ISSN 1039-3218

The Effects of Bioturbation in Port Phillip Bay

Fiona L. Bird
Department of Environmental Management
Victoria University of Technology
P.O. Box 14428 MMC, Melbourne, 3000
Victoria, Australia

Technical Report No. 14

CSIRO Institute of Natural Resources and Environment
Port Phillip Bay Environmental Study
21st Floor, 625 Little Collins Street
Melbourne, Victoria 3000.

August 1994

CONTENTS

EXECUTIVE SUMMARY

A wide range of invertebrates reside in burrows or burrow through sediment, generally to either seek shelter or to obtain food. Bioturbation, defined here as the reworking and irrigation of sediment by burrowing organisms, can affect the chemical, biological and physical properties of benthic sediments. Physical properties of the sediment are generally altered and biological communities can be restricted by factors including destabilised sediment and increased turbidity. Mineralisation of organic matter is often promoted as a result of the introduction of oxygen to greater depths, and nutrient flux is increased by an increase in the water-sediment interface.

In the muddy sediments of Port Phillip Bay deposit-feeders represent 41% of the total macrobenthic biomass and have been estimated to process 85% of all the organic matter utilised by benthic macroinvertebrates in Port Phillip Bay. Four important deposit-feeders have been identified in Port Phillip Bay - the sea urchin *Echinocardium cordatum*, the ghost shrimp *Neocallichirus limosus*, the bivalve *Theora lubrica* and the polychaete *Phyllochaetopterus socialis*. These four species collectively constitute 24% of the total macrobenthic biomass in Port Phillip Bay according to estimates made during the 1970s.

Based on abundance of species in Port Phillip Bay (determined during the 1970s) and the sediment processing rates of similar species elsewhere, it was estimated that *N. limosus* would process in the order of 8×10^5 tonnes of sediment Bay-wide each day. Estimates of sediment processing rates for the other three major deposit-feeding species could not be made owing to a lack of information.

Burrow irrigation rates were also estimated using abundance data from the 1970s and information on related species elsewhere. Bay-wide burrow flushing rates for *N. limosus* were estimated to be about 3×10^{10} l/hr and for *P. socialis* were about 6×10^7 l/hr. *E. cordatum* do not make permanent burrows but move through the sediment instead. Bay-wide pumping (as opposed to burrow irrigation) rates for *E. cordatum* were estimated to be about 3×10^9 l/hr. No estimates could be made of Bay-wide irrigation rates by *T. lubrica* owing to a lack of information. With the exception of *T. lubrica* it was estimated that the remaining three of these important species process about 2.9×10^{14} l of water annually for respiration. This equates to the entire volume of the Bay being processed almost on a monthly basis.

A possible scenario of the overall effect of bioturbation in Port Phillip Bay is proposed. In the absence of bioturbation it is likely that ammonium concentrations would be much higher than are currently measured in the water column. Therefore it is likely that bioturbation plays a major role in limiting primary production in Port Phillip Bay.

1.0 Introduction

Port Phillip Bay, Victoria, receives inflows of large volumes of organic matter from various sources including the Yarra River and the Western Treatment Plant at Werribee. Nitrogen loads in the order of 7000 tonnes/year are added to the Bays waters, and it is known that most of the nutrient pool is contained in the sediments (Wilson *et al.* 1993). Port Phillip Bay sediments are also inhabited by many species of burrowing invertebrate, some of which are present in high numbers (Wilson *et al.* 1993). Bioturbation is defined here as the reworking and irrigation of sediment by burrowing organisms. Burrowing organisms can affect the chemical, biological and physical properties of benthic sediments. Aeration of sediments by burrowers enhances nutrient cycling by increasing the aerobic zone so that oxidation reactions such as nitrification of ammonia are increased. Nutrient flux between sediments and overlying waters is also increased due to an increased area of the water-sediment interface. Burrows provide a greater surface area for diffusion and also allow diffusion to occur in several directions (not just from the sediment to the overlying water). This suggests that the burrowing organisms living in Port Phillip Bay sediments may have a significant effect on the Bay's nutrient dynamics.

1.1 Objectives

This report aims to provide information about the likely effects of bioturbation (i.e. by burrowing organisms) on sediment dynamics and diffusion of various nutrients in marine environments, and also to provide an assessment of the extent and potential effects of bioturbation in Port Phillip Bay.

1.2 Bioturbation

In recent years marine ecologists have become increasingly aware of the important role burrowing organisms play in the reworking of benthic sediments. A wide range of invertebrates reside in burrows or burrow through the sediment, generally to either seek shelter or to obtain food. Burrowing suspension-feeders filter food from water they pump through their burrows and deposit-feeders ingest sediment and its associated organic material, bacteria and fungi. The two main consequences of sediment reworking when benthic organisms burrow are:

1. Burrowing organisms mix oxygen-bearing waters into the sediment;
2. Sediment is resuspended by burrow construction and feeding methods.

Both processes have been termed bioturbation, and the consequences have important ramifications for chemical and geological processes occurring in benthic sediments. Mixing activities of benthic burrowers accelerates diffusion and transport of ions or compounds that have adsorbed to particles or are in solution in interstitial water (Rhoads 1974).

2.0 Ecological Importance of Bioturbation

Bioturbation, or burrowing activities, affect several properties of the sediment and its associated organisms. Physical properties of the sediment, such as sediment size profile, are altered and biological communities are restricted by factors such as destabilised sediment and turbidity. Nutrient cycling is promoted as a result of the introduction of oxygen to greater depths, and nutrient flux is increased by an increase in the water-sediment interface. Sometimes the concentration of organic carbon increases in the sediment owing to the storage of food and faeces, and the presence of new microhabitats in the sediment promotes the growth of micro-organisms. All of these changes are a result of the burrowing and feeding activities of benthic fauna.

