100,000m^{-2}$ (pumping power = $1.5x10^{-8}Js^{-1}m^{-2}$, interface magnification x16). *Pygospio*'s irrigation effect, even at extreme tube-bed densities, is clearly trivial in comparison to the increased diffusion rates promoted by the increased surface area of its tubes. The spionid *Polydora ciliata* grows up to three times the size of *Pygospio*; sediment-water interface fluid transport rates in *P.ciliata* tube aggregations were not significantly different to those in non-tube-dense controls (Noji, 1994).

In the case of empty, or "relic" burrows and tubes, there should be no substantial effect on sediment-water fluxes because of the lack of irrigation behaviour, except where such relic tubes occurred in high density or in close proximity to inhabited tubes (Aller, 1984). However, Libelo *et.al.* (1994) discovered that turbulent tube-tip-flows could reduce water pressure in the immediate vicinity of the tube-mouth, causing a Bernoulli-type "passive pumping" ventilation effect.

An increase in oxygen penetration of sediments may be caused through interaction of surface roughness elements with impinging flow. Work by Ziebis *et.al.* (1996a; 1996b) showed that sediment topographic features generated by the burrowing shrimp *Callianassa truncata* could promote increased penetration of oxygen into surficial sediments. The rising sediment surface presents resistence to passing water, increasing local velocity and fluid pressure on the sediment surface. Oxygen penetrated to nearly 40mm upstream of a 10mm high *Callianassa* mound subjected to a flow velocity of $10cms^{-1}$; oxygen failed to penetrate deeper than 4mm in control sediment, irrespective of flow speed. The implications of this observation for spatial variation in oxygen penetration around biogenic sedimentary structures exposed to flowing water are great. *Pygospio* tube-beds, although only submerged by flowing water for a small proportion of the tidal cycle, may induce spatial variations in flow pressure and consequent changes in exchange rates of overlying and interstitial waters. **Chapter 6** addresses the possibility of spatial variations in tube-bed population fitness in response to varying conditions of anoxia. Although no direct measurements of sediment oxygen concentration were made, the depth of the RPD was monitored. The depth of the RPD is an indirect indicator of local conditions of oxygen penetration into sediment. The RPD, or "redoxcline", viewed in cut sediment vertical profiles was seen to rise nearer the surface with increasing summer temperatures, as metabolic rates increased and the sediment oxygen demand went up. The RPD lay at greater depth in non-bed sediments than in tube-bed sediments, indicating greater depth penetration of oxic conditions. A shallower RPD in tube-bed intertubular sediment may have been the result of lower penetration of oxygenated water into poorly sorted intertubular sediment; sediment oxygen demand of tube-beds is also likely to be higher, supporting as it does a denser community of bacteria (see below). Measurements of RPD depth made in 1995 at the flood-tide-facing bed-edge did not indicate any increased oxygen penetration; it may have been that the RPD rebounded towards the surface during the prolonged period of exposure experienced by beds before sampling. Measurements made on submerged beds may have shown a different result.

4.5.2 Sediment Ammonium Concentration.

Excretion and ventilation by tube-dwelling polychaetes regenerates nutrient mineral ion concentrations in surficial sediments (Weinberg & Whitlach, 1983). Among the major waste products of metabolism in annelids are urea and ammonium (Dales, 1963). Where population densities of sedentary animals are very great, combined rates of excretion of these potentially toxic metabolites might be expected to be high, leading to localised conditions of eutrophication.

Variability in ammonium concentration between replicate samples was high. The scale of sampling may have formed a significant source of this error. Local redox conditions and concentrations of mineral ions are highly microspatially and temporally variable, depending on the sub-millimetre scale distribution in the sediment of moisture, silt and clay flocs, particles of decaying organic detritus, and living organisms (Aller, 1982). The approach taken in this study was to look for larger scale trends in sediment quality, and to simply assess the differentiation of tube-bed from non-bed.

Data collected in June 1995 showed a significant difference ($p<0.001$) in pooled 0-5cm depth sediment ammonium concentrations when pooled tube-bed transect stations were compared with pooled non-bed stations. This difference was most pronounced in the uppermost 0-1cm sediment horizon ($p<0.001$). Ammonium concentration was correlated positively with both station mean *Pygospio* density and transect station position, though more strongly with the latter. This suggests that local ammonium concentration was dependent on a variety of factors other than *Pygospio* density and that these combined factors tended to vary with bed-position. There were no significant differences between ammonium concentrations at the tube-bed edge and other transect stations.

Ammonium is removed by diffusion and irrigation to the overlying water during submersion, where it is oxidised (Aller, 1978; 1980b). The results presented here suggest that ammonium concentration does not increase during exposure, however. The build-up of such a metabolite is possibly averted behaviourally, by a reduction in excretion rate during exposure. Populations of nitrifying bacteria, responsible for microbial conversion of ammonium to nitrate, may have been more active in tube-beds, responding to locally elevated oxygen concentrations in the vicinity of tubes. The

reliance of microflora on ammonium as a ready nitrogen source may also explain the absence of a build-up. A dense community of microphytobenthos would take up ammonium from the sediment, and replenish sediment oxygen. The cycling of ammonia and oxygen between worms and algae is suggested by the ammonium data which shows no build up in time during aerial exposure or with increasing worm density. Such a synergism has been suggested by Jeffrey *et.al.* (1992) between the terebellid polychaete *Lanice conchilega* and the epitubular alga *Ectocarpus*.

4.5.3 The Microbial Community.

The involvement of tubes in sediment stabilisation, pore-water chemistry change, oxygenation of deeper strata and nutrient circulation enhances bacterial and algal biomass and production (Brey, 1991).

Depth integrated chlorophyll *a* concentration was significantly higher in tube-bed stations than in non-bed stations ($p<0.05$). Much of the difference was accounted for by the uppermost 1cm sediment horizon, in which tube-bed concentrations were approximately 1.4x those in non-bed sediment. These measurements supported earlier field observations of increased diatomaceous coverage of tube-bed sediment, exemplified by a rich golden-brown colour at the sediment surface. Chlorophyll *a* concentration varied significantly with depth, generally decreasing away from the surface at every station. Actively photosynthesising organisms would be expected to concentrate themselves near the surface to maximise exposure to light. Chlorophyll *a* concentration in the uppermost 1cm was significantly positively correlated with *Pygospio* density; depth integrated chlorophyll *a* was significantly negatively correlated with *Pygospio* density, however. Correlations with transect station position showed the same sign but were non-significant. There were no significant differences between chlorophyll *a* concentrations at the tube-bed edge and other transect stations.

Noji (1994) measured a 2.5x higher chlorophyll *a* concentration (around 50μg chl*a* cm^{-2}) on *Polydora ciliata* (Spionidae) tube aggregations compared with control sediments. Führböter *et.al.* (1982) discovered cyanobacteria at greater depths among *Pygospio* tube aggregations than in control sediment. Mills (1967) noted increased

chlorophyll *a* concentrations in the presence of a high density population of tube-dwellers, in this case the amphipod *Ampelisca*.

Distributions of phaeopigments (inactive and detrital photopigments) exhibited even stronger patterns. Tube-bed and non-bed stations contained significantly different levels of phaeopigments ($p<0.001$ at all depths). Variation in phaeopigment concentration with depth was not significant in the majority of cases, reflecting the photosynthetic inactivity of these pigments. Ratios of chlorophyll *a* to phaeopigment concentrations illustrate the overall trend for increasing levels of detrital material at the expense of active photopigment with depth, and show that this effect is more pronounced in tube-bed sediments. The increased proportion of phaeopigments on tube-beds is consistent with the increased input of detrital material into tube-beds suggested by the granulometric and organic data. Algal cells living in tube-bed sediment were perhaps more strongly subjected to smothering by incoming fine particulate matter, hindering their vertical, light-seeking migration and shading them from incident light. Subsequent death and breakdown of active chlorophyll would increase phaeopigment levels at depth, producing the observed pattern. Phaeopigment concentration was positively correlated with both transect station position and *Pygospio* density, though more strongly with transect station. This perhaps reflects the detrital nature of phaeopigments, whose distribution is not determined actively in response to local *Pygospio* density, but passively, the result of both detrital input and algal mortality.

The hypothesis that tube-bed ammonium concentration is to some extent regulated by an associated algal community is supported by the present data. The bacterial community may perform a similar function: tube-beds supported a significantly more abundant community of bacteria than did non-bed sediment ($p<0.001$ at 0-1cm and 1-5cm depth horizons). Mean total bacterial numbers in the uppermost 1cm of tube-bed sediment reached $9.78 \times 10^8 g^{-1}$, over 5x more than in the top 0-1cm of adjacent non-bed sediment. These data are again a simple approximation, based on a small number of samples taken at single point in time. Variation in bacterial abundance occurred at the very small scale, and standard deviations of replicate means were very high. A complete study of sediment bacterial populations would require a sampling strategy of very much greater resolution. The tendency for tube-beds to contain more

abundant bacterial communities is clear, however. Bacteria are known to associate closely with macrofaunal tubes (Aller & Aller, 1986). The excretion of the amino-acid creatine by polychaetes also provides a quickly available energy source for the sediment microbial flora (L.E.Hawkins, pers.comm.).

A variety of bioturbating behaviours are documented which enhance bacterial growth, maximising the benefits of accelerated microbial nutrient cycling (Hylleberg, 1975; Aller & Yingst, 1978; Yingst & Rhoads, 1980; Aller & Yingst, 1985; DeWilde, 1991). Sediment particle manipulation (during feeding and tube / burrow construction) results in solid / dissolved nutrient redistribution, providing microbial food at all depths and allows the upward transfer of reduced particles leading to their oxidisation. Bioturbation also selectively concentrates nutrients into faecal pellets which serve as microbial growth substrate; and causes breakdown of such aggregates to increase available surface area of nutrient. Alongi (1985) noted that protozoa attracted to tubes would stimulate bacterial growth through "grazing" behaviour; nematodes have also been implicated as grazers (Findlay & Tenore, 1982).

4.6 Summary & Conclusion

- Physical measurements were made to assess the impact of a dense array of tube-dwelling, deposit- and suspension-feeding polychaetes on the muddy-sand flat of LCS.
- Tube-beds contained higher quantities of silt and clay, suggesting an enhanced depositional regime; mechanisms by which this might be achieved were discussed. Intertubular tube-bed sediment was consequently less well sorted than non-bed sediments. Tube-wall sediment contained less fine material than surrounding, intertubular sediment.
- Dense arrays of tubes significantly enhance sediment permeability, causing tube-beds to drain more quickly than non-bed sediment. Tube-beds sampled during aerial exposure contained less moisture than non-bed areas.
- Intertubular sediment contains significantly more organic material than non-bed sediment; this may be due to increased detrital input and the adsorption of organic particulates onto silt and clay in tube-beds.

- Tube-beds are significantly more resistant to shear stresses than non-bed areas. This effect is probably caused by increased sediment adhesion through the presence of an increased proportion of silt and clay, and through mucous binding by the associated microbial community. Decreased water content can also increase shear strength.
- The sediment-water interface is magnified by approximately 16x in the presence of a theoretical *Pygospio* tube bed of density 100,000m^{-2}; this will have a concomitant effect on solute diffusion rates. Irrigation by tube-bed density *Pygospio* populations is likely to be insignificant in increasing net rates of solute exchange across the sediment-water interface.
- The RPD was closer to the surface in tube-bed sediment. Measurements were taken during low tide, when the poorly sorted, more highly organic intertubular tube-bed sediment became anoxic.
- Ammonium concentration was significantly greater in tube-bed sediment than in non-bed sediment. Excretion by the dense tube-bed *Pygospio* population and the associated biotic community must have been responsible for this. No significant build-up of ammonium was observed during aerial exposure: concentration may have been regulated by microbial action.
- Distribution of chlorophyll a indicated a significantly more abundant community of photosynthetic organisms in tube-bed sediment; distribution of photopigments with depth suggested increased accretion of detrital plant material in tube-beds.
- Direct counts revealed a denser community of bacteria in tube-bed sediment than in non-bed areas.
- Edge-bed sediment did not appear to demonstrate any physical differences related to variation in incident tidal flow velocity.
- Measurements made in this chapter suggest that a tube bed maintains a set of environmental conditions distinct from the surrounding sediment. In many cases these conditions appear to be influenced less by their position within a high-density patch than by the local density of actively feeding, excreting, tube-building *Pygospio*. "Tube-bedness" is thus a condition determined at the small

scale. Larger, bed-scale variations in conditions are considered in the final chapter.

- *Pygospio* themselves are transient occupants of the sediment, occurring in any one area in densities that must be assumed to be temporally variable. A tube-bed uninhabited by *Pygospio* cannot be a self-sustaining sedimentological entity and any region within a tube-bed that loses its occupants, through migration or mortality, must presumably revert to a non-bed condition. The implications of this observation for the spatio-temporal dynamics of tube-beds will be discussed further in the final chapter.

Chapter 5.
The Tube Bed Community

5.1 Introduction

It has long been recognised that soft-bottom community structure is influenced by the nature of the local physico-chemical environment (Sanders, 1958; Gray, 1974). **Chapter 4** showed that a number of benthic sedimentary characteristics are affected by the presence of high-density aggregations of tube-building *Pygospio*, and the present chapter examines the impact of *Pygospio* tube-bed building on the macroinfaunal community.

Much research has concentrated on determining community structuring mechanisms. Among the mechanisms postulated have been adult-larval interactions (Woodin, 1976; Wilson, 1981) and inhibition and facilitation models of succession (Connell & Slatyer, 1977; Gallagher *et. al.*, 1983; Whitlach & Zajac, 1985). These theories involve effects produced by established, adult benthos that actively or passively encourage or discourage immigration by settling larvae. Predation (Reise, 1978; Ambrose, 1984) has been cited as one of a number of disturbances that acts as a community structuring agent. "Refuge" formation by the activity of one or more members of a community can reduce local disturbance and encourage increases in community diversity (Woodin, 1981).

Where communities are dominated by dense monospecific populations, amensalistic interactions may prevail. Woodin (1976) viewed soft-bottom community structuring from the perspective of "functional group" interactions, in which "tube-dweller", "bioturbator" and "suspension-feeder" functional groups should each be inimical to the others. Dense communities of tube-dwellers would be maintained by competitive exclusion, while abundant bioturbators would be expected to undermine tube-dwellers physically. More recent work has cast doubt upon the validity of certain aspects of this theory (Weinberg, 1984; Wilson, 1984b; Tamaki, 1985), and further attempts to identify the role of such forces in structuring benthic communities have yielded equivocal results.

Wilson (1984a) noted that "the paradigm for spatial competition of dense infaunal assemblages (>40,000 macrofaunal animals per m^2) is too simplistic to be of predictive value". As a component of this study of dense *Pygospio* aggregations, it has been possible to revisit the question of how a dense, dominant monospecific population impacts the associated macrofaunal community, and to attempt to shed more light on the mechanisms of community structuring at work.

5.2 Methods

5.2.1 Sampling Strategy.

Macrofaunal samples were taken as described in **Chapter 4**. In June 1994 three random, replicate meiofaunal cores were taken at each transect station each with an area of $2.5 \times 10^{-4} m^2$. These were horizontally sectioned (0-1/1-5/5-10cm horizons) in the field, then fixed and stained on return to St. Valery (as above).

In the following analyses each core sample was treated and analysed individually.

5.2.2 Laboratory Methods.

Macrofauna samples were processed in the same way as *Pygospio* samples (**Chapter 4**). Meiofauna samples were processed by elutriation: the sample was stomached in a plastic bag with excess water, and the supernatant decanted off through a sieve; this was repeated three times to resuspend any meiofauna remaining in the sample. Organisms retained on a 43µm mesh were enumerated and sorted.

5.2.3 Univariate Analysis.

For each core sample, the Shannon-Weiner diversity index H' was calculated (excluding *Pygospio*) as

$$H' = -\sum_{i=1}^{S} p_i \log_2 p_i \qquad (7)$$

where p_i represents the proportion of the total number of individuals accounted for by species i.

In a consideration of diversity, it is important to determine the relative contributions of species richness and equitability. Total number of individuals N, and species richness (both excluding *Pygospio*) were found for each core sample: richness was taken as Margalef's index d, calculated as

$$d = (s - 1) / \log_e N \qquad (8)$$

where s = number of species

N = number of individuals.

Equitability was expressed as Pielou's evenness index j, calculated as

$$j = H'_{(observed)}/H'_{max} \qquad (9)$$

where H'_{max} represents the theoretical diversity which would be achieved were all species equally abundant (mathematically, $H'_{max} = \log_2 s$).

Absolute diversity indices, calculated directly from relative species abundance data, are sample size dependent (Lambshead & Platt, 1988), and comparisons of indices calculated from samples of differing size may thus be compromised. Pielou (1975) noted that it was impossible to estimate the evenness of a highly species rich community from samples: however large, the sample may be unrepresentative of the actual community.

The V statistic was introduced by Caswell (1976) as a relative, rather than absolute, measure of equitability. As such, V may be considered to be less sample-size dependent than more traditional diversity indices. Calculation of V involves the construction of an ecologically "neutral" model community in which no biological interactions occur between the species: V then represents the deviation of a sample's observed diversity with that predicted from the neutral model. V is calibrated against neutrality (a value of 0): positive values demonstrate that the community is over-equitable while negative values indicate dominance; V may therefore be viewed as an equitability measure.

V was used in the present study as a further index of the LCS community's response to tube-bed conditions. Negative deviations from the neutral model potentially signify conditions of increased competition or disturbance, in which the community has become dominated by one or a few species.

V is found from

$$V = (H' - E(H')) / \text{standard deviation}(H') \qquad (10)$$

where H' = Shannon-Weiner diversity index;

$E(H')$ = neutral diversity as calculated by the program CASWELL, (Goldman & Lambshead, 1989) implemented in the PRIMER software package (see Clarke & Warwick, 1994).

5.2.4 Multivariate Analysis.

To qualitatively assess the impact of *Pygospio* on community structure, Bray-Curtis similarity was calculated for contemporaneous core-samples: the Bray-Curtis coefficient has been advocated as one of the most suitable algorithms for use in benthic infaunal abundance studies (Burd *et. al.*, 1989; Clarke & Warwick, 1994). Of other measures, NESS (Normalised Expected Species Shared; Grassle & Smith, 1976) has been developed specifically for use in such studies; the choice of Bray-Curtis over NESS was ultimately based on the availability of computing software.

Samples were ranked and labelled by *Pygospio* density before removal of the species from the data set. *Carcinus maenas* was excluded on the basis of its mobility and *Bathyporeia pilosa* and polydorids removed on account of their extreme rarity. All data were root(root x) transformed before analysis in order to reduce the influence of more abundant species on the results.

Classification (e.g. Everitt, 1980) was performed on the resulting similarity matrices. The method used was hierarchical agglomerative clustering, in which samples are nested on the basis of their similarity into successively larger groups. This showed how samples clustered with respect to *Pygospio* density. Ordination was also carried out using the multi-dimensional scaling (MDS) technique (Kruskal & Wish, 1978).

This indirect gradient method was used to examine the change in species abundance sets with increasing *Pygospio* density. These algorithms are all implemented in PRIMER. Results of cluster analysis were superimposed on the MDS ordinations for presentation. Ordination allowed the data to be displayed incorporating symbols to represent both *Pygospio* density and information derived from the univariate study.

Species responsible for sample similarity groupings (and thus those covarying most strongly with *Pygospio*) were revealed by similarity percentage analysis, as implemented under SIMPER, part of the PRIMER package.

No statistical test of significance was possible on the resulting ordinations: samples were ranked and grouped by *Pygospio* density and ANOSIM, the multivariate corrolate of ANOVA, cannot be used to define and validate sample groupings established *a posteriori*.

5.3 Results

5.3.1 Seasonal Trends.

Figures 5.1 and **5.2** illustrate abundances of the more dominant species as they fluctuated during the study period. Note that each datum point represents mean species abundance at a point in time; samples from both tube-bed and non-bed are pooled.

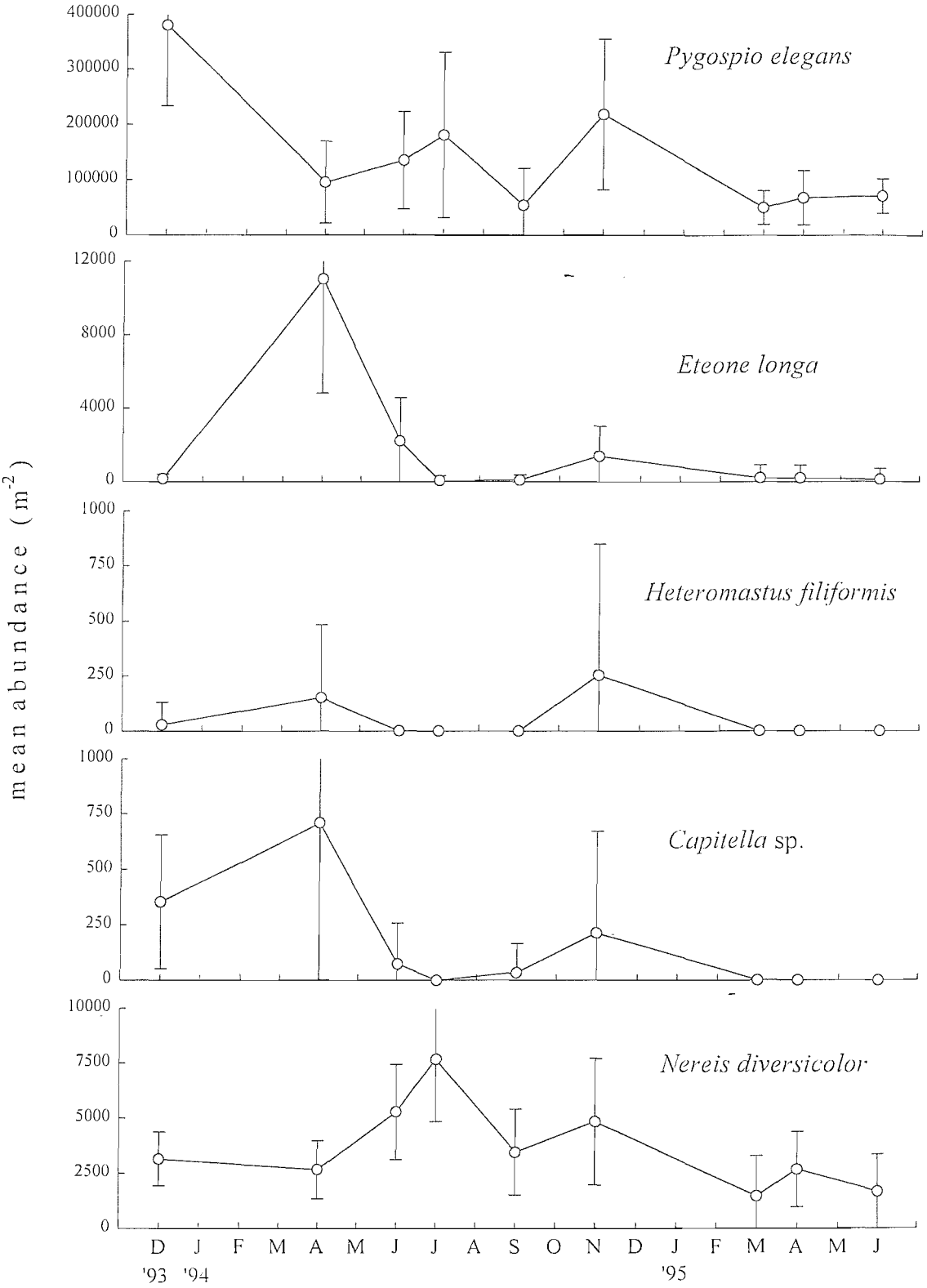


Figure 5.1: Population dynamics of the dominant species during the study period. Mean abundance +/- 1 standard deviation.

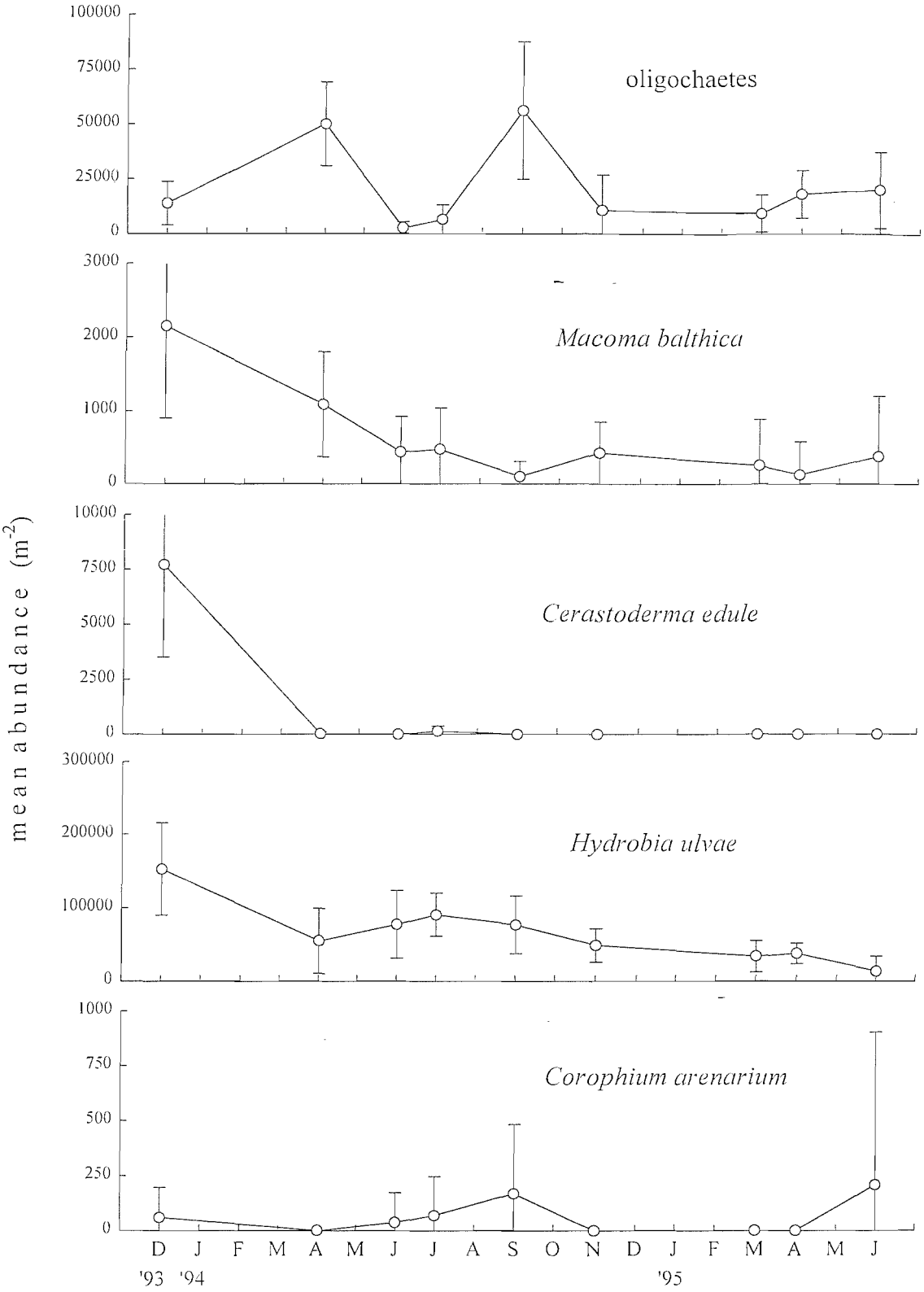


Figure 5.2: Population dynamics of the dominant species during the study period. Mean abundance +/- 1 standard deviation.

Pygospio elegans was present in extremely high densities throughout the period of field sampling, although a general decline in the species was apparent towards the end of the study, in spring / summer 1995. Later observations, made after the main sampling period in November 1995, gave no indication of any resurgence in *Pygospio* colonisation, densities remaining below 75,000m^{-2}. **Chapter 2** demonstrated that recruitment in the spionid is widely spread in time, with pulses of varying strength from spring to autumn: this was exemplified in an increased abundance in summer 1994, and again in autumn 1994 - the latter presumably the evidence of a late summer / autumn recruitment. The relatively low mean abundance recorded from September 1994 was probably the result of having sampled a "pseudo-bed" of generally low tube-worm density. The highest densities (~600,000m^{-2}) were found at the beginning of the sampling campaign in winter 1993, indicating very successful recruitment in the previous months.

Eteone longa, an errant phyllodocid, and the capitellids *Heteromastus filiformis* and *Capitella* sp. all showed similar patterns of density peaks in spring and autumn. In each case densities remained relatively low, except for *Eteone* during spring 1994, and no clear recruitment patterns could be discerned.

Nereis diversicolor, a predator and detritivore, was a prominent component of the infauna throughout the study. A recruitment was clearly seen in summer 1994, but this was not obviously repeated in 1995.

Oligochaetes (*fam.* Tubificidae) persisted at relatively low levels during the winters of 1993 and 1994, showing increased abundances in spring and autumn (50,000-60,000m^{-2}).

The small tellinid bivalve *Macoma balthica* was present at all sampling dates, but no clear seasonal patterns could be seen, other than an initial drop-off from the peak densities found in winter 1993. A more dramatic decline at this time was shown by *Cerastoderma edule*, represented in December 1993 almost entirely by juveniles approximately 2mm in length; it crashed altogether thereafter, only to return in low densities (200m^{-2}) in summer 1994.

The gastropod *Hydrobia ulvae* was abundant all year around, with a weak recruitment pulse in summer 1994. The amphipod *Corophium arenarium* was only present in any number during each summer, reaching densities of around $200m^{-2}$.

Seasonal patterns of diversity, richness, equitability and deviation from neutral diversity, are illustrated in **Figure 5.3**. The influences of species richness and equitability on diversity are graphed in **Figure 5.4**.

From **Figure 5.3**, a cycle of increased species richness was demonstrated in the winter months, dropping through the rest of the year. However, Shannon-Weiner diversity, and the equitability measures J and V all showed a seasonal pattern of peaking in spring and autumn. Shannon-Weiner diversity could be seen from **Figure 5.4** to be more consistently influenced by equitability than richness. The last three time-sets inverted this relationship - possibly as a result of the change in core size in 1995; however, the smaller core did not seem to exclude any species, and there was no concomitant drop in species richness at this time.

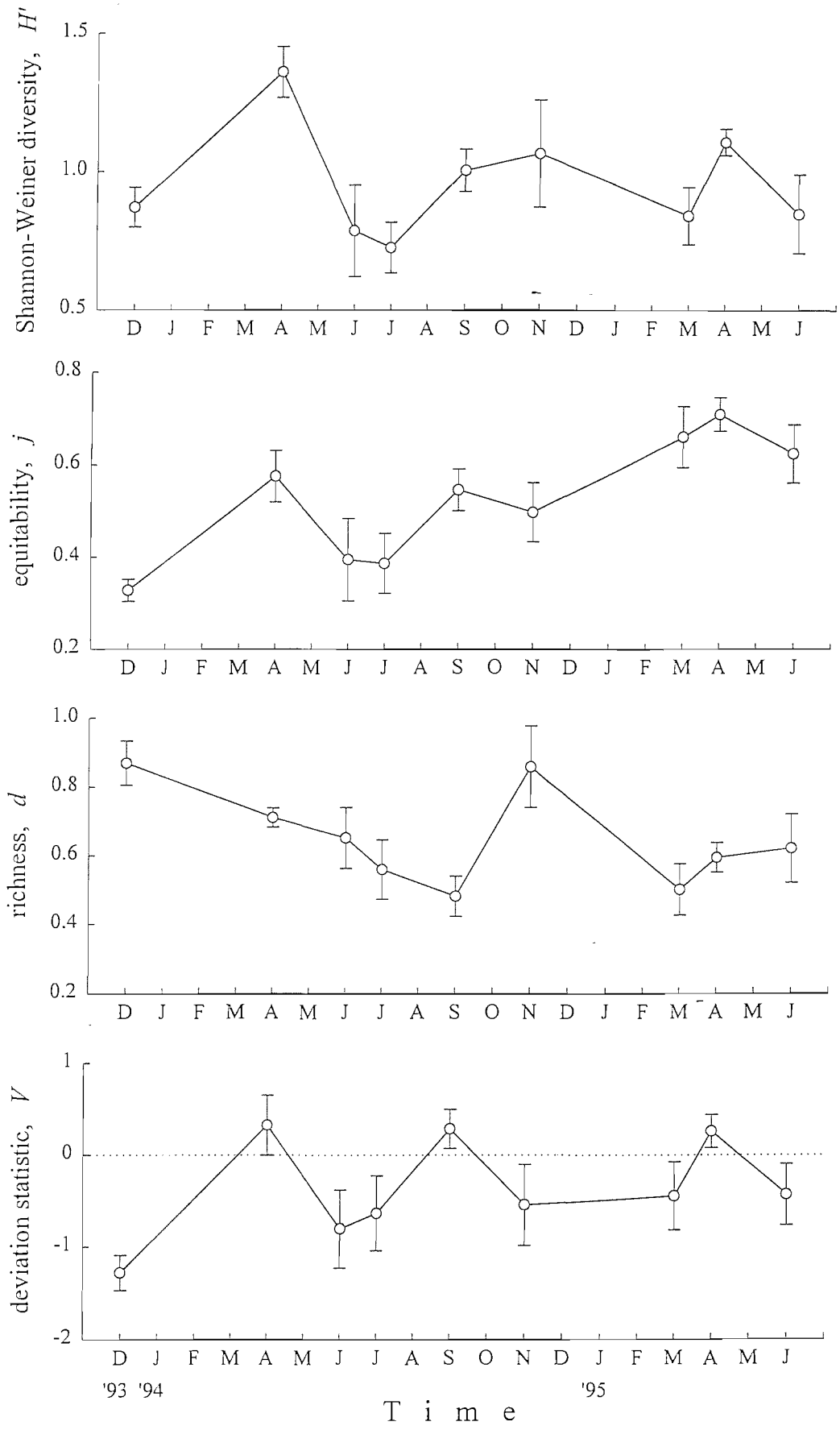


Figure 5.3: Seasonal patterns of diversity, equitability, species richness and deviation from neutral diversity.

data represent means; error bars represent 95% confidence limits

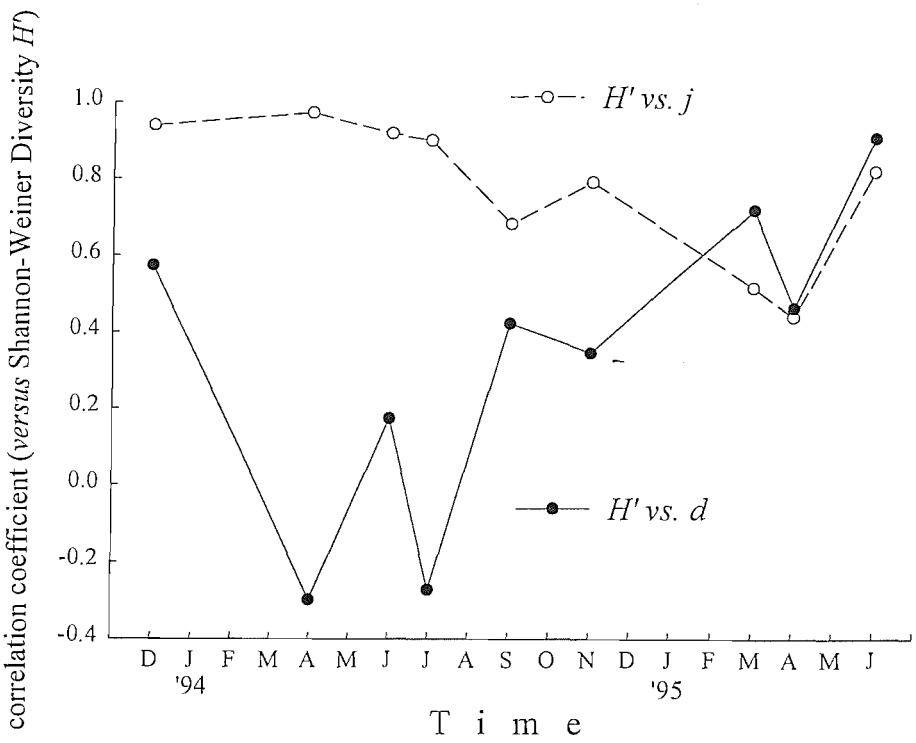


Figure 5.4: Relative influences of species richness and equitability on Shannon-Weiner diversity.

5.3.2 Impact of High *Pygospio* Densities On The Community.

Regression analysis was employed to test for any possible influence of the seasonal abundance of *Pygospio* on the seasonal patterns of: total number of individuals (excluding *Pygospio*), diversity, richness, equitability, and deviation from neutral diversity, as shown in **Table 5.1**. All variables were found to be normally distributed, and parametric methods were employed. Levels of statistical significance are represented by the symbols: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; n.s., not significant.

Table 5.1: Relationships between seasonal patterns of *N*, *H'*, *d*, *j* and *V*, and *Pygospio* population fluctuations.

Pygospio* density in time *vs.	r^2
number of individuals, *N*	0.37, n.s.
Shannon-Weiner diversity, *H'*	0.03, n.s.
species richness, *d*	0.65**
equitability, *j*	0.61*
deviation from neutral model, *V*	0.54*

An analysis of the relationship between *Pygospio* density and community diversity was performed on all samples. **Figure 5.5** shows pooled *H'* and pooled *V* data, each plotted against *Pygospio* density-classes, incrementing in steps of 50,000 individuals m^{-2}. The equitability index *j* was not examined further as its behaviour was very similar to that of *V*. *V* was thus used in preference because of its lesser sensitivity to sample size. **Figure 5.6** illustrates *N* and *d* data manipulated in the same way.

H' and *V* demonstrated significant interactions with *Pygospio* density: graphically both may be seen to peak at 150,000-200,000 *Pygospio* m^{-2} ,both indices also showing a tendency fall away to either side of this density-class. One-tailed *t*-tests suggested that 150,000-200,000 *Pygospio* m^{-2} represented a threshold density at which the tube-worm ceased to "facilitate" the associated community and began to "inhibit" it: comparison of the mean *H'* value of this "threshold" density and that of pooled densities greater than 250,000 *Pygospio* m^{-2} showed the significantly deleterious effect of increasing *Pygospio* density on Shannon-Wiener diversity ($p=0.007$). Similar examination of *V* indicated significantly increased negativity, *i.e.*, increased dominance suggesting increased levels of disturbance or competition ($p<0.001$). A study of lower tube-worm densities found a significant increase in mean *H'* as *Pygospio* abundance increased beyond 50,000m^{-2} ($p=0.037$). *V* failed to show any significant evidence for such facilitation, however ($p=0.18$).

Mean number of individuals and species richness were both found to be significantly higher at the threshold density than at <50,000 tube-worms m^{-2}-($p=0.008$ and $p=0.047$ respectively). However, no inhibition of the community was discovered beyond the threshold density, both *N* and *d* continuing to rise (mean *N* and *d* for densities >250,000m^{-2} significantly higher than those at threshold density: $p=0.04$ and $p=0.001$ respectively).