2.1 Physical parameters of sediment

Constant reworking of sediment disturbs the vertical profile of the sediment. With some tropical callianassid ghost shrimps, fine grains of sediment are ejected from the burrows and coarse sediments are buried in deep chambers leading to an increase in sediment particle size with increased depth (Suchanek 1983). A similar result has been reported from the Great Barrier Reef, where tropical callianassids produced a 5 to 60 cm thick surface layer of gravel free sediment above gravel-rich sediment (Tudhope and Scoffin 1984). Sediment processing also modifies the grain size distribution of surface sediments (Suchanek *et al.* 1986) and decreases the shear strength of superficial sediment layers (Rhoads and Boyer 1982). It increases sediment permeability (Meadows and Tait 1989), pore-water content (Davis 1993) and physical resuspension (Colin *et al.* 1986). For example, callianassid ghost shrimps in a tropical lagoon were found to resuspend 0.05 mg/l/day of sediment per burrow (Colin *et al.* 1986). The formation of pellets in faeces production also increases grain size and porosity of sediment (Rhoads and Boyer 1982). The presence of burrows can either increase the stability of the sediment (if burrow walls are armoured or bound with mucous) or decrease the stability if the burrows are open and sediment in burrow walls is neither compacted nor bound with mucous (Jones and Jago 1993). Bioturbation may reintroduce polluted sediment to the water-sediment interface (Pemberton *et al.* 1976; Officer and Lynch 1989) where contaminants such as radionuclides can be incorporated into the food chain (McMurty *et al.* 1985; Suchanek and Colin 1986; Suchanek *et al.* 1986). Many chemical properties of sediment are correlated with grain size, so that any spatial segregation of particle types will result in a change in chemical composition and reaction rates (Aller 1982).

2.2 Biological effects

Bioturbation is known to limit the presence and/or abundance of benthic communities associated with the surrounding sediment (Posey 1986a; Posey *et al.* 1991). Posey (1986b) found that abundances of sedentary species decreased in dense beds of callianassid ghost shrimp, without a change in faunal richness. Branch and Pringle (1987) found that nematode numbers halved in the presence of callianassids, compared to a callianassid free zone, and Riddle *et al.* (1990) found that bioturbation decreased the abundance of small infaunal species such as polychaetes and crustaceans. Bioturbation limits benthic populations by restricting migration (Tamaki 1988), affecting the feeding ability of suspension-feeders by clogging feeding structures (Rhoads and Young 1970) and by restricting settlement of larvae (Rhoads and Young 1970; Aller and Dodge 1974). Bioturbation has also been found to have a negative effect on seagrass productivity and percentage cover (Suchanek 1983).

2.3 Nutrient cycling

2.3.1 Nitrogen

Oxygen is introduced into the sediment via irrigation of burrows. Loose packing of the sediment and oxygenated conditions can sustain aerobic bacterial populations at unusual depths (Miller 1984). Ammonia is one product of the decomposition of organic matter by decomposing and ammonifying bacteria. Nitrifying bacteria oxidise ammonium to form nitrate and nitrite (nitrification). One benefit of sediment processing is that ammonium is reduced in the pore water and therefore fluxes decrease, and the ammonium concentration in the water column also decreases. Under anaerobic conditions, denitrification is an important sink for nitrogen, which results in the removal of nitrate and export of nitrogen gas out of the sediment (Law *et al.* 1991). By enlarging the zone of nitrification, the concentration of nitrate and nitrite increases, denitrification is promoted, and nitrogen gas is released from the sediment (Hüttel 1990).

Decomposition pathways depend on the presence of an electron acceptor (Aller 1982). Oxygen is used preferentially, then interstitial nitrate, and finally when the nitrate supply is exhausted sulfate reduction becomes the dominant process (Grundmanis and Murray 1977). Porewater composition in different sediment layers depends on the particular decomposition pathway at that depth (Hüttel 1990).

In benthic sediments ammonium is produced in two ways; via microbial decomposition of organic matter and via excretion by fauna (Henriksen *et al.* 1983; Fukuhara and Sakamoto 1988). Current evidence suggests that excretion is the major source of ammonia in sediments, and Kristensen *et al*. (1991) calculated that excretion accounts for 80% of the ammonium released from burrows of the nereid polychaete, *Nereis virens*.

The burrow wall is the key microenvironment for biogeochemical processes because it is the site of solute exchange between ambient sediment and burrow water (Aller *et al*. 1983). Tube linings and organically enriched burrow walls have a substantial influence on burrow chemistry (Aller 1983; Aller *et al.* 1983). For example, the burrow of the polychaete *Onuphis jenneri* is lined with a muco-polysaccharide layer whereas callianassid shrimp *Upogebia affinis* burrows are not, but *U. affinis* individuals are known to incorporate decomposing plant material into the burrow wall. This difference in substrate lining may influence the abundance and types of microbes present and hence control local chemical processes (Aller *et al.* 1983). Callianassid (*Upogebia affinis*) burrows were found to be sites of more intense nitrification-denitrification and microbial activity than polychaete (*Onuphis jenneri*) tubes (Aller *et al.* 1983). Burrow water composition is sensitive to the adsorption-permeability properties of the inner burrow wall or lining (Aller *et al*. 1983). Also different solutes have different diffusive permeabilities through burrow walls so that diffusion rates for each solute group may be quite different (Aller 1983). The potential nitrification rate of the burrow wall of the amphipod, *Corophium volutator*, was nearly three times that of the adjacent 1cm of sediment (Henriksen *et al*. 1983). Sayama and Kurihara (1983) found that oxidised nitrogen concentrations decreased dramatically only a few millimetres from the burrow wall of the polychaete *Neanthes japonica*, whereas Ott *et al*. (1976) measured oxidation effects extending 6mm into the surrounding sediment from callianassid burrows. In the inner oxidised zone around the bivalve, *Mya arenaria*, potential nitrification rates were estimated to range from 600 to 1200 μmol NO^{-3}/cm^3/day whilst in the 1cm thick layer surrounding this, the potential nitrification rates were significantly lower (Henriksen *et al*. 1983).