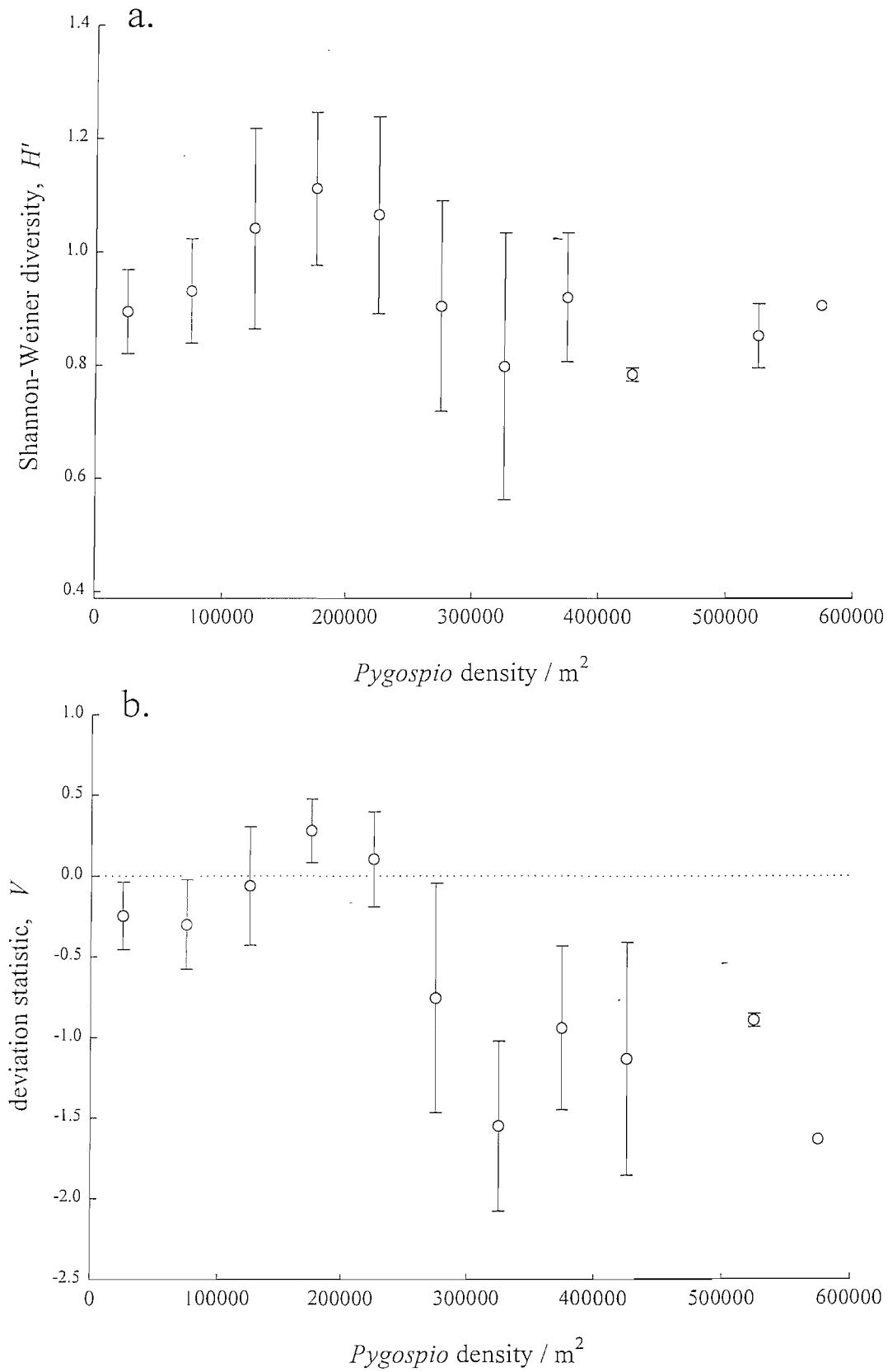


Figure 5.5: a. Shannon-Weiner diversity *versus Pygospio* density-class; **b.** deviation from neutral model of diversity (*V*), *versus Pygospio* density-class.

data represent means; error bars are 95% confidence limits

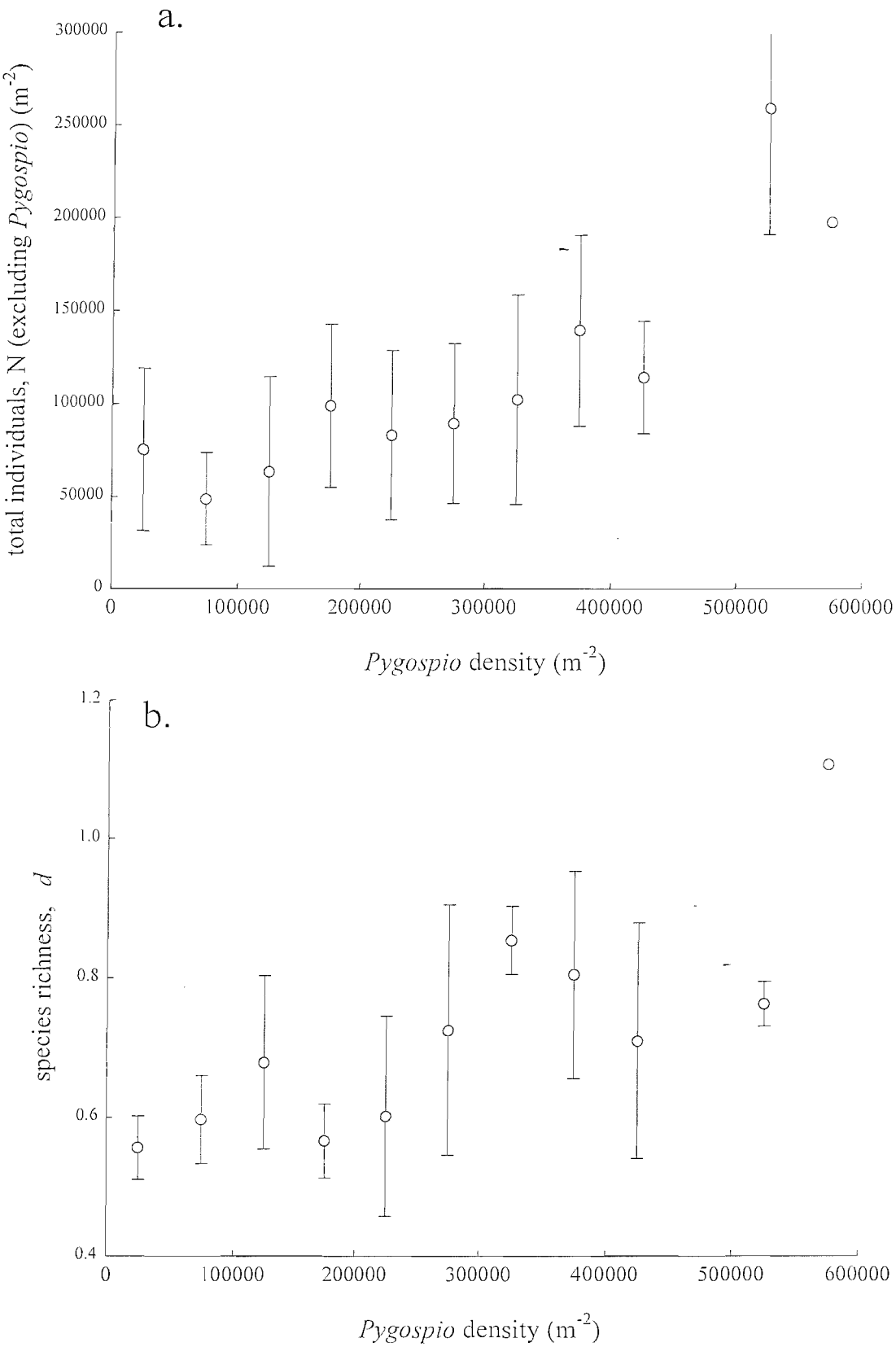


Figure 5.6: a. Total number of individuals (excluding *Pygospio*) *versus Pygospio* density-class; **b.** species richness, *d*, *versus Pygospio* density-class.
data represent means; error bars represent a. standard deviation; b. 95% confidence limits

The meiofaunal study from June 1994 demonstrated that the interstitial fauna of the Somme was entirely dominated by nematodes. No effort was made in this study to identify the nematode taxa involved. Nematode abundance data is plotted in **Figure 5.7** against *Pygospio* density.

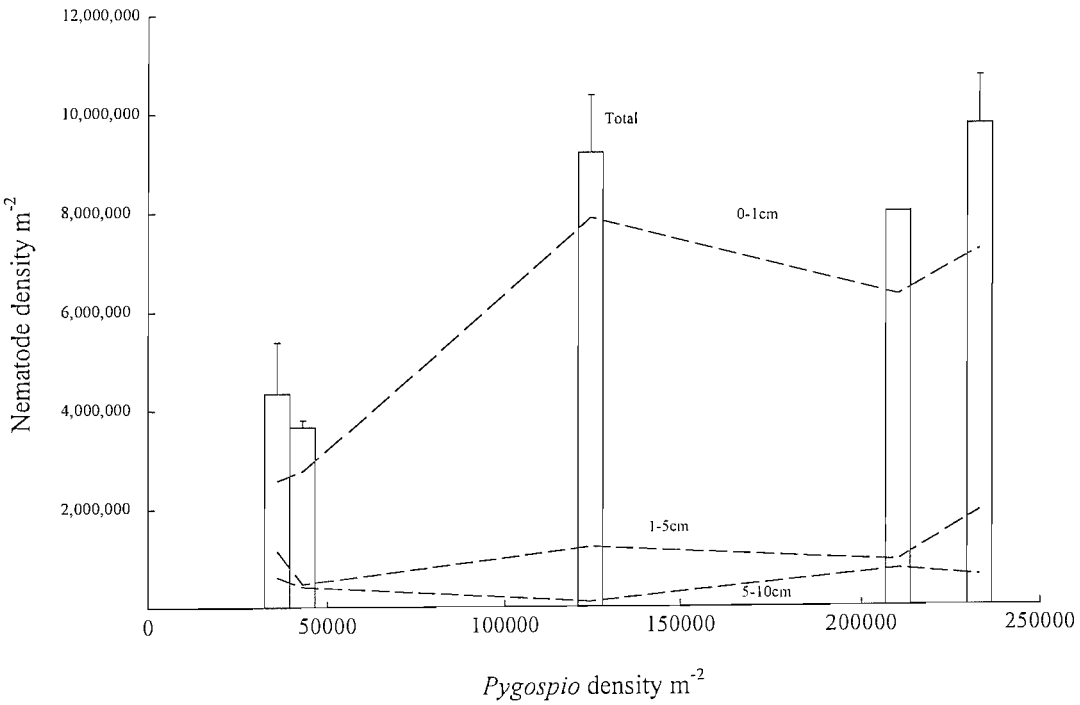


Figure 5.7: Mean nematode density ± 1 standard deviation, as a function of *Pygospio* density.

One-way ANOVA indicated a significant interaction between *Pygospio* and nematode densities ($p = 0.002$).

5.3.3 Qualitative Study: Univariate Method.

A univariate study of *Pygospio* density *versus* species density patterns among contemporaneous samples was made. In this instance, parametric analysis could not be justified because of the strongly non-normal, right-skewed distribution of the abundance data; Spearman Rank correlations, relying only on relative abundances, were therefore employed. **Table 5.2** displays correlations of densities of *Pygospio versus* other species that were found to be significant to at least the 1% level.

Table 5.2: Spearman Rank Correlations of *Pygospio* density *versus* species density.

Pygospio elegans ***versus***	**coefficient**	**date**
Eteone longa	+0.79***	April 1994
Nereis diversicolor	+0.72**	June 1994
Nereis diversicolor	+0.72**	November 1994
oligochaetes	+0.90**	June 1994
Macoma baltica	-0.67**	April 1994
Cerastoderma edule (juv.)	+0.71**	December 1993
Hydrobia ulvae	+0.72**	December 1993
Hydrobia ulvae	+0.66**	April 1994

5.3.4 Qualitative Study: Multivariate Method.

Figures 5.8 to **5.16** display MDS ordinations of samples from each of the nine time-sets gathered during the course of the study. Such ordinations present core samples as symbols, the relative distances between which represent the similarities of their respective communities. Note that, in view of the increased replication of sampling in 1995, in **Figures 5.14** through **5.16** mean values per transect station are presented. The inclusion of every replicate core give a less clear picture.

The following key explains the symbology used: for each time-set, graph **a.** overlays *Pygospio* density and sample clustering information; graph **b.** overlays the deviation statistic *V* in an attempt to indicate the relative level of disturbance and / or competition at each station.

---

graph a.

symbol diameter proportional to core sample *Pygospio* density.

line drawn, where possible, to mark division of core samples at *Pygospio* density of <50,000m^{-2}>.

to demarcate clusters of samples of similarity level of 85% (unless line is dotted: 90%) and labelled "*i, ii, iii*" *etc.*

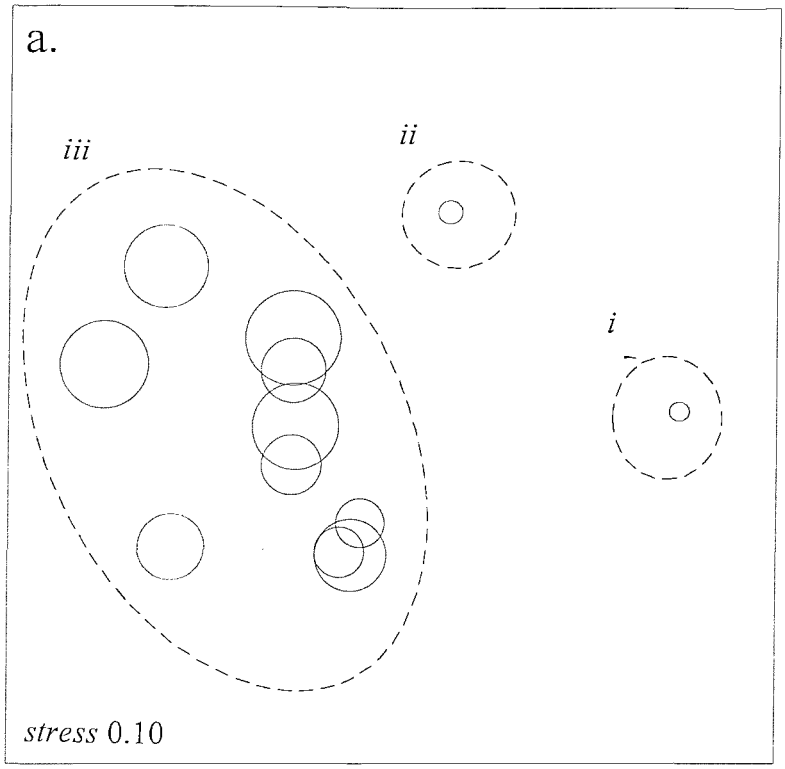
stress: a figure expressing the efficacy of the two dimensional MDS ordination in representing the "high dimensional" nature of a species-abundance data matrix. Stress values of <0.15 indicate a satisfactory level of accuracy.

graph b.

symbol proportional to the magnitude of the sample's deviation from "neutral diversity" (*V*). Thick-edged circles represent positive values; thin-edged circles, negative values.

Key to **Figures 5.8** through **5.16**.

It is again noted that ordination compresses multidimensional vectors of similarity into two dimensions; superimposed clustering information derived from classification analysis should not be viewed as constraining to the interpretation of the ordination.



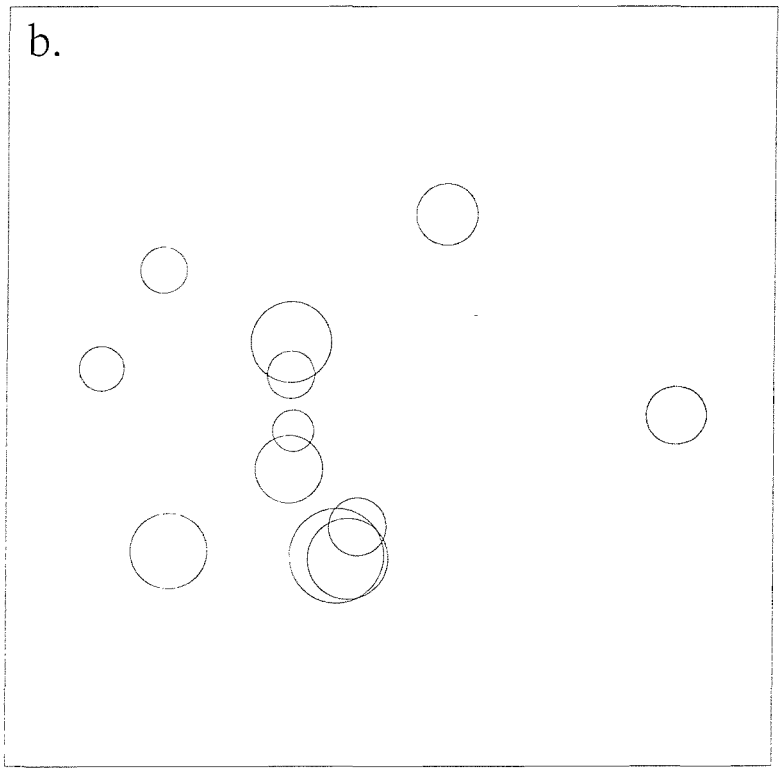
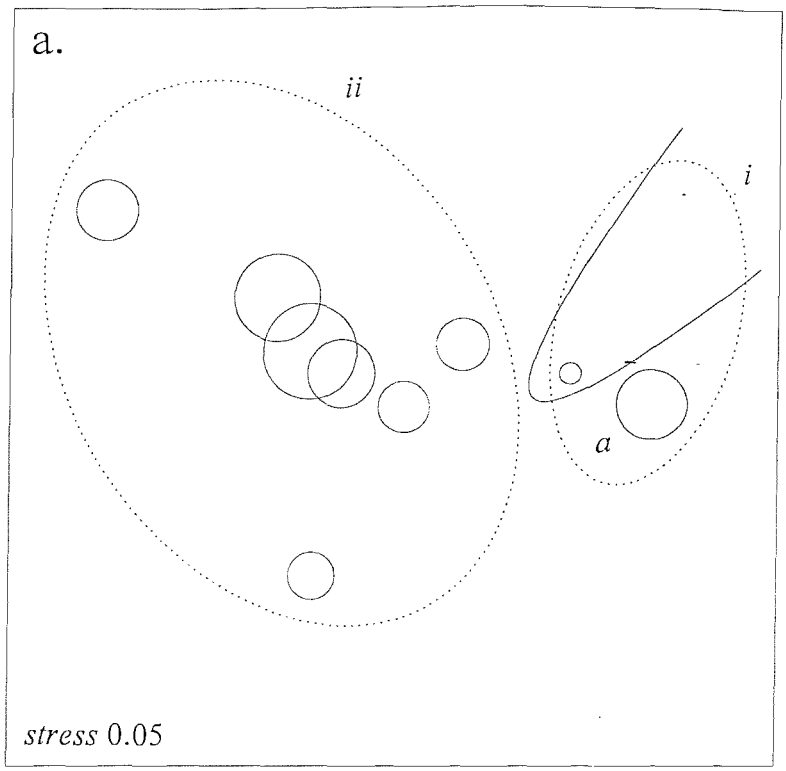


Figure 5.8: MDS Ordination of December 1993 Samples.



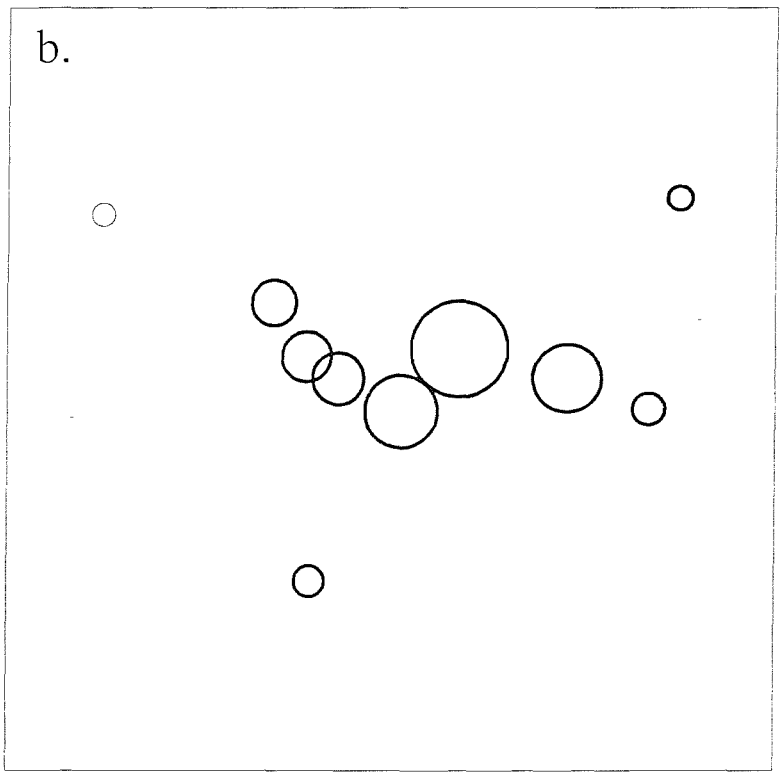
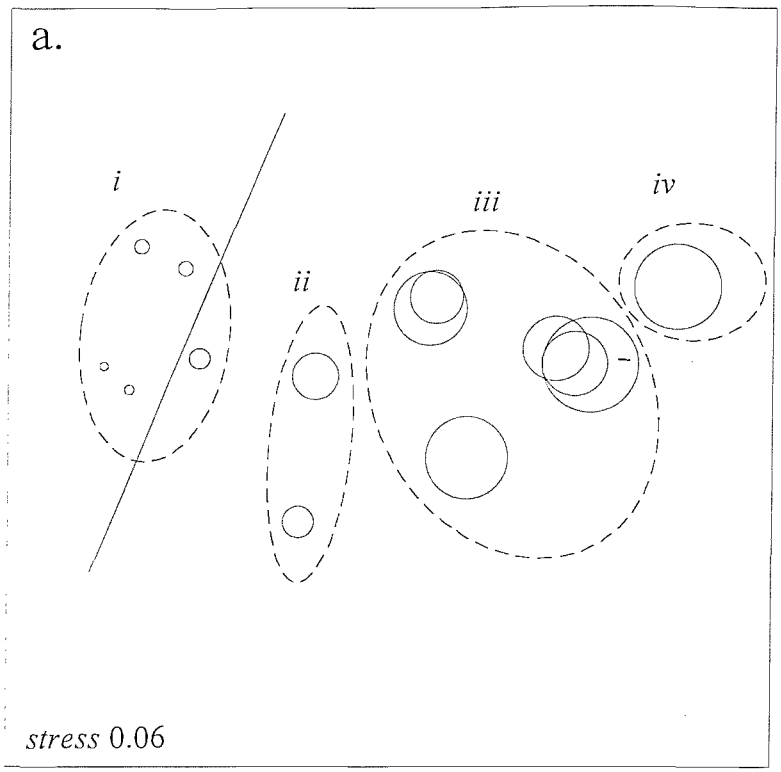


Figure 5.9: MDS Ordination of April 1994 Samples



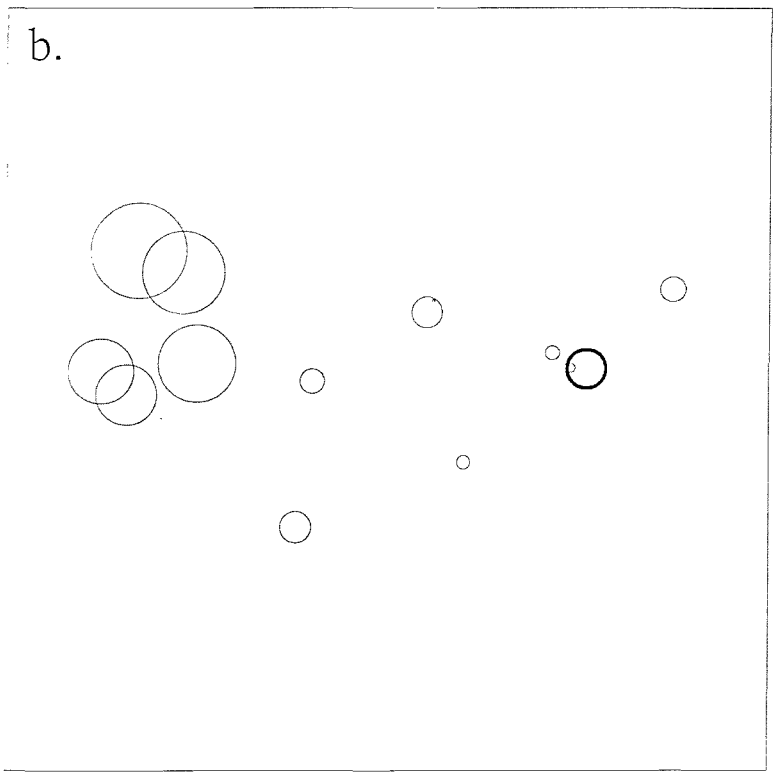
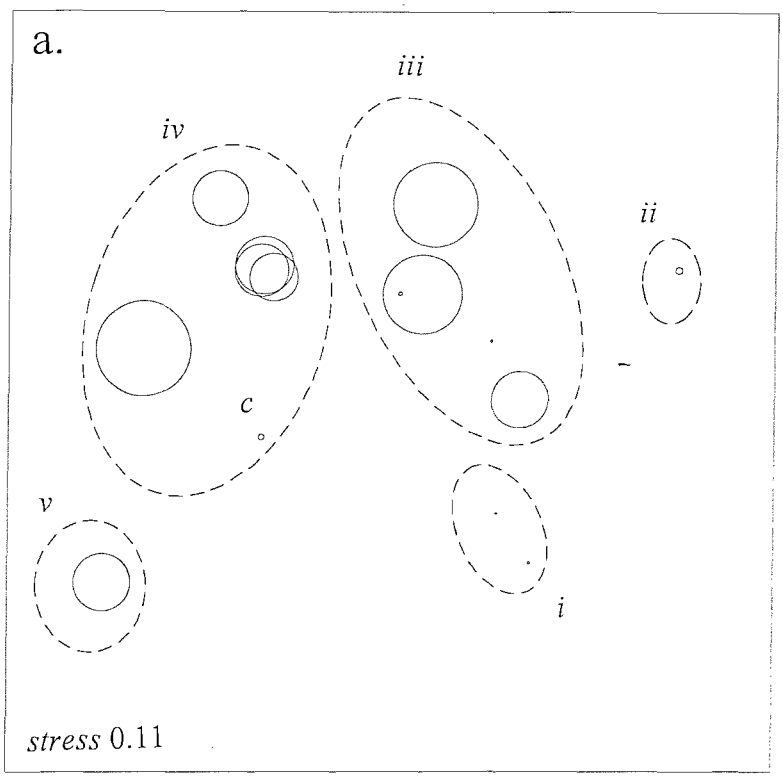


Figure 5.10: MDS Ordination of June 1994 Samples



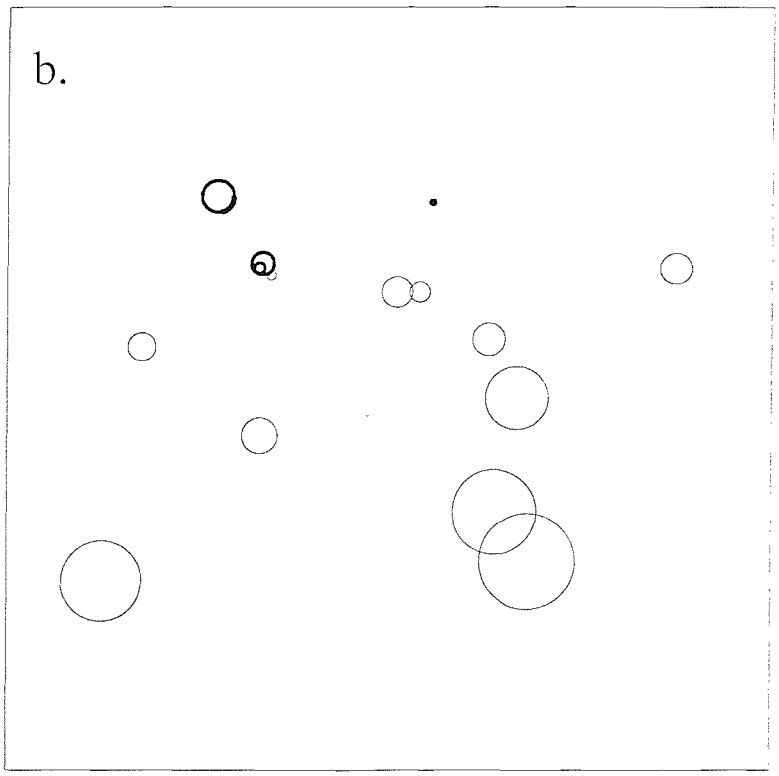
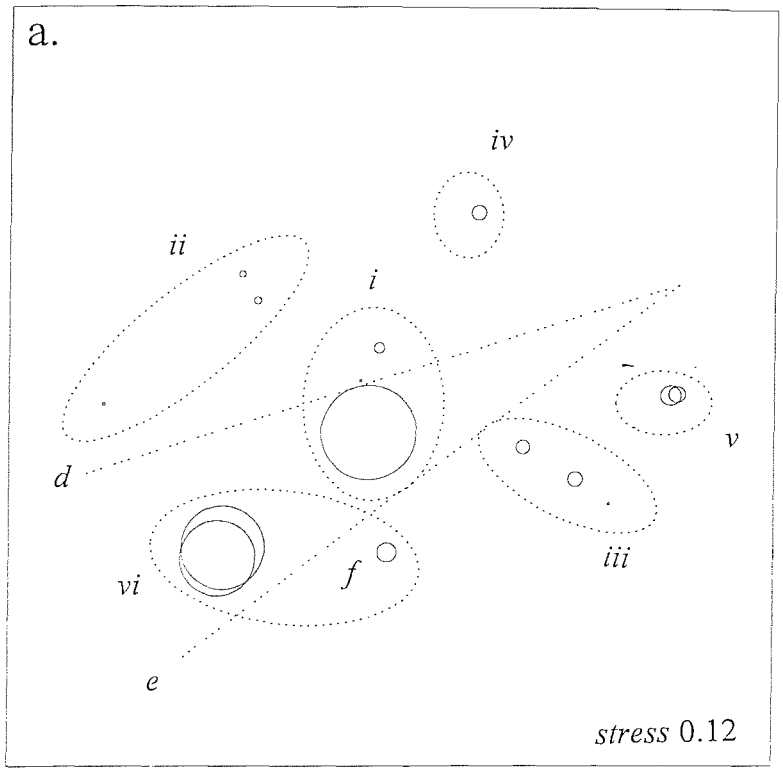


Figure 5.11: MDS Ordination of July 1994 Samples



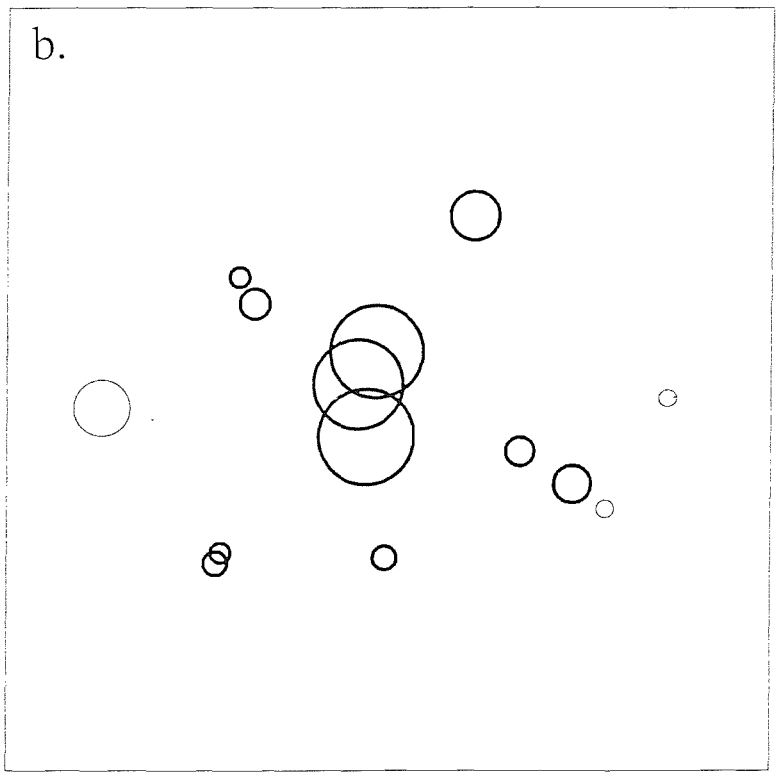
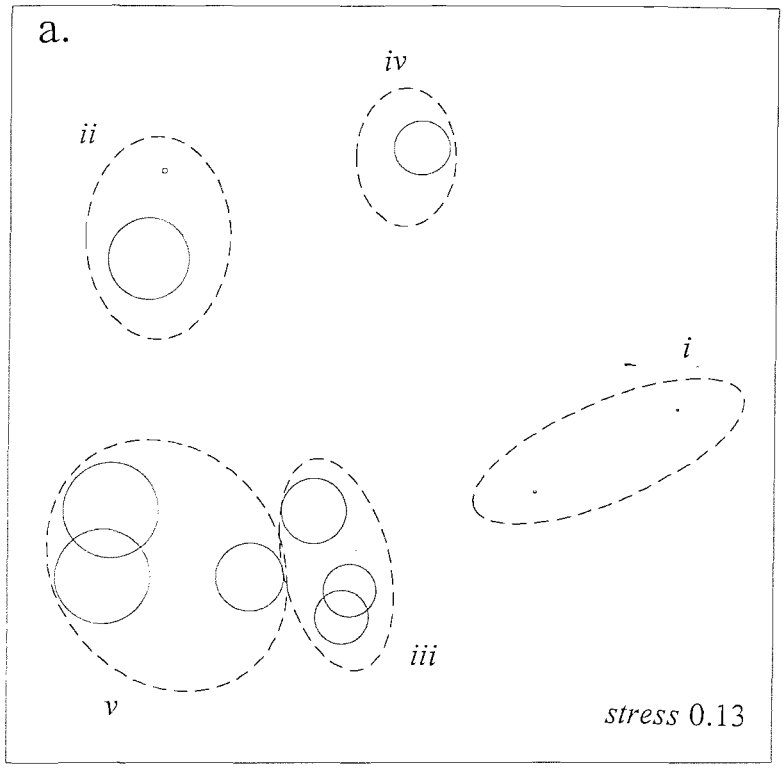


Figure 5.12: MDS Ordination of September 1994 Samples.



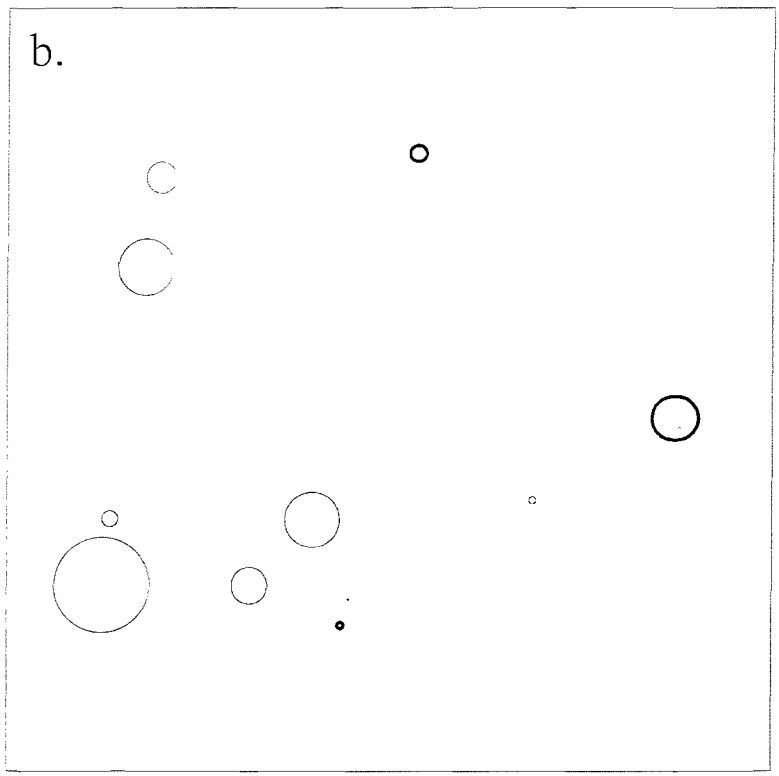
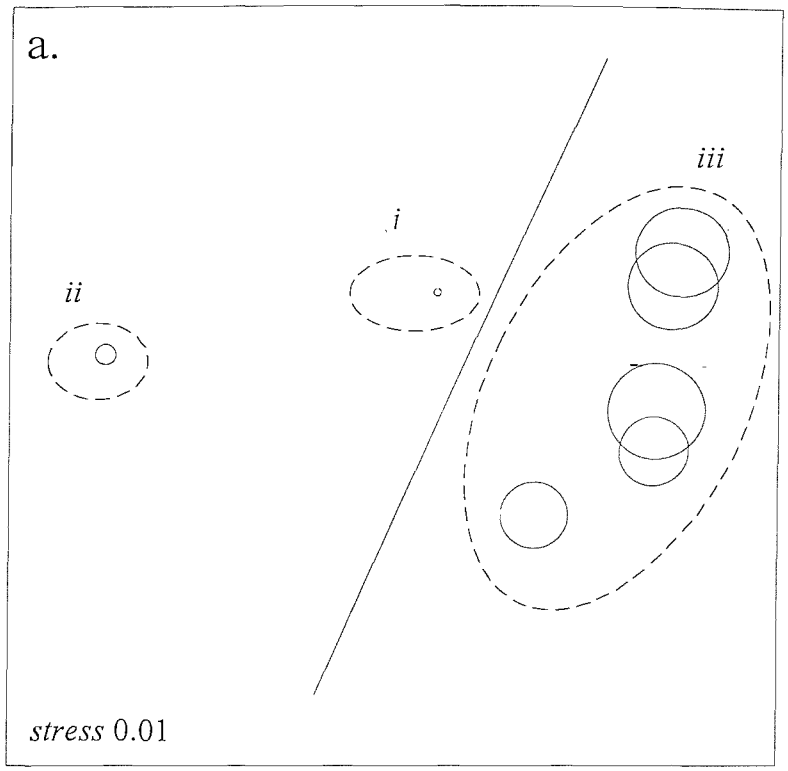


Figure 5.13: MDS Ordination of November 1994 Samples



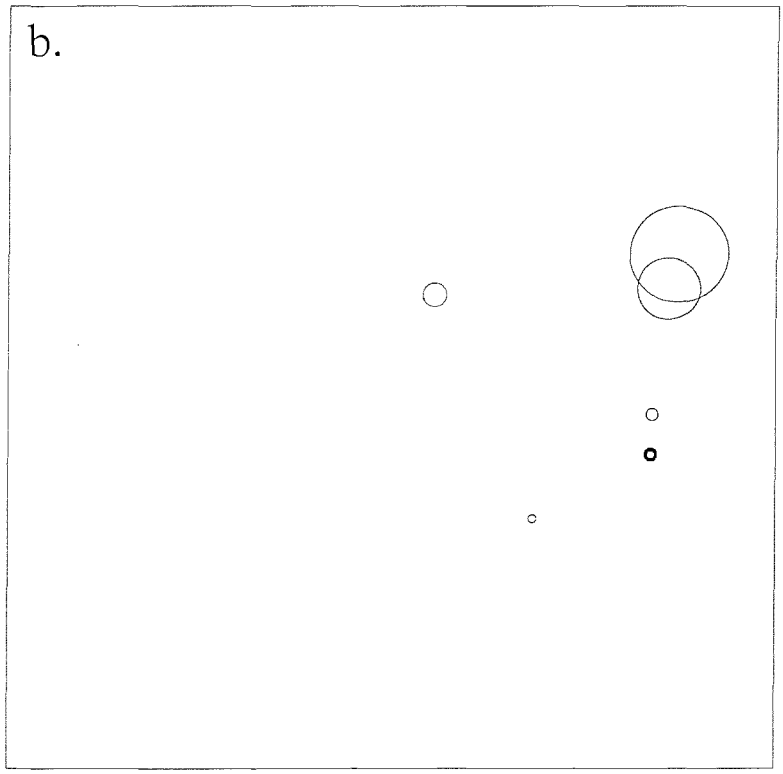
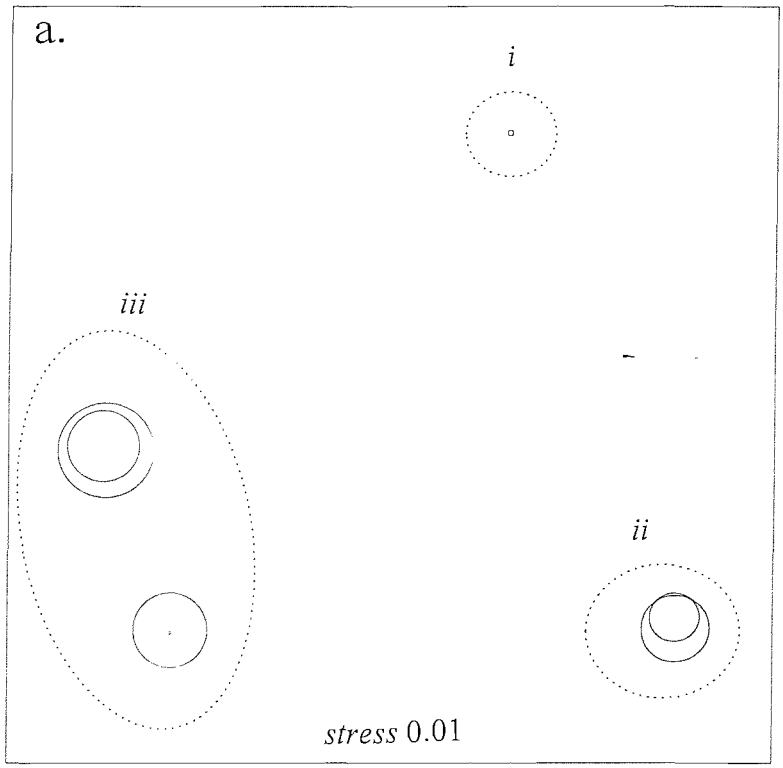


Figure 5.14: MDS Ordination of March 1995 Samples



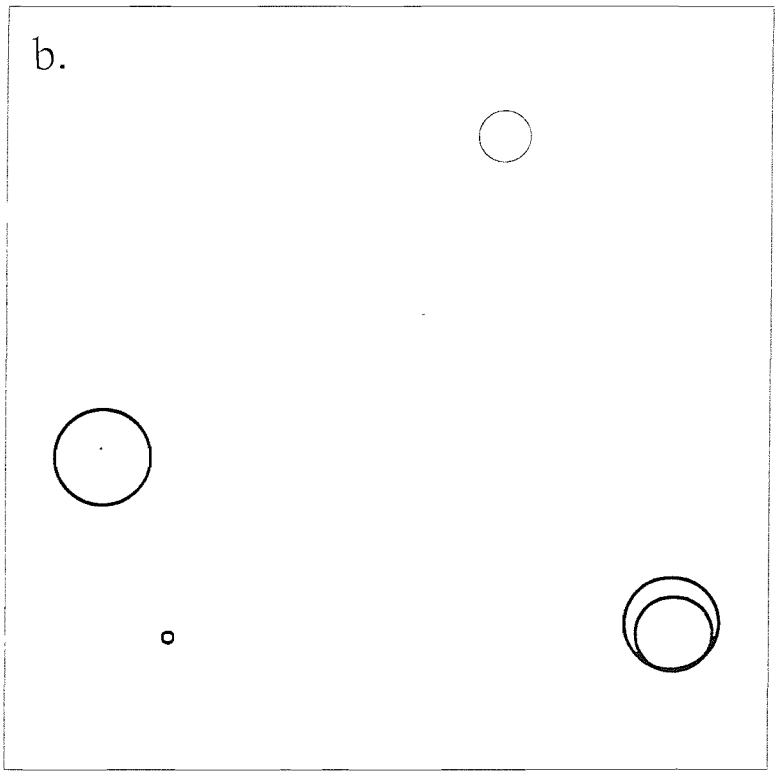
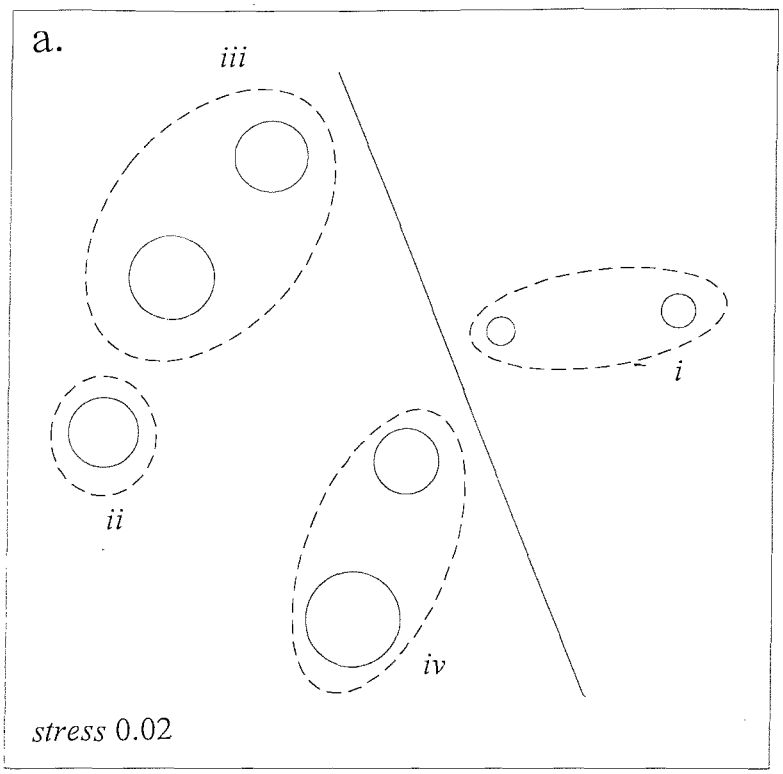


Figure 5.15: MDS Ordination of April 1995 Samples.



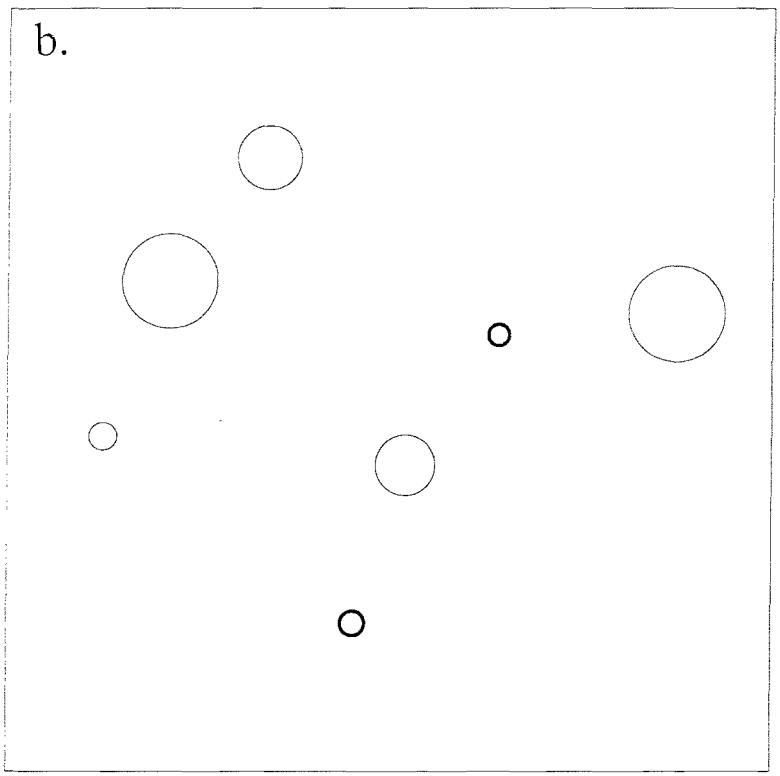


Figure 5.16: MDS Ordination of June 1995 Samples

December 1993.

- Sample clusters were defined at 85% Bray-Curtis similarity by classification analysis. Clusters *i* and *ii* contained one sample each and *Pygospio* densities exceeded 200,000m^{-2}, while in cluster *iii* all *Pygospio* densities exceeded 300,000m^{-2} (**Figure 5.8a**). Good agreement was noted between the ordination, which showed a gradient of *Pygospio* densities, and this classification.
- Similarity percentage analysis identified those species most responsible for the sample clustering in cluster *iii*. *Hydrobia* accounted for 35% of the similarity, *Cerastoderma* for 17%, oligochaetes for 16% and *Nereis* for 13%.
- Clusters *i* and *ii* were separated from cluster *iii* by *Macoma* and *Hydrobia*, each accounting for 17% of the dissimilarity between groups.
- **Figure 5.8b** shows that all samples deviated negatively from neutral diversity. No gradient in this equitability measure was clear from the ordination, however.

April 1994.

- The sample of second-lowest *Pygospio* density was removed from this ordination as its very high dissimilarity caused the MDS calculation to provide a "degenerate solution" in which all other, relatively similar stations collapsed to a single point.
- Two sample clusters were defined at 90% similarity. Sample cluster *i* contained the three replicate samples from a non-bed transect-station: two samples of <50,000 *Pygospio* m^{-2} and a third (marked *a*) which retained non-bed community characteristics irrespective of the high abundance of the spionid. Sample *a* therefore marked an imperfection in the agreement between the ordination and classification as based on *Pygospio* density (**Figure 5.9a**).
- Taxa responsible for discrimination between clusters i and ii were *Hydrobia*, *Eteone* and oligochaetes. These accounted for 45%, 17% and 13% respectively of the dissimilarity between these clusters. These three species also tended to be the best indicators of both cluster *i* (responsible for 24%, 18% and 32% respectively of the similarity) and cluster *ii* (31%, 21% and 25% similarity respectively).

- From **Figure 5.9b** it may be seen that a single sample deviated from neutral diversity.

June 1994.

- Samples separated into four clusters at the 85% level. Cluster *i* again contained the five lowest *Pygospio* density stations while clusters *iii* and *iv* contained tube-worm densities of >150,000m^{-2}. Very good agreement was found between the ordination (showing a gradient of *Pygospio* densities) and this classification analysis (**Figure 5.10a**).
- *Hydrobia* and *Nereis* were both responsible for clustering of clusters *i* (47% and 18% similarity respectively) and *ii* (47% and 29% similarity respectively). *Eteone* accounted for a further 19% of cluster *i*'s similarity.
- Species discriminating between cluster *i* and clusters *iii* + *iv* (taken together) most appreciably were *Eteone, Hydrobia* and *Macoma* (27%, 19% and 18% dissimilarity respectively). Separation of clusters *iii* and *iv* was primarily due to *Corophium* (40% dissimilarity).
- **Figure 5.10b** also illustrates a gradient of increasing positive deviations from a neutral model (indicating increasing evenness), broadly corresponding to the gradient of decreasing *Pygospio* density.

July 1994.

- Five sample clusters were classified at 85% similarity. Six core samples contained fewer than 50,000 *Pygospio* m^{-2}, but these did not tend to be well clustered. This data set demonstrated the weakest agreement between the ordination and classification analyses (**Figure 5.11a**).
- Cluster *i* contained the first and third least dense *Pygospio* populations; the second and fourth such samples were found in cluster *iii*, related to samples of higher *Pygospio* density by low levels of *Hydrobia* and *Nereis* (45% and 25% similarity) and high abundances of oligochaetes (17% similarity). Another low spionid density sample (marked *c*), in cluster *iv*, was associated with higher *Pygospio* density populations on the basis of a dense oligochaete population (accounting for 12% of the similarity) and a lack of *Macoma*, a species otherwise commonplace only at low *Pygospio* densities. The sample of the

sixth least *Pygospio* density represented cluster *ii* and was separated from cluster *i* by altogether lacking oligochaetes - the only sample so to do. Cluster *v* was characterised by the inclusion of *Eteone*.

- In **Figure 5.11b**, positively deviating $\bar{V}$ was seen among samples of intermediate-to-high *Pygospio* densities; the ordination placed such samples together, demonstrating the existence of a gradient. More strongly negative deviations were found among stations of low-to-intermediate tube-worm abundance.

September 1994.

- Only three samples, in the middle of the transect, exceeded densities of 50,000 *Pygospio* m^{-2}. Samples taken from transect-stations to one side of this high density region associated above line *d* while samples from stations to the other side associated below line *e*. Gradients relative to both *Pygospio* density and transect relative position were therefore evinced by the ordination (**Figure 5.12a**).
- Six clusters were recognised by classification at 90% similarity. Classification analysis showed a lack of concord with the ordination in some cases. Cluster *vi* contained two of the high *Pygospio* density samples; however, a low tube-worm density sample (marked *f*) shared this cluster by virtue of a relatively abundant oligochaete population (38% similarity). The third sample of high *Pygospio* density was dissimilar to the other two due to a lack of *Corophium* (representing 51% of the dissimilarity).
- The third sample of high spionid density clustered closely with two samples of the very lowest *Pygospio* density in cluster *i*, where they all are shown by **Figure 5.12b** to have strongly positively deviated from neutral diversity: all were relatively dominated by oligochaetes (43% of observed similarity), with abundant *Hydrobia* (38% similarity).
- Cluster *vi* was well characterised by *Hydrobia*, oligochaetes and *Nereis* (accounting for 39%, 38% and 12% of the similarity respectively). Cluster *ii* (with low *Pygospio* densities) was distinguished by the presence of *Macoma* (33% mean dissimilarity with all other clusters). Cluster *v* was similarly

discrete, owing its position to the presence of *Eteone* (accounting for 37% of mean dissimilarity with all other clusters).

November 1994.

- Samples were classified at the 85% similarity level into five clusters (**Figure 5.13a**).
- Cluster *i* contained the two lowest *Pygospio* density samples. The third sample of spionid density <50,000m^{-2} was grouped elsewhere, in cluster *ii*, through a shared presence of *Heteromastus*. *Heteromastus* accounted for 25% of dissimilarity between clusters *i* and *ii*. Cluster *i* was otherwise isolated from clusters of higher *Pygospio* density by *Hydrobia*, high abundances of *Macoma* and the absence of *Capitella* (35%,22% and 22% of the dissimilarity respectively).
- Cluster *v* (densest *Pygospio*) was distinguished by the presence of *Capitella* (28% average dissimilarity with other clusters). *Hydrobia, Nereis,* oligochaetes and *Eteone* were responsible for clustering in cluster *v* (34%, 22%, 15%, 15% respectively of the similarity) and cluster *iii* (34%, 21%,18% and 12% respectively of the similarity).
- Relatively strong negative deviations from neutral diversity were common to the samples of higher *Pygospio* density (**Figure 5.13b**).

March 1995.

- Three clusters of core-samples averaged by transect station were realised at the 85% level of similarity. Clusters *i* and *ii* contained <50,000 *Pygospio* m^{-2} (**Figure 5.14a**). A very low richness (2 species) in cluster *ii* accounted for the dissimilarity between these two clusters. The ordination and classification were in good agreement.
- Cluster *iii* was classified primarily by *Hydrobia* and oligochaetes (42% and 29% internal similarity respectively); *Nereis* and *Eteone* contributed most strongly to the average dissimilarity between cluster *iii* and clusters *i* + *ii* taken together (27% and 25% respectively), both polychaetes being more commonly found at high *Pygospio* densities.

- All but one transect-station exhibited negative mean deviations from neutral diversity. Negative deviations were strongest among the stations of high *Pygospio* density (**Figure 5.14b**). *V* cannot be calculated where the number of species is two or less, and so **Figure 5.14b** lacks a datum point for cluster *ii*.

April 1995.

- Transect-station averaged data shown in **Figure 5.15a** indicated the presence of three clusters classified at the 90% similarity level. Two stations included *Pygospio* at average densities under 50,000m^{-2}; the least dense *Pygospio* station clustered with the most dense stations in cluster *iii*, where *Hydrobia*, oligochaetes and *Nereis* (responsible for 37%, 30% and 19% of the similarity) occurred with similar patterns of abundance.
- **Figure 5.15b** otherwise shows cluster *iii* to include those stations of generally very slight deviation from a neutral model of diversity - with the exception of the station of highest *Pygospio* density (at 126,000m^{-2}), which strongly positively deviated from neutrality.

June 1995.

- Cluster *i* contained those stations of <50,000m^{-2} average *Pygospio* abundance (**Figure 5.16a**).) Abundant *Hydrobia* and *Macoma*, and absent *Corophium* were responsible for separating cluster *i* from all other clusters (representing 33%, 32% and 20% of the average dissimilarity respectively). *Eteone*, *Nereis*, *Macoma* and *Corophium* all contributed to dissimilarities between clusters *ii*, *iii* and *iv*.
- **Figure 5.16b** shows that all but two stations deviated negatively from neutral diversity.

5.4 Discussion

5.4.1 The Somme Bay *Pygospio* Tube-bed Community.

Macrobenthic surveys since the early 1980's have identified the Somme Bay as a fairly disturbed, low diversity environment, where opportunistic behaviour is common and there is a general lack of demographic stability (Desprez *et. al.*, 1992). In the mid-northern area of the estuary studied only 14 species / taxa were identified,

maximally 11 co-occurring at any one time, of a total 22 identified from the Somme Bay as a whole (Ducrotoy *et. al.*, 1986). A lack of any clear demographic pattern was also found, although the sampling strategy lacked fine temporal resolution. Emerging from the time-based analysis of the data was the tendency of species equitability to increase during the spring and autumn, perhaps in concert with periods of increased nutrient availability. This view is supported by the occurrence of peak densities at these times of oligochaetes and capitellid polychaetes; both taxa are considered to be indicators of organic enrichment.

5.4.2 Perspectives on Community Structuring.

Chapter 4 has shown that tube-beds provide an unusual combination of potential community structuring conditions. They harbour abundant microbial communities and are relatively organic-rich, and as such offer an increased resource availability to macrofauna. They are stronger in their resistance to shearing forces, and thus may offer a refuge (*sensu* Woodin, 1986) from physical disturbance such as tidal action or the foraging behaviour of predatory birds and fish. They contain high density populations of *Pygospio* with which other species must compete for food and space; and they potentially offer a distinct range of cues that affect rates of larval recruitment.

5.4.2.1 The Supply-side: Facilitation and Inhibition Models of Recruitment.

Community structuring mechanisms involving tube-dwellers have been well documented - most notably those involving interactions with the larvae of other species. The ecology of adult-larval interactions, determining rates of immigration to benthic communities, has generated much research interest. Such interactions were qualified by Connell and Slatyer (1977) as being characterised by inhibition, tolerance or facilitation. The view has been that inhibition prevails (Woodin, 1976; Dean & Hurd, 1980); however, more recent studies have developed a wider perspective, successional events being determined by local habitat conditions (Whitlach & Zajac, 1985) of flow, geology, community diversity, species / functional group composition, and especially density (Woodin, 1976; 1979).

When submerged, *Pygospio* may facultatively switch to a suspension-feeding mode to suit conditions of food availability (Taghon *et. al.*, 1980): in densities such as those found in the Somme Bay, it is reasonable to assume that suspension-feeding *Pygospio* has a considerable impact on settling larvae. Elsewhere, larvae of *Abarenicola pacifica* (Wilson, 1981) and the ampharetid *Hobsonia florida* (Smith, 1980) have been reported as suffering predation by *Pygospio*, and the closely related spionid *Polydora ligni* has been observed ingesting bivalve larvae (Breeze & Phibbs, 1972); Weinberg found a population of the same genus to consume the more sizeable larvae of the bivalve *Gemma gemma*, confounding Woodin's original suggestion that larger burrowing molluscs should be able to gain a foothold among dense patches of smaller tube-dwellers (1984). In the vicinity of a *Porites* coral reef, a "feeding analog" of a dense spionid tube-bed, zooplankton densities were found to be depleted by 60% (Glynn, 1973).

Inhibition stimuli of a chemical nature have been investigated by Woodin *et. al.* (1993). A "recruitment filter" of allelochemicals was suggested as a common feature in soft-bottom communities: the abundance of invertebrates (especially Hemichordates, Polychaetes and Phoronids) producing noxious, biogenic, halogenated aromatics was noted. Production of such allelochemicals by *Pygospio* has not been observed, but remains an interesting possibility. The converse, a chemical stimulation to attract settlers, has been discovered occurring between conspecifics (Pawlik, 1986)

Facilitation of larval settlement by dense tube patches has been reported (Gallagher *et. al.*, 1983). Facilitation may involve both active larval "choice" and passive, flow-mediated "trapping" of larvae. Flow-mediated facilitation of larval settlement has been experimentally verified at small spatial scales for larvae falling at speeds $<10 mms^{-1}$ (Eckman, 1979b; 1979a; 1982; 1983; Jumars & Nowell, 1984b; Nowell & Jumars, 1984). In this case larvae are treated as passively sinking particles; the effect of tube aggregations on local boundary layer flow was treated with in **Chapter 4**. *Pseudopolydora kempi japonica* tubes were found to facilitate recruitment of the tube-building peracarid crustacean *Tanais* sp.; *Tanais* tubes facilitated recruitment of *Tanais* sp., *Macoma balthica* and oligochaetes; and *Hobsonia florida* tubes facilitated recruitment of *P. kempi japonica*, *Tanais* sp., *M. balthica*, *Manayunkia*

aesturina (Sabellidae) and oligochaetes. Gallagher *et. al.* (1983) also planted simulated tubes (wooden sticks mimicking those of *H. florida*): abundances of *Tanais* sp. and oligochaetes were positively correlated with the presence of such tubes. In total, 8 of 9 experimental treatments yielded facilitation responses. However, Whitlach & Zajac (1985) noted that the facilitation observed by Gallagher *et. al.* (1983) may have been due to relatively low densities in their experimental populations.

Active larval "choice" of settlement site (implying sensitivity of the larva to the requisite stimuli) can be said to be influenced by a variety of biotic and environmental factors, among them: substrate texture, orientation and stability; substrate exposure to extremes of flow, light intensity, temperature and salinity; food availability; potential for success in sexual reproduction; potential competition and / or predation; actual chemical/physical inhibition by a competitor, or passive chemical / physical deterrence by an amensal; or chemical / physical active or passive inducement to settle by a conspecific or commensal. Eckman (1979a) noted that a factor in enhanced settlement may have been the trapping of food material by tube-tips, which then actively attract site-selective larvae. Larvae have also been found to selectively settle in less-recently disturbed sediments (Woodin *et. al.*, 1995), suggesting a further facilitation mechanism. Eckman (1979a) also reported active site selection by larvae on the basis of local patterns of flow.

5.4.2.2 Functional Groups.

Diversity is fundamentally affected by species interactions such as competition and predation. Such interactions broadly depend on the functional groups of the species involved.

Sanders (1958) correlated trophic mode with preferred sediment type and noted how groups of organisms united in their life-habit maintained exclusive communities. Rhoads & Young (1970) went further in their "trophic group amensalism" hypothesis. Suspension- and deposit- feeders were said to maintain discrete, homogenous communities: deposit feeder reworking of sediment caused pelletisation and increased grain sizes, with increased sediment water-content (Levinton, 1977) and consequent

destabilisation of the substrate. Stable-substrate seeking larvae of suspension feeders were thereby inhibited.

Doubt has been cast on the trophic group amensalism hypothesis by Snelgrove & Butman (1994), who noted that many species are not associated with specific sediment types; and that many species may alter their trophic mode.

Woodin (1976) took a broader approach and distinguished three main functional groups based not only on feeding guild but also mobility: **1**. non-tubicolous, mobile deposit feeders; **2**. filter-feeding bivalves; and **3**. tube-builders of differing trophic types. No experimental work has been done to examine the exclusion of burrowers by densely aggregated tubicolous species. Wilson (1981) showed that *Pygospio* was suffocated by the faecal deposits of *Abarenicola pacifica.*

Woodin (1983) discussed the facilitation of larval settlement discovered by Gallagher *et. al.* (1983). She noted that they had only demonstrated interactions between members of the same functional group (tube-builders), with no inter-functional group interactions that could result in inhibition. A functional-group type amensalism between the tellinid bivalve *Macomona liliana* and the spionid polychaete *Boccardia syrtis* was observed by Cummings *et.al.* (1996); survivorship of recently settled juveniles of *M.liliana* was significantly lower amongst dense tube aggregations of the polychaete.

A *Pygospio* population of only 30,000m^{-2} was studied and found to over-exploit its total foraging area by a factor of 1.8 (Brey, 1991). Actual evidence of competition involving *Pygospio* appears to be limited in the literature to discussions of spionid-dominated communities; this work is reviewed in the next chapter in the context of intra-specific competition in *Pygospio.*

5.4.2.3 Refuges.

Biogenic refuges have been described from hard substrata, where they allow small organisms with limited attachment to the substrate to exist in the face of strong physical disturbance (Walters & Wethey, 1996). In soft bottoms, tubes built by the large onuphid polychaete *Diopatra cuprea* have also been found to provide larvae and juveniles with a refuge from predation or disturbance (Woodin, 1978; 1981). Wilson

(1979) observed refugee fauna in the tubes of the maldanid polychaete *Petaloproctus socialis*. Mattila (1995) noted higher species richness and abundance within *Zostera* beds than without them, and attributed this to a predation refuge effect. Woodin's definition of a refuge included any structure shielding against a disturbance: *Pygospio* tube-beds might thus be seen as biogenic refuges from physical disturbances such as tidal scour and predation, as they are stronger in their resistance to shearing stresses.

5.4.3 Observed Responses by the Community as a Whole to Increasing *Pygospio* Density.

From the evidence presented in this chapter it would seem that increasing abundances of *Pygospio elegans* may influence Shannon-Weiner diversity both beneficially and detrimentally, suggesting some degree of density dependence. Conditions of peak diversity were reached at tube-worm abundances of 150,000-200,000m^{-2}. It has been seen that a rise in diversity occurs in the presence of >50,000 *Pygospio* m^{-2}, a density representing an areal coverage by worm tubes of around 4%. This is also notably the region of *Pygospio* density at which the physical conditions characteristic of "tube-beds" become apparent in the Somme Bay (**Sampling Strategy** and **Chapter 4**). This suggests that some combination of physical changes wrought on the sediment by tube-bed formation is at least in part responsible for observed increase in community diversity.

Patterns of unimodal, domed diversity responses have been found to gradients of disturbances such as grazing pressure (Lubchenko, 1978; Carpenter, 1981) and frequency of substrate damage (Sousa, 1979). At high frequencies of disturbance, only quickly establishing opportunists could survive; while at very low frequencies, slower-growing, more able competitors would dominate: at intermediate frequencies, a variety of species could coexist. Species richness is clearly influential in determining this diversity response. These ideas are synthesised in the "Intermediate Disturbance Hypothesis" (Connell, 1978; Huston, 1979).

Peaking diversity at certain densities of *Pygospio* do not represent an intermediate disturbance, however. The significant peak in diversity is seen instead as occurring at an optimum stage where diversity-increasing facilitation / refuge / resource

effects balance with diversity-decreasing inhibition / amensalism / competition effects. This theory is explored further below.

In the present study the equitability component was found to contribute most to the observed diversity increase. As *Pygospio* density increased towards 150,000 - 200,000m^{-2} *V* showed no significant response, remaining close to neutrality and indicating a fairly even community. At the same time, numbers of individuals (*N*) and species (*d*) both rose significantly, evidence of increasing productivity and resources present in the tube-bed sediment: overall diversity (*H'*) was seen to significantly increase in response to this facilitation. Peak diversities were identified in samples of between 100,000-250,000 spionids m^{-2} (areal coverage 8-20% tubes).

N and *d* continued to demonstrate a significant positive correlation with rising *Pygospio* as densities rose above 200,000m^{-2}. Further increases in *N* and *d* perhaps resulted from a continuing response to the increased resource offered by *Pygospio* tube-beds. Increasing *Pygospio* density correlated positively with organic content and microbial abundance in the uppermost sediment horizons (**Chapter 4**) Increased microbial biomass raises the environmental carrying capacity for deposit feeders (Levinton & Lopez, 1977). Increased entrainment of larvae by tube-tip interaction with boundary layer flow may have also enriched tube-bed species diversity. Shear strength was positively correlated with *Pygospio* density and was significantly higher on tube-beds than off (**Chapter 4**): high *Pygospio* densities may thus have provided a shelter from erosion to a quasi-cryptofaunal assemblage exposed to the dynamic LCS environment.

Over the same increase in *Pygospio* density the community appeared to significantly negatively deviate from predicted, "neutral" diversity as the community became dominated by a few species attracted to, or able to compete at, very high *Pygospio* densities. Increasing dominance was perhaps a sign of disturbance resulting from certain tube-bed physical conditions, *e.g.* increased deposition of detritus fuelling productivity and promoting anoxia, and poor sorting of sediment which would hinder mobility. It may equally have represented the effect of *Pygospio* to some extent competitively excluding other species by increasing its monopoly on resources such as nutrient (Thistle, 1981) and space (Levin, 1982, 1984 #166). The number of species did

not appear to be compromised, perhaps as most species were able to persist, albeit at low levels, dominated by a few species.

Such a pattern of facilitation at low polychaete densities grading into inhibition at higher densities was predicted, though not demonstrated, by Whitlach & Zajac (1985).

5.4.4 The Natural History of Species Interactions in the Somme Bay.

In the tube-bed biofacies of the Somme Bay, most of the species present appeared to interact in some way with the community dominant *Pygospio*. *Nereis diversicolor* demonstrated positive correlations with the tube-worm; the nereid has been observed preying on *Pygospio* in aquarium culture (personal observation) and was presumably attracted to concentrations of its prey without being adversely hindered in its movement by the dryer, more compacted and mucous-bound bed conditions. The strongest correlation was noted during November 1994 when 600-700 nereids m^{-2} occurred in *Pygospio* patches of nearly 400,000m^{-2}. In species-wise multivariate classifications *Nereis* clustered with *Pygospio* at a similarity level of at least 80% in 5 of 9 sample sets.

The errant phyllodocid *Eteone longa* was cited by Dupont (1975) as the primary predator of *Pygospio* in the Somme Bay: although pairwise species correlation indicated only one highly significant correlation, multivariate analysis showed both *Nereis* and *Eteone* to consistently, significantly account for similarity clustering of high-density *Pygospio* samples. The lack of a stronger association may to a certain extent have resulted from the hindrance of *Eteone*'s movements by dense *Pygospio* tubes.

The sessile, deposit-feeding capitellids *Heteromastus filiformis* and *Capitella sp.* appeared with insufficient regularity or density to show any clear relationships with *Pygospio*, apart from the distinctive presence of *Capitella* in the cluster of samples of highest *Pygospio* density in November 1994. Both species are small and construct a burrow, and might be thought of as belonging to the same functional group as *Pygospio*. Amensalistic interactions between these species are thus perhaps rare. *Capitella sp.* is the classic opportunist polychaete, having been found responding

favourably to conditions of extreme physical and biogeochemical disturbance (1976; Tsutsumi, 1990; Chareonpanich *et. al.*, 1993); this may lend it a greater ability to tolerate the high levels of organic enrichment predominating in tube-beds.

Oligochaetes are similar in terms of response to disturbance and organic enrichment as *Pygospio*. Although not identified to species in this study, oligochaete diversity in the Somme Bay is low: only *Tubificoides benedi* and *Tubifex sp.* are present (Desprez, 1994). Densities of oligochaetes were found to strongly positively correlate with those of *Pygospio* in summer 1994, and multivariate analysis identified oligochaetes' predisposition to tube beds. In classification analysis oligochaetes clustered with *Pygospio* at at least 80% similarity in 5 of 9 sample sets.

Corophium volutator showed no relationship to *Pygospio* in the univariate study; when present, however, this tube-dwelling amphipod did tend to occur only at higher tube-worm densities, suggesting some sort of functional group facilitation. Similarly, Reise (1978) discovered *Corophium* beds harbouring dense *Pygospio* populations in the Wadden Sea, noting up to 100,000 tubes m^{-2}, a figure presumably incorporating *Pygospio* and both limbs of *Corophium* dwellings.

Macoma balthica provided evidence to support the functional group hypothesis: dissimilarities between high and low *Pygospio* density samples highlighted by multivariate analysis were repeatedly found to involve *Macoma*. The small tellinid, usually around 1cm in length, buries itself to a depth of around 5cm and may have found burrowing through the thickness of the tube-bed to be prohibitively difficult. The bivalve was found able to persist at high tube-worm densities, however, perhaps benefitting from substrate stability and thus protection from erosion. Timing of settlement is crucial, *Macoma* settling into established tube-worm patches colonising less successfully than those present before *Pygospio* has monopolised space. Spionids have been implicated in predation on settling *Macoma* larvae (Segarsträle, 1962).

Conversely, at Königshafen on the North Sea, *Pygospio* (density = 11,000m^{-2}) was found to abandon aggregates of *Macoma* of density 3365m^{-2} (c.f. ~500m^{-2} in the Somme Bay), the spionid recoiling from the touch of the bivalve's feeding siphons, unable to compete for food with the more efficient deposit-feeder (Reise, 1983a). Reise also noted an amensalism between the tube-worm and *Cerastoderma*; however in

this case he suggested that it was physical disruption of the sediment by the cockle's movement that evicted the tube-builder. Smidt (1951) and Flach (1996) have documented similar interactions from the Wadden Sea: the latter study indicated almost complete destruction of the *Pygospio* population (maximum density in absence of *Cerastoderma* = 30,000m^{-2}) when cockle areal coverages exceeded 10 - 15%. Sauriau (1992) described mortality of settling *Pygospio* larvae caused by cockle bioturbation and Noyer (1993) described inhalation of settling *Pygospio* larvae by the cockle.

In the present study, the *Cerastoderma* population crashed during late 1993 - early 1994. This was the latest in a series of such events that have been recorded in the Somme Bay over the last 15 years. Low cockle densities prevailed between 1982-1987, with mass mortalities in 1982, '83, '85, '89 and '90 (Rybarczyk *et. al.*, 1996) and these events have been tied to oxygen depletion caused by cockle auto-eutrophication (Rybarczyk *et. al.*, 1993). Notably, cockle population declines have been exploited by *Pygospio* (*e.g.* 1983-1986), reacting opportunistically to vacated space during periods of high disturbance (Ducrotoy *et. al.*, 1987). Although *Pygospio* was not noted preying on settling cockle larvae, the formation of dry, compact beds was cited as a hinderance to the successful settlement and implantation of spat (Noyer, 1993); elsewhere, the spionid *Polydora* has been found to impair growth of molluscs by suffocation through enhanced deposition (Michaelis, 1978). Newell (1979) found microbial growth, enhanced by deposit feeder bioturbation, to result in decreased oxygenation and pH of resuspended particles, with consequent negative effects on suspensivores; Noyer (1993) related this to the *Pygospio* and *Cerastoderma* populations in the Somme Bay.

An exceptionally successful recruitment by *Cerastoderma* in the 1987 led to the collapse of the *Pygospio* population, leading to the postulation of a cycle of alternating *Pygospio* / cockle dominance (Rybarczyk, 1993). The present study provides further evidence: *Pygospio* densities were predominantly very low throughout 1992 (**Chapter 2**), meaning the opportunist must have undergone a population explosion sometime between winter 1992 and winter 1993; the extreme high densities of December 1993 suggest a time nearer the latter, coincident with the onset of decline of *Cerastoderma*. The high cockle densities of December 1993 were predominantly due to the presence of

abundant, recently settled juveniles: these clearly failed to mature into an adult population and *Pygospio* retained its dominance. Gray (1981) has described *C. edule* as an unusually long lived opportunist, showing blanket-like recruitment by larvae, slow growth in response to low food levels and the maximisation of gamete production at the expense of growth.

The gastropod *Hydrobia ulvae*, a surficial deposit feeder, twice demonstrated significant positive correlations with *Pygospio* in the univariate study. Deployment of this species is in part tidally-mediated, the animal floating up on the flood and rafting about before settling, left behind by the ebb. *Hydrobia*, otherwise only able to crawl slowly, is therefore fairly mobile and it is suggested that small-scale circulatory patterns were primarily responsible for its distribution; the raised tube-bed surface would certainly affect such patterns, but a consideration of the hydrodynamics of such recruitment is outside the scope of this study. In the cases of positive correlation the gastropod would also have benefited from the increased availability of nutrient at the tube-bed surface. A numerically dominant member of the Somme Bay community, *Hydrobia*'s abundance was the main reason for employing a root (root x) transformation on the data before multivariate analysis. The snail accounted for much in the analysis of sample similarities, and multivariate, species-wise classification uncovered the close association between *Hydrobia* and *Pygospio*: these species clustered at 80% similarity or more in 7 of the 9 sample sets.

The study of meiofauna indicated the dominance of nematodes in the Somme Bay, no other meiofaunal taxa having been found in the samples examined. Nematode abundances increased on to tube-beds by a factor of 2.25, from non-tube-bed levels. Reise (1983b) found an increase in meiofaunal abundance of 43% in *Pygospio* patches, compared to areas lacking the tube-worm, whilst a similar facilitation has been noted in beds of the related spionid *Polydora ciliata* (Noji, 1994). Opportunistic nematodes were attracted to the high resource availability of tube-beds, while small enough in size to avoid space-related competition.

5.5 Summary

- Univariate indices of community diversity showed increased species richness during winter, while the community was most diverse and equitable in spring and autumn.
- *Pygospio* density appears to mediate the diversity of the associated macrobenthic community. Peak Shannon-Weiner diversities were encountered at *Pygospio* densities under 100,000-250,000m^{-2} .
- Lower diversity at low extremes of *Pygospio* density (<50,000m^{-2}) were seen as representing conditions of lower resource availability and the lack of a physical refuge provided by a tube-bed.
- Increased diversity with increasing *Pygospio* density probably resulted from increased nutrient availability, increased sediment stability, and entrainment of larvae by tube tips.
- Decreased diversity at extremely high *Pygospio* densities (>250,000m^{-2}) was due in part to over-domination by a minority of species, importantly *Hydrobia*. Dominant species were tolerant of conditions in tube-beds of increased competition for food and space and amensalistic interactions.

Chapter 6.
Pygospio Tube-Bed Population Diversity

6.1 Introduction

Results presented in **Chapter 4** suggested a strong link at the small scale between *Pygospio* population density and the physical attributes of sediment. In a number of cases, physical sedimentary attributes appeared to be locally determined by the density of the tube-builder. In a species with indeterminate growth and a potentially flexible reproductive strategy, localised variations in environmental conditions could cause intra-population variations in fitness, potentially affecting the allocation of energy and resources to growth and reproduction. Might then the formation of a tube-bed in turn structure the *Pygospio* population that generated it? Do gradients or patches of varying *Pygospio* population structure exist inside and outside of tube-beds?

In this chapter, measurements of population variation in somatic size and reproductive status were made to address these questions. Levels of tube occupancy were also estimated, and the dispersion of *Pygospio* tubes within a bed examined, to investigate possible variations in mortality, emigration and tube-spacing. This work would provide insights into the response of *Pygospio* at an individual level to life in an extremely dense population, subject to competitional interactions for food, space and tube-building materials.

Similar lines of questioning have been adopted in other studies of populations of sedentary individuals, especially plants (Linhart, 1974; Thompson, 1978; 1985); and in studies of communities restricted to discrete patches, *e.g.* those dwelling in cowpats (Denholm-Young, 1978). For example, Thompson (1978) observed density-dependent differences in growth rate and fitness within a monospecific patch of the umbellifer *Pastinaca sativa*. Differential mortality altered patch shape as individuals in high-density areas died-off, yielding space and resources to adjacent individuals.

Variations within the population of organisms that build and maintain the tube-bed may have implications for the way in which tube-beds grow and decline in time and space; the role of the *Pygospio* population in directing tube-bed development is discussed further in the final chapter.

6.2 Methods

6.2.1 Field Sampling Strategy.

The collection of *Pygospio* samples was described in **Chapter 4** (section **4.2.3**) Note that the reduction in core size and increased replication in 1995 allowed a better assessment of *Pygospio* response to tube-bed relative position.

6.2.2 Collection of Morphometric and Reproductive Data.

A tube-bed station and a non-bed station were chosen from each sample set taken prior to 1995. Choices were made on the basis of density: the tube-bed was represented by the station of highest *Pygospio* density and the non-bed by the station of lowest *Pygospio* density. At least 100 (or all individuals present in sample) tube-stripped *Pygospio* individuals were randomly subsampled per station for analysis.

In 1995 when core sizes decreased and spatial sampling resolution improved, 20 individuals (or all individuals present in sample if less than 20) were randomly subsampled from each of 6 replicate cores per transect station (see **Table SS.1** for transect station positions). The influence of tube-bed-relative position on population structure could then be investigated.

Individuals were then prepared and examined as described in **Chapter 2** (Section **2.3.1**), with additional measurements as noted below.

For each individual the following characteristics were noted and measured:

- width of the fifth setiger;
- total setiger number (where whole);
- evidence of asexual reproduction by fragmentation;
- sex;

- presence of coelomic oocytes in females;
- mean number of true oocytes, measured from 5 randomly picked gametogenic setigers, per gravid female;
- mean diameter (across long axis) of true oocytes, measured from 5 randomly picked setigers, per gravid female;
- number of gametogenic setigers in females (where whole);
- number of oocytes and embryos in externally-borne brood capsules;
- length, and number of setigers, of brooded larvae.

Female fecundity was calculated as:

number of gametogenic setigers x mean number of oocytes per setiger (11)

Fecundity could only be calculated for whole individuals. The total number of gametogenic setigers showed only a weak relationship with width of the fifth setiger ($r^2 = 0.30$) and thus could not be estimated from a regression.

A simple index of female "reproductive output" was calculated. This index was derived to represent total gonadal production over total somatic production, and was found as:

(fecundity x mean oocyte diameter) / width of the fifth setiger (12)

Reproductive output as calculated thus represented a size-specific gonadal output, proportional to the volume of gonadal production per unit volume of somatic production. This simple, derived index was used to examine spatial trends in reproductive investment in the context of the present study. As this index relied for its calculation on measurements of fecundity, it was again only calculated for whole individuals.

6.2.3 Estimation of Tube Density and Occupation.

The ratio of *Pygospio* density to tube density was calculated. This would then reveal the proportion of tubes that contributed to tube-bed structure but that were uninhabited, either through mortality or emigration.

An assessment of amount of tube material per unit sediment volume only became practical with the introduction of smaller macrofauna core samples in 1995. These small cores allowed the recovery of all tubes from a known volume of sediment ($5.7x10^{-4}m^2$ x 5cm depth), and the removal of all worms dwelling within them.

Tubes were washed on GF/C Whatman filter paper and dried to constant weight at 70°C; dry weight was recorded. Tubes were then placed in a muffle furnace at 550°C for 24 hours, cooled in a dessicator and reweighed. Weight lost was ascribed to the oxidation of the mucous tube-wall. To allow conversion of these data to total tube length per unit volume of sediment, the lengths of tubes in 40 samples were measured and totalled. Tubes were then ashed as above and total weight per sample was regressed on total length per sample.