The depth of the nitrification zone in the burrow wall depends on the irrigation activity of the inhabitant (Henriksen *et al.* 1983). High irrigation activity, combined with high nitrification rate, will increase the nitrate concentration in the burrow wall which in turn will increase the nitrate release into the water column (Henriksen *et al.* 1983; Hüttel 1990; Law *et al.* 1991). In some cases irrigation of burrows results in nitrification occurring in an intermediate (at 20 to 30 cm depths in Puget Sound, USA) sedimentary zone, below and above which denitrification predominates (Grundmanis and Murray 1977).

Krantzberg (1985) suggested that deposition and decomposition of faecal pellets may represent a significant route for nitrate release from sediments. The presence of faecal pellets also increases the surface area for nitrifying bacteria (Henriksen *et al*. 1983). Faecal pellets of the bivalve, *Malcoma balthica*, from the sediment surface showed high rates of potential nitrification in the order of 5200 μmol NO^{-3}/cm^3/day (Henriksen *et al*. 1983). Sayama and Kurihara (1983) found that denitrification occurs in intact faecal pellets of the polychaete *Neanthes japonica* even under extremely aerobic conditions, suggesting that faecal pellets may offer anaerobic and organically rich micro-sites.

2.3.2 Phosphorus

Sediment resuspension, commonly caused by the actions of burrowing organisms, promotes the rapid and enhanced release of phosphorus (Wisniewski 1993). A continual influx of oxygenated water into the burrows causes a decrease in phosphate concentrations in the interstitial water (Clavero *et al.* 1992, 1994). Fluxes of phosphate from callianassid (*Callianassa rathubunae* and *Calliax jonesi*) burrows (assuming one shrimp per mound and 4.4 mounds per m^2) were found to be 0.2 μmol/m^2/day (Murphy and Kremer 1992).

2.4 Nutrient flux to overlying water

Net fluxes of nutrients at the water sediment interface increase in the presence of benthic activity (Waslenchuk *et al.* 1983; Hopkinson 1987; Aller and Aller 1992) and studies of nutrient flux may be misinterpreted if the influence of extensive burrowing is ignored (De Vaugelas and Buscail 1990). Burrows are known to increase the surface area for solute exchange between the burrow and adjacent sediment (Aller 1982; Fukuhara and Sakamoto 1987), and nutrient profiles in the surrounding pore-water are altered (Hüttel 1990). The one-dimensional concept of diffusion from the sediment to the overlying water is complicated by the construction and irrigation of burrows by macrofauna. In a bioturbated zone, solutes can diffuse along lateral concentration gradients into burrow cavities as well as along vertical concentration gradients, so that solute diffusion actually occurs three-dimensionally (Aller 1982, 1983).

Dworschak (1983) found burrow walls of the callianassid shrimp *Upogebia pusilla* to be the same tan colour of oxidised surface sediment compared to the black colour of the surrounding anoxic sediment, and the same phenomenon has been observed for an intertidal species in Western Port, Victoria (F. Bird, pers.obs.). Dworschak (1981) suggested that *Upogebia pusilla* increases the water-sediment interface 3 to 5-fold and Ott *et al.* (1976) calculated a 10 to 16-fold increase for very dense populations of *Upogebia litoralis*. This value was higher than the 2.6 fold increase estimated for *Callianassa bouvieri* (Dworschak and Pervesler 1988) and for the 25% increase estimated for *Callianassa japonica* (Koike and Mukai 1983). The effect on transport rates of solutes changes seasonally and depends on macrofauna density (Aller and Aller 1992) and size (Aller 1982). The magnitude of flux depends on the nutrient concentration differences between the burrow and sediment, and continual irrigation maintains reasonably constant burrow water nutrient concentrations (Aller 1982). Exchange also depends on burrow shape, lining properties (Aller *et* al. 1983) and both size and spacing of burrows (Aller 1980).

Nitrogen loss from the sediments was doubled in the presence of the polychaete *Nereis diversicolor* individuals compared to a control devoid of macrofauna (Clavero *et al*. 1994). Another polychaete, *Nereis virens*, increased the net fluxes of dissolved inorganic nitrogen across the water-sediment interface by a factor of 2 to 4 (Kristensen *et al*. 1991). Burrow water of some callianassid shrimps contain two to three times higher concentrations of nitrate/nitrite compared to overlying waters and double the concentration of ammonia (Koike and Mukai 1983). In the presence of macrofauna, ammonium production rates from the sediment increased by 20 to 30 % (Aller and Yingst 1985). Influence on ammonium flux by the bivalve *Theora lata* changed seasonally (Yamada and Kayama 1987), with largest fluxes during summer (Regnault *et al*. 1988). The increase in ammonium flux due to the bivalve, *Malcoma balthica*, was 61 μmol/m^2/hr in organically rich sediment which was 30% more than that accounted for by excretion (Henriksen *et al*. 1983). Fluxes of ammonium from callianassid (*C. rathubunae* and *Calliax jonesi*) burrows (assuming one shrimp per mound and 4.4 mounds per m^2) was found to be 97 μmol NH_4/m^2/day (Murphy and Kremer 1992). This flux rate was measured in a tropical reef environment with coarse, calcareous sandy sediment (Murphy and Kremer 1992), and therefore is also not comparable to the callianassid burrows of central Port Phillip Bay muds.

2.5 Carbon accumulation

An increase in organic matter was found in burrow linings (Reichardt 1988; De Vaugelas and Buscail 1990). In some cases plant debris is stored in chambers to decompose, and is either ingested or worked into the burrow wall to promote growth of micro-organisms (Dworschak 1987a). Deposit-feeders often selectively ingest small sediment particles (Devine 1966; Hughes 1969; Whitbaard and Duinveld 1989) which are relatively higher in organic carbon than ambient sediment (Rashid 1985; Self and Jumars 1988; Stamhuis 1992). One consequence is that faecal pellets are also higher in organic content than ambient sediment (Hylleberg and Gallucci 1975), up to 5 times as in the pellets of the bivalve *Malcoma balthica* (Henriksen *et al*. 1983). Callianassid faecal pellets can be either ejected from burrows (Barnes 1965; Shinn 1968; Yamada and Kayama 1987) or stored in chambers (Dworschak 1983; De Vaugelas and Buscail 1990) and their fate sometimes depends on sediment type (De Vaugelas *et al.* 1986). Storage of faecal pellets in back-filled tunnels suggests that burrows may act as nutrient sinks (De Vaugelas and Buscail 1990).