Tube density could then be estimated for each sample set. For each sample set, total tube length was divided by *Pygospio* density to obtain mean tube length per *Pygospio* individual. Tube density was then calculated assuming a normal distribution of tube-lengths in the population.

6.2.4 Direct Assessment of Small Scale Dispersion of Tubes.

The small scale dispersion of *Pygospio* tubes was examined. Five cores of mouth area $5.7x10^{-4}m^2$ were taken to 5cm depth from a mid-tube-bed area in July 1995. These cores were sealed and transported intact back to the laboratory where the uppermost 1cm of sediment was carefully removed and resin impregnated. Sediment was impregnated under vacuum in a Logitech IU-20 Vacuum Impregnator, using Logitech Epotech 301 low-viscosity mounting resin. Once impregnated, the sediment was cut horizontally in half and a thin section prepared from a freshly-exposed surface using a low-speed, oil-lubricated saw to prevent sample re-hydration and distortion. Drawings of horizontal thin-sections were made under low power light microscopy using a *camera lucida*.

Spatial patterns have both "intensity" and "form" (Thrush, 1991). Measurements of intensity, *e.g.* the ratio of the variance to the mean, or Moritisa's index, estimate the deviation of a distribution from random. Such measures can give no indication of any actual spatial pattern (form) present in the data, however. Measures of "spatial autocorrelation" may be used to highlight spatial patterning to which measures of intensity are insensitive. Spatial autocorrelation is exhibited by distributions of spatial data which depart from random (Cliff & Ord, 1973). Deviation from random implies that some structuring quality influences the distribution. In the case of the spatial distribution of polychaetes, such structuring qualities may include amensalistic competition, toleration or gregariousness.

Two coefficients of spatial autocorrelation, Moran's I and Geary's c, have been advocated for use in marine benthic studies (Cliff & Ord, 1973; Jumars *et. al.*, 1977; Thrush *et. al.*, 1989). One method of calculation of these indices relies on the provision of a data matrix representing the two-dimensional spatial distribution and abundance of a population. Such a data matrix was derived from each cross-sectional core. A 10x10grid of cells was superimposed on each core, and the abundance of *Pygospio* recorded in each cell; each cell represented an area of $2mm^2$. A high degree of spatial resolution was thus achieved.

The degree of a cell's spatial interaction with adjacent, occupied cells is quantified by the calculation of a second matrix of "weights". Each cell is weighted according to the number of number of neighbouring cells which are occupied. The method of weight calculation in turn depends on the nature of the effect each "cell" will have on adjacent cells. In the present case, a cell represented the immediate field of influence of one or more active *Pygospio* individuals (an area of $2mm^2$); *Pygospio* forage radially from the tube over a short range, and so each cell was assigned a weight on the basis of the number of occupied cells within a three-cell, or 6mm radius.

Geary's c and Moran's I are calculated as follows:

$$c = \left(\frac{n-1}{2W}\right) \frac{\sum_{i=1}^{n}\sum_{\substack{j=1 \\ i\neq j}}^{n} w_{ij}(x_i - x_j)^2}{\sum_{i=1}^{n} z_i^2} \qquad (13)$$

$$I = \left(\frac{n}{W}\right) \frac{\sum_{i=1}^{n}\sum_{\substack{j=1 \\ i\neq j}}^{n} w_{ij} z_i z_j}{\sum_{i=1}^{n} z_i^2} \qquad (14)$$

where n = number of cells

$x_{i,j}$ = variate value at cell i, j

$z_{i,j}$ = standardised variate value = $x_{i,j}$ - (mean x)

W = weight; $w_{i,j}$ = 1 if d<3; 0 if d>3

d = euclidean distance between cells

I and c are normally distributed (Cliff & Ord, 1973) and may be tested for significance using parametric techniques.

Geary's c = 1 in the case of a random distribution; c > 1 indicates negative spatial autocorrelation, or a uniform distribution. Values of c < 1 indicate positive spatial autocorrelation, or a more contagious or clumped distribution.

Moran's I must be related to a value calculated from I and n; $I = -(n-1)^{-1}$ in the absence of spatial autocorrelation. In the present case, where n = 100, I = -0.01 for a random distribution. I approaches 1 as positive spatial autocorrelation increases.

6.3 Results

Where calculated, levels of statistical significance are represented by the symbols: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; n.s., not significant.

6.3.1 Variability in Somatic Size Distribution.

The somatic size of an individual was expressed in terms of its total number of setigers. Where animals were broken total setiger number was estimated using the regression equation described in **Chapter 2** (equation 1).

Figure 6.1 plots the mean total setiger number of the tube-bed and non-bed populations sampled during the course of the study. Also shown are edge-bed population data which were calculated during 1995. The significance of the differences in mean total setiger number between the populations were calculated by analysis of variation; significance level is indicated on the graph.

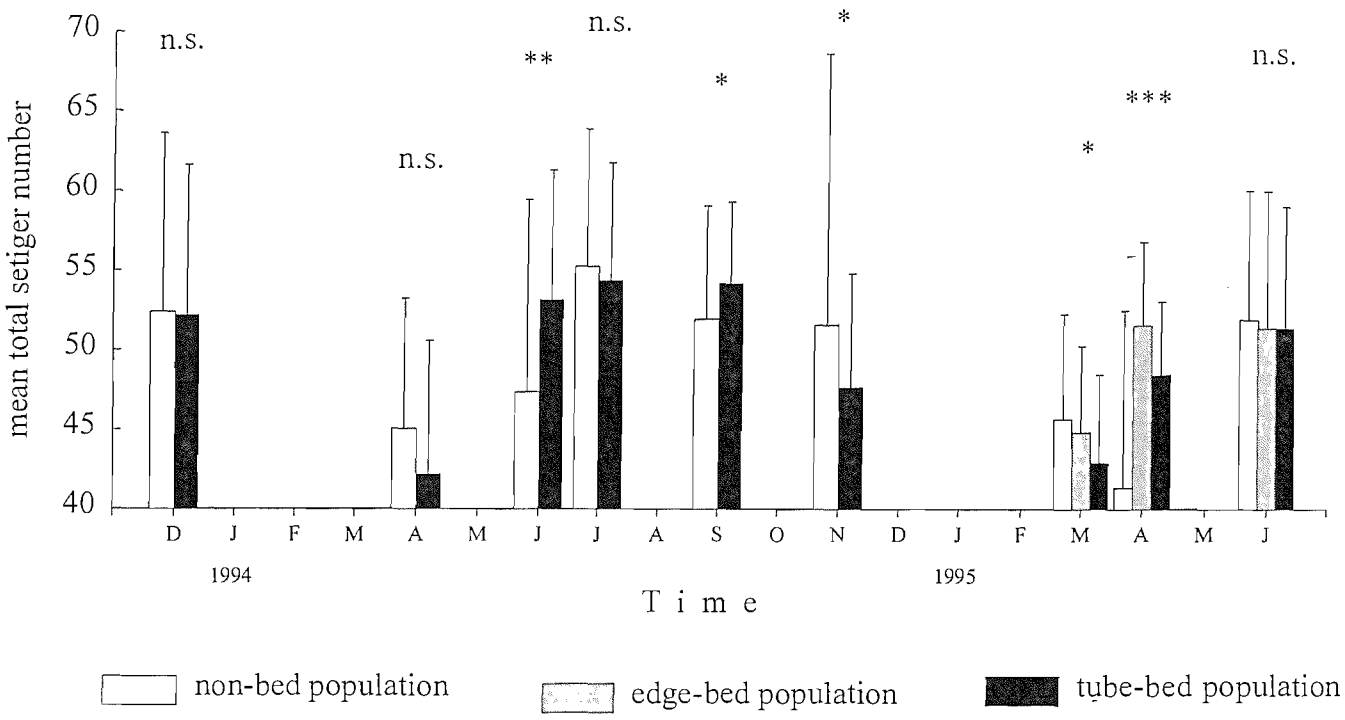


Figure 6.1: Variation in mean somatic size (total setiger number) + one standard deviation, with time and bed-relative position.

Coefficients of correlation were calculated between mean total setiger number and *Pygospio* density. Increased spatial resolution of sampling in 1995 also allowed the calculation of correlations of mean total setiger number with transect station position (as represented in **Table SS.1**). **Table 6.1** below presents the results of these calculations, where significant at $p \leq 0.1$.

Table 6.1: Correlations of mean total setiger number with position and *Pygospio* density.

Date	Coefficient of correlation	
	Pygospio	Station
December 1993	n.s.	-
April 1994	-0.91*	-
June 1994	+0.89*	-
July 1994	n.s.	-
September 1994	+0.85*	-
November 1994	-0.77, n.s.	-
March 1995	n.s.	-0.73, n.s.
April 1995	n.s.	+0.88**
June 1995	n.s.	-0.69, n.s.

The sign and strength of the correlation of total setiger number with *Pygospio* density appeared to vary widely in time; this temporal variability is also borne out in **Figure 6.1**. Significance criteria for sample sets taken before 1995 were more stringent because of the lower level of spatial resolution.

6.3.2 Variability in Reproductive Status.

The following population reproductive characteristics were determined per sample:

- The proportion of the sample comprising morphologically mature males;
- The proportion of females, greater than 40 setigers in length, carrying oocytes in the coelom. Individuals with fewer than 40 setigers were identified as

"immature" for the purposes of this study: only 1.2% of all females carrying oocytes in the coelom had fewer than 40 setigers. Similarly, Gudmundsson (1975) found that no female shorter than 35 setigers carried oocytes.

- An index of reproductive output was calculated for each gravid female, and the mean index found per station. The calculation of this index relied on measurements performed on unbroken, gravid females: unfortunately, a high proportion of individuals sampled prior to 1995 were broken, perhaps the result of the large core size used and an *in situ* sieving technique. The yield of data required for the estimation of reproductive output was therefore low. For this reason, station mean index of reproductive output was only calculated for sample sets taken in 1995.

Figure 6.2 illustrates the variation in reproductive state with respect to tube-bed position. 1995 data represent stations pooled into off-, edge- and tube-bed groups. Reproductive output index could not be calculated at the non-bed station in April 1995, as there were no unbroken, gravid females present. Analyses of variation were performed to compare mean reproductive output indices.

Where present, brooded larvae were found to have 3 setigers: there was no spatial variation in apparent larval developmental mode.

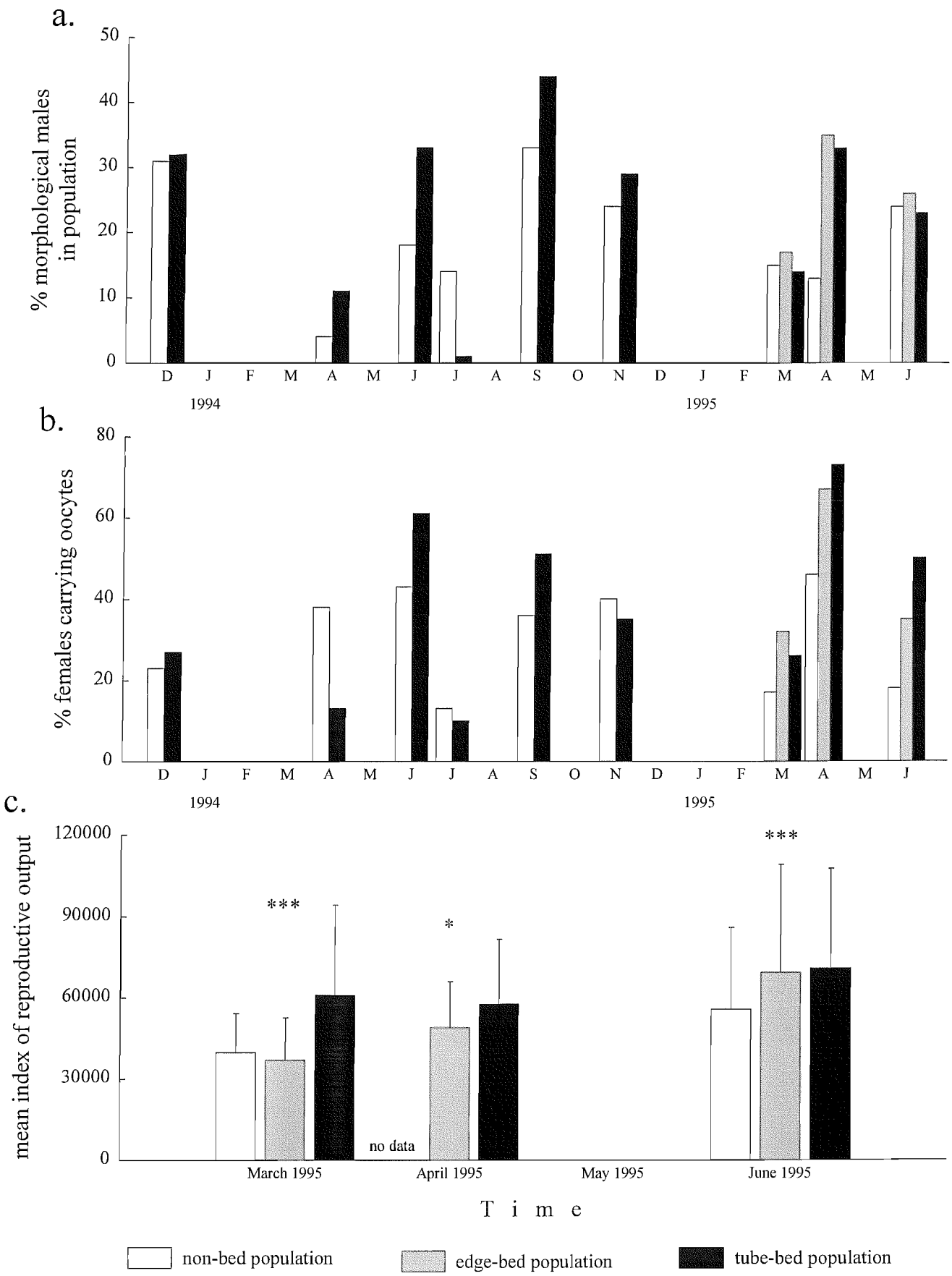


Figure 6.2: Variation in reproductive state with tube-bed position: **a.** percentage of the population comprising morphologically distinct males; **b.** proportion of females bearing oocytes; **c.** mean index of reproductive output, + one standard deviation.

Coefficients of correlation were calculated between the percentage of males present and *Pygospio* density. Correlations with transect station position were also performed on data collected during 1995. The results are shown below in **Table 6.2**; correlation coefficients of significance $p \leq 0.1$ are shown.

Table 6.2: Correlations of % males present with position and *Pygospio* density.

Date	Coefficient of correlation	
	Pygospio	Station
December 1993	n.s.	-
April 1994	n.s.	-
June 1994	+0.92**	-
July 1994	n.s.	-
September 1994	+0.73, n.s.	-
November 1994	n.s.	-
March 1995	n.s.	n.s.
April 1995	+0.95***	n.s.
June 1995	+0.81*	n.s.

The proportion of males in the population tended to correlate positively with increasing *Pygospio* density; although there were non-significant, negative correlations in July 1994 and March 1995. No significant interaction with tube-bed transect station position was noted.

Coefficients of correlation were also calculated for station mean percentages of gravid females and the station mean index of reproductive output with mean station *Pygospio* density and transect station position; significant results (where $p \leq 0.1$) are given in **Table 6.3** below.

Table 6.3: Correlations of female reproductive characteristics with position and *Pygospio* density.

Date	Coefficient of correlation			
	% gravid females		reproductive output	
	Pygospio	Station	*Pygospio*	Station
March 1995	n.s.	+0.76*	n.s.	+0.81, n.s.
April 1995	n.s.	+0.91**	n.s.	n.s.
June 1995	+0.95***	+0.69, n.s.	+0.73, n.s.	+0.86*

6.3.3 Variability in the Ratio of *Pygospio* Density to Tube Density.

The regression of the dry weight of mucous tube-wall material per sample on total tube length per sample produced the following relationship:

$$\text{total tube length} = 115.335 + (\text{weight tube mucous} \times 171.637) \qquad (15)$$

This equation was used to estimate tube lengths ($r^2 = 0.69$; $p < 0.001$; $n = 40$). Mean tube length per individual was calculated for each sample set. This is illustrated by **Figure 6.3**, which plots total sample tube-lengths against sample *Pygospio* density. A trend for increasing tube length per individual with time was apparent: mean tube length per individual is shown on the figure.

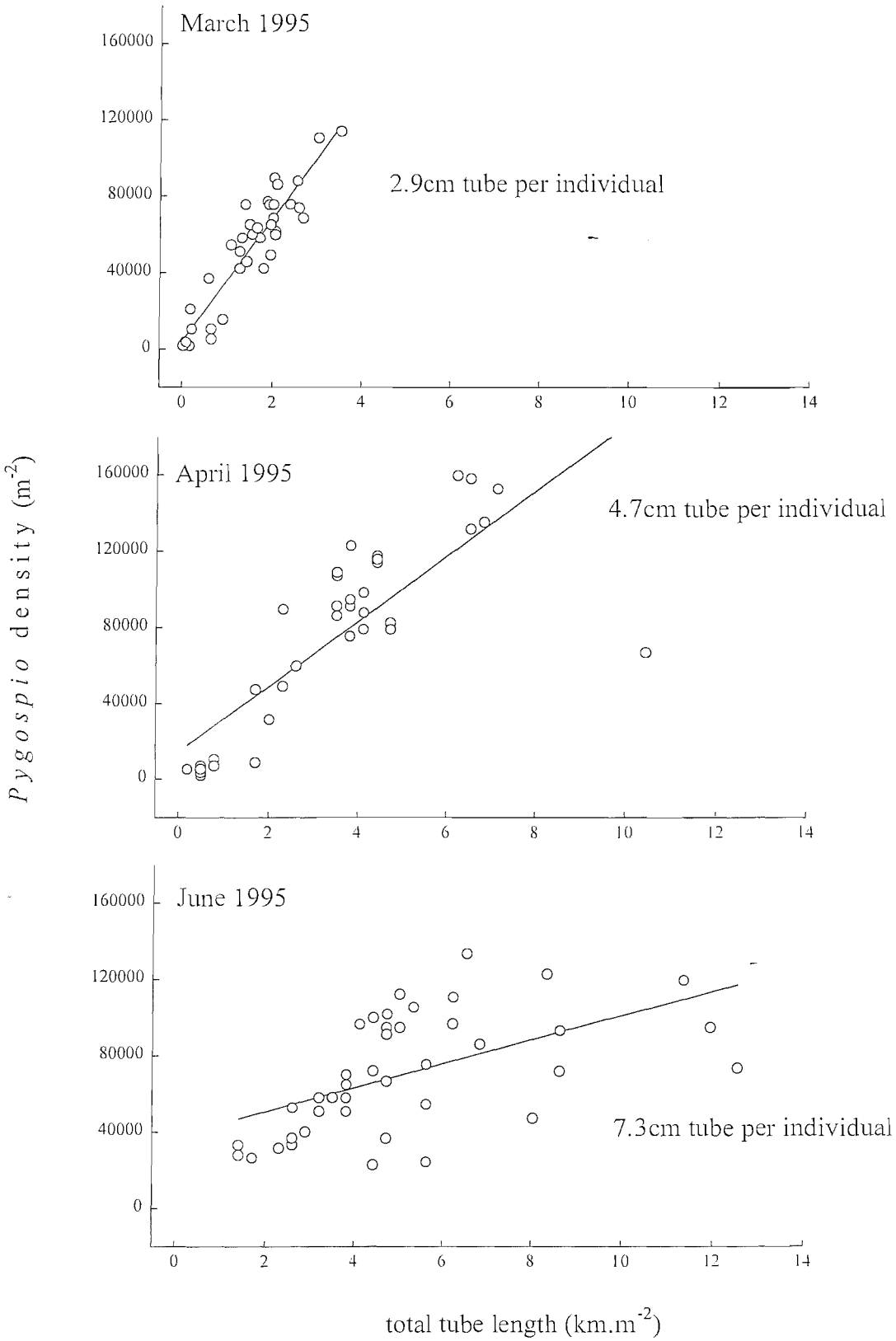


Figure 6.3: Relationship between total tube length in sample and *Pygospio* density per core sample. Lines are fitted to show average tube length per individual worm. March, April and June 1995.

Sample tube density was then calculated, assuming a constant tube-length per individual within each sample set. The ratio of *Pygospio* density to tube density could then be found per sample.

The mean ratio of *Pygospio* density to tube density was calculated per transect station, and could then be correlated with both mean station *Pygospio* density and transect station position. Resulting correlation coefficients of significance $p \leq 0.1$ are presented in **Table 6.4**.

Table 6.4: Correlations of (*Pygospio* density : tube density) ratio with position and *Pygospio* density.

Date	Coefficient of correlation	
	Pygospio	Station
March 1995	n.s.	n.s.
April 1995	+0.94**	n.s.
June 1995	+0.84*	n.s.

Although non-significantly, negatively correlated in March 1995, the ratio of *Pygospio* density to tube density was significantly positively correlated with *Pygospio* density in April and June 1995. Correlations with transect station position were non-significant, but positive in all cases.

Spatial variation in the *Pygospio* density : tube density ratio is illustrated by **Figure 6.4**. In each case, the edge-bed station appeared to have significantly more occupied tubes than the other areas (by analysis of variation).

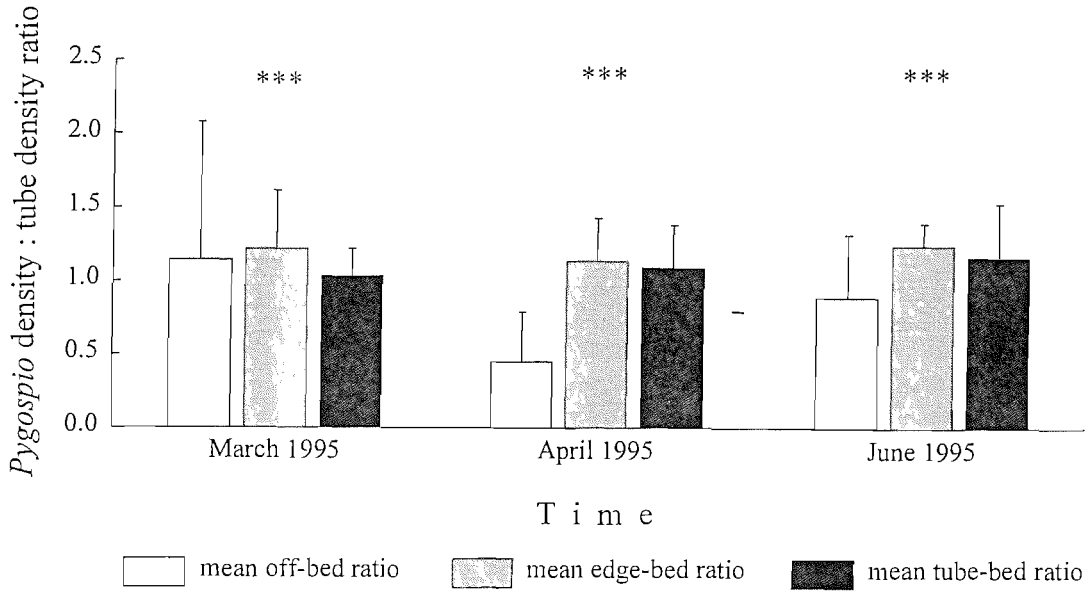


Figure 6.4: spatial variation in mean ratio of *Pygospio* density to tube density (+ one standard deviation). March, April and June 1995.

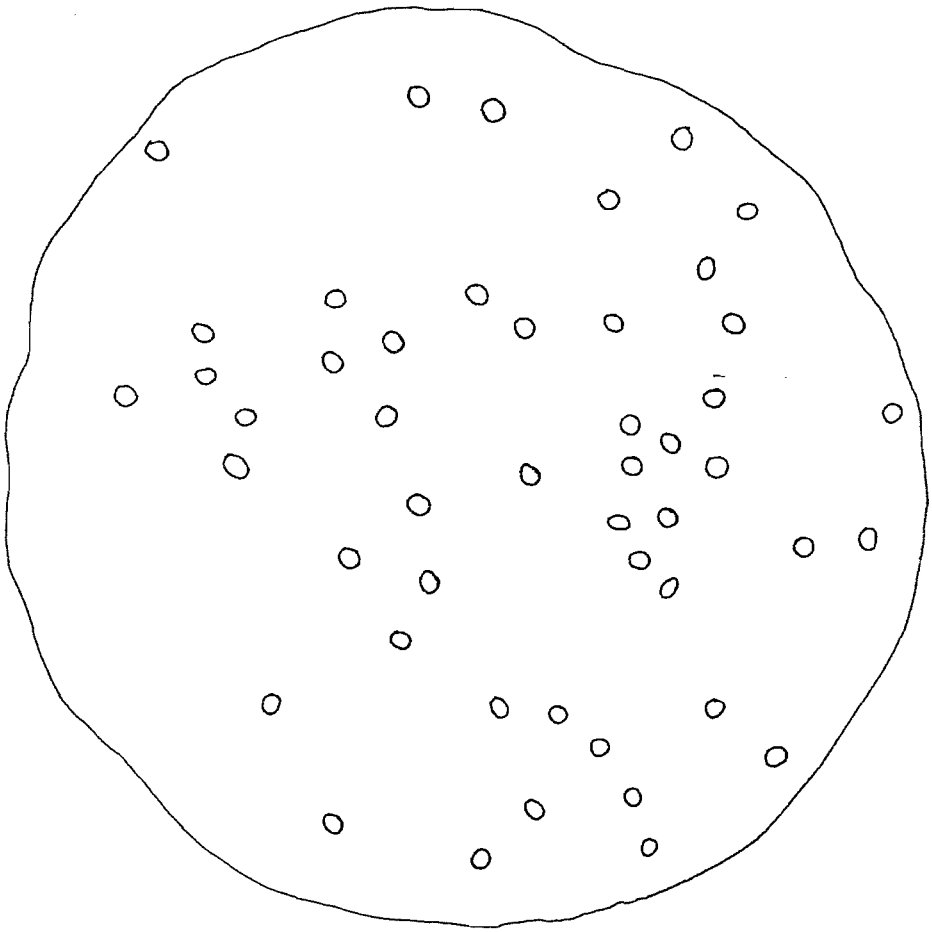
6.3.4 Small-scale Dispersion of *Pygospio* Tubes.

Figure 6.5 presents enlarged drawings (scaled x4.4) of horizontal sections through five resin-embedded cores. Original core diameter was 2.7cm.

Examination of these sections under low power microscopy revealed many circular spaces, of 0.5-1.0mm internal diameter, jacketed internally by a ring of organic material: the internal cross-sectional appearance of *Pygospio* tubes. Approximate *Pygospio* density, based on counts of tube-sections, was as follows in **Table 6.5**. No other macrofaunal species capable of constructing such tubes at such density were present at the time of sampling.

Table 6.5: Estimated *Pygospio* density per core.

Core number	estimated density /m^2
#1	82,500
#2	47,500
#3	80,500
#4	65,000
#5	68,500



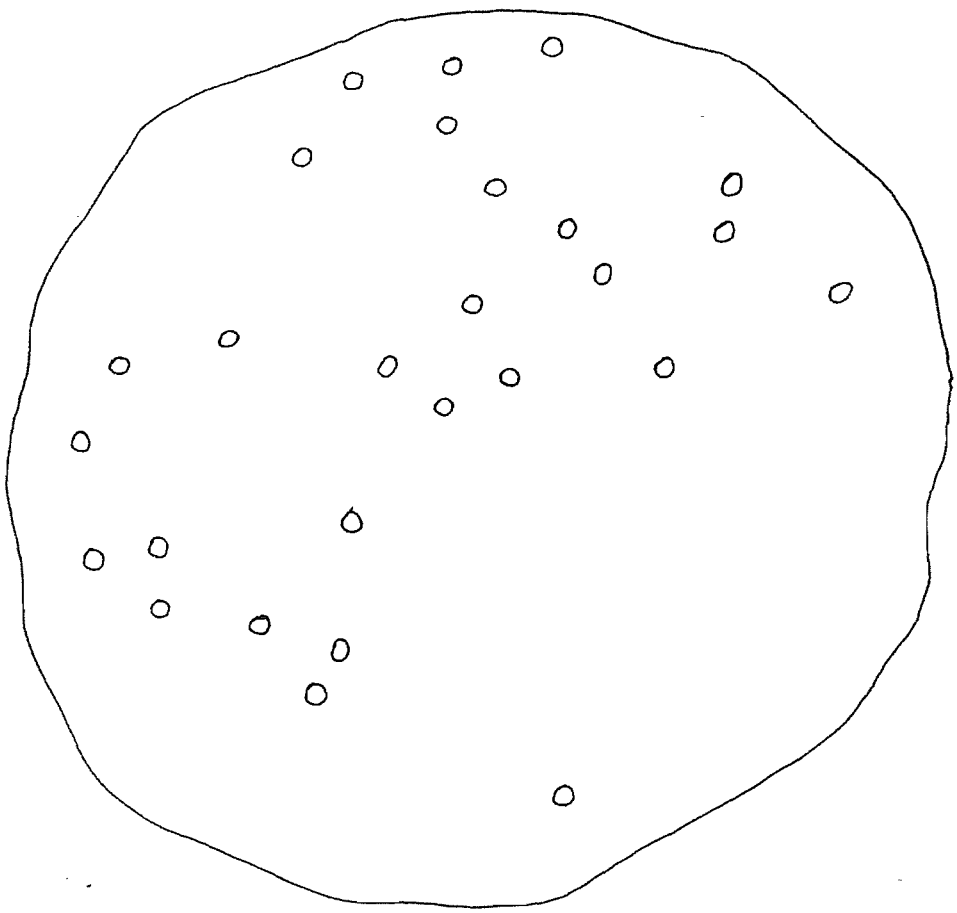
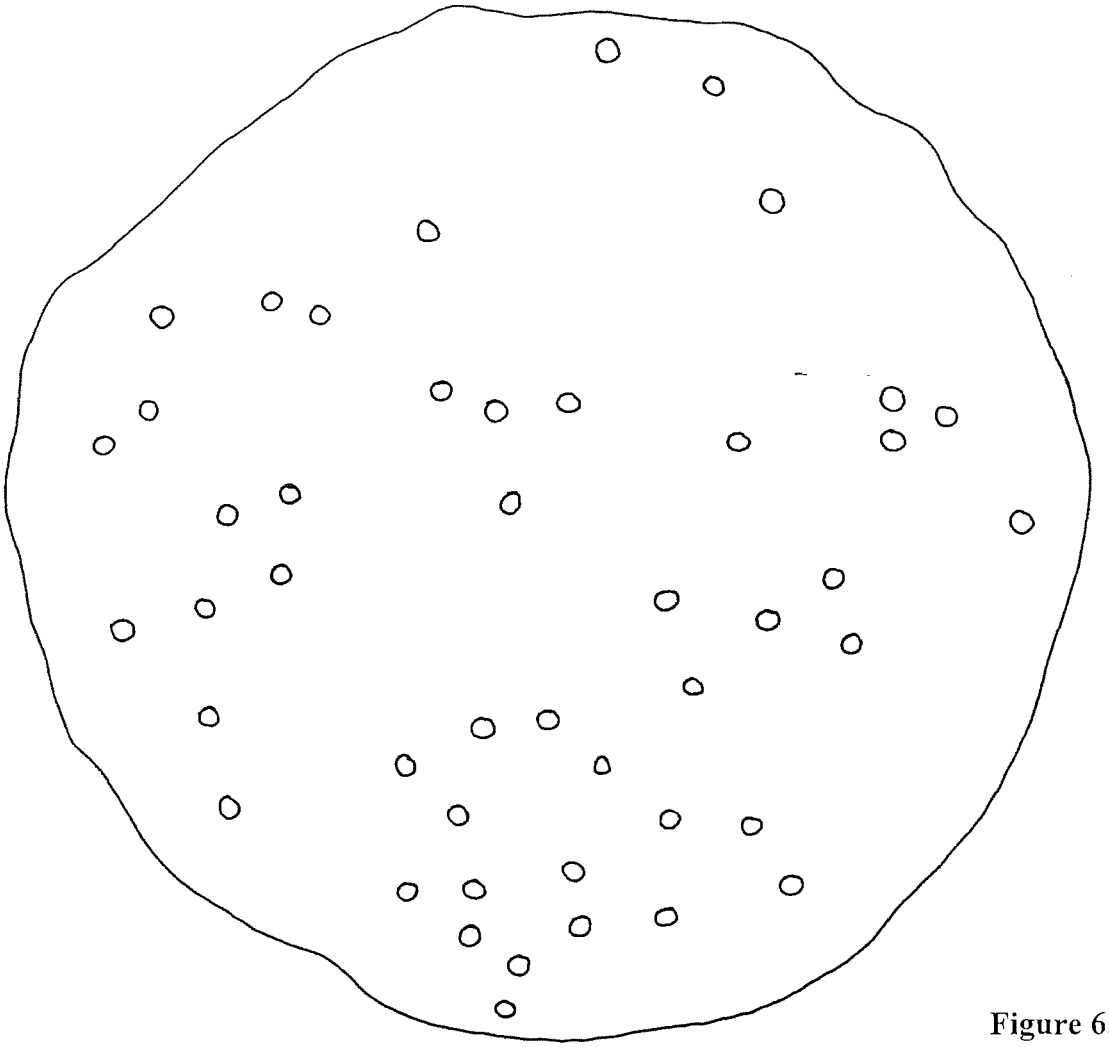


Figure 6.5:
Horizontal sections of tube-bed cores #1 and #2. Scaled x4.4.



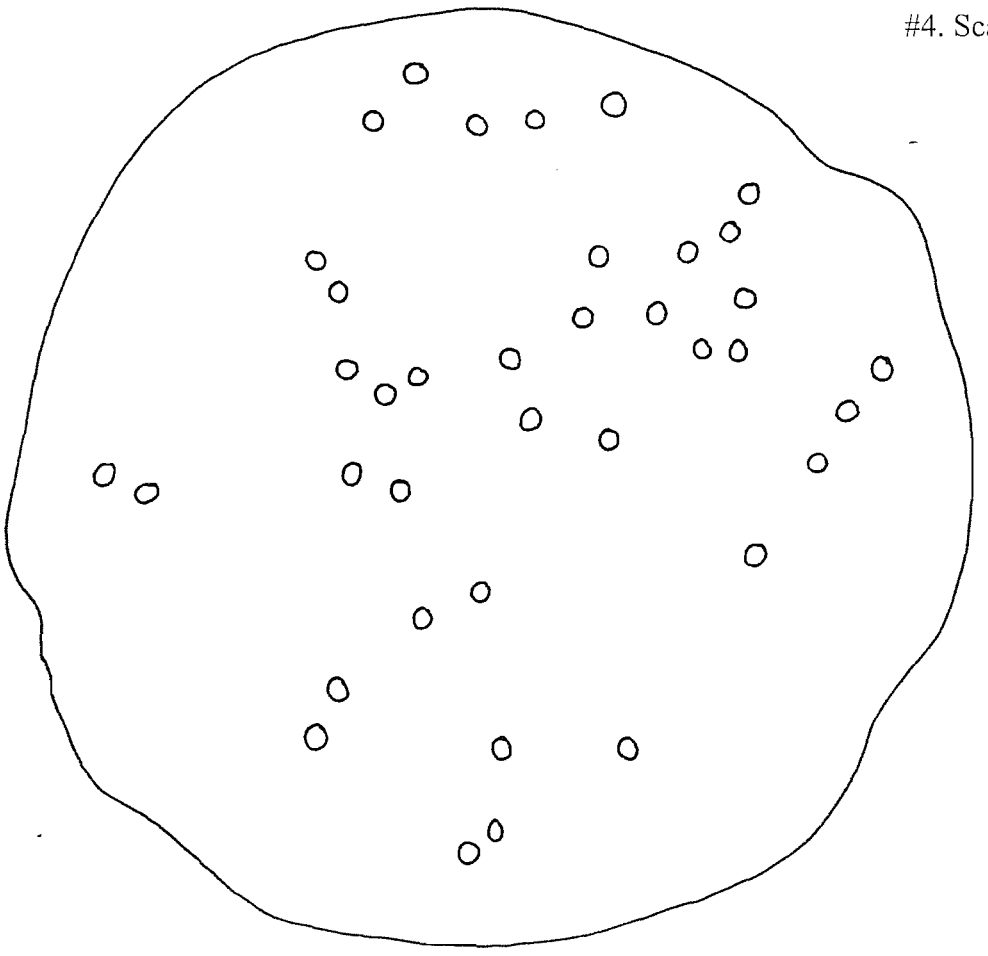


Figure 6.5 *continued*: Horizontal sections of tube-bed cores #3 and #4. Scaled x4.4.

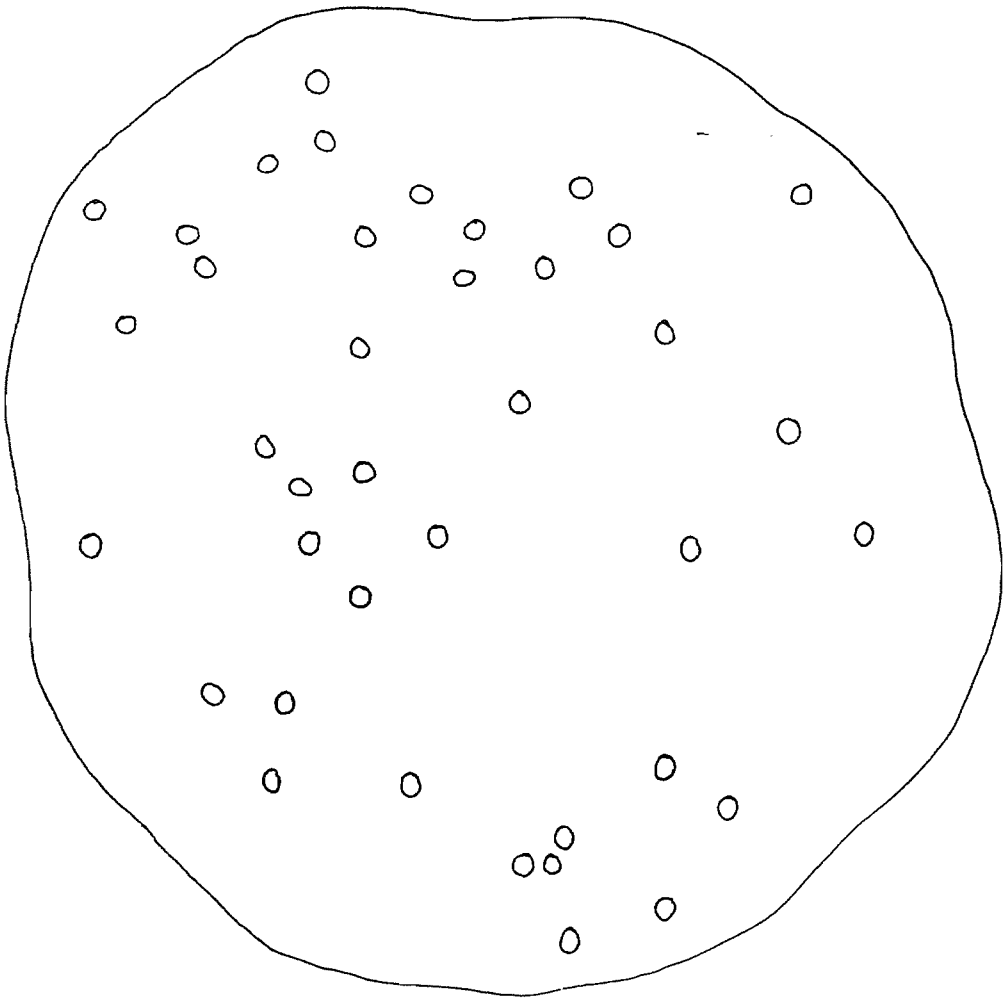


Figure 6.5, *continued*: Horizontal section through tube-bed core #5. Scaled x4.4.

Spatial autocorrelation analysis was performed on the distribution of *Pygospio* in these cores. Between 0 and 3 individuals were present per $2mm^2$ cell. Calculated values of Moran's *I* and Geary's *c* are given in **Table 6.6** below. The expected values of *I* and *c* for a random distribution were -0.01 and 1 respectively.

Table 6.6: Results of spatial autocorrelation.

Core number	Moran's *I*	Geary's *c*
#1	+0.028	1.067
#2	+0.038	1.007
#3	-0.023	1.013
#4	+0.010	1.068
#5	-0.031	0.974

Pygospio distribution did not significantly deviate from random in any core ($p>0.05$ in all cases).

6.4 Discussion

6.4.1 Variability in Somatic Size Distribution.

No effort was made to fit the present data to a pattern of seasonal growth: temporal resolution was not adequate for this purpose. The approach taken in the present chapter was to look at spatial variation only.