2.6 Microbial growth rates

In sediments largely undisturbed by burrowing invertebrates, microbial biomass is usually higher at the water-sediment interface and decreases with depth (Novitsky and Karl 1986). Microbial mediated decomposition reactions are stimulated by macrobenthos in several ways, for example, increasing the surface area of the organic detritus, increasing electron acceptor supply by irrigation, particle reworking and multidimensional diffusion (Aller 1982). Continual irrigation of burrows causes a distinct composition of burrow water which in turn creates a unique micro-environment for micro-organisms (Koike and Mukai 1983). Reichardt (1988) suggested that a consequence of bioturbation is a shift of microbial activity from the sediment surface to subsurface layers, chiefly burrow walls. It is possible that sediment is altered by some species of burrowing invertebrate to promote microbial growth and provide a rich food supply in usually nutrient-poor sediment (Miller 1984). A species of deposit-feeding amphipod (*Parhyalella whelpleyi*) increases the rate of micro-organism production by decreasing detritus particle size, thus increasing its biologically active surface (Fenchel 1970).

Accumulating organic matter in burrow linings changes the organic content of the sediment and enhances bacterial numbers (Branch and Pringle 1987). Plant material collected and stored in burrows provides substrate for bacterial growth and may enhance meiofaunal production within the burrow (Ott *et al*. 1976; Nash *et al.* 1984). Decomposing plant material is worked into the burrow walls to support bacterial or fungal growth which is subsequently harvested by the inhabitant (Ott *et al*. 1976). By changing the surface area of organic matter and stimulating microbial activity, grazing by benthic macroinvertebrates is thought to maintain micro-organisms in a highly productive phase of growth (Aller 1982).

Fine particles are often selectively incorporated into the burrow wall (Dobbs and Gurket 1988). Oxygen consumption by bacteria on sediment particles is directly proportional to the particle surface area, so that if oxygen flux to a surface is kept constant, a surface composed mainly of fine grains should be more reactive for such processes as remineralisation than a surface composed of coarse grains (Aller 1982). Burrow linings are thought to be mainly aerobic but the presence of anaerobic microhabitats may promote survival of sulfate-reducing bacteria (Dobbs and Gurket 1988). An increase in bacterial abundance, by between 30% and 100% (Branch and Pringle 1987), and activity (Reichardt 1988) has been found in burrow linings of *Callianassa kraussi*. Bacteria numbers declined rapidly within millimetres of the burrow wall (Branch and Pringle 1987).

3.0 Port Phillip Bay

3.1 Important burrowing invertebrates

In the muddy sediments of Port Phillip Bay, deposit-feeders represent 41% of the total macrobenthic biomass and are estimated to process 85% of all the organic matter utilised by benthic macroinvertebrates in Port Phillip Bay (Wilson *et al.* 1993).

Mobile deposit-feeders move vertically and laterally within the sediment causing mixing and transport of particles together with dissolved gases and interstitial water (Rhoads 1974). The influence of a deposit-feeding species on sediment properties is dependent on size, mobility, feeding depth and rate, particle size selectivity and population densities (Aller 1978).

Four important deposit-feeders have been identified in Port Phillip Bay, and each of these species contributes to a significant proportion of the total macrobenthic biomass. The species are, the burrowing spatangoid sea urchin, *Echinocardium cordatum* (8% of total biomass), the ghost shrimp, *Neocallichirus limosus* (7%), the bivalve, *Theora lubrica* (= *T. fragilis*) (5%) and the Chaetopterid polychaete, *Phyllochaetopterus socialis* (4%) (Wilson *et al*. 1993).

Suspension-feeders represent 42% of the total macrobenthic biomass of Port Phillip Bay (Wilson *et al*. 1993). Suspension-feeders trap organic matter from water pumped through their filters. Bivalves, the major suspension-feeders found in Port Phillip Bay, are usually buried in the sediment to avoid predation and to maximise food capture. Suspension-feeders, however, do not actively burrow to the same extent as deposit-feeders, nor do they process sediment for food. Therefore they are not considered to be significant bioturbators in Port Phillip Bay and will not be further discussed in this report.

4.0 Burrow Architecture

The principal species of deposit-feeders found in Port Phillip Bay burrow in different ways. The crustacean, *Neocallichirus limosus*, builds burrows which are permanent even though the structure is continually being altered. The polychaete, *Phyllochaetopterus socialis*, also resides in a permanent structure which is lined with a leathery tube. Conversely, the urchin, *Echinocardium cordatum*, ploughs through the sediment, continually moving to new locations, presumably as does the bivalve, *Theora lubrica*, although this fact has not been documented. Each type of burrow or burrowing activity would have a different effect on the sediment and nutrient dynamics of the system.

4.1 *Neocallichirus limosus*

N. limosus is a small species of ghost shrimp (up to 30 mm long) in the family Callianassidae (Poore 1975). Most research on callianassids has been performed on larger tropical species inhabiting reef lagoons where sediments are usually much coarser than Port Phillip Bay, or in seagrass beds (Suchanek 1983). Callianassid ghost shrimps are common bioturbators which build extensive burrow systems and continually process sediment during feeding and burrow construction. Each species creates a unique burrow plan (Suchanek *et al.* 1986), but burrow architecture usually demonstrates characteristics of three major ecological types; filter/suspension feeders, detritus/deposit feeders, and seagrass/algae harvesters (Suchanek 1985; Griffis and Suchanek 1991). It is not known which feeding category *N. limosus* belongs to, but Wilson *et al*. (1993) suggest that it is probably the detritus/deposit feeding type.

Deposit-feeding callianassids build temporary, deep, complex burrows in which they process sediment for organic matter. A burrow complex of different levels of chambers indicates active searching for organic-rich sediment (Pervesler and Dworschak 1985; Dworschak 1987b). Inside the burrows, sediment is continually taken up, its organic matter gleaned and the residue transported to another part of the burrow or up to the surface (Dworschak 1987b). The organic components of ingested sediment are utilised (Pohl 1946; Fenchel *et al.* 1975), and fine particles are selected because they have a greater surface area and are more likely to consist of organic matter than larger particles (Rashid 1985; Self and Jumars 1988; Stamhuis 1992). In the New Zealand species *Callianassa filholi* (which is closely related to *Callianassa ceramica* from Port Phillip Bay), sand grains up to 0.03 mm diameter are ingested from sediment, of which they form an insignificant proportion (Devine 1966). *Callianassa subterranea* selectively consume particles < 0.05 mm diameter, producing an increase of 3 to 4 fold in faeces over parent sediment (Witbaard and Duineveld 1989). Ejecta have a lower organic content than surface sediment (De Vaugelas and Buscail 1990) with a reduction of organic carbon and nitrogen by up to 50% (Suchanek *et al.* 1986). Concentrations of organic carbon and humic matter were thirty times higher in the stomach contents of *Callichirus laurae* than in surface sand (De Vaugelas and Buscail 1990), indicating that selective food uptake occurs to maximise organic gain from sediment.

The presence of a lining in callianassid burrows depends on sediment type, with a thick lining observed in sandy sediments and no lining in muddy sediments (De Vaugelas *et al.* 1986). If a lining is present, it can be composed either of finer grains than the surrounding sediment (Shinn 1968; Dobbs and Gurket 1988) or of grains of average size (Dworschak 1983). In the case of *Callianassa trilobata*, particles <63 mm diameter accounted for 13-16% of total sediment in the burrow, but only 3% in the adjacent sediment (Dobbs and Gurket 1988).

Burrow dynamics change seasonally (Tunberg 1986) and are affected by physical parameters such as salinity (Dworschak 1983), macrophyte cover (Dworschak 1987b) and shell content of sediment (Coleman and Poore 1980). Burrow size is known to vary with sediment type (Griffis and Chavez 1988), and architectural differences associated with sediment type may reflect limitations in terms of structural support as well as differences in feeding methods associated with that sediment type (Griffis and Suchanek 1991). Species which can use a variety of feeding modes may change their primary mode in response to the food availability of the habitat (Griffis and Chavez 1988). The ratio of burrow to burrow openings is not consistent over species, with a range of ratios from 1 shrimp to 2 openings, to 1 shrimp to 4.29 openings (Hailstone and Stephenson 1961; Ott *et al*. 1976; Dworschak 1981; Miller 1984). The ratio also changes with sediment type for a single species, with more openings in muddy sediment than sandy sediments (Miller 1984). This variation indicates that estimates of shrimp density from counts of burrow openings are likely to be inaccurate.

4.2 *Echinocardium cordatum*

E. cordatum is a small cosmopolitan species in the order Spatangoida, with a test length ranging from 23 to 50 mm (Buchanan 1966, 1967). Individuals observed offshore from the Isle of Man and Plymouth in the United Kingdom, burrow to a maximum depth of 18 cm and maintain contact with the overlying seawater via a respiratory tunnel (Nichols 1959). Burrow depth differs with sediment type (Nichols 1959; Buchanan 1966; Foster-Smith 1978) and may be only 5 cm deep in silty environments (Buchanan 1966). *Meoma ventricosa*, a species also in the order Spatangoida, burrows to greater depths in cold temperatures (Chesher 1969).

E. cordatum ingests exclusively surface sediment, collected by tubefeet which extend to a radius of 3 to 4 cm around the funnel opening. The particles enter the respiratory tube, are directed downwards as a mucous string and finally are transported by tube feet to the mouth (Buchanan 1966; De Ridder 1982). Buchanan (1966) compared the growth rate and reproductive frequency of two populations in different substrates, and found that the population in clean sand (compared to silty sand) was the most successful because the morphology and behaviour of its feeding mechanism was best suited to process coarser sediment. *E. cordatum* moves through silty sediment very slowly, but can move through sand at a rate of 6 to 8 cm/h (Buchanan 1966). At regular intervals during movement (every 2 to 3 cm) a new respiratory funnel is constructed (Nichols 1959).

4.3 *Theora lubrica*

Little is known about the small (maximum shell length 12 mm) deposit-feeding bivalve *T. lubrica*, from the family Semelidae, except that it is very similar to the species *Theora lata* which dominates a similar system to Port Phillip Bay, the Inland Sea of Japan (Poore and Rainer 1979). *T. lata* (maximum shell length 13 mm) inhabits sediment to a maximum depth of 26 mm and maintains connection with the overlying water by an inhalant and an exhalant siphon. Food and water are drawn in through the inhalant siphon and water and faecal pellets are excreted from the exhalant siphon (Yamada and Kayama 1987). Similarly, a deposit-feeding bivalve of similar size, the Nuculanid, *Yoldia eightsi*, burrows through, processes and regularly expels sediment from its mantle cavity via the inhalant siphon (Davenport 1988). *Yoldia limulata* burrows to depths of 1 cm to 8 cm depending on shell size, and moves through sediment (horizontally and vertically) searching for food (Bender and Davis 1984). Another Nuculanid, *Nucula proxima* (maximum shell length 12 mm), obtains 65% to 95% of organic carbon from sedimentary organic matter and 2% to 35% from bacteria (Cheng and Lopez 1991). A much studied deposit-feeding species, *Malcoma balthica* (Bivalvia, Tellinacea) (maximum shell length 38 mm), has been found to feed by extending its long inhalant siphon to surface sand, drawing in material, sorting it and then ejecting unsuitable particles (Brafield and Newell 1961). *M. balthica* can also survive as a suspension feeder (Brafield and Newell 1961), and a population in southern Sweden showed a marked difference in feeding habit depending on sediment type; deposit-feeding in muddy sand and filter-feeding in sandy sediment (Olafsson 1986). Burrow depth varies with valve size, and a maximum depth of 12 cm was observed with an increase during winter (Zwarts and Wanink 1989). Another species, *M. nasuta* (maximum shell length 88 mm), is primarily a deposit-feeding bivalve and has a high degree of diet selectivity where 97% of the surface material is ejected as pseudofaeces during sorting in the mantle cavity (Hylleberg and Gallucci 1975).