No clear and consistent relationship between tube-bed-relative position and somatic size was found; significant spatial variations did occur, however, suggesting a patchy size distribution, perhaps based on time since settlement. Tube-bed relative gradients of size were clear from correlations of mean somatic size with tube-bed relative position, but these varied in sign. In March and June 1995 animals were on average smaller as one progressed onto a bed, although these relationships were only significant at $p<0.1$. By contrast, a strongly significant increase in average size onto a

tube-bed was observed from data collected in April 1995; this pattern largely resulted from a very low mean non-bed total setiger number (**Figure 6.1**).

Both positive and negative significant correlations between mean size and mean *Pygospio* density were found; moreover these occurred over a similar range of *Pygospio* densities. The implications are that *Pygospio* somatic size is dependent on more than one density related factor, and that resources were not limiting to growth, even at extremely high conspecific densities. Negative correlation suggests competitional interactions while positive correlations imply some benefit is derived from life at high density, *i.e.*, in the context of somatic size, the tube-bed offers a better resource base. Somatic size must to some degree be determined by the interaction of these opposing factors.

6.4.2 Variability in Reproductive Status.

The predominance of significant positive correlations between the percentage of males in the population and mean *Pygospio* density suggests that mature males' spatial concentration is related to the availability of females for copulation. Living at higher conspecific density must increase the chances of finding a sexually mature female. No significant variations with spatial position were apparent from the correlative study; however, 1995 data suggested a maximum concentration of males at edge-bed stations.

In July 1994 males appeared to be more concentrated in non-bed areas, and the percentage of males demonstrated a negative, though non-significant, correlation with mean *Pygospio* density. This is explained in terms of the population's reproductive seasonality, as described in **Chapter 2**; the period July to August marks the end of the breeding season, when remaining males perhaps no longer actively seek females.

All significant correlations between both the proportion of females carrying oocytes and the mean index of reproductive output, and *Pygospio* density and transect station position, were positive. Both the proportion of females carrying oocytes and the index of reproductive output may be taken as indicators of reproductive success. By this measure, it would again therefore seem as though high-density aggregations of *Pygospio* are more "successful". Again, the physical impact of *Pygospio* on the sediment must be involved: increased removal rate of toxic metabolites may improve

the survival of brooded larvae, while an improved nutrient availability enables females to devote more energy and resources to reproduction.

Irrespective of these trends, there was no spatial variation in larval developmental type. Clearly *Pygospio* in the Somme does not respond to varying environmental conditions by changing larval developmental mode, thereby altering fecundity and dispersive capability. All brooded larvae occurred in capsules of around 20, and all displayed the swimming setae associated with a planktonic developmental phase. There was no sign of asexual reproduction.

6.4.3 Variability in Tube Occupancy.

The scatterplots in **Figure 6.3** showed differences in the regressions of total tube length on *Pygospio* density for tube-beds sampled in different months. The apparent increase in estimated mean tube length per individual through spring is construed as an increasing tube-length per individual in time. Two pieces of evidence support this explanation and validate the methodology used. Firstly, mean somatic size increased over the period March to June 1995 (**Figure 6.1**), and it is probable that larger individuals build deeper tubes to accommodate their length. Secondly, x-radiographs of vertical profiles through tube-bed sediment, which are presented in **Appendix 3** and discussed in **Chapter 7**, do indicate an increase in the depth penetration of tubes over this period; furthermore, the depths of tubes apparent from the x-radiographs tally well with the mean tube lengths estimated here.

An increase in the ratio of *Pygospio* density to tube density is interpreted as an increase in the proportion of tubes that are occupied. The significantly positive correlations of this ratio with *Pygospio* density in April and June 1995 therefore suggest that fewer tubes are unoccupied at higher *Pygospio* densities. Assuming that tube non-occupancy results from mortality or emigration, this suggests that some benefit is derived from living at high density. If the degree of tube occupancy is taken as a measure of the fitness of a population, then this result supports the conclusion that high-density *Pygospio* populations are fitter than lower density populations. This effect must be ascribed to the role of *Pygospio* in conditioning and improving stability of the sediment in which it dwells. Aller (1980a) suggested that increasing contagion of

distributions of sessile, tube-building benthos was a way of improving the efficiency of waste metabolite removal, and avoiding autoeutrophication.

A significant maximum in tube-occupancy was apparent at the edge of each sampled tube-bed when compared with both tube-bed and non-bed stations. This suggests some that further benefit is derived from living at a tube-bed's edge. A possible reason for such an effect is increased boundary flow velocity, and thus oxygen penetration into the sediment, as discussed in **Chapter 4**. The potential for such spatial heterogeneity is discussed at a later point in this chapter.

The increase in tube occupancy with increasing *Pygospio* density suggests that adverse intraspecific interactions such as competition are tolerated. This is further tested in the next section. Brey (1991) analysed the potential feeding area of *Pygospio* individuals, and estimated that a Kiel Bay summer population of density 30,000m^{-2} could potentially overexploit the available area by a factor of x1.8. Approximately 30% of tubes in this population had lost their occupants. Individuals living at such densities must therefore encounter restrictions to their foraging behaviour. *Pygospio* tolerates palp encounters with conspecifics (personal observations). Taghon (1992) hypothesised that deposit feeding, with a wider potential exploitation area than suspension feeding, should incur greater density dependance effects, and noted that emigration rate was greater among actively deposit feeding spionids. Frithsen & Doering (1986) observed very dense assemblages of spionids suspension feeding, and described this as a behavioural reduction of competition.

6.4.4 Tube Dispersion.

The spatial autocorrelation study revealed no significant spatial interaction between *Pygospio* individuals. Levin (1981) detected territoriality in the spionid *Pseudopolydora paucibranchiata* using a nearest-neighbour technique, in which mean actual distance between individuals is compared with the mean distance expected from a purely random distribution. *P.paucibranchiata* individuals were spaced more uniformly than expected. Aquarium observations of this species indicated aggresive defensive behaviour and guarding of space, food and tube-building materials, resulting in maximum spacing to avoid intraspecific conflicts. *P.paucibranchiata* is a larger and

more aggresive spionid than *Pygospio*. The same technique revealed more-or-less random dipersion in the spionid *Streblospio benedictii*, suggesting a greater tolerance of interspecific encounters in this species (Levin, 1981). However, significant over-dispersion (*i.e.* increased spacing) was found at the highest *S.benedictii* densities, suggesting some density-dependent competition. Overdispersion was noted in *S.benedictii* at densities of only 16,500m^{-2}, while the *Pygospio* densities recorded during the present study of dispersion ranged between 47,500m^{-2} and 82,500m^{-2}. The randomly distributed *Pygospio* population sampled here clearly tolerated much higher conspecific densities than did Levin's *S.benedictii*, a species similar in size and feeding behaviour to *Pygospio elegans*. That no overdispersion (significantly negative spatial autocorrelation) was found at such high *Pygospio* densities indicates that this species is extremely high-density tolerant.

Wilson (1983) noted that survivorship of *Pygospio* was not at all influenced by cohabitation with the larger spionid *Pseudopolydora kempi*. Wilson (1984b) found the two spionids occurring sympatrically. He proposed a "spacing hypothesis", wherein *Pygospio* actively avoided competition. He also noticed the secondary effect of a spatial partitioning of feeding: *P. kempi* was found to be more predisposed to suspension feed than *Pygospio*, allowing a certain degree of non-competitive coexistence:

6.4.5 Gradients of Spatial Heterogeneity Within Tube-Beds.

A tube-bed could be considered as a discrete patch in space, perhaps influenced directionally by tidal action. Hypotheses might then be erected concerning the spatial variation in condition of its sedentary *Pygospio* population relative to tube-bed position, *i.e.* in terms of proximity to the bed's edge. Deceleration of tidal flow at the sediment - water boundary results from the passage of water across the tube-bed surface, made "rough" by a dense array of projecting tube-tips (**Chapter 4**). Gradients of flow-related conditions may then be envisaged. The scale of such gradients is likely to be limited given the size and density of *Pygospio* tubes; flow presumably reaches a turbulence maximum within a short distance of the bed-edge, after which homogenous conditions of flow predominate.

In **Hypothesis A**, eutrophication is exacerbated away from the bed-edge region onto the bed by the increased deposition of organic detritus and silt, coupled with the retarded hydrodynamic removal of toxic metabolites. At the bed-edge a stronger boundary layer pressure causes greater penetration of oxygenated water into the sediment and redeploys waste more efficiently to the water column. Hypothesis A thus predicts a diversity gradient within the population with more favourable conditions, and thus perhaps fitter worms, at the bed-edge.

Conversely, under **Hypothesis B** increased depositional rates with distance onto a tube-bed produce more favourable conditions providing that the accumulation of metabolites is avoided by efficient irrigation and microbial cycling. Higher silt accretion rates fall within limits tolerated by *Pygospio*, and contribute to a more cohesive sediment offering a more effective refuge from erosion. Worms dwelling further from the edge might be expected to show greater fitness in this case.

Hypothesis C holds that no spatial variations in boundary-flow conditions exist that might structure the fitness of a tube-bed population along a gradient; flow is not progressively slowed as it encroaches further onto a tube-bed. Boundary flow rate and turbulence are determined at the local scale by local *Pygospio* tube density.

Increased fitness can be expressed in terms of somatic size, abundance and / or an improved reproductive output: a non-propagative mode of development (*i.e.* brooded larvae or asexual fragmentation) might also be chosen to monopolise on beneficial local physical conditions. The higher spatial resolution data taken-in 1995 allowed the validity of these three hypotheses to be examined. Population data were examined over the small spatial range represented by the transect stations "0" "+5" "+10" and "+15"; *i.e.* the bed-edge and three successive 5cm increment advances onto the tube-bed. Non-bed and far on-bed stations were disregarded in this analysis.

Over this range there were no significant correlation with position in any of the following: mean abundance of *Pygospio*; proportion of mature males; proportion of gravid females; or the mean index of reproductive output. Mean somatic size showed a significant ($p<0.05$) decrease onto tube-beds over this range in March and April 1995. Mean somatic size has previously been shown to vary in a way that cannot be predicted by available data, so no conclusions are drawn about this relationship. Although pooled

data from all stations have been found to show maximum tube-occupancy at bed-edges (**6.4.3**), no significant spatial gradient from the bed-edge onto the bed was observed in the present analysis.

These findings support Hypothesis C, that there is no small-scale gradient of spatial population variation. It is inferred that there are no gradients of flow-related structuring agents that act within a tube-bed population near the bed-edge, and local *Pygospio* density is the primary population structuring agent.

6.5 Summary

- Mean somatic size varied spatially, but there was no consistent relationship with either *Pygospio* density or tube-bed relative position. Comparisons of sample sets indicated that significant positive and negative correlations with mean somatic size occurred over the same range of *Pygospio* densities; clearly there are conflicting density-dependent factors involved in the determination of somatic size, such as competition and resource availability.
- A significant positive correlation existed between the proportion of the population represented by morphologically mature males and overall *Pygospio* density. Males are likely to seek areas of high conspecific density so as to improve their chances of finding a sexually mature female. No significant spatial variation was noted.
- Larval developmental mode did not vary spatially: all brooded larvae appeared destined for planktonic development. This supported the observation made in **Chapter 3** that *Pygospio* in the Somme does not alter reproductive mode in response to environmental conditions.
- The proportion of females bearing oocytes, and the mean index of female reproductive output both significantly positively correlated with *Pygospio* density and tube-bed transect station position. This suggested a higher level of reproductive success in reponse to both conspecific density (*c.f.* mate availability) and the physical conditions engendered in tube-bed sediment by a dense *Pygospio* population.

- A lower proportion of tubes appeared unoccupied at higher *Pygospio* densities; moreover, the lowest levels of tube-non-occupancy were noted in the edge-bed when compared against both tube-bed and non-bed. Unoccupied tubes were construed as evidence of mortality or emigration, *i.e.* a sign of unfavourable conditions.
- A direct examination of inter-tubular spacing revealed a random spatial distribution of *Pygospio* tubes; this suggested that no density-related spacing effects occur up to densities of approximately 80,000m^{-2}.
- Support was given to the hypothesis that *Pygospio* density is the primary population structuring agent within tube-beds.

Chapter 7.
Tube-Bed Sedimentology

7.1 Introduction

Localised variations in direction and velocity in sediment-carrying tidal currents bring about both deposition and erosion on estuarine intertidal mud flats. The direction and velocity of tidal flow are influenced by topographical features, and changes in the disposition of sedimentary structures may result in changes in local hydrodynamic conditions. Spatially variable, patchy distributions of sediment types are produced. Topographically raised tube-beds may interact with, and alter, local hydrodynamic conditions and become sedimentologically distinct from surrounding areas. Empirical evidence supporting this was presented in **Chapter 4**.

Examination of vertical profiles through sediments from coastal shelves and ocean basins has led to the discovery of "lamination patterns" that provide insights into their sedimentological environment (Kemp, 1990; Schimmelmann *et. al.*, 1990; Baumgartner *et. al.*, 1991; Christensen *et. al.*, 1994). "Laminae" are millimetre-scale horizontal bands differentiated by their mineralogy or granulometry (Collinson & Thompson, 1982). They may be formed over many cycles of deposition and erosion by variations in the direction and velocity of currents during deposition and by the input of sediments from different sources.

In estuarine intertidal sand- and mud-flats, lamination is usually tidally induced; following the depositional phase of the high tide, exposure and dessication causes drying of subsequent layers of freshly deposited material (Kindle, 1930). This can be more exaggerated in higher shore areas where dessication is more prolonged. However, macroinfaunal bioturbation can "lead to the wholesale destruction of lamination" (Allen, 1970), and densely populated areas such as mud-flats are generally found to contain little or no such depositional record. Even so, it may be argued that the potential for lamination in LCS *Pygospio* tube-beds is high. The great macrotidal range and double low water of the Somme Bay prolongs the period of exposure and potential dessication on the mid-to-upper tidal flats of LCS. Tube-beds have been

shown to drain more efficiently, exacerbating dessication. It has also been shown that deposition of fine material is greater in tube-beds than adjacent areas. Furthermore, *Pygospio* tubes appear to increase the shear strength of sediment, protecting the depositional record from erosion (**Chapter 4**). The spionid itself disturbs the sediment comparatively little once tube-building is completed, and may even exclude such sediment-homogenising influences as *Cerastoderma* (**Chapter 5**).

Preliminary work in July and September 1994, involving x-radiography of cores, exposed the persistence of lamination in tube-bed sediments of the Somme Bay. Such lamination was deemed a potential source of information regarding differential deposition regimes on and around tube-beds, and further samples were taken for profiling. In the present chapter sedimentological profiles of tube-beds and non-bed regions are examined, and the impact of *Pygospio* aggregations on their depositional environment is assessed.

Implications for the dynamics of the tube-beds themselves will be discussed further in **Chapter 8**.

7.2 Methods

A number of techniques for the structural analysis of unconsolidated wet sediments have been developed (Bouma, 1969). Two in particular have found popular use; these are **a:** x-radiography of thin slabs of material (Calvert & Veevers, 1962; Bouma, 1964; Schimmelmann *et. al.*, 1990; Baumgartner *et. al.*, 1991) and **b:** the casting of resin or lacquer "peels" into plane cut sediment surfaces (Burger *et. al.*, 1969). These methods were employed in this study. Other methods considered and tested during this study, but not used, included the "soft-impregnation" of sediment for sectioning using formaldehyde-set gelatine (Jensen & Crawford, 1984), and the production of ultra-thin, resin-embedded, polished sections for examination by scanning electron microscopy (Brodie & Kemp, 1994). The former method was eventually rejected because of the difficulty in achieving complete impregnation to an adequate depth; the latter method proved to be of too high resolution, being more suited to studies of far finer sediments.

For the present study, equipment was designed to enable the recovery of 40cm deep cores from which both an x-ray image and a resin peel could be made. This new approach allowed direct comparison of the two methods, each yielding unique information.

A single core of diameter 10cm was taken to 40cm depth, then extruded into a longitudinally-cut half-core "cradle", this being closed with a second "cradle". The cradles were taped tightly together and the open ends taped over. On return to the laboratory the core was cut longitudinally in two with a sharpened stainless steel plate using the cradle-edges as a guide. Care was taken not to let the core fracture or tear. Each half-core surface was next shaved as flat and smooth as possible using a razor blade, avoiding shell fragments standing proud of the cut surface.

Sections were prepared for **x-radiography** using a perspex plate which was placed against the smooth core face: 0.5cm high stainless steel runners riveted onto the plate cut into the sediment, defining the walls of a slab. Remaining sediment was removed using a wide blade which sat across the runners to ensure an even, flat cut. The resulting 0.5cm thick, 7.5cm wide slab was exposed to x-rays in a Hewlett Packard Faxitron 43855B x-radiography cabinet for 180s at 56kV, and a radiograph negative produced. Contact prints were then made from the negative. Sediment granulometry and density controlled x-ray passage through the sample: more highly x-ray penetrated areas, where sample density was low and porosity was high, show as lighter areas on the contact prints.

Peels were prepared from the second half core: this was allowed to dry out for 2 days before treatment. 130ml of hot resin (CIBA - Araldite components GY257 : HY830 : HY850 in a 20 : 9 : 1 ratio) was poured evenly across the flat surface, being contained on all sides by tin foil walls while a Plaster of Paris cap at the core top preserved surface features. A hardboard plate was placed against the resin and weighted down with sandbags. After 2 days the resin-set sediment was peeled away and unimpregnated sediment washed off with warm water to reveal a topographic representation of the vertical sediment structure. This was then photographed under oblique lighting, so as to emphasise contour detail. Resin penetrated more deeply into

coarser and more porous sediment and this allowed peel topography to be used as an aid in the identification of different textures in the sediment.

7.3 Results

All x-radiograph plates are presented in **Appendix 3**_X-radiograph plates **X.3** to **X.8** were cropped to 25cm length to fit the page and allow for x1 scaling. No significant detail was lost below 25cm depth.

A pilot study in July 1994 demonstrated the potential of x-radiography for the examination of tube-bed structure. Radiographs were taken through whole 5.2cm diameter cores intact within plastic coring tubes. An x-radiograph of the top 8.5cm of a mid-tube-bed core is shown in **Plate X.1**. *Pygospio* tubes are clearly visible to a depth of 4cm; tube density was approximately 300,000m^{-2} (from macrofauna analysis of the corresponding area). Note the apparent lamination (alternating sediment horizons of differing granulometry and thus opacity to x-rays) present within the sediment. No such structuring was observed in off-bed cores.

Cores were taken during September 1994 for further x-radiograph analysis. A rectangular corer was developed that took a 15cm square, 1cm wide sediment sample: such thin samples presented a clearer x-radiograph image. However, this design of corer proved to buckle during sediment penetration, giving a wedge-shaped sample; therefore it was not used again. Once more, off-bed cores appeared homogeneous in profile, while tube-dense cores showed more marked variations in sediment x-ray opacity. **Plate X.2** shows the profile of a flood-tide facing bed-edge core containing many shallow laminae in the uppermost 6cm. Tube density was in the region of 175,000m^{-2}; maximum tube length was around 6cm.

Sediment profiles taken in March 1995 are illustrated in **Plates 7.1-7.3** (peels) and **X.3-X.6** (x-radiographs).

Plate 7.1 March 1995; **a:** off-bed #1; **b:** off-bed #2. Peels. x0.7.

Plate 7.2 March 1995; **a:** edge-bed; **b:** 5cm onto bed. Peels. x0.7.

Plate 7.3 March 1995; **a:** 10cm onto bed; **b:** mid-bed. Peels. x0.7.

Plate 7.1a: March 1995. Off-bed #1, peel. x0.7

Plate 7.1b: March 1995. Off-bed #2, peel. x0.7

cm

Plate 7.2a: March 1995. Edge of bed, peel. x0.7

Plate 7.2b: March 1995. 5cm onto bed, peel. x0.7

cm

Plate 7.3a: March 1995. 10cm onto bed, peel. x0.7

Plate 7.3b: March 1995. Mid bed, peel. x0.7

cm

Off-bed #1 (Plate 7.1a / X.3a): a thick peel (approximately 1cm thick) showed the uppermost 6cm to 7cm of the profile to contain predominantly coarse sediment. The x-radiograph in this region appeared homogeneous and well penetrated by x-rays, confirming the well-mixed, coarse nature of the sediment. Both the peel and x-radiograph indicated lamination from 8cm to 25cm. Laminae were 2-4mm in thickness. Below 25cm depth the peel became shallower and the x-radiograph darker, indicating the presence of finer, denser sediment; there was less apparent lamination. A shelly layer lay at 18cm. The x-radiograph showed a *Macoma* shell at 3cm depth, the trace of its siphon preserved within the thin section.

Off-bed #2 (Plate 7.1b / X.3b): although identified in the field as a non-tube-bed station, this core did in fact contain *Pygospio* tubes, seen in the x-radiograph to around 5cm depth. Unfortunately the thin section was damaged at the top during preparation, making it difficult to interpret the resulting x-radiograph image in the uppermost region. Otherwise, the top 9cm were predominantly composed of fine sediment: the peel was less than 5mm thick in this region. Coarser sediment was present beneath this.

Lamination was faintly apparent from 11cm to 14cm in both peel and x-radiograph: beneath this the sediment was too reworked to preserve any laminar structure. Many *Nereis* burrows were apparent in the x-radiograph, penetrating to a depth of around 20cm. A shelly layer, composed mainly of *Cerastoderma* shell fragments, lay at 15cm to 20cm, matching the approximate shell-layer depth of off-bed core #1.

Edge-bed (Plate 7.2a / X.4a): the x-radiograph indicated dense *Pygospio* tubes penetrating the sediment to 3-4cm depth; estimated tube density was 65,000m^{-2}. Tubes were also very well preserved in the peel. X-ray penetration and thus sediment density appeared heterogeneous in the upper 3cm. The uppermost 5mm were very well penetrated by x-rays. Beneath this lay a short series of laminar horizons, alternating on the x-radiograph as light and dark bands. Darker bands (of finer, denser sediment) were 1-3mm in depth; the two distinct lighter horizons were 5-10mm deep. Such light /

dark variation showed the abrupt changes in sediment granulometry and thus x-ray opacity in these uppermost 3cm. A "shelf-like" peel top, formed by increased penetration of resin into the sediment, also indicated a predominantly coarse texture near the surface. This peel structure was apparent in all tube-dense cores, but absent from off-bed core #1 in which no tubes were present. The peel was shallower beneath this surface horizon, indicating fine sediment to a depth of 6.5cm.

A lamination signal was preserved in the peel from 8cm to around 28cm, although it was disturbed by *Nereis* burrow traces. A *Nereis* burrow, infilled by resin, was particularly well delineated by the peel. A shell layer was apparent around 30cm below the surface.

5cm onto bed (Plate 7.2b / X.4b): tubes were visible to a depth of 3-4cm; estimated tube density was 55,000m^{-2}. Surficial sediment appeared layered in the x-radiograph image. The uppermost 2-3mm were of fine material, and this was followed by a less dense horizon some 2mm deep. A finer, 2mm layer lay beneath. Another 7-8mm horizon, of lower density sediment, underlay this. The 1-2cm thick peel top indicated the predominating coarseness of the surface sediment. The peel also indicated a 2-3cm deep region of finer sediment lying beneath this uppermost, heterogeneous region. The x-radiograph below 5cm was lighter, suggesting less dense sediment. A laminated region was apparent in the peel at around 15cm depth. Shell layers lay at 18cm and 32cm depth.

10cm onto bed (Plate 7.3a / X.5a): tubes were present to around 3-4cm depth; estimated tube density was 50,000m^{-2}. Damage to the x-radiograph, notably fractures at 1.5cm and 2.5cm, prevented its useful interpretation. However, the pattern of a thick peel top (to 2.5cm) followed by a shallower region (to 7cm), was again seen in this on-bed core. Lamination was apparent beneath 28cm in both the peel and x-ray. A shelly layer was found at 20cm depth.

Mid-bed (Plate 7.3b / X.5b): tubes were apparent to 4cm depth; estimated tube density was 90,000m^{-2} . Again the thick peel top indicated high sediment porosity.

Careful examination of the x-radiograph surface indicated the presence of around six very shallow (1mm) light and dark horizons underlain by a 1cm deep horizon of less dense material. Both peel and x-radiograph indicated a further region of fine sediment to around 12-14cm: the high sediment density in this region caused very poor resin penetration in the peel, especially at 3-5cm depth. Beneath this region sediment appeared coarser.

Lamination was seen in the peel between 14cm and 20cm depth. The pronounced area of relief on the peel at 10cm was almost certainly the result of a fracture in the core-half: no corresponding feature was noted in its companion x-radiograph. Shell layers lay at 20cm and 30cm, and contributed to the difficulty in obtaining an intact thin section for x-radiography.

Profiles were also taken in April 1995, and are described below. **Plates X.6-X.8, Appendix 3**, present x-radiographs of these profiles. Peels were not made of these cores. Descriptions are given below.

1.5m off-bed (Plate X.6a): very few *Pygospio* tubes could be seen in the cross-sectional profile. Estimated tube density was 1,000 m^{-2}; tubes penetrated to around 3cm depth. Good penetration by x-rays indicated predominantly low-density sediment throughout the profile. Surficial sediment was homogeneous to a depth of 4cm, beneath which lamination was apparent.

0.75m off-bed (Plate X.6b): *Pygospio* tubes were entirely absent from this profile, which appeared virtually structureless except for a number of *Nereis* burrows.

Edge-bed (Plate X.7a): edge profile contained *Pygospio* tubes to depths of over 5cm; estimated tube density was 125,000m^{-2}. Tubes appeared to have a curved growth orientation. The surficial 1-2cm offered good x-ray penetration, indicating lower sediment density; beneath this region sediment was denser and more opaque to x-rays.

10cm onto bed (Plate X.7b): *Pygospio* tubes were built to 5-6cm depth; estimated tube density was 100,000m^{-2}. A heterogeneous pattern of x-ray penetration was apparent in the uppermost 5cm. No clear vertical trend could be seen.

1m onto bed (Plate X.8): *Pygospio* tubes reached over 6cm in length in this mid-bed core; estimated tube density was 60,000m^{-2}. Again, the uppermost 5cm contained a definite horizontal pattern of more and less x-ray-opaque horizons. The localised destruction of such structures in the vicinity of *Nereis* burrows was well captured by the x-radiograph; *Pygospio* tubes did not appear to cause such destruction of sediment lamination. Surface sediment was denser and more opaque to x-rays to around 1cm depth. A 1cm horizon of less dense sediment underlay this. A 2mm horizon of high density sediment separated this from a further 3cm region of lower density.

7.4 Discussion

7.4.1 The Tubes of *Pygospio elegans*.

X-radiograph images of longitudinal sections through tube-beds show tubes built by *Pygospio* to be 3-6cm in length. Other studies have found tubes to penetrate to a depth of 4cm-7cm (Dupont, 1975; Brey, 1991; Reise, 1983), occasionally down to 9-10cm (Holme, 1949; Hertweck, 1994).

Maximum depth of tube penetration as seen in profile x-radiograph appeared to vary in time. In March 1995 tubes penetrated to 3-4cm in all tube-bed cores; by April maximum tube length was 5-6cm and in July 1995 tubes were reaching depths of around 7cm. This may be a sign of the maturation of the *Pygospio* population through spring into summer. A similar increase in tube-length over this period was noted during the assessment of tube density in **Chapter 6**.

Dupont (1975), working at HHS in the Somme Bay, observed that beneath the extant layer of tubes in a dense population there lay the "ghosts" of tubes of past generations, protected by their burial from erosion. No such "ghost" tubes were visible in x-radiographs taken during the present study from LCS, however. It is assumed that

such relics might only persist in low-energy, highly-depositional environments such as HHS.

7.4.2 Sedimentological profiles.

Profiles of LCS non-tube-bed sediments were taken as a control. The relatively coarse and homogeneous sediment of the upper 10-20cm indicated a high-energy hydrodynamic regime. Profiles taken on tube-beds showed a different pattern, however. Sedimentary structures were better preserved in these, indicating the greater stability of the tube-bed environment. The deeply resin-impregnated tops of tube-bed peels indicated the prevalence at the surface of a more porous, granular sediment, while the uppermost 2-3cm of tube-bed x-radiograph profiles revealed a laminar structure, with mm-cm scale horizons of more- and less- x-ray opaque sediments.

It is postulated that two factors were at work to create this structuring. Firstly, the flow-related entrainment of fine particulates by tubes; and secondly the egestion of mucous-bound, consolidated pellets at the surface by *Pygospio* (for review see **Chapter 4**). It was the presence of these pelletised layers that most probably caused the increased penetration of resin at the peel-tops. The presence of distinct layers is perhaps the result of a two stage deposition process. While the tube-bed is submerged, tidal currents interact with the tube-tips to bring about deposition. *Pygospio* suspension-feeds during this period, and "messy-eating" contributes to the input of material to the surface. A dense layer of unconsolidated silt and clay is thereby laid down. During the prolonged period of exposure, deposition continues as the result of egestion at the surface, giving rise to a more granular, porous layer of faecal pellets. Dessication would strengthen this deposit during exposure. As further deposits accumulate above and worms continued to build upwards to keep pace with the rising bed surface, material entrained by tubes and the feeding activity of *Pygospio* is compacted down into a sub-surface region, pelletised egesta dewatering and breaking down under microbial action. Such an horizon of finer, denser deposits was noted beneath the surficial laminar region in all tube-dense cores. Around 7cm in depth, this region was characterised by low x-ray penetrability and by shallower areas on peel surfaces. No such distinct sub-surface region was recorded from any of the non-bed profiles.

This sub-surface region of mud is perhaps one of the most important factors in the stabilisation of tube-bed sediments, lending tube-beds a more cohesive frame than surrounding areas. In the field, observations of the remnants of storm-eroded tube-beds revealed darker, exposed deposits of muddier sediment

Deeper lying zones of lamination were observed in all March 1995 peel profiles, their structure preserved by burial under 10-20cm of sediment. It is unlikely that this deeper lamination recorded the past presence of dense *Pygospio* populations, however. It is felt that Pygospio-induced lamination can persist only near the sediment surface, depending as it does on vertical variations in sediment bulk density. At such depths, this *Pygospio*-induced lamination would have compacted down into a more homogenous region of fine, densely-packed silt and clay. These deeper structures must instead represent the undisturbed fragments of background, tidally-induced lamination of horizons of differing granulometry.

A tube-bed situated in an area exposed to low erosive forces might continue to accrete without regular disruption through erosion. A long-established tube-bed, harbouring few efficient bioturbators, might then preserve the lamination resulting from cyclical inundation and dessication, incorporating a record of deposition into its structure. If the theory of increased deposition into tube-beds is correct, then laminae deposited in the presence of tubes would be thicker than those deposited onto uninhabited sediment. The age of a tube-bed could then be inferred by comparing the disposition of thick and thin laminae within a longitudinal profile section of the sediment, were depositional rates known. No quantitative study of depositional rates was performed in the present study, and so no attempt has been made to "age" tube-bed deposits.

7.4.3 Ichnological significance.

The effects of benthic organisms on their sedimentological environment has been observed from ancient, as well as recent sediments. Ichnology is the study of trace fossils, and may lend much to the interpretation of ancient, buried sedimentary environments. Trace fossil assemblages (ichnofacies), and associated bioturbation patterns, can provide information on conditions of sedimentation rate and substrate

type, as well as on oxygenation and nutrient content (Wetzel, 1991). In view of the apparent effects of dense *Pygospio* populations on sedimentation in estuarine, tidal sandy-mudflats, and as a component of the present examination of *Pygospio* tube-beds, it is important here to consider the potential importance of *Pygospio* as a trace-fossil-generating organism.

The ichnogenus *Pygospioides* was first described by Häntzschel *et.al.* (1968) from Helmstedt in Niedersachen, Germany, named after the high density *Pygospio* populations of the North Sea coast waddens which the ichnofacies resembled. *Pygospioides* tubes are 0.75-1mm in diameter and up to 10cm in length; the top third shows the forking often described in recently-built *Pygospio* tubes. The similar ichnogenus *Skolithos* is taken to represent the burrow of a suspension-feeding polychaete; it is a simple, unbranched vertical shaft, 4-10mm in diameter, built perpendicularly to the bedding plane (Wetzel, 1991). *Skolithos* ichnofacies are indicative of estuarine conditions (Howard & Frey, 1975). *Skolithos* is a widely recognised taxon, one popularly applied to the simple trace fossils built by small, suspension feeding polychaetes. Apart from its original description, *Pygospioides* has only been described by Sellwood (1970), however. This suggests either that *Pygospio* tube-aggregations (not uncommon in modern benthic environments) are badly preserved in the sedimentary record; or that they are placed in *Skolithos*. It should be remembered that branching characteristic of *Pygospioides* is not necessarily a diagnostic feature of *Pygospio* tubes, and may depend on local hydrodynamic conditions.

It is proposed that the discovery and identification of ancient *Pygospio* communities would be of great interest to those piecing together the palaeo-ecology of a deposit. High density fossil assemblages of the sorts of tubes built by opportunistic polychaetes would point to an environment perhaps disturbed by organic enrichment and eutrophication, or prone to regular hydrodynamic re-structuring.

The ghost-tubes discovered by Dupont (1975) beneath the extant surface layers of tubes demonstrate how *Pygospio* tube-structures can survive to become trace fossils. Sedimentological profiles of the salt-marshes adjacent to the HHS sampling area would

certainly yield interesting data on the sedimentological history of the area, casting more light on the role of *Pygospio* tube-beds in sediment conditioning and stabilisation.

7.5 Summary

- **Chapter 4** has shown how dense arrays of tubes can-lend sediment an increased shear strength. However, interaction between infaunal tubes and the boundary-layer flow of water can also lead to reduced shear stresses acting on the sediment surface.
- The same flow related effect can lead to increased deposition of suspended matter. Sessile, suspension feeding infauna augment the rate of deposition further.
- A record of increased deposition may be preserved in the sediment, especially where erosion and is weak and bioturbation minimal.
- The vertical depth structure of *Pygospio* tube-bed and non-bed sediments were examined to depths of 30-40cm by casting peels and taking x-rays.
- No signals of extinct, buried populations of tube-aggregations were found at LCS. There was thus no evidence that tube-beds build on top of older, dead beds at this station.
- Tube-bed sediments contained more clearly structured vertical horizons than non-bed sediments. Notably, a subsurface region of silt and clay was apparent within tube-bed cores, concentrated there by the conditions of increased deposition. This deposit is presumed to play an important role in the maintenance of the structural integrity of a tube-bed.
- The potential of *Pygospio* as a trace-fossil generating organism is highlighted.
- This chapter has described a new approach to the study of a "reef"-forming organism in the soft-bottom benthic environment. By employing methods more usually practised by geologists, some important insights into the construction of tube-beds have been developed. The importance and relevance of sedimentological processes to tube-bed dynamics will be discussed in the final chapter.

Chapter 8.
Tube-Bed Formation and Dynamics

8.1 Introduction

The four preceding chapters have addressed biotic and abiotic structuring mechanisms operating at the scales of the individual, population and community. In this final chapter an appreciation is made of dynamics at the scale of the tube-bed itself. The mechanisms which may be involved in tube-bed formation and dynamics are first reviewed. These fall into the general categories of tube-bed foundation, development, and succession. A synthesis is then presented, which attempts to model tube-bed dynamics conceptually.

8.2 Tube-Bed Foundation

For a population to attain the density required for tube-bed formation in the absence of asexual reproduction or non-dispersive larval development, certain conditions must apply. There must be a massive, gregarious settlement of larvae, or a less-densely settled patch must preferentially accrete larvae to high density at the expense of surrounding sediment. Furthermore, adults may actively migrate to areas of higher density. Lastly, a tube-bed may represent an area of lower mortality or emigration.

Species-specific preferences for substrate and environmental conditions will lead larvae to recruit to patches that are similar in terms of their physical conditions. In common with the larvae of other intertidally-occurring invertebrates, *Pygospio* is positively phototactic for the duration of its planktonic existence, ensuring a roughly littoral distribution (Thorson, 1950; Hempel, 1957). Tube-building larvae are known to be discriminating about the granulometric character of their destined substrates (Crisp, 1974b). Smidt (1951) performed experiments on planktonic larvae of *Pygospio* to qualify this larval choice, and found that a natural sand or mud substratum stimulated settlement; a sterile or absent substrate, or one containing pebbles, had a negative effect. The increased organic load associated with tube-beds may therefore facilitate

larval settlement into previously established patches. Grain size has been shown to be of importance in the settlement of the closely related, tube-building spionid *Polydora ciliata*. Hempel (1957) found that tube-building behaviour in this species required settlement into sediment with a range of grain sizes between 50μm and 200μm. Kiseleva (1967) observed settlement of *P.ciliata* only in sediments with grain-size distributions predominantly finer than 250μm.

Preferential immigration into tube-beds may result from passive, flow induced deposition of larvae. This subject has already been examined in **Chapter 5**, in the context of the mechanism by which community diversity of tube-beds is generated. Larval behavioural responses to local boundary layer flow conditions may operate; tube-dwelling species might thus attract settlement of conspecific larvae. Such behavioural responses were found in the sabellariid tube-builder *Phragmatopoma lapidosa californica* (Pawlik *et. al.*, 1991; 1993). The implications for preferential settlement into tube-beds exhibiting surface roughness is clear. Natural, chemical cues have also been implicated in the induction or prevention of settlement of the larvae of many species. Among the polychaeta, *Phragmatopoma californica* produces free fatty acids, and thereby attracts conspecific larvae (Pawlik, 1986); this response to a chemical stimulus is distinct from the species' response to flow already mentioned. No other instances of a species-specific chemical cue are known in the polychaeta. Chemical inducers of settlement can, however, include the simple presence of organic matter and microbial films; this has been demonstrated for the capitellid *Capitella* sp. (Butman & Grassle, 1992).

Hannerz (1956) detailed the metamorphosis of a generic spionid larva. He found it was induced by sand "from the natural biotope". The pre-metamorphic larva was described as behaving as if "a narcotic had been added to the water", lying on the surface either motionless or vibrating. After a minute or less the larva began to crawl sinuously, occasionally attempting to burrow prostomium-first into the substrate. If burrowing was not immediately accomplished, the larva would swim away, sporadically re-attempting to burrow. During burrowing, palps previously held flat along the back were directed forward. Many larval setae were seen to be lost during penetration. Once in the sediment, larval trochs swiftly became inactive and were shed

after around one hour. Larval ciliation was completely lost after around five hours, while the prostomium began to elongate. Full adult morphology was not attained rapidly: Hannerz noted that larval pigmentation was still visible after two months, at which time gametogenesis began.

The formation of dense patches may partly result from differential mortality following a blanket larval settlement. Post-settlement mortality of newly-metamorphosed juveniles may be very high: Bachelet (1990) noted 42% mortality in *Pygospio* within one month of settlement and almost 95% mortality after four months. Lambeck & Valentijn (1987) observed 90% mortality in the spionid *Polydora ligni* within two months of settlement.

Although the growth of benthic populations is usually seen as involving larval recruitment, immigration of adults to established populations may be of importance. Günther (1992) stressed the possibility of population re-seeding by adult dispersion after disturbance events. In the case of *Pygospio* in the Somme Bay, erosion may cause localised redistribution of adults carried in torn-away bundles of tube-bound sediment (personal observation). Adult *Pygospio* individuals may also migrate (Wilson, 1983), especially if subjected to amensalistic interactions with other species. There have been many reports of adult *Pygospio* floating in the water-column (Linke, 1939; Armonies, 1988; Heiber, 1988; 1994).

8.3 Tube-Bed Development

The growth and maintenance of a tube-bed as a physical, sedimentological entity may depend in part upon the activity of the *Pygospio* population that generated it. Of further consequence is the supply of material that contributes to its structure, and the combination of erosive and depositional forces that acting upon it.

8.3.1 Structuring Mediated by *Pygospio*.

Pygospio density has been shown in **Chapter 4** to have a significant impact on sediment condition. *Pygospio* causes the accretion of suspended material such as silt, clay, and organic detritus into tube-beds through biodeposition, and through building a tube which passively traps sediment. A cohesive sedimentary frame is established

(**Chapter 7**). The *Pygospio* population also encourages growth of the microbial community, leading to further sediment strengthening by mucous binding.

The spionid clearly has a primary role in the creation of a tube-bed. Intra-tube-bed variability in the *Pygospio* population must therefore be considered as a potential structuring factor also. Thus, if *Pygospio* are the primary tube-bed structuring agents, might differential mortality and fitness in space influence the development of the tube-bed? The potential causes of spatial variability in a tube-bed *Pygospio* population were examined in **Chapter 6**. Although tube-bed-dwelling populations were apparently more reproductively successful than those inhabiting non-bed areas, no significant spatial variations in population structure within a tube-bed were discovered. No mechanism can therefore be postulated whereby the tube-bed population's spatial structure has any impact on a tube-bed's spatial development.