Scrobicularia plana, from the family Tellinacea, (shell length ranging from 20 to 50 mm), is capable of filtering particles of 4 μm to 40 μm size with an efficiency of nearly 100% (Hughes 1969). *M. balthica* moves horizontally at a rate of 1.25 cm/min (Brafield and Newell 1961) and *Y. eightsi* can plough through surface layers over 5 to 10 cm in a few seconds (Davenport 1988), whereas *S. plana* rarely moves horizontally (Hughes 1969).

4.4 *Phyllochaetopterus socialis*

P. socialis is a very small member of the Chaetopterus family (approximately 1.5 to 2.5 cm long) which is permanently confined to a branched, leathery or parchment-like vertical tube (Barnes 1965; Day 1967). A considerable extent of the tube lies horizontally on the sediment surface, and tube length ranges from 3 to 6 cm long (Barnes 1965). One or more worms may inhabit each tube (Barnes 1965). *P. socialis* is both a suspension-feeder and a deposit-feeder. A mucous bag strains food particles from water flowing through the burrow, and palps transport particles directly from the tube and sediment surfaces to the mouth (Barnes 1965). Faeces are removed from the burrow by cilial movement on the palps (Barnes 1965). The tube length of a species from the same family which has a similar structure and habit to *P. socialis*, *Spiochaetopterus oculatus*, depends on sediment type. Tubes are considerably shorter in muddy sediments than in sand (Barnes 1964), so the surface area of burrow exposed to the water would be less in muddy than sandy sediments.

5.0 Sediment Processing

Sediment processing during burrow construction and feeding activities of deposit-feeders occurs continually. Some sediment is transported to the surface, some buried in chambers, some compacted into the burrow wall, and some is gleaned of its organic matter. Large volumes of sediment are processed daily, with an estimated 3.2×10^7 tonnes (dry weight) of sediment being processed in Port Phillip Bay each year (Wilson *et al*. 1993). In the Bay, four major groups of invertebrates contribute significantly to this value; polychaetes are estimated to turnover 44% of the Bays sediments, echinoderms 31%, crustaceans 22%, and molluscs 3% (Wilson *et al*. 1993).

Even though burrowing and feeding activities are species and site specific, it is possible to compare species of similar sizes which reside in similar sediments and feed in the same way. However, those values presented in the following pages are indications only of the potential sediment processing rates of the Port Phillip Bay species and may not reflect the actual values.

5.1 *Neocallichirus limosus*

Sediment turnover rates are not known for *N. limosus*, but some values (especially for tropical species of callianassid) have been documented. Feeding by deposit-feeding callianassids involves continual sediment processing. In some tropical species, coarse sediment (> 1.4 mm diameter) is stored in chambers and fine sediment (< 1.4 mm diameter) is ejected from the burrow (Suchanek 1983, 1985). The volume of sediment expelled from burrows is dependent on temperature and changes temporally (Rowden *et al*. 1992).

Callianassa armatus was found to turn over the upper centimetre of tropical lagoon sediment between 3 and 8.5 times per year depending on the population density (De Vaugelas *et al.* 1986). Other estimates of turnover rates for various tropical callianassid shrimp species range between 0.4 and 1111 g/day per burrow in sandy environments and 58 and 90 g/day per burrow in muddy environments (de Vaugelas 1985; de Vaugelas *et al.* 1986). Rapid processing of sediment may be necessary to gain adequate nutrition from sediment with generally low organic content (Suchanek *et al.* 1986). Tropical species are larger in size than the species found in Port Phillip Bay, and the lagoon sediment is coarser and lower in organic content than the finer sand and silty sediments of temperate habitats. A deposit-feeding species from the North Sea, *Callianassa subterranea*, was found to turn over an approximate quantity of 1.75 g (dry sediment)/day per burrow (Witbaard and Duineveld 1989). This value is an order of magnitude less than tropical species, but whether it is primarily the result of differences in animal size, organic content of sediment, sediment processing rates or a combination of these is unknown. *C. subterranea* is a small species, similar in size to *N. limosus*, and similarly resides in muddy sediments. As previously stated, sediment processing rates would be species and site specific, but due to the similarities between the two species, it is possible that rates are comparable. If the values are comparable, a bay-wide sediment processing rate for *N. limosus* would be in the order of 8×10^5 tonnes/day, based on abundance data from the zoobenthos study completed in the 1970s (Poore *et al*. 1975).

5.2 *Echinocardium cordatum*

Sediment turnover rates are not available for *E. cordatum*. *Meoma ventricosa*, a species in the same order (Spatangoida), has a maximum test length of 144 mm (*E. cordatum* maximum test length 50 mm), and burrows to depths of less than 10 cm. It ingests sandy substrate non-selectively and, in a tropical lagoon, this species has been found to turnover sediment at a rate of approximately 330 cm^3/h/urchin (Chesher 1969). A turnover rate for *E. cordatum* can not be extrapolated from this value because the species are very different sizes and reside in different sediment types.

5.3 *Theora lubrica*

Little is known about *T. lubrica*, including sediment processing rates. Processing of sediment by *Y. limatula* during feeding results in expulsion of loose pseudofaeces into the water column, causing sediment resuspension. *Y. limatula* increases turbidity in experimental aquaria by 55% to 65% via sediment resuspension. Ten to 200 times body weight is expelled daily as pseudofaeces and elongate faeces (Bender and Davis 1984). The amount of sediment expelled is proportional to body size up to a length of 18 mm, after which greater quantities are expelled, but less frequently (Bender and Davis 1984). Large individuals of the bivalve *Y. eightsi* (shell length about 30 mm) expel approximately 4.55 g (dry wt)/day (Davenport 1988), and small individuals of the species *Y. limatula* (shell length about 15 mm) expel approximately 1.21 g (dry wt)/day (Bender and Davis 1984). Expulsion rates increase with an increase in temperature (Bender and Davis 1984). In the absence of information about the feeding structures and/or habits of *T. lubrica*, few comparisons between it and other species can be drawn, especially species from different taxonomic families.

5.4 *Phyllochaetopterus socialis*

Sediment turnover rates are not available for *P. socialis* or any other members of the polychaete family, Chaetopteridae. The Amphictenid polychaete *Pectinaria gouldii* lives in a tapered tube, 4 to 6 cm long, and is positioned with its head downwards where it feeds on the available sediment. The sediment is ingested, passes through the gut and is deposited on the sediment surface (Gordon 1966). Individuals process 6 g/day of sediment and this rate is directly dependent on sediment temperature (Gordon 1966). Particles larger than 1mm are unmanageable, and remain in the ambient sediment. Forty-five percent of the available organic carbon is utilised from the sediment ingested (Gordon 1966). Sediment reworking rates of the Maldanid polychaete, *Axiothella rubrocinta*, which feeds in a similar way to *P. gouldii*, are influenced by several factors, including temperature, salinity, organic carbon content of sediment, sedimentation rate and grain size (Kudenov 1982). *P. socialis* does not feed in the same way as *P. gouldii*, so these sediment processing rates are not comparable.

6.0 Burrow Irrigation

Aquatic burrowing organisms face the problem of coping with reduced oxygen concentration in burrow water. Oxygen consumption by microflora and meiofauna lining the burrow, as well as by the inhabitant, can cause hypoxic conditions. Oxygen can diffuse into the burrow from overlying water, but this process alone may not necessarily maintain burrow water at viable concentrations (Atkinson and Taylor 1988). An additional problem faces intertidal species. Burrow inhabitants are likely to experience severe hypoxia at low tides because the animals are unable to irrigate their burrows (Atkinson and Taylor 1988). It is common for individuals to move towards burrow openings at low tide (Farley and Case 1968; Hill 1981). Oxygen concentration in the burrow water and depth of penetration into the burrow wall decreases during resting periods, whereas during high irrigation activity oxygen penetration into the burrow wall is comparable to that of the sediment surface (Henriksen *et al*. 1983). Irrigation also removes faeces and metabolites from the burrows (Barnes 1965).

Again burrow irrigation rates would be species and site specific, depending on the individuals requirements and tolerance to anoxic conditions. However closely related species, with similar feeding habits, that reside in similar sediment type, may have comparable flushing rates. The following values for Port Phillip Bay are only estimates and should therefore be regarded cautiously.

6.1 *Neocallichirus limosus*

Callianassids create water current by the beating of pleopods (Atkinson and Taylor 1988). Water volumes pumped through individual *Callianassa* burrows in tropical lagoons ranged between 93.33 and 187.5 ml/hr (Colin *et al.* 1986). These values were higher than those calculated for the deposit-feeding *Callianassa japonica* from Japan, where pumping rates ranged from 32 to 89 ml/hr (Koike and Mukai 1983). Even though burrow flushing rates are species and site specific, *C. japonica* is a similar size to *N. limosus* and is also found in a temperate environment, so burrow ventilation rates of the two species may be similar. If this is the case tentative estimates of Bay-wide burrow flushing rates of *N. limosus*, based on abundance data from Poore *et al*. (1975), would be in the order of 3×10^{10} l/hr.

With the species *Upogebia pusilla*, the smallest individual (10 mm long) was found to exchange its burrow water approximately 1.3 times per hour and the largest individual (60 mm long) exchanged its burrow water 4.1 times per hour (Dworschak 1981). Pumping rates were dependent on animal and burrow size (Dworschak 1981). Dissolved oxygen in burrow water ranged from 12 to 45% saturation (Koike and Mukai 1983), and concentrations are not evenly distributed along the burrow axis (Whitbaard and Duineveld 1989). Tolerance to anoxic conditions varies with species, with survival times ranging from 9 hours to 80 hours (Felder 1979; Mukai and Koike 1984).

6.2 *Echinocardium cordatum*

E. cordatum does not make permanent burrows, but moves through sediment in search of food. Connection with overlying water is via a respiratory tube which is continually re-established during movement (Nichols 1959). Oxygen rich water is circulated through the respiratory tube and over the test via cilia currents (Nichols 1959; Foster-Smith 1978). If *E. cordatum* is deprived of oxygen, individuals will move to the surface, presumably in search of oxygen (Nichols 1959). Large individuals of *E. cordatum* (test length 5 to 5.7 cm) pump water at an average rate of 90 ml/h, and small individuals (test length 2.5 to 3 cm) pump water at an average rate of 13 ml/h (Foster-Smith 1978). Based on the mean of these values and previously recorded abundance data (Poore *et al*. 1975), Bay-wide water pumping rates for *E. cordatum* would be in the order of 3×10^9 l/hr.

6.3 *Theora lubrica*

In the absence of information on irrigation rates by *T. lubrica*, results from studies of other deposit-feeding species are presented. However, as with the sediment processing rates, until more is known about the feeding and burrowing activity of *T. lubrica* or closely related species, no direct comparisons can be made. *Mya arenaria,* (shell length 80 mm), a species at least double the size of *T. lubrica*, (shell length 15 mm), was found to have a maximum pumping rate ranging between 200 and 750 ml/h per individual (Foster-Smith 1978). The pumping rate of *M. nasuta*, which resides in silty sand, varied with size and ranged between 23 ml/h (shell length 35 mm) and 110 ml/h (shell length 49 mm) (Specht and Lee 1989). The pumping rate of *Scrobicularia plana* (shell length 40 mm), which resides in muddy sediment, changed with temperature and reached a maximum of about 210 ml/h (Hughes 1969).