8.3.2 Tube-Bed Seasonality.

Sediment stability is not constant, and the integrity of a tube-bed may be affected by seasonal change. Seasonal temperature changes and nutrient fluxes alter the productivity of the benthic community (Yingst & Rhoads, 1978; Rhoads & Boyer, 1982), and therefore the amount of sediment-binding mucous produced. Build-up of exopolymers and other metabolites occurs with time, potentially leading to a temporal gradient in sediment stability (Grant *et. al.*, 1982). Such a seasonal effect on shear strength was not tested for; although data presented in **Chapter 4** does appear to display seasonal patterns, the sampling strategy was not designed to test for temporal variation, and this observation was not tested for significance.

Seasonal depression of bioturbation in winter may allow sediment binding activities to become more effective (Myers, 1977a; 1977b). Bioturbation has been described as the deciding factor in the determination of the net stability of sediment (Yingst & Rhoads, 1978).

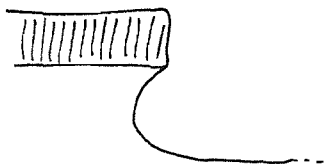
The quantity of suspended material imported to an estuary by a river varies seasonally, as it depends on the frequency of and intensity of precipitation. Storms increase riverine flow rates and thus erosion along river banks. Comparison of meteorological data presented in **Chapter 2** (**Figure 2.6b** and **Figure 2.7**, suspended

particulates) indicates a clear relationship between the flushing rate of the River Somme and the amount of suspended particulate matter in the river water.

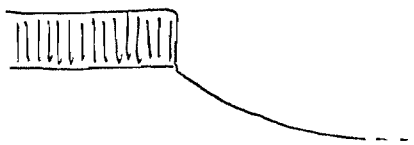
8.3.3 Abiotic Structuring Forces.

Hydrodynamic activity has a strong influence on the development of tube-beds. This is well illustrated in the Somme Bay. The building of a seawall dyke in 1969 suppressed the course-shifting of the River Somme channel, and enabled the seaward progression of salt-marsh vegetation (Ducrotoy *et. al.*, 1985). The consequent reduction in hydrodynamic activity in the Somme Bay was most significantly felt at the HHS site, situated directly behind the dyke. Dupont (1981) described the morphology of *Pygospio* tube-beds at HHS and classified the variety of tube-bedforms he found there. He distinguished between four basic types of tube-bed; each was formed of the familiar, simple array of tubes, but differed in appearance because of local conditions of flow. Dupont's (1981) four tube-bed types are listed below, with reproductions of his drawings. Note that HHS sediment is predominantly composed of silt and clay, compared to the muddy sand of LCS.

- *à encourbellement* (carved-out tube-beds), where strong erosive currents had sculpted away the less-stable sediment below a tube-bed; this clearly demonstrates the increased resistance to erosion conferred by dense aggregations of tubes.



- *à rupture de pente* (with a bed-edge gradient change), found bordering channels were slower flows predominated. Otherwise this bed-form is similar to the "carved-out" form.



- *en gradins* (stepped), which clearly shows that *Pygospio* may settle and build tubes on top of extinct tube-bed formations. Gentle flows had failed to erode these successive "generations" of tube-bed, indicating that tube-beds can retain their structure in the absence of an inhabiting *Pygospio* population. Dupont noted that such constructs do not last long, however, and described them as a senile stage of tube-bed development.

- *trapèzoidaux* (sloping), found in coarser sediment (*i.e.* containing an admixture of sand). Large sloping tube-beds were found, separated by drainage channels. Dupont noted the relics of tube-beds buried to depths of 70cm beneath the extant, surface tube-bed.

The LCS beds monitored in the present study harboured higher densities of *Pygospio* (>100,000m^{-2}) than were found by Dupont at HHS (where they rarely exceeded 50,000m^{-2}). More exposed LCS beds observed in the present study-most closely resembled Dupont's "sloped" form. More dramatic edge formations found at HHS were caused by strongly directional scouring by flow along tidal drainage channels, which form along paths of least resistance in very silty conditions. Such channels were not a feature of the more exposed and sandy LCS.

LCS tube-beds never reached heights above mean sediment level of more than 5-10cm, while at HHS Dupont (1981) recorded tube-beds that dominated the surrounding sediment by up to 40cm. Also, HHS tube-beds were frequently found having been built atop extinct tube-bed aggregations, whereas no evidence of relic tube-beds was found at LCS. These differences must be ascribed to the difference in

hydrodynamic activity between the two sites. LCS tube-beds were literally flattened by the flow while HHS tube-beds were able to grow in height relatively undisturbed.

The asymmetry of the Somme Bay tide is undoubtedly an important factor in the determination of tube-bed morphology. The difference in tidal flow velocities, with a fast flood and slower ebb, confers some degree of orientation to a tube-bed. This effect is found at LCS, which is exposed to the incoming tide; no such orientation has been observed or reported at HHS, where tidal flows are attenuated by the seawall dyke. An analogy may be made here with dune formation. During exposure to an incident flow, the stoss is eroded while deposition occurs in the lee. This effect is more marked during the stronger flood flows, and tube-beds appear to face the sea with sloping edges, while the ebb-facing edge shows less of a gradual gradient. "Blow outs", where pits or weakened areas of sediment preferentially erode, show the same orientation to tidal flow.

8.4 Tube-Beds and Succession

Successional cycles usually begin with some form of disturbance and defaunation which may render the environment temporarily inhospitable. Disturbances might result from unusually cold winters, physical damage by storms, trawling or dumping, pollution by toxic inorganic compounds, or eutrophication and oxygen depletion.

The following section begins with a consideration of defaunated, post-disturbance sediment and its colonisation by a pioneer tube-bed forming species. The fate of this tube-bed forming population is then addressed. It may decline, or persist.

8.4.1 Post-disturbance Colonisation by Tube-Bed Forming Populations.

Disturbances (either natural or experimentally induced) that bring about defaunation result in the recolonisation of the sediment by opportunist species which swiftly achieve high densities (Grassle & Grassle, 1974; McCall, 1977). The pattern of such recolonisation is "virtually independent of the causes of defaunation" (Noji & Noji, 1991). The timing of the disturbance is important if opportunists are to recolonise successfully, however, and must coincide with a plentiful supply of larvae in the

plankton (Zajac & Whitlach, 1982; Levin, 1984a). Zajac & Whitlach (1991) emphasised the importance of the demographic responses of all the component species in a community. The importance of the timing of disturbance was demonstrated by them in simulations based on recruitment and population growth rate data of *Polydora ligni*: the model population was less successful in re-establishing after a spring disturbance than after a summer disturbance. The importance of larval supply and recruitment success has become encapsulated in the theory dubbed "Supply-side ecology" (Gaines & Roughgarden, 1985; Lewin, 1986).

The first successional stage usually includes spionid polychaetes, many of which are capable of massive proliferation: *e.g. Polydora ciliata*, *Polydora ligni*, *Pygospio elegans* and *Streblospio benedictii* (Persoone, 1965; McCall, 1977; Rumohr, 1980). A *Polydora ciliata* population of density 1,000,000m^{-2} has been recorded (Daro & Polk, 1973). Hutchinson (1967) described spionids as exhibiting a quick response to newly-created habitats. Such opportunistic, tube-dwelling species can tolerate adverse conditions of eutrophication. The ability to colonise eutrophic areas has been seen as a reflection of life history adaptations rather than a tolerance of hypoxia (Warren, 1984), and the formation of dense populations has been described as a mechanism to increase diffusion rates between eutrophic sediments and their overlying waters (Aller, 1982). Such species are important in "conditioning" disturbed substrates for recolonisation (Rumohr, 1980; Gallagher *et. al.*, 1983; Reise, 1983b; Schmager-Noji, 1988; Chareonpanich *et. al.*, 1993).

8.4.2 Disturbances to Tube-Beds.

Once the structure of a tube bed is physically undermined, eroded patches and decreasing tube densities may stimulate flows that enhance scouring. Daro & Polk (1973) described *Polydora ciliata* tube-beds being quickly fragmented and washed away by water currents while Rumohr (1980) observed the total displacement of a *Polydora* tube-bed by boring molluscs (genus *Saxicava*) over a period of a year. Similarly, Noyer (1993) documented the rapid displacement of a dense *Pygospio* population by *Cerastoderma edule* in the Somme Bay. Unfortunately this amensalism could not be tested further given the absence of *Cerastoderma* from the present data

set. The rapid destruction of a *Pygospio* tube-bed on the foreshore of the Wirral, UK following local sediment disturbance was monitored by Hoare (pers. comm. in Eagle, 1975). The smothering effect of algal mats in eutrophied areas has been shown to reduce *Pygospio* populations (Nicholls *et. al.*, 1981; Soulsby *et. al.*, 1982; Hull, 1987; Bonsdorff, 1992).

Physical disturbance by megafaunal predators is a further consideration: Carey (1987) observed break-up of *Lanice conchilega* tube-beds being exacerbated by the browsing activities of Eider duck, while Fager (1964) described the dissection of an *Owenia fusiformis* tube-bed into "hummocks" by a school of bat rays. Spionids are a food source for demersal fish (De Vlas, 1979). Among the most severe disturbances in coastal regions are those caused by human activities. In the Somme Bay, shell fishing and bait digging occur all year round; furthermore, the site LCS is also known as Le Crotoy's beach, and represents a popular recreational resort during the summer months.

Carter (1976) noted the influence of meteorological conditions, and found that in many areas winter weather caused greater disturbances to infaunal communities than could be counteracted by biological sediment binding. Hydrodynamic and meteorological influences on the *Pygospio* population have been discussed in **Chapter 2**. The absence of severe storms in 1985 may have been a contributing factor in the proliferation of *Pygospio* at both LCS and HHS.

Highly-dense spionid populations may "self-destruct", through food depletion (Whitlach & Zajac, 1985). Trueblood *et.al.* (1994) observed a decline in *Pygospio* density in Boston Harbour and speculated that the original population of 83,000m^{-2} had out-grazed the diatom on which it predominantly fed. The complex interaction of many environmental variables makes it difficult to pinpoint with certainty the cause of a population crash. Theories of auto-eutrophication or other self-induced mortalities are therefore difficult to test. In the present study, no clear indications of density-aggravated mortality in the Somme Bay population were found. Environmental carrying capacity in not thought to have been exceeded even by *Pygospio* populations of many 100,000's m^{-2}: mean somatic size did not appear to show any consistent patterns of decrease with increasing population density, for example. Nor did the study of intertubular spacing indicate any competitive interactions, at least at densities

between 40,000m^{-2} and 80,000m^{-2} (**Chapter 6**). In **Chapter 4** a theory of microbial cycling was advanced to explain how metabolite build-up (and thus auto-eutrophication) was avoided during the prolonged emersion experienced by LCS at low tide.

Disturbance to tube-beds may result from competition between the tube-bed building species and co-habitants. Noji & Noji (1991) noted that, "in most cases, spionids are completely replaced by subsequent colonisers". Pianka (1972) described spionids as poor competitors. Chesney (1985), however, argued that supposedly weakly competitive pioneering species are not always ousted by later seres. He noted that such competitive exclusion must involve maximum exploitation of resources by incoming successor species, and invoked a non-equilibrium view of soft-bottom succession, in which patches of pioneering species could flourish for extended periods. Non-equilibrium theory will be addressed in the following section.

8.4.3 The Persistence of Opportunist Populations.

For most of the past century, the dominant view has been that community structuring is determined by inter-specific interactions such as competition and predation: *i.e.* that a community is at equilibrium, with a stable species composition through time. The view now attaining acceptance is that the population dynamics of a soft-bottom community may be viewed as a series of successional events (Gleason, 1927) and the benthic habitat seen as a spatio-temporal mosaic containing patches which vary in successional maturity (Johnson, 1973; Caswell, 1978; Remmert, 1991). This view represents a "non-equilibrium" theory, in which the dominating structuring parameters are frequency and intensity of disturbance events, and the success of recruitment. "Equilibrium" is now considered an unusual state for natural ecosystems; ecosystems might be more accurately thought of a recovering from the most recent disturbance (Reice, 1994). This is especially true in the case of the highly dynamic coastal regions of the North and Baltic Seas (Arntz & Ruhmor, 1982).

Disturbance effectively retards, or even resets, the successional sequence. MacArthur (1960) noted that pioneer species may persist under a regime of near continuous disturbance. In effect, the community of a chronically disturbed

environment is caught in a continually cycling primary seral stage. Examples of persistent populations of pioneering / opportunistic species exist in the literature, *e.g.* Turner (1983) and Eagle (1975). The *Pygospio* population of the hydrodynamically active, organically enriched Somme Bay constitutes another example.

8.5 Synthesis: Tube-Bed Dynamics

8.5.1 Conditions Required for Tube-Bed Formation, Foundation and Growth.

The high-density populations that produce tube-beds require a highly productive environment for their support. The Somme Bay receives organically enriched allochthonous input from the agricultural catchment area of the Somme Valley (Rybarczyk, 1996). Furthermore, the LCS site has the most productive benthic community of the Bay (Desprez, 1994).

For successful high density recruitment, reproduction must be geared to ensure the availability of propagules (larval or asexual) at the right time and in the right place for the monopolisation of available sediment. In the Somme Bay population these conditions are fulfilled by the extended period of sexual reproduction and a planktonic mode of larval development. The number of broods per year was increased to two in this population by the release at an early developmental stage of larvae into highly productive Somme Bay waters; reliance for the supply of nutrient for larval growth and development was thus also shifted from the parent to the environment, potentially allowing parents to devote even more resources to reproduction.

A minimum settlement density required for successful tube-bed foundation is postulated. In the absence of a dense settlement, erosion may be induced by flow around newly-built tubes at low density, and the chances of a recruitment failure increased through suffocation and resuspension. Newly settled larvae are immediately competent to build tubes, but may be at increased risk of resuspension because of their small size, and the lack of penetration to depth of their tubes. Preferential settlement of larvae into tube-beds may then occur through flow-related deposition; settlement may also be facilitated by larval sensitivity and attraction to microbial biofilms and higher levels of organic matter that are characteristic of tube-beds. However, a tube-bed is considered as being primarily formed during one single massive and successful

recruitment to a patch of sediment. Secondary, preferential settlement into the new tube-bed must rely on the presence of a high density of earlier settlers for positive cues such as increased organic load, or passive, flow-related depositional effects to become effective. Secondary settlement over an extended period causes the wide range of somatic sizes noted from single tube-bed populations. Tube-bed densities may then become further augmented by the immigration of adults; it appears for example that mature males are attracted to high conspecific densities. The exact mechanism for such attraction is not known.

Tube-bed growth is mediated by the twin processes of erosion and deposition. Tube-beds show both preferential deposition and resistance to erosion. Tube-bed elevation is indicated by the lengthening of tubes with tube-bed age as the inhabitant works to keep its tube's top open at the sediment surface. Active, surface-level-tracking growth is evinced by x-radiographs in which the tube's growth through the sediment is curved to meet the surface at a perpendicular (**Plate X.7a**; also x-radiographs taken of June 1995 sediment, not included for presentation). Presumably a worm builds a straight tube, such that the tube meets the surface at a perpendicular, as a tube meeting the surface at an angle would cause the inhabitant to contort unnecessarily to fully exploit its foraging area. A curving tube could then only mean that the orientation of the surface had moved away from horizontal at some time in the past, and the worm had altered its building trajectory to complement the new surface orientation. Tube length thus serves as a good indication of tube-bed maturity.

It is noted that a tube-bed forming threshold density of 50,000m^{-2} was apparent from sampling in the Somme Bay; the physical appearance of a tube-bed might thus be thought of as an emergent property of *Pygospio* populations of density greater than this. The morphology of a tube-bed is primarily determined by hydrodynamic conditions. No spatial heterogeneity in intra-bed population structure was found that might cause heterogeneous tube-bed growth. In the Somme Bay, *Pygospio* tube-beds established in exposed areas such as LCS do not attain heights above surrounding sediment of more than 10cm, whereas tube-beds built in more quiescent areas such as HHS can reach well over 30cm in height. Tube-bed edges adjacent to fast-flowing tidal channels may

be eroded into cliff-like formations; more gradual, sloping edges are formed where flow is not channelled.

8.5.2 Factors Involved in Tube-Bed Decline.

The decline of a tube-bed may be conceived as being either gradual or catastrophic. Gradual decline might result from adverse competition, eutrophication, or age. Neither of the two former phenomena are felt to play a part in the dynamics of Somme Bay tube-beds. A tube-bed may however have a certain "life-span", however, determined by the natural life-span of the population of primary and secondary recruits already mentioned. A tube-bed is considered to be the construct of a single, massive settlement event and subsequent, preferential secondary settlement. It is thought unlikely that tube-beds are "re-used" by the following year's generation. Cultured individuals, stripped of their tubes and presented with both clean sediment and unoccupied tubes, invariably made fresh tubes. In the field, it is also likely that unmaintained tubes would soon become smothered and buried. It is difficult to quantify the life-span of a tube-bed based on the senescence of its *Pygospio* population. No measurements have been made of *Pygospio*'s natural life-expectancy in the natural environment. Given the extended period of settlement, *Pygospio* tube-beds of a range of maturity may be present in the Bay at any one time.

The catastrophic collapse of tube-beds is thought to occur as the result of meteorological activity, and is likely to be most intensely felt over the winter months. Storms of sufficient violence to resuspend or smother very large (many m^2) areas of sediment may occur. Tube-beds, as discrete entities, also fragment under the influence of more mild physical disturbances. Small tube-bed remnants, with large surface area to volume ratios, are then more susceptible to erosion.

Resuspended adults are scattered within Bay waters to resettle elsewhere. Were this redistribution of individuals in space a frequent occurrence, one would expect a random spatial variability in population structure. The presence of density dependent and spatial patterns of population structure does support the view that tube-beds last long enough to have an impact on the populations they contain.

8.5.3 Factors Involved in Tube-Bed Persistence.

The *Pygospio* population in the Somme Bay has demonstrated extended periods during which it has dominated the macroinfaunal community. These high densities have been concentrated in a spatio-temporally shifting patchwork of tube-beds, almost continually reseeded from the plankton. *Pygospio*'s persistence is ascribed to the frequent small-to-medium scale disturbances to the sediment caused by hydrodynamism and eutrophication / anoxia which "reset" the successional clock. *Pygospio* is provided with suitable conditions for recolonisation of disturbed substrates, and the establishment of a more mature seral stage, which could perhaps competitively exclude *Pygospio*, is prevented. Under the intermediate disturbance hypothesis, the Somme Bay represents a situation of frequent disturbance and low community diversity.

8.5.4 The Benefits of Tube-Bed Formation to the *Pygospio* Population.

A tube-bed offers a resource; increased deposition of organic detritus, and enhanced sediment irrigation foster an abundant microbial community. By the same token, metabolites are efficiently removed from the sediment and autoeutrophication avoided. A tube-bed offers a refuge from erosion; increased sediment cohesiveness and stability allows residents to resist resuspension by strong localised hydrodynamic activity. Small tube-dwelling species may otherwise be unable to tolerate life in such physically disturbed areas. If it can be tolerated, further benefits may accrue from exposure to strong currents, including an increased rate of nutrient import and higher levels of water oxygenation. High conspecific densities prevalent in tube-beds increase the likelihood, and perhaps rate, of sexual activity. This is especially important when the small size, poor mobility and requirement for copulation in *Pygospio* is considered. The Somme Bay population may lack asexual behaviour because of the relative proximity of sexually mature conspecifics.

8.6 Suggestions for Further Work

During the course of this multidisciplinary study many different approaches to understanding tube-bed dynamics were considered. The diversity of these different approaches meant that not all of them could be included in the time-scale available, however. Some of these methods deserve mention here as they are perceived as interesting avenues of further investigation.

8.6.1 Use of Molecular Techniques to Investigate the Possibility of Sub-speciation.

In **Chapter 3** suggestions were made for the further study of the question of *Pygospio*'s taxonomy. A study involving both an analysis of population reproductive biology and molecular techniques will show if the mechanism determining *Pygospio*'s reproductive response is inherited or adaptive.

8.6.2 Monitoring Tube-Bed Dynamics: the Application of Remote Sensing.

The spectrum of solar radiation reflected from an area of the Earth's surface can be measured using recently developed "remote sensing" technology (Curran, 1994). The quality of light is determined by the nature of the substrate from which it was reflected; a correctly calibrated spectroradiometer can therefore determine the quality of a reflecting surface from a distance. Remote sensing has found wide application in mapping where accurate, large scale spatial information is required; geologists map mineral deposits; meteorologists map the distribution of gasses in the atmosphere, and oceanographers map the distribution of temperature, suspended sediment and algal blooms in the oceans. Remote sensing has also found application in coastal studies; Coulson *et.al.* (1980) mapped the distribution of sediment algae in Chichester Harbour.

The ability of spectroradiometers to qualify differences in surface texture, moisture content, mineral composition and abundance of chlorophyll make remote sensing a potentially useful method of mapping the distribution of *Pygospio* tube-beds at the scale of the whole estuary. *Pygospio* beds have been seen to alter sediment physical qualities: tube-beds are resistant to erosion and therefore tend to lack ripple

marks; they drain more quickly and may thus be drier at low tide; and they support more abundant communities of chlorophyll-bearing microphytobenthos.

The use of remote sensing apparatus owned by the Natural Environment Research Council was considered for the present study. However, current available technology is limited in the spatial resolution of its measurements and the scale of horizontal variation in Somme sediment elevation and habitation was felt to be too fine to be reliably detected by low-level, airborne equipment.

When improved spectrophotometer resolution becomes easily available, its application to determining the actual scale of tube-bed formation in the Somme Bay would undoubtedly prove interesting to those compiling sediment budgets for the system. Silt and clay brought in by the Somme, or released from salt-marsh sediment, is trapped to some extent by *Pygospio* tube-beds.

8.6.3 Assessment of Tube-Beds' Role in Salt-Marsh Encroachment.

The role of *Pygospio* tube-beds in facilitating salt marsh encroachment has been the topic of some speculation (*e.g.* Dupont, 1981), but no actual study. Clumps of the pioneering salt marsh grass *Spartina* sp, growing from *Pygospio* tube-beds, are a familiar sight in the Somme Bay. *Spartina* clearly favour tube-beds as a substrate: this is most probably because of the increased stability tube-beds offer. The increased output of nitrogenous metabolites associated with dense macrobenthic communities may also offer a richer nutrient resource to the developing plant. Salt-marsh growth may lead to land reclamation, and thus is of some larger environmental and economic interest. It would thus be interesting to determine the involvement of tube-bed sediment stabilisation and conditioning in this context. The vertical profiling methodologies outlined in **Chapter 7** may be of use here. Deep cores taken into the sediment underlying the salt marsh directly behind HHS may reveal the preserved traces of tube beds.

8.6.4 Towards a Mathematical Model of Tube-Bed Dynamics.

Interactions between individual units of biological systems, e.g. individuals or species, contribute to the larger scale patterns of distribution in ecosystems. Were the

nature of these interactions known, the spatio-temporal dynamics of a system might be modelled, given the proper modelling conditions (Bascompte & Solé, 1995).

Until recently, ecological modelling techniques have ignored the role of spatial structuring. However, mathematical modelling of the spatial and growth dynamics of complex, biologically-driven systems has recently been much enhanced by the availability of powerful computers. The "cellular automaton" (hereafter CA) modelling environment is an approximation of a reaction-diffusion model in which both space and time are treated discreetly; as such it is computationally quite simple (Wolfram, 1983; 1986).

A CA is formed of a regular grid of cells, each of which is characterised by one or more discreet variables. At time = 0, the CA grid is "seeded" with cells of random or predetermined state. Interactions between cells are specified by "transition rules" and given ranges of influence; at each discrete time-step (t=1; t=2, *etc.*) the state of a cell is updated by the states of the other cells which have been assigned an influence over it. Of special interest is the way in which a set a very simple transition rules can generate highly complex and unexpected "emergent" patterns.

CA have found wide employment in biology (Caswell & Etter, 1993; Ermentrout & Edelstein-Keshet, 1993); it has been used to model the growth of cancerous tumours (Qi *et. al.*, 1993), growth patterns of clonal plants (Inghe, 1989), wildfire propagation in forests (Clarke *et. al.*, 1994), interspecific competition in plant communities (Silvertown *et. al.*, 1992), succession in plants (Colasanti & Grime, 1993; Hendry & McGlade, 1995), and in fungi (Halley *et. al.*, 1994). The adaptive nature of dispersal in disturbed regimes has been modelled using CA by Etter & Caswell (in press).

Although a mathematical model lay outside the scope of this thesis, CA were considered as an environment for modelling the spatio-temporal dynamics of tube-beds. The role of spatial proximity in determining the status of CA cells was seen as having interesting parallels with the apparent *Pygospio* density dependance of tube-bed construction. Preliminary transition rules were drawn up to operate at the level of the individual: a cell might for example have the following states: unoccupied; one *Pygospio* present; one unoccupied tube present. A cell might also have a secondary,

coupled state describing its resistance to erosion; this would in turn depend on the presence of a tube, the time the cell has spent accreting silt and the proximity of other tube-containing cells. Other density-dependent transition rules, concerning competition, *Pygospio* feeding behaviour, metabolite build-up and irrigation, reproductive success and larval settlement rate could be invoked. It was hoped that insights gained from the present work would allow for the compilation of a realistic set of such transition rules and the development of a model of *Pygospio* tube-bed dynamics. However, building physical forcing agents such as boundary layer fluid dynamics into the transition rules at the correct scale proved too great a conceptual obstacle. The valid and correct translation of such intrinsically complex processes into such a model may in fact be impossible to do realistically (R. Etter, pers. comm.).

If physical factors such as boundary flow conditions could be built in, it is felt that a mathematical model of this nature would be the most productive way forward in the study of tube-beds. A whole range of conditions could be simulated, and hypotheses concerning tube-bed dynamics could be more thoroughly tested.

References.

Allen, J. R. L. (1970). **Physical Processes of Sedimentation: An Introduction.** Allen & Unwin.

Allen, J. R. L. (1985). **Experiments in Physical Sedimentology**. Allen & Unwin.

Aller, J. Y. & Aller, R. C. (1986). Evidence for localised enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. **Deep Sea Research: Oceanographic Research Papers, 33**, 755-790.

Aller, R. C. (1978). The effects of animal-sediment interactions on geochemical processes near the sediment-water interface. In M. L. Wiley (Ed.), **Estuarine Interactions** (pp. 157-172).

Aller, R. C. (1980a). Quantifying solute distributions in the bioturbated zone of marine sediments by defining an average microenvironment. **Geochimica and Cosmochimica Acta, 44**, 1955-1965.

Aller, R. C. (1980b). Relationship of tube-dwelling benthos with sediment and overlying water chemistry. In K. R. Tenore & B. C. Coull (Eds.), **Marine Benthic Dynamics** (pp. 285-308). University of South Carolina Press.

Aller, R. C. (1982). The effects of macrobenthos on chemical properties of marine sediment and overlying waters. In P. L. McCall & M. J. S. Tevesz (Eds.), **Animal-Sediment Relations** (pp. 53-102). New York: Plenum.

Aller, R. C. (1984). The importance of relict burrow structures and burrow irrigation in controlling sedimentary solute distributions. **Geochimica and Cosmochimica Acta, 48**, 1929-1934.

Aller, R. C. (1988). Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In T. H. Blackburn & J. Sørenson (Eds.), **Nitrogen Cycling in Coastal Marine Sediments.** (pp. 301-338). John Wiley & Sons.

Aller, R. C. & Yingst, J. Y. (1978). Biogeochemistry of tube dwellings: a study of the sedentary polychaete *Amphitrite ornata* (Liedy). **Journal of Marine Research, 36**, 201-254.

Aller, R. C. & Yingst, J. Y. (1985). Effects of the marine deposit feeders *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia) and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates and microbial distributions. **Journal of Marine Research, 43**, 615-645.

Alongi, D. M. (1985). Microbes, meiofauna, and bacterial productivity on tubes constructed by the polychaete *Capitella capitata*. **Marine Ecology Progress Series, 23**, 207-208.

Ambrose, W. G. J. (1984). Role of predatory infauna in structuring marine soft-bottom communities. **Marine Ecology Progress Series, 17**, 109-115.

Anger, K. (1977). Benthic invertebrates as indicators of organic pollution in the Western Baltic Sea. **International Revue der Gesampten Hydrobiologie, 62**, 245-254.

Anger, K., Anger, V., & Hagmeier, E. (1986). Laboratory studies on larval growth of *Polydora ligni, Polydora ciliata* and *Pygospio elegans* (Polychaeta, Spionidae). **Helgoländer Meeresuntersuchungen, 40**, 377-395.

Anger, V. (1984). Reproduction in *Pygospio elegans* (Spionidae) in relation to its geographical origin and to environmental conditions - a preliminary report. **Fortschritte der Zoologie, 29**, 45-51.

Armonies, W. (1988). Active emergence of meiofauna from intertidal sediment. **Marine Ecology Progress Series, 43**, 151-159.

Armonies, W. (1994). Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. **Helgoländer Meeresuntersuchungen, 48**, 299-320.

Arntz, W. E. & Ruhmor, H. (1982). An experimental study of macrobenthic colonisation and succession, and the importance of seasonal variation in temperate latitudes. **Journal of Experimental Marine Biology and Ecology, 64**, 17-45.

Bachelet, G. (1990). Recruitment of soft-sediment infaunal invertebrates: the importance of juvenile benthic stages. **La Mer, 28**, 199-220.

Bailey-Brock, J. H. (1979). Sediment trapping by chaetopterid polychaetes on an Hawaiian fringing reef. **Journal of Marine Research, 37**, 643-646.

Banse, K. (1986). Vertical distribution and horizontal transport of planktonic larvae of echinoderms and benthic polychaetes in an open sea. **Bulletin of Marine Science, 39**, 162-175.

Bascompte, J. & Solé, R. V. (1995). Rethinking complexity: modelling spatiotemporal dynamics in ecology. **Trends in Ecology and Evolution, 10**, 361-366.

Bastrop, R., Röhner, M., & Jürss, K. (1995). Are there two species of the polychaete *Marenzellaria* in Europe? **Marine Biology, 121**, 509-516.

Batten, S. D. (1994) **Correlative studies of the ecophysiology and community structure of benthic macrofauna.** Ph.D. Thesis, Southampton University.

Baumgartner, T. R., Ferreira-Bartrina, V., Cowen, J., & Soutar, A. (1991). Reconstruction of a 20th Century varve chronology from the central Gulf of California. In J. P. Dauphin & B. R. T. Simoniet (Eds.), **The Gulf and Peninsular Province of the Californias. AAPG Memoirs 47** (pp. 603-616).

Belgrano, A. & Dewarumez, J. M. (1995). The influence of tidal-induced variability on the distribution of meroplankton larvae in the Southern Bight of the North Sea. **Oceanologica Acta, 18**, 523-530.

Bellan, G. (1977). A discussion of the relationship between systematics and ecology in polychaetous annelids. In D. J. Reish & K. Fauchald (Eds.), **Essays on Polychaetous Annelids, In Memory of Dr. Olga Hartman.** (pp. 449-460). Los Angeles: Allan Hancock Foundation, University of Southern California.

Bick, A. & Gosselk, F. (1985). Arbeitsschlüssel zur Bestimmung der Polychäeten der Ostsee. **Mitteilungen des Zoologisches Museums in Berlin, 61**, 171-272.

Blake, J. A. (1969). Reproduction and larval development of *Polydora* from Northern New England (Polychaeta, Spionidae). **Ophelia, 7**, 1-63.

Blake, J. A. & Kudenov, J. D. (1981). Larval development, nutrition and growth for two *Boccardia* species (Polychaeta, Spionidae) from Victoria, Australia. **Marine Ecology Progress Series, 6**, 175-182.

Boer, P. L. (1981). Mechanical effects of microorganisms on intertidal bedform migration. **Sedimentology, 28**, 129-132.

Boicourt, W. C. (1982). Estuarine larval retention mechanisms on two scales. In V. Kennedy (Ed.), **Estuarine Comparisons** (pp. 445-457). New York: Academic Press.

Bonsdorff, E. (1992). Drifting algae and zoobenthos - effects on settling and community structure. **Netherlands Journal of Sea Research**, **30**, 57-62.

Boudreau, B. P. & Marinelli, R. L. (1994). A modelling study of discontinuous biological irrigation. **Journal of Marine Research**, **52**, 947-968.

Bouma, A. H. (1964). Notes on X-ray interpretation of marine sediments. **Marine Geology**, **2**, 278-309.

Bouma, A. H. (1969). **Methods For The Study of Sedimentary Structures.** John Wiley & Sons.

Breeze, W. P. & Phibbs, F. D. (1972). Ingestion of bivalve molluscan larvae by the polychaete annelid *Polydora ligni*. **Veliger**, **14**, 274.

Brey, T. (1991). Interactions in soft-bottom benthic communities - quantitative aspects of behaviour in the surface deposit feeders *Pygospio elegans* (Polychaeta) and *Macoma balthica* (Bivalvia). **Helgoländer Meeresuntersuchungen**, **45**, 301-316.

Brodie, I. & Kemp, A. E. S. (1994). Variation in biogenic and detrital fluxes and formation of laminae in late Quaternary sediments from the Peruvian coastal upwelling zone. **Marine Geology**, **116**, 385-398.

Buchanan, J. B. (1984). Sediment analysis. In N. A. Holme & A. D. McIntyre (Eds.), **Methods for the Study of Marine Benthos**

Burd, J. B., Nemec, A., & Brinkhurst, R. O. (1989). The development and application of analytical methods in benthic marine infaunal studies. **Advances in Marine Biology**, **26**, 170-249.

Burger, J. A., Klein, G.dV. & Sanders, J. E. (1969). A field technique for making epoxy relief-peels in sandy sediments saturated with salt-water. **Journal of Sedimentary Petrology**, **39**, 338-341.

Butman, C. A. & Grassle, J. P. (1992). Active habitat selection by *Capitella* sp.1 larvae. 1. Two-choice experiments in still-water and flume flows. **Journal of Marine Research**, **50**, 669-715.

Cadman, P. S. & Nelson-Smith, A. (1990). Genetic evidence for two species of lugworm (*Arenicola*) in South Wales. **Marine Ecology Progress Series, 64**, 107-112.

Calvert, S. E. & Veevers, J. J. (1962). Minor structures of unconsolidated marine sediments revealed by X-radiography. **Sedimentology, 1**, 256-286.

Carey, D. A. (1983). Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes. **Canadian Journal of Fisheries and Aquatic Sciences, 40**(suppl. 1), 301-308.

Carey, D. A. (1987). Sedimentological effects and paleoecological implications of the tube-building polychaete *Lanice conchilega* Pallas. **Sedimentology, 34**, 49-66.

Carpenter, R. C. (1981). Grazing by *Diadema antillarum* (Phillipi) and its effects on the benthic algal community. **Journal of Marine Research, 39**, 749-765.

Carter, L. (1976). Seston transport and deposition in Pelorus Sound, South Island, New Zealand. **New Zealand Journal of Geology and Geophysics, 20**, 335-351.

Caswell, H. (1976). Community structure: a neutral model analysis. **Ecological Monographs, 46**, 327-354.

Caswell, H. (1978). Predator-mediated coexistence: a non-equilibrium model. **American Naturalist, 112**, 127-154.

Caswell, H. (1981). The evolution of "mixed" life histories in marine invertebrates and elsewhere. **American Naturalist, 117**, 529-536.

Caswell, H. & Etter, R. J. (1993). Ecological interactions in patchy environments: from patch-occupancy models to cellular automata. In S. A. Levin, T. M. Powell, & J. H. Steele (Eds.), **Lecture Notes in Biomathemetics, No.96: Patch Dynamics** (pp. 93-109). Springer-Verlag.

Chareonpanich, C., Montani, S., Tsutsumi, H., & Matsuoka, S. (1993). Modification of chemical characteristics of organically enriched sediment by *Capitella* sp.1. **Marine Pollution Bulletin, 26**, 375-379.

Chesney, E. J. J. (1985). Succession in soft-bottom benthic environments: are pioneering species really outcompeted? In **Proceedings 19th EMBS** (pp. 277-286).

Chia, F. S. (1974). Classification and adaptive significance of developmental patterns in marine invertebrates. **Thalassia Jugoslavica, 10**, 121-130.

Chia, F.-S., Gibson, G., & Qian, P.-Y. (1996). Poecilogony as a reproductive strategy of marine invertebrates. **Oceanologica Acta, 19**, 203-208.

Christensen, C. J., Gorsline, D. S., Hammond, D. E., & Lund, S. P. (1994). Non-annual laminations and expansion of anoxic basin-floor conditions in Santa Monica Basin, California Borderlands, over the past four centuries. **Marine Geology**(116), 399-418.

Christiansen, F. B. & Fenchel, T. M. (1979). Evolution of marine invertebrate reproductive patterns. **Theoretical Population Biology, 16**, 267-282.

Claparède, E. (1863). **Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere.**

Clarke, K. C., Brass, J. A., & Riggan, P. J. (1994). A cellular automaton model of wildfire propagation and extinction. **Photogrammetric Engineering and Remote Sensing, 60**, 1355-1367.

Clarke, K. R. & Warwick, R. M. (1994). **Change In Marine Communities: An Approach To Statistical Analysis And Interpretation.** Natural Environmental Research Council.

Cliff, A. D. & Ord, J. K. (1973). **Spatial Autocorrelation**. London: Pion Ltd.

Colasanti, R. L. & Grime, J. P. (1993). Resource dynamics and vegetation processes: a deterministic model using two dimensional cellular automata. **Functional Ecology, 7**, 169-176.

Coles, S. M. (1979). Benthic microalgal populations on intertidal sediments and their role as precursors to salt-marsh development. In R. C. Jeffries & A. J. Davy (Eds.), **Ecological Processes in Coastal Environments.** Oxford: Blackwell.

Collinson, J. D. & Thompson, D. B. (1982). **Sedimentary Structures**. Allen & Unwin.

Connell, J. H. (1978). Diversity in tropical rainforests and coral reefs. **Science, 199**, 1302-1310.

Connell, J. H. & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organisation. **American Naturalist, 111**, 1119-1144.

Coulson, M. G., Budd, J. T. C., Withers, R. G., & Nicholls, D. N. (1980). Remote sensing and field sampling of mudflat organisms in Langstone and Chichester Harbours, Southern England. In J. H. Price, D. E. G. Irvine, & W. F. Farnham (Eds.), **The Shore Environment, Vol. 1. Systematics Association Special Volume no. 17a** (pp. 241-263). Academic Press.

Crisp, D. J. (1974a). Energy relations of marine invertebrate larvae. **Thalassia Jugoslavica, 10**, 103-120.

Crisp, D. J. (1974b). Factors influencing the settlement of marine invertebrate larvae. In P. T. Grant & A. M. Mackie (Eds.), **Chemoreception in marine organisms** (pp. 177-265). New York: Academic Press.

Cronin, T. W. (1982). Estuarine retention of larvae of the crab *Rhithropanopeus harrisii*. **Estuarine and Coastal Shelf Science, 15**, 207-220.

Cullen, D. J. (1973). Bioturbation of superficial marine sediments by interstitial meiobenthos. **Nature, 242**, 323-324.

Cummings, V. J., Pridmore, R. D., Thrush, S. F., & Hewitt, J. E. (1996). Effect of the spionid polychaete *Boccardia syrtis* on the distribution and survival of juvenile *Macocomona liliana* (Bivalvia: Tellinacea). **Marine Biology, 126**, 91-98.

Curran, P. J. (1994). Imaging Spectrometry. In J. Hill (Ed.), **Imaging Spectrometry as a Tool for Environmental Observation.** Kunner Academic.

Dade, W. B., Davis, J. D., Nichols, P. D., Nowell, A. R. M., Thistle, D., Trexler, M. B., & White, D. C. (1990). Effects of bacterial exopolymer adhesion on the entrainment of sand. **Geomicrobiology Journal, 8**, 1-16.

Dales, R. P. (1963). **Annelids**. London: Hutchinson & Co.

Daro, M. H. & Polk, P. (1973). The autoecology of *Polydora ciliata* along the Belgian coast. **Netherlands Journal of Sea Research, 6**, 130-140.

Davey, J. T. & Watson, P. G. (1995). The activity of *Nereis diversicolor* (Polychaeta) and its impact on nutrient fluxes in estuarine waters. **Ophelia, 41**, 57-70.

Day, J. H. (1967). **A Monograph on the Polychaeta of Southern Africa. Part 2: Sedentaria.** British Museum (Natural History).

Day, R. L. & Blake, J. A. (1979). Reproduction and larval development of *Polydora giardi* Mesnil (Polychaeta: Spionidae). **Biological Bulletin (Woods Hole), 128**, 67-76.

De Vlas, J. (1979). Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. **Netherlands Journal of Sea Research, 13**, 117-153.

Dean, T. A. & Hurd, L. E. (1980). Development in an estuarine fouling community: the influence of early colonists on later arrivals. **Oecologia, 22**, 99-117.

Denholm-Young, P. A. (1978) **Studies on decomposing cattle dung and its associated fauna.** DPhil. Thesis, Oxford University.

Desprez, M. (1994). **L'ecosysteme Baie de Somme. Distribution des peuplements benthiques et ichtyologiques de l'espace intertidal et de ses abords.** (Rapports scientifiques et techniques du GEMEL No.

Desprez, M., Rybarczyk, H., Wilson, J. G., Ducrotoy, J.-P., Sueur, F., Olivesi, R., & Elkaim, B. (1992). Biological impact of eutrophication in the Bay of Somme and the inducton and impact of anoxia. **Netherlands Journal of Sea Research, 30**, 149-159.

deVries, M. C., Tankersley, R. A., Forward, R. B. J., Kirby-Smith, W.W., & Luettich, R. A. J. (1994). Abundance of estuarine crab larvae is associated with tidal hydrological variables. **Marine Biology, 118**, 403-413.

DeWilde, P. A. W. J. (1991). Intreactions in burrowing communities and their effects on the structure of marine benthic ecosystems. **Symposia of The Zoological Society of London, 63**, 107-117.

deWolf, P. (1974). On the retention of marine larvae in estuaries. **Thalassia Jugoslavica, 10**, 415-424.

Dorsett, D. A. (1961). The reproduction and maintenance of *Polydora ciliata* Johnst. at Whitstable. **Journal of The Marine Biological Association of the U.K., 41**, 383-396.

Duchêne, J. C. (1984). Reproductive biology of *Boccardia polybranchiata* (Carazzi) in Kerguelen (Subantarctic Province). **Polar Biology, 2**, 251-257.

Duchêne, J. C. (1989). Adelphophagie et biologie larvaie chez *Boccardia polybranchiata* (Carazzi) (Annélide Polychète Spionidae) en province subantarctique. **Vie et Milieu, 39**, 143-152.

Ducrotoy, J. P., Elkaim, B., Lafite, R., & Dupont, J. P. (1986). Essai d'application des notions de confinement au milieu paralique de Baie de Somme. **Journal de Recherche Oceanographique, 11**, 88-89.

Ducrotoy, J.-P., Desprez, M., & Dupont, J.-P. (1985). Short and long term biosedimentary evolution of two *Macoma balthica* communities. In J. G. Wilson & W. Halcrow (Eds.), **Estuarine Management and Quality Assessment** (pp. 105-130). New York: Plenum Press.

Ducrotoy, J.-P., Desprez, M., & Elkaïm, B. (1987). Crise de la production de coques (*Cerastoderma edule*) en Baie de Somme. 2. Impact de la dynamique biosedimentaire. **Revue des Travaux de l'Institute des Pêches Maritimes, 49**, 231-241.

Dupont, J.-P. (1975). Présence de biolithosores á *Pygospio elegans* Claparède (Polychaètes sédentaires) dans la baie de Somme. **Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Serie D., 280**, 1773-1776.

Dupont, J.-P. (1981) **Relations entre bios et phénoménes sédimentaires intertidaux: le modéle de la Baie de Somme.** Ph.D. thesis, Rouen University.

Dyer, K. R. (1979). Estuaries and estuarine sedimentation. In K. R. Dyer (Ed.), **Estuarine Hydrography And Sedimentation.** (pp. 1-19). Cambridge University Press.

Eagle, R. A. (1975). Natural fluctuations in a soft bottom benthic community. **Journal of The Marine Biological Association of the U.K., 55**, 865-878.

Eckelbarger, K. J. (1986). Vittelogenic mechanisms and the allocation of energy to offspring of polychaetes. **Bulletin of Marine Science, 39**, 426-443.

Eckelbarger, K. J. & Grassle, J. P. (1983). Ultrastructural differences in the eggs and ovarian follicle cells of *Capitella* (Polychaeta) sibling species. **Biological Bulletin (Woods Hole), 165**, 379-393.

Eckman, J. E. (1979a). **Particle deposition in animal-tube waters: description, identification of relevant parameters and biological significance**. Friday Harbour Laboratory Library.

Eckman, J. E. (1979b). Small-scale patterns and processes in a soft substratum intertidal community. **Journal of Marine Research, 37**, 437-457.

Eckman, J. E. (1982) **Hydrodynamic effects exerted by animal tubes and marsh grasses and their importance to the ecology of soft-bottom, marine benthos.** Ph.D Thesis, University of Washington.

Eckman, J. E. (1983). Hydrodynamic processes affecting benthic recruitment. **Limnology and Oceanography, 28**, 241-257.

Eckman, J. E. & Nowell, A. R. M. (1984). Boundary skin friction and sediment transport about an animal-tube mimic. **Sedimentology, 31**, 851-862.

Eckman, J. E., Nowell, A. R. M., & Jumars, P. A. (1981). Sediment destabilisation by animal tubes. **Journal of Marine Research, 39**, 361-374.

Ermentrout, G. B. & Edelstein-Keshet, L. (1993). Cellular automata approaches to biological modelling. **Journal of Theoretical Biology, 160**, 97-133.

Etter, R. J. & Caswell, H. (in press). The advantage of dispersal in a patchy environment: effects of disturbance in a cellular automaton model. In C. Young & K. Eckelbarger (Eds.), **Reproduction, Larval Biology and Recruitment in the Deep-Sea Benthos.** Columbia University Press.

Everitt, B. (1980). **Cluster Analysis** (2nd ed.). Heinemann, London.

Fager, E. W. (1964). Marine sediments: effects of a tube-building polychaete. **Science, 143**, 356-359.

Fauchald, K. (1977). The Polychaete worms: definitions and keys to the orders, families and genera. **Natural History Museum of Los Angeles County Science Series, 28**.

Fauchald, K. & Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. **Oceanography and Marine Biology Annual Review, 17**, 193-284.

Fauvel, P. (1927). Polychètes sedentaires. **Faune de France, 16**, 1-494.

Featherstone, R. P. & Risk, M. J. (1977). Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. **Journal of Sedimentary Petrology, 47**, 446-450.

Findlay, S. & Tenore, K. R. (1982). Effect of a free-living marine nematode (*Diplolaimella chitwoodi*) on detrital carbon mineralisation. **Marine Ecology Progress Series, 8**, 161-166.

Flach, E. C. (1996). The influence of the cockle, *Cerastoderma edule*, on the macrozoobenthic community of tidal flats in the Wadden Sea. **Marine Biology, 17**, 87-98.

Foster, N. M. (1971). Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. In Hummelinck (Eds.), **Studies on the Fauna of Curaçao and Other Caribbean Islands: No. 129** (pp. 1-181).

Foster-Smith, R. L. (1978). An analysis of water flow in tube-living animals. **Journal of Experimental Marine Biology and Ecology, 34**, 73-95.

Frithsen, J. B. & Doering, P. H. (1986). Active enhancement of particle removal from the water column by tentaculate benthic polychaetes. **Ophelia, 25**, 169-182.

Frostick, L. E. & McCave, I. N. (1979). Seasonal shifts of sediment within an estuary mediated by algal growth. **Estuarine and Coastal Shelf Science, 9**, 569-576.

Führböter, A., Dette, H. H., Manzenrieder, H., & Niesel, S. (1982). In Situ-Untersuchungen der Erosions-stabilität von Wattböden. 2. Meßzeitraum 1982. **Braunschweig (Leichtweiss-Inst.): Ber 552**.

Gaines, S. D. & Bertness, M. D. (1992). Dispersal of juveniles and variable recruitment in sessile marine species. **Nature, 360**, 579-580.

Gaines, S. D. & Roughgarden, J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. **Proceedings of the National Academy of Sciences (USA), 82**, 3707-3711.

Gallagher, E. D., Jumars, P. A., & Trueblood, D. D. (1983). Facilitation of soft-bottom benthic succession by tube-builders. **Ecology, 64**, 1200-1216.

George, J. D. (1967). Cryptic polymorphism in the cirratulid polychaete *Cirriformia tentaculata*. **Journal of The Marine Biological Association of the U.K., 47**, 59-75.

Gerdes, G. & Krumbein, W. E. (1985). Beobachtungen zur Lebensweise von *Pygospio elegans* (Spionidae, Polychaeta Sedentaria) im Farbstreifensandwalt von Mellum. **Verhandlungen der Gesellschaft fur Okologie, 13**, 49-54.

Giard, A. (1905). La poecilogenie. **Bulletin Scientifique de la France et de la Belgique, 39**, 153-187.

Giere, O. (1968). Die Fluktuationen des marinen Zooplanktons im Elbe-Ästuar. Beziehungen zwischen Populationschwankungen und hydrographischen Faktoren in Brackwasser. **Archiv Hydrobiologie, suppl. 31**, 389-546.

Gleason, H. A. (1927). Further views on the succession concept. **Ecology, 8**, 299-326.

Glynn, P. W. (1973). Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope, part II: plankton community with evidence for depletion. **Marine Biology, 22**, 1-21.

Goldman, N. & Lambshead, P. J. D. (1989). Optimisation of the Ewens / Caswell neutral model program for community diversity analysis. **Marine Ecology Progress Series, 50**, 255-261.

Grant, J. (1988). Intertidal bedforms, sediment transport and stabilisation by benthic microalgae. In P. L. deBoer (Ed.), **Tide Influenced Sedimentary Environments and Facies** (pp. 499-510). D.Reidel Publishing Company.

Grant, W. D., Boyer, L. F., & Sanford, L. P. (1982). The effect of biological processes on the initiation of sediment motion in non-cohesive sediments. **Journal of Marine Research, 40**, 659-677.

Grassle, J. F. & Grassle, J. P. (1974). Opportunistic-life histories and genetic systems in marine benthic polychaetes. **Journal of Marine Research, 32**, 253-284.

Grassle, J. F. & Smith, W. (1976). A similarity measure sensitive to the contribution of rare species and its use in the investigation of variation in marine benthic communities. **Oecologia, 25**, 13-22.

Grassle, J. P. & Grassle, J. F. (1976). Sibling species in the marine pollution indicator *Capitella* (Polychaeta). **Science, 192**, 567-569.

Gray, J. (1974). Animal-sediment relationships. **Oceanography and Marine Biology Annual Review, 12**, 223-261.

Gray, J. S. (1981). **The Ecology of Marine Sediments.** Cambridge University Press.

Gremare, A., Marsh, A. G., & Tenore, K. R. (1988). Short-term reproductive responses of *Capitella* sp.1 (Annelida: Polychaeta) fed on different diets. **Journal of Experimental Marine Biology and Ecology, 123**, 147-162.

Grube, A. E. (1850). **Die Familien der Anneliden mit Angabe ihrer Gattungen und Arten.** Berlin.

Gudmundsson, H. (1979) **Reproductive Biology of Four Species of Spionid Polychaete.** Ph.D Thesis, University of Newcastle-upon-Tyne.

Gudmundsson, H. (1985). Life-history patterns of polychaete species of the family Spionidae. **Journal of The Marine Biological Association of the U.K., 65**, 93-111.

Guérin, J.-P. (1991). Elevage de spionidés (Annélides, Polychètes) en cycle complet: 3. Description du développment larvaire de *Boccardia semibranchiata*. **Annales de l'Institut océanographique, Paris, 67**, 145-154.

Guérin, J.-P. & Kerambrun (1984). The role of reproductive characters in the taxonomy of spionids, particularly in the *Malacoceros fuligiosus* complex. In A. Fischer & H. D. Pfannenstiel (Eds.), **Polychaete Reproduction. Progress in Zoology** (pp. 319-333). New York: Gustav Fischer Verlag.

Günther, C.-P. (1992). Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales? **Netherlands Journal of Sea Research, 30**, 45-56.

Hadrys, H., Balick, M., & Schierwater, B. (1992). Applications of random amplified polymorphic DNA (RAPD) in molecular ecology. **Molecular Ecology, 1**, 55-63.

Halley, J. M., Comins, H. N., Lawton, J. H., & Hassell, M. P. (1994). Competition, succession and pattern in fungal communities: towards a cellular automaton model. **Oikos, 70**, 435-442.

Hannan, C. A. (1984) **The Role of Passive Sinking in a Near-Bottom Turbulent Flow Environment.** Ph.D. Thesis, MIT & Woods Hole Oceanographic Institution.

Hannerz, L. (1956). Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil and Poecilochaetidae n.fam. in the Gullmar Fjord, Sweden. **Zoologiska Bidrag fran Uppsala, 31**, 1-204.

Hansbo, S. (1957). A new approach to the determination of the shear strength of clay by the fall cone test. **Proceedings of the Swedish Geotechnical Institute, 14.**

Häntschel, W. & Reineck, H.-E. (1968). Fazies-Untersuchungen im Hettangium von Helmstedt (Niedersachen). **Mitteilungen Geologisches Staatsinstitut Hamburg, 37**, 5-39.

Hartman, O. (1936). New species of Spionidae (Annelida: Polychaeta) from the coast of California. **University of California Publications in Zoology, 41**, 45-52.

Hartmann-Schröder, G. (1971). **Die Tierwelt Deutschlands. Part 58: Annelida: Borstenwürmer. Polychaeta.** Fischer, Jena.

Havenhand, J. N. (1993). Egg to juvenile period, generation time, and the evolution of larval type in marine invertebrates. **Marine Ecology Progress Series, 97**, 247-260.

Heiber, W. (1988) **Die Faunengemeinschaft einer großen Stromrinne des Wursten Wattengebietes (Deutsche Bucht).** University of Bonn.

Hempel, C. (1957). Über den Rohrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta sedentaria) der Deutschen Kusten. **Helgoländer Wissenschaftliche Meeresuntersuchungen, 6**, 100-155.

Hendry, R. J. & McGlade, J. M. (1995). The role of memory in ecological systems. **Proceedings of The Royal Society of London, B259**, 153-159.

Hernoth, L. & Ackefors, H. (1979). The zooplankton of the Baltic proper. **Reports of The Fisheries Board of Sweden, 2**, 5-60.

Hertweck, G. (1994). Zonation of benthos and lebensspuren in the tidal flats of the Jade Bay, Southern North Sea. **Senckenbergiana Maritima, 24**, 157-170.

Hoagland, K. E. & Robertson, R. (1988). An assessment of poecilogeny in marine invertebrates: phenomenon or fantasy? **Biological Bulletin (Woods Hole), 174**, 109-125.

Hobson, K. D. (1976). Notes on benthic sedentariate polychaeta Annelida from British Columbia, Canada, and Washington, USA. **Syesis, 9**, 135-142.

Hobson, K. D. & Green, R. H. (1968). Asexual and sexual reproduction of *Pygospio elegans* in Barnstable Harbour, Massachusetts. **Biological Bulletin (Woods Hole), 135**, 410.

Holme, N. A. (1949). The fauna of sand and mud banks near the mouth of the Exe Estuary. **Journal of The Marine Biological Association of the U.K., 28**, 189-237.

Howard, J. D. & Frey, R. W. (1975). Estuaries of the Georgia Coast, USA, III: regiona; animal-sediment characteristics of Georgia estuaries. **Senckenbergiana Maritima**, 7, 32-55.

Hull, S. C. (1987). Macroalgal mats and species abundance: a field experiment. **Estuarine and Coastal Shelf Science, 25**, 519-532.

Huston, M. (1979). A general hypothesis of species diversity. **American Naturalist, 113**, 81-101.

Hutchinson, G. E. (1967). **A Treatise on Limnology. Vol.2: Introduction to Lake Biology and the Limnoplankton.** New York: John Wiley.

Hylleberg, J. (1975). Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. **Ophelia, 14**, 113-137.

Inghe, O. (1989). Genet and ramet survivorship under different mortality regimes - a cellular automaton model. **Journal of Theoretical Biology, 138**, 257-270.

Jackson, J. B. C. (1986). Modes of dispersal of clonal benthic invertebrates: consequenses for species distributions and genetic structure of local populations. **Bulletin of Marine Science, 39**, 565-587.

Jeffrey, D. W., Madden, B., Rafferty, B., Dwyer, R., Wilson, J., & Allott, N. (1992). **Dublin Bay Water Quality Management Plan: Technical Report 7: Algal Growths and Foreshore Quality.** Environmental Research Unit, Trinity College Dublin.

Jensen, A. C. & Crawford, D. (1984). **Biological activities relating to the transfer of radionuclides.** (Department of the Environment Report no. DOE/RW/84/085. University of Southampton, Department of Oceanography.

Johnson, R. G. (1973). Conceptual models of benthic communities. In T. J. M. Schopf (Ed.), **Models in Palaeobiology** (pp. 148-159). San Francisco: Freeman Cooper & Co.

Jollivet, D., Desbruyères, D., Ladrat, C., & Laubier, L. (1995). Evidence for differences in the allozyme thermostability of deep-sea hydrothermal vents polychaetes Alvinellidae: a possible selection by habitat. **Marine Ecology Progress Series, 123**, 125-136.

Jumars, P. A. & Nowell, A. R. M. (1984a). Effects of benthos on sediment transport: difficulties with functional grouping. **Continental Shelf Research, 3**, 115-130.

Jumars, P. A. & Nowell, A. R. M. (1984b). Fluid and sediment dynamical effects on marine benthic community structure. **American Zoologist, 24**, 45-55.

Jumars, P. A., Nowell, A. R. M., & Self, R. F. L. (1981). A simple model of flow-sediment-organism interaction. **Marine Geology, 42**, 155-172.

Jumars, P. A., Thistle, D., & Jones, M. L. (1977). Detecting two-dimensional spatial structure in biological data. **Oecologia, 28**, 109-123.

Kemp, A. E. S. (1990). Sedimentary fabrics and variation in lamination style in Peru continental margin upwelling sediments. **Proceedings of the Ocean Drilling Program, Scientific Results, 112**(43-58), 43-58.

Khlebovich, V. V. (1977). Response of White Sea organisms to lowered salinity resulting from discharge of fresh waters into sea inlets. **Hydrobiological Journal, 11**, 67-69.

Kindle, E. M. (1930). **The intertidal zone of the Wash, England.** (Report of The Committee on Sedimentation 1928-29 No. 92). National Academy of Sciences - National Research Council, Washington D.C.

Kiseleva, A. G. (1967). **Ukrainian Academy of Sciences, 1**, 85-90.

Kristensen, E. (1981). Direct measurement of ventilation and oxygen uptake in 3 species of tubicolous polychaetes (*Nereis* spp.). **Journal of Comparative Physiology [B], 145**, 45-50.

Kristensen, E., Jensen, M. H., & Aller, R. C. (1991). Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual polychaete (*Nereis virens*) burrows. **Journal of Marine Research, 49**, 355-377.

Kruskal, J. B. & Wish, M. (1978). **Multidimensional Scaling**. Sage Publications, Beverly Hills, California.

Lafite, R. (1986). **Etude sedimentologique de la Baie de Somme.** Rapport IFREMER / Université de Rouen.

Lambeck, R. H. D. & Valentijn, P. (1987). Distribution, dynamics and productivity of a colonising (*Polydora quadrilobata*) and an established (*P.ligni*) polydorid polychaete in Lake Grevelingen: an enclosed estuary in the SW Netherlands. **Netherlands Journal of Sea Research, 21**, 143-158.

Lambshead, P. J. D. & Platt, H. M. (1988). Analysing disturbance with the Ewens / Caswell neutral model: theoretical review and practical assessment. **Marine Ecology Progress Series, 43**, 31-41.

Leschke, M. (1903). Beitrage zur Kenntnis der pelagischen Polychaetenlavren der Kieler Forde. **Helgoländer Wissenschäftliche Meeresuntersuchungen**, 7, 113-134.

Levin, L. A. (1981). Dispersion, feeding behaviour and competition in two spionid polychaetes. **Journal of Marine Research, 39**, 99-117.

Levin, L. A. (1982). Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. **Journal of Experimental Marine Biology and Ecology, 65**, 107-119.

Levin, L. A. (1984a). Life history and dispersal patterns in a dense infaunal polychaete assemblage - community structure and response to disturbance. **Ecology, 65**, 1185-1200.

Levin, L. A. (1984b). Multiple patterns of development in *Streblospio benedictii* Webster (Spionidae) from 3 coasts of North America. **Biological Bulletin (Woods Hole), 166**, 494-508.

Levin, L. A. (1986a). Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedictii* Webster - a mesocosm study. **Biological Bulletin (Woods Hole), 171**, 143-160.

Levin, L. A. (1986b). The influence of tides on larval availability in shallow waters overlying a mudflat. **Bulletin of Marine Science, 39**, 224-233.

Levin, L. A. & Bridges, T. S. (1995). Pattern and diversity in reproduction and development. In L. McEdward (Ed.), **Ecology of Marine Invertebrate Larvae** (pp. 1-48). CRC Press.

Levin, L. A. & Creed, E. L. (1986). Effect of temperature and food availability on reproductive response of *Streblospio benedictii* (Polychaeta, Spionidae) with planktotrophic or lecithotrophic development. **Marine Biology, 92**, 103-113.

Levin, L. A., Zhu, J., & Creed, E. (1991). The genetic basis of life-history characters in a polychaete exhibiting planktotrophy and lecithotrophy. **Evolution, 45**, 380-397.

Levinton, J. S. (1977). Ecology of shallow water deposit feeding communities: Quissett Harbour, M.A. In B. C. Coull (Eds.), **Ecology of Marine Benthos** (pp. 191-228). University of South Carolina Press.

Levinton, J. S. & Lopez, G. R. (1977). A model of renewable resources and limitation of deposit-feeding benthic populations. **Oecologia, 31**, 177-190.

Lewin, R. (1986). Supply-side ecology. **Science, 234**, 25-27.

Libelo, E. L., MacIntyre, W. G., Seitz, R. D., & Libelo, L. F. (1994). Cycling of water through the sediment-water interface by passive ventilation of relict biological structures. **Marine Geology, 120**, 1-12.

Light, W. J. (1978). **Spionidae (Polychaeta, Annelida). Invertebrates of the San Francisco Bay Estuary System.** Boxwood Press.

Linhart, Y. B. (1974). Intra-population differentiation in annual plants. 1. *Veronica peregrina* L. raised under non-competitive conditions. **Evolution, 28**, 232-243.

Linke, O. (1939). Die Biota des Jadebusenwattes. **Helgoländer Wissenschäftliche Meeresuntersuchungen, 1**, 201-348.

Lorenzen, C. J. (1967). Determination of chlorophyll and pheopigmants: spectrophotometric equations. **Limnology and Oceanography, 12**, 343-346.

Lubchenko, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability. **American Naturalist, 112**, 23-39.

MacArthur, R. H. (1960). On the relative abundance of species. **American Naturalist, 94**, 25-36.

Mackin, J. E. & Aller, R. C. (1984). Ammonium adsorption in marine sediments. **Limnology and Oceanography, 29**, 250-257.

Manchenko, G. P. & Radashevsky, V. I. (1994). Genetic differences between two allopatric sibling species of the genus *Polydora* (Polychaeta: Spionidae) from the west Pacific. **Biochemical Systematics and Ecology, 22**, 767-773.

Marcano, G. & Cazaux, C. (1994). Influence de l'advection tidale sur la distribution des larves d'annelides polychetes dans les chenaux du bassin d'Arcachon. **Bulletin de la Société Zoologique Française, 119**, 263-273.

Marinelli, R. L. (1994). Effects of burrow ventilation on activities of a terebellid polychaete and silicate removal from sediment pore waters. **Limnology and Oceanography, 39**, 303-317.

Mattila, J. (1995). Does habitat complexity give refuge against fish predation? some evidence from two field experiments. In A. Eleftheriou, A. D. Ansell, & C. J. Smith (Eds.), **Biology and Ecology of Shallow Coastal Waters: Proceedings of the 28th European Marine Biology Symposium.** (pp. 261-268). Iraklio, Crete: Olsen & Olsen.

Mayer, M. S., Schaffner, L., & Kemp, W. M. (1995). Nitrification potentials of benthic macrofaunal tubes and burrow walls: effects of sediment NH^{4+} and animal irrigation behavior. **Marine Ecology Progress Series, 121**, 157-169.

Mayr, E. (1963). **Animal Species And Evolution**. Cambridge, Massachussetts: Harvard University Press.

McCall, P. A. (1977). Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. **Journal of Marine Research, 35**, 221-266.

McCall, P. L. & Fischer, J. B. (1980). Effects of tubificids oligochaetes on physical and chemical properties of Lake Erie sediments. In R. O. Brinkhurst & D. G. Cook (Eds.), **Aquatic Oligochaete Biology** New York: Plenum Press.

Meadows, P. S. & Hariri, M. S. B. (1991). Effects of two infaunal polychaetes on sediment shear strength and permeability: an experimental approach. **Symposia of The Zoological Society of London, 63**, 313-316.

Meadows, P. S. & Tait, J. (1989). Modification of sediment permeability and shear strength by two burrowing invertebrates. **Marine Biology, 101**, 75-82.

Meadows, P. S., Tait, J., & Hussain, S. J. (1990). Effects of estuarine infauna on sediment stability and particle sedimentation. **Hydrobiologia, 190**, 263-266.

Meadows, P. S. & Tufail, A. (1986). Bioturbation, microbial activity and sediment properties in an estuarine ecosystem. **Proceedings of The Royal Society of Edinburgh, 90B**, 129-142.

Mesnil, F. & Caullery, M. (1917). Un noveau type de dimorphism évolutif chez une Annelide polchète (*Spio martinensis* Mesnil). **Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Serie D., 165**, 646-648.

Michaelis, H. (1978). Zur Morphologie und Ökologie von *Polydora ciliata* und *Polydora ligni* (Polychaeta, Spionidae). **Helgoländer Wissenschäftliche Meeresuntersuchungen, 31**, 102-116.

Mileikovsky, S. A. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. **Marine Biology, 10**, 193-213.

Mills, E. L. (1967). The biology of an ampelescid crustacean pair. **Journal of The Fisheries Research Board of Canada, 24**, 305-353.

Morris, H. M. (1955). A new concept of flow in rough conduits. **Transactions of The American Society of Civil Engineering, 120**, 373-398.

Munro, C. C. A. (1930). Polychaete worms - Discovery Reports 2.

Muskananfola, M. R. (1994) **The influence of biological, sedimentological and physical factors on sediment stability in intertidal waters.** Ph.D. Thesis, Southampton University.

Mustaquim, J. (1988). Electrophoretic variation of isozymes in *Polydora ciliata* complex (Polychaeta: Spionidae). **Comparative Biochemistry and Physiology, 91B**, 197-205.

Myers, A. C. (1977a). Sediment processing in a marine subtidal sandy bottom community. 1. Physical aspects. **Journal of Marine Research, 35**, 609-632.

Myers, A. C. (1977b). Sediment processing in a marine subtidal sandy bottom community. 2. Biological consequences. **Journal of Marine Research, 35**, 633-647.

Nair, P. S., Brncic, D., & Kojima, K. (1971). Isozyme variation and evolutionary relationships in the *mesophragmatica* species group of *Drosophila*. **Studies in Genetics 6. University of Texas, 7103**, 17-28.

Newell, R. C. (1979). Biology of intertidal animals. **Marine Ecological Surveys** (45-47).

Nicholls, D. J., Tubbs, C. R., & Haynes, F. N. (1981). The effect of green algal mats on intertidal macrobenthic communities and their predators. **Kieler Meeresforschung Sonderhaven, 5**, 511-520.

Nickels, J. S., Bobbie, R. J., Lott, D. F., Martz, R. F., Benson, P. H., & White, D. C. (1981). Effect of manual brush cleaning on the biomass and community structure of the microfouling film formed on aluminium and titanium surfaces exposed to rapidly flowing seawater. **Applied Environmental Microbiology, 41**, 1442-1453.

Noji, C. I.-M. (1994). Influence of the tube building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes. In J. C. Dauvin, L. Laubiers, & D. J. Reish (Eds.), **Actes de la 4ème Conférence Internationale des Polychètes, Angers.** (pp. 493-501).

Noji, C. I. M. & Noji, T. T. (1991). Tube lawns of spionid polychaetes and their significance for recolonisation of disturbed benthic substrates. **Meeresforschung, 33**, 235-246.

Nowell, A. R. M. & Church, M. A. (1979). Turbulent flows in a depth limited boundary layer. **Journal of Geophysical Research, 84**, 4816-4829.

Nowell, A. R. M. & Jumars, P. A. (1984). Flow environments of aquatic benthos. **Annual Review of Ecology and Systematics, 15**, 303-328.

Nowell, A. R. M., Jumars, P. A., & Eckman, J. E. (1981). Effects of biological activity on the entrainment of marine sediment. **Marine Geology, 42**, 133-153.

Noyer, G. (1993) **Dynamique des populations de *Pygospio elegans* et *Cerastoderma edule* en Baie de Somme.** Memoire de Maîtrise, Université P.et M.Curie, Paris.

Olive, P. J. W., Garwood, P. R., & Bentley, M. G. (1981). Oosorption and reproductive failure in Polychaeta in relation to their reproductive strategy. **Bulletin de la Société Zoologique Française, 106**, 263-268.

Palmer, A. R. & Strathmann, R. R. (1981). Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. **Oecologia, 48**, 308-318.

Paterson, D. M., Crawford, R. M., & Little, C. (1990). Subaerial exposure and changes in the stability of intertidal estuarine sediments. **Estuarine and Coastal Shelf Science, 30**, 541-556.

Pawlik, J. R. (1986). Chemical induction of larval settlement and metamorphosis on the reef-building tube-worm *Phragmatopoma californica* (Sabellariidae: Polychaeata). **Marine Biology, 91**, 59-68.

Pawlik, J. R. & Butman, C. A. (1993). Settlement of a marine tube-worm as a function of current velocity: interacting effects of hydrodynamics and behaviour. **Limnology and Oceanography, 38**, 1730-1740.

Pawlik, J. R., Butman, C. A., & Starczak, V. R. (1991). Hydrodynamic facilitation of gregarious settlement of a reef-building tube-worm. **Science, 251**, 421-424.

Pechenik, J. A. (1979). Role of encapsulation in invertebrate life-histories. **American Naturalist, 114**, 859-870.

Persoone, G. (1965). The importance of fouling in the harbour of Ostende in 1964. **Helgoländer Wissenschäftliche Meeresuntersuchungen, 12**, 444-448.

Pianka, E. R. (1972). r- and K- selection or b- and d- selection? **American Naturalist, 106**, 581-588.

Pielou, E. C. (1975). **Ecological Diversity**. Wiley, New York.

Qi, A.-S., Zheng, X., Du, C.-Y., & An, B.-S. (1993). A cellular automaton model of cancerous growth. **Journal of Theoretical Biology, 161**, 1-12.

Qian, P.-Y. (1994). Effect of food quantity on growth and reproductive characteristics of *Capitella* sp. (Annelida: Polychaeta). **Invertebrate Reproduction and Development, 26**, 175-185.

Ramberg, J. P. & Schram, T. A. (1982). A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data (Polychaeta: Spionidae). **Sarsia, 68**, 233-247.

Rasmussen, E. (1953). Asexual reproduction in *Pygospio elegans* Claparède (Polychaeta sedentaria). **Nature, 171**, 1161-1162.

Rasmussen, E. (1973). Systematics and ecology of the Isefjord marine fauna, Denmark. **Ophelia, 11**, 1-493.

Read, G. B. (1975). Systematics and biology of polydorid species (Polychaeta: Spionidae) from Wellington Harbour. **Journal of The Royal Society of New Zealand, 5**, 395-419.

Refors, L. (1933). Ein Vertreter der Familie Spionidae (Annelida Polychaeta) aus dem Finnischen Meerbusen. **Memoranda Societatis pro Fauna et Flora Fennica, 9**.

Reice, S. R. (1994). Nonequilibrium determinants of biological community structure. **American Scientist, 82**, 424-435.

Reineck, H. E. & Singh, I. B. (1980). **Depositional Sedimentary Environments** (2nd ed.). Springer Verlag.

Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. **Helgoländer Wissenschäftliche Meeresuntersuchungen, 31**, 55-101.

Reise, K. (1983a). Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. **Marine Ecology Progress Series, 12**, 229-236.

Reise, K. (1983b). Experimental removal of lugworms from marine sand affects small zoobenthos. **Marine Biology, 74**, 327-332.

Remane, A. & Schlieper, C. (1950). **Die Biologie des Brackwassers In Die Binnengewasser.** Stuttgart: Thienemann.

Remmert, H. (1991). The mosaic-cycle concept of ecosystems - an overview. In H. Remmert (Ed.), **The Mosaic-Cycle Concept of Ecosystems; Ecological Studies no. 85** (pp. 1-21). Springer-Verlag.

Rhoads, D. C. (1974). Organism-sediment relations on the muddy sea-floor. **Oceanography and Marine Biology Annual Review, 12**, 263-300.

Rhoads, D. C. & Boyer, L. F. (1982). The effects of marine benthos on physical properties of sediments: a successional perspective. In P. L. McCall & M. J. S. Tevesz (Eds.), **Animal-Sediment Relations: The Biogenic Alteration of Sediment.** (pp. 3-52). New York: Plenum Press.

Rhoads, D. C., Yingst, J. Y., & Ullman, W. J. (1978). Seafloor stability in central Long Island Sound, Pt.1. Temporal changes in erodability of fine grained sediment. In M. L. Wiley (Ed.), **Estuarine Interactions** (pp. 221-244). New York: Plenum Press.

Rhoads, D. C. & Young, D. K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structure. **Journal of Marine Research, 28**, 150-178.

Rice, S. A. (1991). Reproductive isolation in the *Polydora ligni* complex and the *Streblospio benedictii* complex (Polychaeta: Spionidae). **Bulletin of Marine Science, 48**, 432-447.

Rice, S. A. & Simon, J. L. (1980). Intraspecific variation in the pollution indicator polychaete *Polydora ligni* (Spionidae). **Ophelia, 19**, 79-115.

Riemann, F. & Schrage, M. (1978). The mucus-trap hypothesis in feedng of aquatic nematodes and implications for biodegradation and sediment texture. **Oecologia, 34**, 75-88.

Risk, M. J. & Yeo, R. K. (1980). Animal-sediment relationships in the Minas Basin, Bay of Fundy. In S. B. McCann (Ed.), **The Coastline of Canada.** Geological Survey of Canada.

Rumohr, H. (1980). Der "Benthosgarten" in der Kieler Bucht - Experimente zur Bodentierökologie. **Reports SFB 95, 55**, 1-179.

Rybarczyk, H. (1993) **Processus d'eutrophication et ses consequences sur les peuplements d'un ecosysteme estuarien, un exemple en manche orientale: La Baie de Somme.** Ph.D Thesis, Université de Paris.

Rybarczyk, H., Desprez, M., Ducrotoy, J.-P., & Elkaim, B. (1990). The Bay of Somme (France): a key littoral zone to the English Channel. **Bulletin d'Ecologie, 21**, 25-32.

Rybarczyk, H., Desprez, M., Ducrotoy, J.-P., Olivesi, R., Delesmont, R., Jamet, F., & Elkaim, B. (1993). Dynamics of nutrients and faecal bacteria in a macrotidal estuary, The Bay of Somme (France). **Netherlands Journal of Aquatic Ecology, 27**, 395-404.

Rybarczyk, H., Elkaim, B., Wilson, J. G., & Loquet, N. (1996). L'eutrophisation en Baie de Somme: mortalités des peuplements benthiques par anoxie. **Oceanologica Acta, 19**, 131-140.

Sanders, H. L. (1958). Benthic studies in Buzzard's Bay. 1. Animal-sediment relationships. **Limnology and Oceanography, 3**, 245-258.

Santos, P. J. P. (1994). Population dynamics and production of *Scolelepis gaucha* (Polychaeta, Spionidae) on the sandy beaches of Southern Brazil. **Marine Ecology Progress Series, 110**, 159-165.

Sauriau, P. G. (1992) **Les mollusques benthiques du Bassin de Marennes-Oléron: estimation et cartographie des stocks non-cultivés, compétation spatiale et trophique, dynamique de population de *C.edule*.** Thèse, Université de Bretagne Occidentale.

Sautor, B. & Cazaux, C. (1985). Evolution de deux populations larvaires d'annelides p olychaetes dans le basin d'Arcachon. **Journal de Recherche Oceanographique, 10**, 102-104.

Schimmelmann, A., Lange, C. B., & Berger, W. H. (1990). Climatically controlled marker layers in Santa Barbara Basin sediments and fine-scale core-to-core correlation. **Limnology and Oceanography, 35**, 165-173.

Schlötzer-Schrehardt, U. (1991). Ultrastructural differentiation of nuchal and dorsal organs during postembryonic and sexual development of *Pygospio elegans* Claparède (Polychaeta: Spionidae). **Ophelia, Suppl. 5**, 633-640.

Schmager-Noji, C. I.-M. (1988) **Einfluß rasenbildender Spioniden auf den Stoffaustausch am Meeresboden.** Master's Dissertation, University of Kiel.

Schroeder, P. C. & Hermans, C. O. (1975). Annelids: Polychaeta. In A. C. Giese & J. S. Pearse (Eds.), **Reproduction of Marine Invertebrates, III: Annelids and Echiurans** (pp. 1-213). London: Academic Press.

Segarsträle, S. G. (1962). Investigations on Baltic populations of the bivalve *Macoma balthica* (L.), part II. What are the reasons for the periodic failure of recruitment and the scarcity of *Macoma* in the deeper waters of the inner Baltic? **Commentationes Biologiae Societas Scientiarum Fennica, 24**, 1-26.

Self, R. F. L. & Jumars, P. A. (1978). New resource axes for deposit feeders. **Journal of Marine Research, 36**, 626-641.

Sellwood, B. W. (1970).

Serota, S. & Jangle, A. (1972). **A direct-reading pocket shear vane.** Civil Engineering ASCE.

Silvertown, J., Holtier, S., Johnson, J., & Dale, P. (1992). Cellular automaton models of interspecific competition for space - the effect of pattern on process. **Journal of Ecology, 80**, 527-534.

Simon, J. L. (1968). Occurence of pelagic larvae in *Spio setosa* Verril 1873 (Polychaeta Spionidae). **Biological Bulletin (Woods Hole), 134**, 503-515.

Smidt, E. L. B. (1951). Animal production in the Danish Waddensea. **Meddelelser fra Kommissionen for Danmarks Fiskeri - og Havundersøgelser (Ser Fiskeri), 6.**

Smith, J. E. (1980) **Seasonality, spatial dispersion patterns and migration of benthic invertebrates in an intertidal marsh-sandflat system of Puget Sound, Washington, and their relation to waterfoul foraging and the feeding ecology of the Staghorn Sculpin, *Leptocottus armatus*.** Dissertation, University of Washington.

Snelgrove, P. V. R. (1994). Hydrodynamic enhancement of invertebrate larval settlement in microdepositional environments: colonisation tray experiments in a muddy habitat. **Journal of Experimental Marine Biology and Ecology, 176**, 149-166.

Söderström, A. (1920). **Studien über die Polychaetenfamilie Spionidae.** Uppsala: Almquist & Wiksells, Boktryckeri-Aktiebolag.

Solorzano, L. (1969). **Limnology and Oceanography, 14**, 799-801.

Soulsby, P. G., Lowthion, D., & Houston, M. C. M. (1982). Effects of macroalgal mats on the ecology of intertidal mudflats. **Marine Pollution Bulletin, 13**, 162-166.

Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: the cross-equilibrium maintenance of species diversity. **Ecology, 60**, 1225-1239.

Stopford, S. C. (1951). An ecological survey of the Cheshire foreshore of the Dee Estuary. **Journal of Animal Ecology, 20**, 103-122.

Strathmann, R. R. (1982). Selection for retention or export of larvae in estuaries. In V. S. Kennedy (Ed.), **Estuarine Comparisons** (pp. 521-536). New York: Academic Press.

Strathmann, R. R. & Strathmann, M. F. (1982). The relationship between adult size and brooding in marine invertebrates. **American Naturalist, 119**, 99-101.

Sulkin, S. D. (1984). Behavioural basis of depth regulation in the larvae of brachyuran crabs. **Marine Ecology Progress Series, 15**, 181-205.

Taghon, G. L. (1992). Effects of animal density and supply of deposited and suspended food particles on feeding, growth and small-scale distributions of two spionid polychaetes. **Journal of Experimental Marine Biology and Ecology, 162**, 77-95.

Taghon, G. L., Nowell, A. R. M., & Jumars, P. A. (1980). Induction of suspension feeding in spionid polychaete by high particulate fluxes. **Science, 210**, 562-564.

Tamaki, A. (1985). Detection of non-interference within a mobile polychaete species. **Journal of Experimental Marine Biology and Ecology, 90**, 277-287.

Thamdrup, H. M. (1935). Beiträge zur Okologie der Wattenfauna auf experimentaller Grundlage. **Medd. Komm. Havunder Kbh. Fisheri., 10**, 125.

Thiebaut, E., Dauvin, J. C., & Lagadeuc, Y. (1994). Horizontal distribution and retention of *Owenia fusiformis* larvae (Annelida: Polychaeta) in the Bay of Seine. **Journal of The Marine Biological Association of the U.K., 74**, 129-142.

Thistle, D. (1981). Natural physical disturbances of marine soft-bottoms. **Marine Ecology Progress Series, 6**, 223-228.

Thompson, J. N. (1978). Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialised herbivore. **Ecology, 59**, 443-448.

Thompson, J. N. (1985). Within-patch dynamics of life histories, populations and interactions: selection over time in small spaces. In S. T. A. Pickett & P. S. White (Eds.), **The Ecology of Natural Disturbance and Patch Dynamics.** (pp. 253-264). Orlando: Academic Press.

Thorpe, J. P. & Solé-Cava, A. M. (1994). The use of allozyme electrophoresis in invertebrate systematics. **Zoologica Scripta, 23**, 3-18.

Thorson, G. (1946). Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). **Meddelelser fra Kommissionen for Danmarks Fiskeri - og Havundersøgelser (ser Plankton), 4.**

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. **Biological Reviews, 25**, 1-45.

Thrush, S. F. (1991). Spatial patterns in soft-bottom communities. **Trends in Ecology and Evolution, 6**, 75-79.

Thrush, S. F., Hewitt, J. E., & Pridmore, R. D. (1989). Patterns in the spatial arrangements of polychaetes and bivalves in intertidal sediments. **Marine Biology, 102**, 529-535.

Trask, B. D. & Rolston, J. W. (1950). Relation of strength of sediments to water content and grain size. **Science, 111**, 666-667.

Trueblood, D. D., Gallagher, E. D., & Gould, D. M. (1994). Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. **Limnology and Oceanography, 39**, 1440-1457.

Tsutsumi, H. (1987). Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. **Marine Ecology Progress Series, 36**, 139-149.

Tsutsumi, H. (1990). Population persistance of *Capitella* sp. (Polychaeta; Capitellidae) on a mud flat subject to environmental disturbance by organic enrichment. **Marine Ecology Progress Series, 63**, 147-156.

Tufail, A., Meadows, P. S., & McLaughlin, P. (1989). Meso- and micro- scale heterogeneity in benthic community structure and the sedimentary environment on an intertidal muddy-sand beach. **Scientia Marina, 53**, 319-327.

Turner, T. (1983). Complexity of early and middle successional stages in a rock intertidal surfgrass community. **Oecologia, 60**, 56-65.

Underwood, G. J. C. & Paterson, D. M. (1993). Seasonal changes in diatom biomass, sediment stability and biogenic stabilisation in the Severn Estuary. **Journal of The Marine Biological Association of the U.K., 73**, 871-887.

Vance, R. R. (1973a). On reproductive strategies in marine benthic invertebrates. **American Naturalist, 107**, 339-352.

Vance, R. R. (1973b). More on reproductive strategies in marine benthic invertebrates. **American Naturalist, 107**, 353-361.

Walters, L. J. & Wethey, D. S. (1996). Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. **Marine Ecology Progress Series, 137**, 161-171.

Ward, L. A. (1981). Spionidae (Polychaeta Annelida) from Hawaii, with descriptions of five new species. **Proceedings of The Biological Society of Washington, 94**, 713-730.

Warren, L. M. (1984). How intertidal polychaetes survive at low tide. In P. A. Hutchings (Eds.), **Proceedings of the First International Polychaete Conference, Sydney, Australia.** (pp. 238-253). The Linnean Society of New South Wales.

Weinberg, J. R. (1984). Interactions between functional groups in soft-substrata: do species differences matter? **Journal of Experimental Marine Biology and Ecology, 80**, 11-28.

Weinberg, J. R. & Whitlach, R. B. (1983). Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration. **Journal of Marine Research, 41**, 557-569.

Wetzel, A. (1991). Ecologic interpretation of deep-sea trace fossil communities. **Palaeogeography, Palaeoclimatology and Palaeoecology, 85**, 47-69.

Whitlach, R. B. & Zajac, R. N. (1985). Biotic interactions among estuarine infaunal opportunistic species. **Marine Ecology Progress Series, 21**, 299-311.

Wible, J. G. (1984) **The Effects of Salinity, Temperature and Food on the Growth and Reproductive Output of *Polydora nuchalis* Woodwick 1953 (Polychaeta: Spionidae).** Ph.D Thesis, UCLA.

Wilson, E. O. (1992). **The Diversity of Life**. Penguin Books.

Wilson, H. W. (1979). Community structure and species diversity of the sedimentary reefs constructed by *Petaloproctus socialis* (Polychaeta: Maldanidae). **Journal of Marine Research, 37**, 623-641.

Wilson, W. H. J. (1981). Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica*. **Journal of Marine Research, 39**, 735-748.

Wilson, W. H. J. (1983). The role of density dependance in a marine infaunal community. **Ecology, 64**, 295-306.

Wilson, W. H. J. (1984a). An experimental analysis of spatial competition in a dense infaunal community: the importance of relative effects. **Estuarine and Coastal Shelf Science, 18**, 673-684.

Wilson, W. H. J. (1984b). Non-overlapping distribution of spionid polychaetes: the relative importance of habitat and competition. **Journal of Experimental Marine Biology and Ecology, 75**, 119-127.

Wilson, W. H. J. (1985). Food limitation of asexual reproduction in a spionid polychaete. **International Journal of Invertebrate Reproduction and Development, 8**, 61-65.

Wilson, W. H. J. (1991). Sexual reproductive modes in polychaetes - classification and diversity. **Bulletin of Marine Science, 48**, 500-516.

Wolfram, S. (1983). Statistical mechanics of cellular automata. **Reviews of Modern Physics, 55**, 601-644.

Wolfram, S. (1986). **Theory and Applications of Cellular Automata.** World Scientific.

Woodin, S. A. (1976). Adult - larval interactions in dense infaunal assemblages. Patterns of abundance. **Journal of Marine Research, 34**, 25-41.

Woodin, S. A. (1978). Refuges, disturbance and community structure: a marine soft-bottom example. **Ecology, 59**, 274-284.

Woodin, S. A. (1979). Settlement phenomena: the significance of functional groups. In S. E. Stancyk (Ed.), **Reproductive Ecology of Marine Invertebrates.** (pp. 99-106). University of South Carolina Press.

Woodin, S. A. (1981). Disturbance and community structure in a shallow water sand flat. **Ecology, 62**(1052-1066).

Woodin, S. A. (1982). Browsing - important in marine sedimentary environments - spionid polychaete examples. **Journal of Experimental Marine Biology and Ecology, 60**, 35-45.

Woodin, S. A., Lindsay, S. M., & Wethey, D. S. (1995). Process-specific recruitment cues in marine sedimentary systems. **Biological Bulletin, 189**, 49-58.

Woodin, S. A. & Marinelli, R. L. (1991). Biogenic habitat modification in marine sediments: the importance of species composition and activity. **Symposia of The Zoological Society of London, 63**, 231-250.

Woodin, S. A., Marinelli, R. L., & Lincoln, D. E. (1993). Allelochemical inhibition of recruitment in a sedimentary assemblage. **Journal of Chemical Ecology, 19**, 517-530.

Wooding, R. A., Bradley, E. F., & Marshall, J. K. (1973). Drag due to regular arrays of roughness elements of varying geometry. **Boundary Layer Meteorology, 5**, 285-308.

Yingst, J. Y. & Rhoads, D. C. (1978). Seafloor stability in central Long Island Sound, part II: biological interactions and their potential importance for seafloor erodability. In M. L. Wiley (Ed.), **Estuarine Interactions** (pp. 245-260).

Yingst, J. Y. & Rhoads, D. C. (1980). The role of bioturbation in the enhancement of bacterial growth rates in marine sediments. In K. R. Tenore & B. C. Coull (Eds.), **Marine Benthic Dynamics** (pp. 407-421). University of South Carolina Press.

Yokoyama, H. (1990). Life history and population structure of the spionid polychaete *Paraprionospio* sp. (form a.). **Journal of Experimental Marine Biology and Ecology, 144**, 125-143.

Young, D. K. & Rhoads, D. C. (1971). **Marine Biology, 11**, 242-254.

Zajac, R. N. (1986). The effects of intra-specific density and food supply on growth and reproduction in an infaunal polychaete, *Polydora ligni* Webster. **Journal of Marine Research, 44**, 339-359.

Zajac, R. N. (1991). Population ecology of *Polydora ligni* (Polychaeta, Spionidae), 1. Seasonal variation in population characteristics and reproductive activity. **Marine Ecology Progress Series**, 77, 197-206.

Zajac, R. N. & Whitlach, R. B. (1982). Responses of estuarine infauna to disturbance. 2. Spatial and temporal variation of succession. **Marine Ecology Progress Series, 10**, 15-27.

Ziebis, W., Forster, S., Huettel, M., & Jørgenstern, B. B. (1996a). Complex burrows of the mud-shrimp *Callianassa truncata* and their geochemical impact on the sea bed. **Nature, 382**, 619-622.

Ziebis, W., Huettel, M., & Forster, S. (1996b). Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. **Marine Ecology Progress Series, 140**, 227-237.

Appendix 1.

Taxonomic Description of *Pygospio elegans*

The genus *Pygospio* (Claparède, 1863) belongs to the subfamily Spioninae (Söderström, 1920); that subset of the family Spionidae (Grube, 1850) which discharges eggs into externally-borne egg-sacs and includes *Pygospio, Spio, Microspio* and *Polydora.*

Diagnosis: Spionidae *fam.* (Grube, 1850). Linear body with a variable number of setigers. Body regions delineated only by changes in parapodial shapes and setal types and arrangements. Two long, contractile, deciduous, grooved peristomial palpi present, on either side of the prostomium. Prostomium elongate and anteriorly tapered, bifurcate, rounded or blunt; may bear eyes and frontal horns. No true antennae; prostomium may bear occipital or nuchal papilla. The peristomium surrounds the prostomium and may extend laterally into wings. Cirriform and pinnate branchiae present on a limited number of anterior setigers, or extend along the length of the body: they are located dorsally at the bases of the notopodia often partially fused to the notopodial lamellae. Parapodia biramous, lacking aciculae. Notopodial setae are sheathed capillaries anteriorly and may include posterior hooded hooks. Neuropodial setae are also sheathed capillaries anteriorly, and hooded hooks are present posteriorly. Hooded hooks may include a secondary internal hood. Specialised setae may be present. Pygidium may be drawn out into blunt lobes, digitate cirri and / or a collar or flange. Proboscis lacks teeth and jaws. (Taken from Foster, 1971).

Diagnosis: *Pygospio* (Claparède, 1863). Prostomium lacking frontal horns, pointed posteriorly. Eyespots present. Branchiae fused to notopodial lamellae: female with branchiae beginning posterior to setiger 10; male with additional pair on setiger 2. Notosetae are capillary throughout. Neurosetae are winged anteriorly and hooded hooks posteriorly. Pygidium with four thick glandular cirri or lobes.
(Taken from Day, 1967; and Foster, 1971).

Membership of the genus has been attributed to *P. californica* (Hartman, 1936); *P. dubia* (Munro, 1930); *P. muscularis* (Ward, 1981) and *P. elegans*. Foster (1971) has cast doubt on the place of *P. dubia* in the genus.

Diagnosis: *Pygospio elegans* (Claparède 1863). A small species 10-15mm long with up to 60 segments. Prostomium faintly bilobed and pointed posteriorly while inflated laterally and ventrally, forming a low hood around the prostomium. Eyes four to eight, irregular. Notopodial and neuropodial lamellae subequal: anteriorly neuropodial lamellae are tall and thin while notopodial lamellae are large and angular. Posteriorly, neuropodial lamellae are broader, lower and asymmetrically rounded; notopodial lamellae become shorter and broader at the base. Branchiae are fused to dorsal lamellae and are heavily ciliated. Males have an extra pair on setiger 2 separate from the notopodial lamellae. Branchiae begin from setiger 11 and end between seven and fifteen setigers from the posterior end. In the female, branchiae may be limited to around eight pairs. Notosetae are capillaries throughout. Anterior neurosetae are capillaries but four to five bidentate hooded hooks, or crotchets, are present per setiger from setiger 8; between setigers 8 and 10-14 these may have an unusual "spoonlike" morphology. Each has only a single hood. An interramal patch of cilia occurs laterally. The pygidium has four thick lobes which may be unequal in length. (Taken from Day, 1967; Foster, 1971; and Light, 1978)

Hannerz (1956) detailed larval morphology: anteriorly, the prostomium extends posteriorly forming a nuchal crest; bacillary glands are present. Three pairs of black eyes develop, composed of a central cell and a cup of pigment, though the most lateral pair are compound. The peristomium is laterally and dorsally extended. Palps develop relatively early compared to other spionids, and are attached close to the dorsal median line. Branchiae are entirely lacking in the planktonic form, and do not appear for quite some time in the benthonic form. Two types of cilia occur: one in distinct rows (trochs), and a second uniformly scattered over larger surfaces. "Sensory cilia" also occur. Prototrochs, a well developed nototroch, gastrotrochs (on setigers 5 and 7) and a telotroch are present, as is a short, ventromedial neurotroch. In *P. elegans*, unlike many other spionids, the neurotroch does not end in a "ciliated pit": Hannerz identified this as

a vestigial, palingenetic organ lost in the most advanced species. "Grasping cilia" aiding in coordination of ciliary swimming are well developed. The anterior-most crotchet-bearing setiger (#8) corresponds in larva and adult. Melanin is present, in melanophores.

Appendix 2.
Preparation of Specimens for Scanning Electron Microscopy

Dehydration and Critical Point Drying.

Specimens were changed out of storage alcohol (70%) into 100% acetone via the following dehydration series:

70% alcohol	
90% alcohol	15 minutes
100% alcohol	15 minutes
100% alcohol / 100% acetone (50:50)	15 minutes
100% acetone (2 changes)	15 minutes each

Specimens in 100% acetone, protected in permeable capsules, were placed in an acetone-filled bomb chamber. The chamber was cooled to 10°C, and the pressure lowered to 78 bar. $CO_2(l)$ was introduced until well-mixed with the acetone. The chamber was then heated to 40°C: as the temperature passed 31.8°C (the "critical point" at 78 bar) the mixture passed directly from liquid to gaseous phase without boiling. Pressure was then normalised and the dried specimens removed from the bomb chamber.

The specimen was mounted on a conducting stub using a thin layer of epoxy resin and left to dry overnight before the coating process.

Sputter Coating.

The mounted specimen was put into a pressure tank and placed under vacuum; it was then "sputter coated" in a mixture of gold and paladium, causing the specimen's surface to become conducting to the microscope's electron beam. The specimen was then ready to be examined under scanning electron microscopy.

Appendix 3.
X-radiograph Plates

Plate X.1 July 1994; mid-bed. Scaled x2. The poor image at edges is due to overexposure where the sediment was contained inside a cross-sectionally circular core.

Plate X.2 September 1994; edge-bed. X-radiograph from intensified negative. 1:1 scale. A gradient of decreasing exposure with depth resulted from bad design in the corer, which buckled as it entered the sediment.

Thin section cores (5mm thick) were developed as described in **Chapter 7**. In this way the exposure problems encountered in the earlier x-radiographs (above) were avoided.

Plate X.3 March 1995; **a:** off-bed #1; **b:** off-bed #2. 1:1 scale.

Plate X.4 March 1995; **a:** edge-bed; **b:** 5cm onto bed. 1:1 scale.

Plate X.5 March 1995; **a:** 10cm onto bed; **b:** mid-bed. 1:1 scale.

Plate X.6 April 1995; **a:** 1.5m and **b:** 0.75m off-bed. 1:1 scale.

Plate X.7 April 1995; **a:** edge-bed and **b:** 10cm onto-bed. 1:1 scale.

Plate X.8 April 1995; 1m onto bed (mid-bed). 1:1 scale.

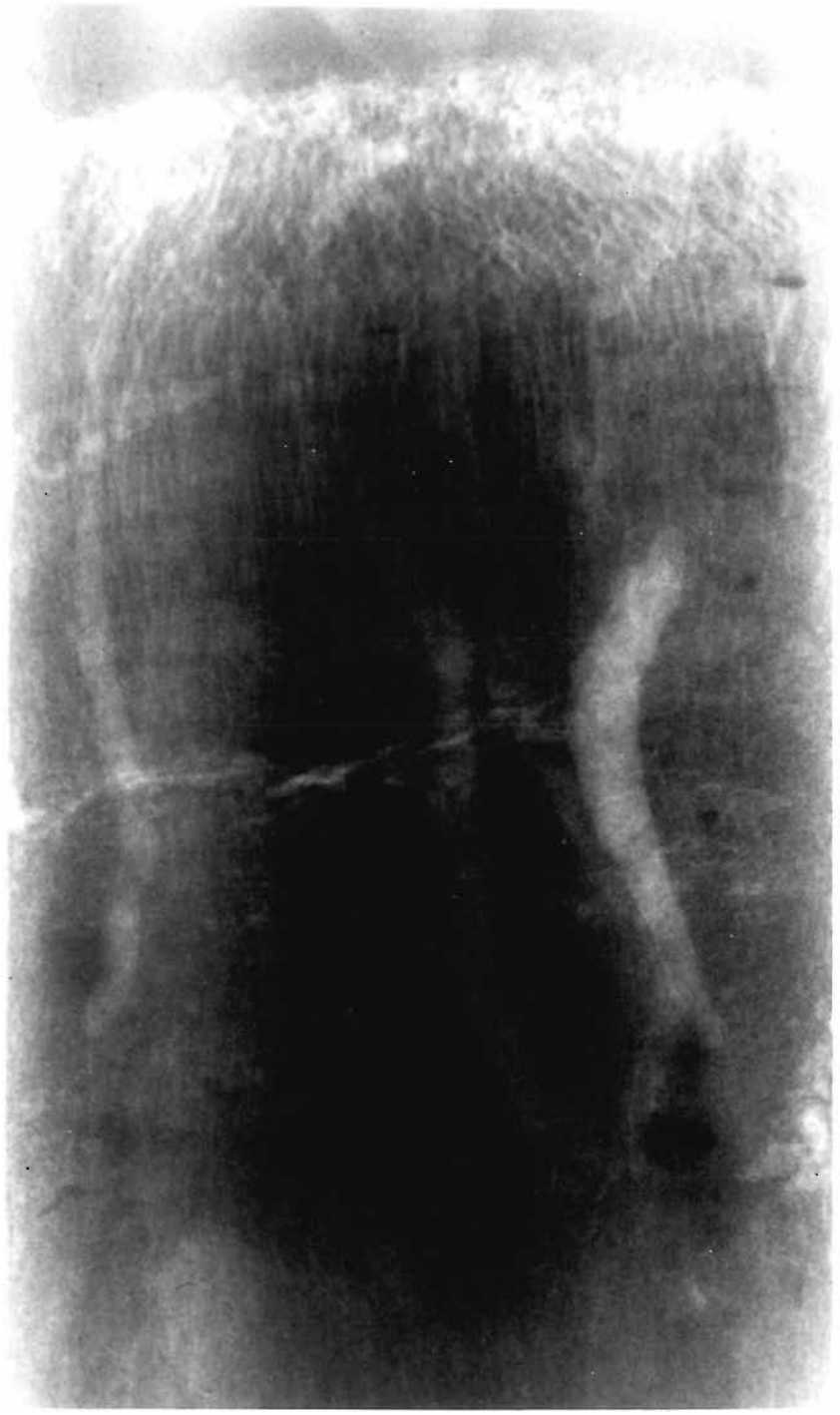


Plate X.1: July 1994, mid-bed. x2.

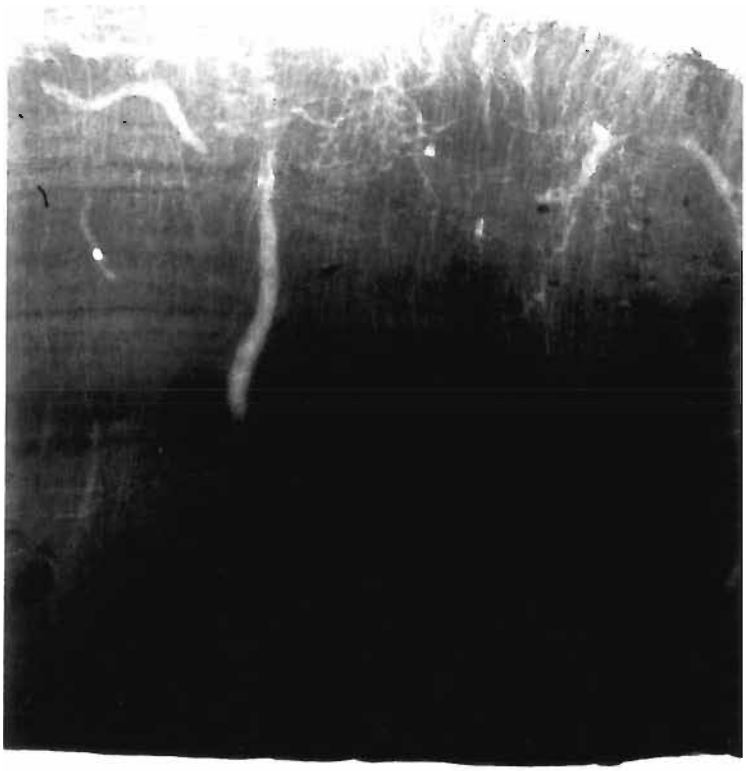
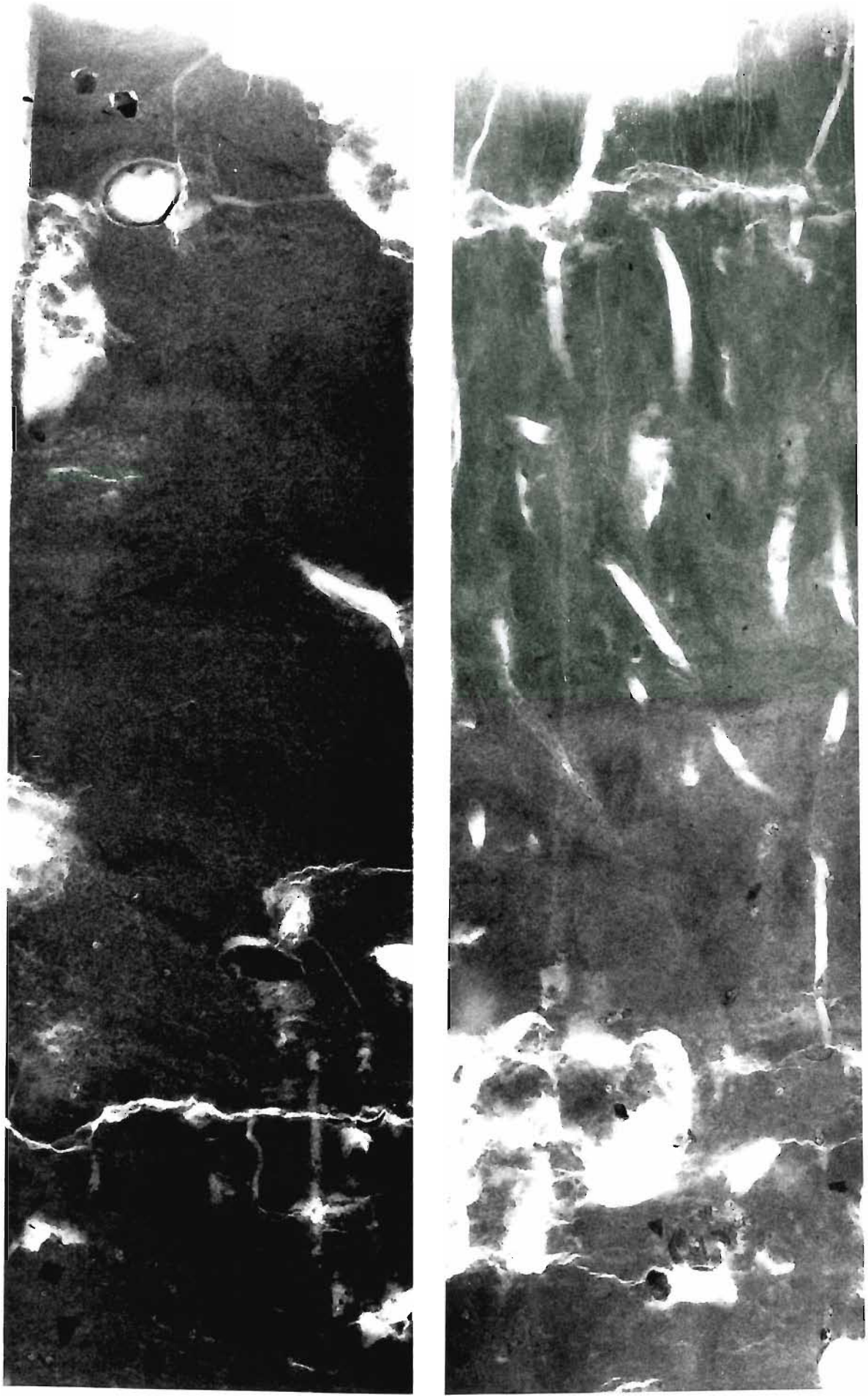
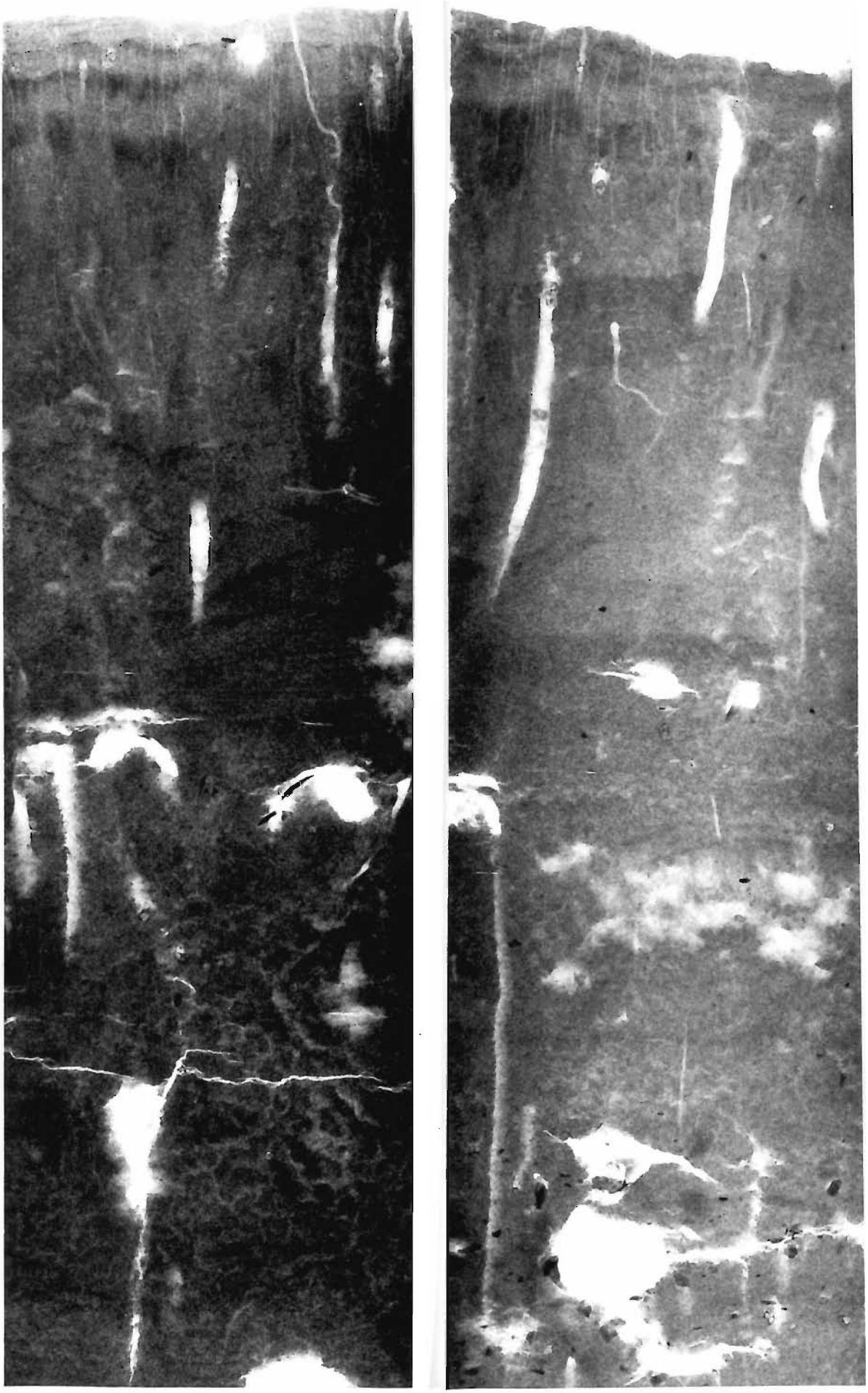


Plate X.2: September 1994, edge-bed. To scale.



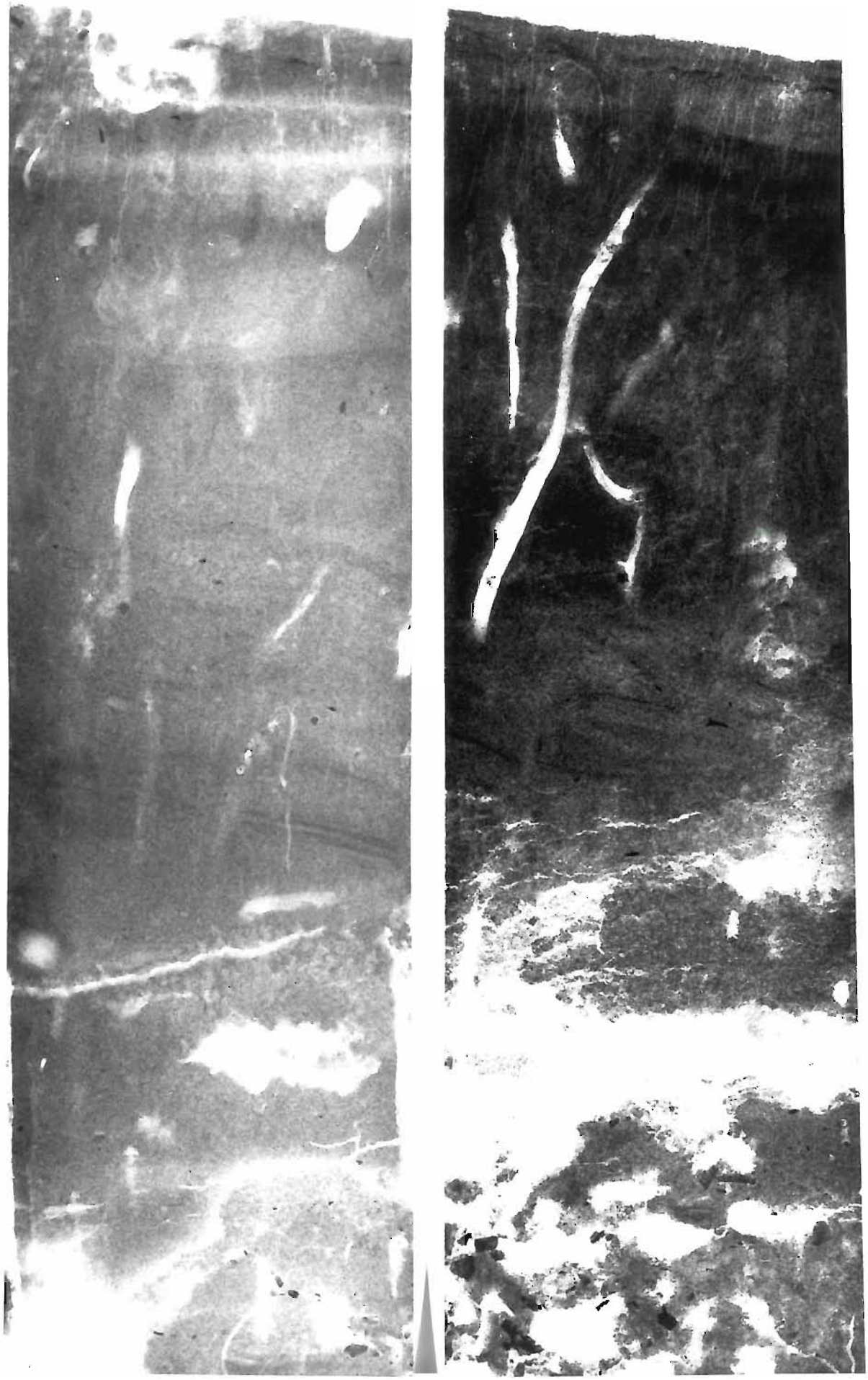
a. b.

Plate X.3: March 1995, **a.** off-bed #1; **b.** off-bed #2. To scale.



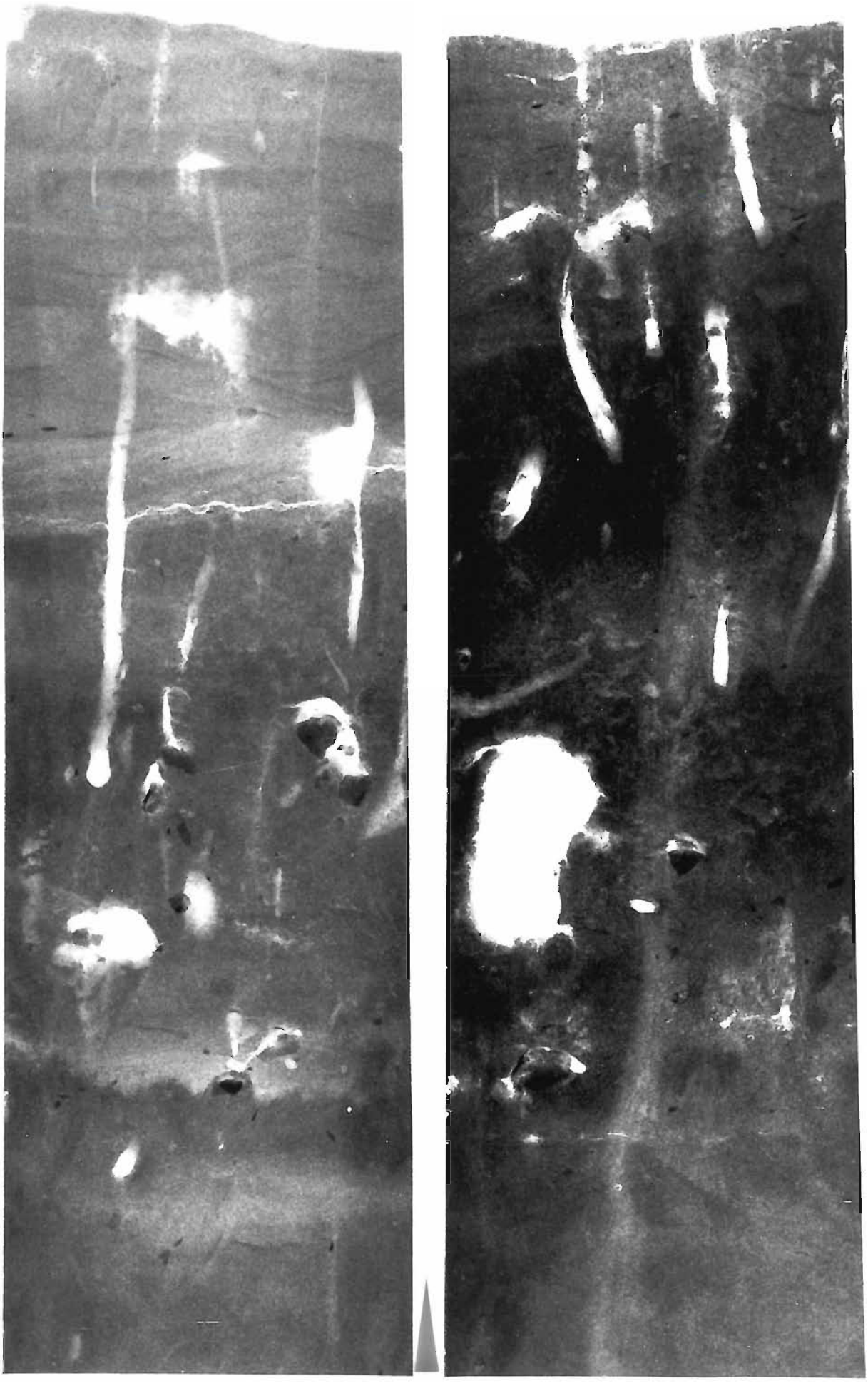
a. b.

Plate X.4: March 1995, **a.** edge-bed; **b.** 5cm onto bed. To scale.



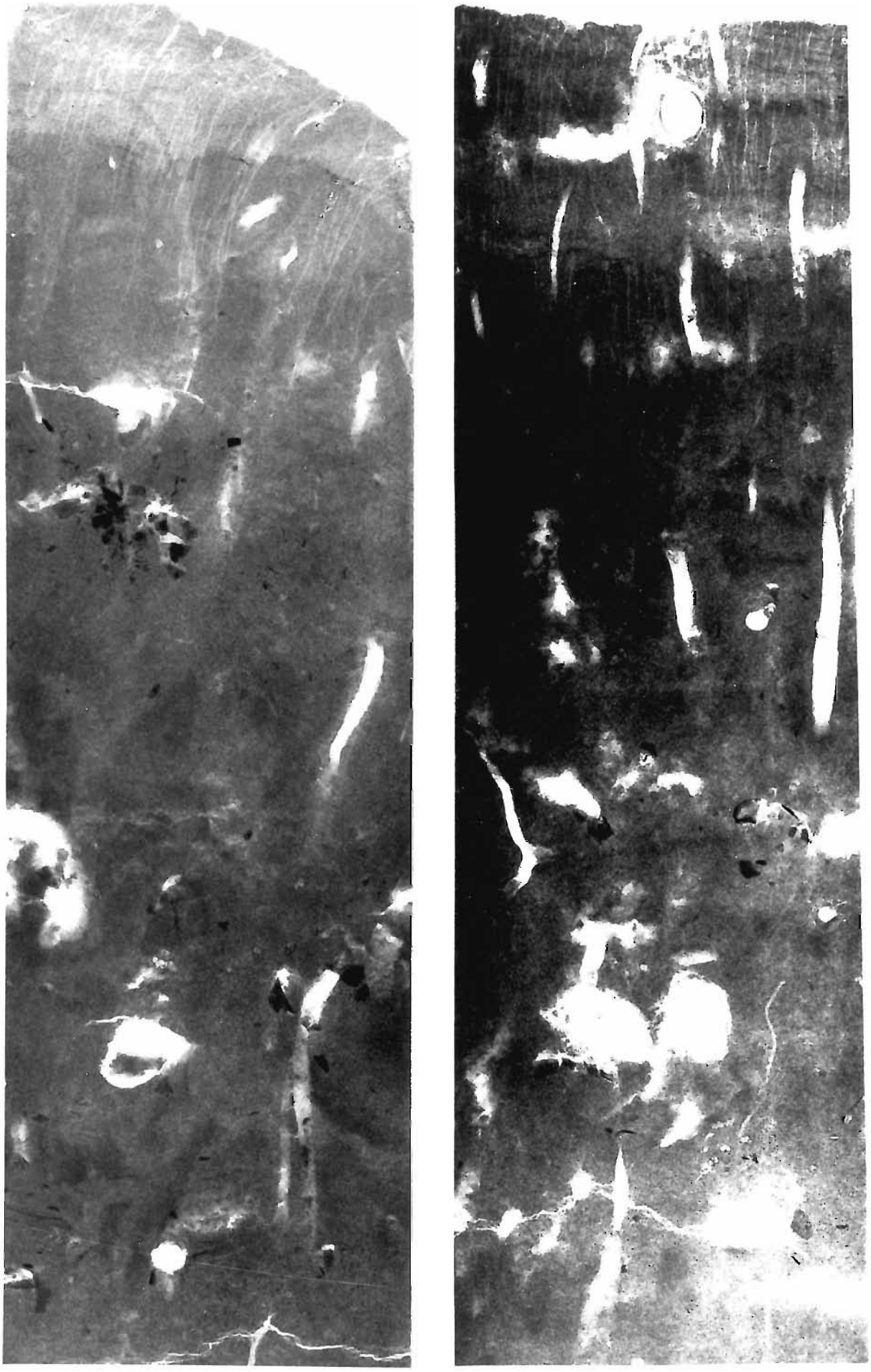
a. b.

Plate X.5: March 1995, **a.** 10cm onto bed; **b.** mid-bed. To scale.



a. b.

Plate X.6: April 1995, **a.** 1.5m off-bed; **b.** 75cm off-bed. To scale.



a. b.

Plate X.7: April 1995, **a.** edge-bed; **b.** 10cm onto-bed. To scale.

Plate X.8: April 1995, 1.0m onto-bed. To scale.