6.4 *Phyllochaetopterus socialis*

Like most sedentary tubicolous polychaetes, *P. socialis* is dependent on water for respiration and to flush its tube (Barnes 1965). Membranelles beating within the notopodial ring drive the current (Barnes 1965), and in *Spiochaetopterus oculatus*, these membranelles never cease beating (Barnes 1964). Burrow irrigation rates are not available for *P. socialis*, but a polychaete from the family Spionidae, *Malacoceros fuliginosa*, which has a similar size (body length between 3 and 4 cm), lives in a vertical tube with one opening and similarly creates its water currents via the beating of cilia, was found to pump water at a rate of 0.8 to 1.75 ml/h (Foster-Smith 1978). As previously stated, burrow irrigation will depend on the specific requirements of a species, however *M. fuliginosa* has a similar habit to *P. socialis*, so pumping rates may be comparable. If this is true, a tentative estimate of Bay-wide pumping rates of *P. socialis*, based on abundance data collected by Poore *et al*. (1975) and a mean of the above rates, would be in the order of 6×10^7 l/hr.

7.0 Conclusions

In conclusion, bioturbation is known to be an important process which effects the physical, biological and chemical properties of benthic sediments. The presence of burrows increases the oxygen content of the sediment which alters nutrient cycling so that the rates of aerobic reactions, such as nitrification, increase. Burrows also increase the surface area of the sediment-water interface which leads to diffusion across multi-dimensional interfaces. This increase in surface area also increases nutrient flux from the sediments to the overlying water, even though the overall increase of flux in the presence of burrows can be partially accounted for by excretion.

A possible scenario of the overall effect of bioturbation in Port Phillip Bay may be as follows. Organic matter, entering the Bay from sewage outfalls, streams, rivers and drains etc., is decomposed to form ammonia. Ammonium, in the presence of oxygen, will be nitrified to form nitrate and nitrite, which in turn will be denitrified in the anaerobic zone of the sediment and removed from the sediments in the form of nitrogen gas or nitrous oxide gas. This series of reactions is promoted in the presence of bioturbation, because sediments are aerated by burrow construction and feeding processes and by continual burrow irrigation. In a system devoid of bioturbation, anaerobic processes would dominate in the sediments because the aerobic zone extends only a few millimetres below the water-sediment interface. Ammonium is not nitrified, and is free to diffuse between the interstitial water and overlying water. Hence ammonium concentrations would be much higher in the water column. Therefore bioturbation may play a major role in limiting primary production in Port Phillip Bay.

It is only now becoming obvious that the presence of burrowing species in Port Phillip Bay is vital to maintain a healthy system, and yet little quantitative information is available on the main bioturbating species. Future research should concentrate on the biology, population dynamics and activities of bioturbating species of Port Phillip Bay so we can better understand their importance in controlling benthic processes.

8.0 References

Aller, R.C. (1978). Experimental studies of changes produced by deposit feeders on pore water, sediment, and overlying water chemistry. *American Journal of Science* **278,** 1185-234.

Aller, R.C., (1980). Quantifying solute distributions in the bioturbated zone of marine sediments by defining an average microenvironment. *Geochimica et Cosmochimica Acta* **44,** 1955-65.

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

Aller, R.C. (1983). The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. *Journal of Marine Research* **41,** 299-322.

Aller, R.C. and Dodge, R.E. (1974). Animal-sediment relations in a tropical lagoon Discovery Bay, Jamaica. *Journal of Marine Research* **32**, 209-32.

Aller, R.C., Yingst, J.Y. and Ullman, W.J. (1983). Comparative biogeochemistry of water in intertidal *Onuphis* (polychaeta) and *Upogebia* (crustacea) burrows: temporal patterns and causes. *Journal of Marine Research* **41,** 571-604.

Aller, R.C. and 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,** 615-45.

Aller, R.C. and Aller, J.Y. (1992). Meiofauna and solute transport in marine muds. *Limnology and Oceanography* **37**, 1018-33.

Atkinson, R.J.A. and Taylor, A.C. (1988). Physiological ecology of burrowing decapods. *Symposia of the Zoological Society of London* **59**, 201-26.

Barnes, R.D. (1964). Tube-building and feeding in the Chaetopterid polychaete, *Spiochaetopterus oculatus*. *Biological Bulletin* **127**, 397-412.

Barnes, R.D. (1965). Tube-building and feeding in Chaetopterid polychaetes. *Biological Bulletin* **129**, 217-33.

Bender, K. and Davis, W.R. (1984). The effect of feeding by *Yoldia limatula* on bioturbation. *Ophelia* **23**, 91-100.

Brafield, A.E. and Newell, G.E. (1961). The behaviour of *Macoma balthica* (L.). *Journal of the Marine Biological Association of the United Kingdom* **41**, 81-7.

Branch, G.M. and Pringle, A. (1987). The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna, and benthic microflora. *Journal of Experimental Marine Biology and Ecology* **107**, 219-35.

Buchanan, J.B. (1966). The biology of *Echinocardium cordatum* (Echinodermata: Spatangoidea) from different habitats. *Journal of the Marine Biological Association of the United Kingdom* **46**, 97-114.

Buchanan, J.B. (1967). Dispersion and demography of some infaunal echinoderm populations. *Symposia of the Zoological Society of London* **20**, 1-11.

Cheng, I-J. and Lopez, G.R. (1991). Contributions of bacteria and sedimentary organic matter to the diet of *Nucula proxima*, a deposit-feeding protobranchiate bivalve. *Ophelia* **34**, 157-70.

Chesher, R.H. (1969). Contributions to the biology of Meoma ventricosa (Echinoidea: Spatangoida). *Bulletin of Marine Science* **19**, 72-110.

Clavero, V., Fernandez, J.A. and Niell, F.X. (1992). Bioturbation by *Nereis* sp. and its effects on the phosphate flux across the sediment-water interface in the Palmones estuary. *Hydrobiologia* **235/236**, 387-92.

Clavero, V., Niell, F.X. and Fernandez, J.A. (1994). A laboratory study to quantify the influence of *Nereis diversicolor* O.F. Muller in the exchange of phosphate between sediment and water. *Journal of Experimental Marine Biology and Ecology* **176**: 257-67.

Coleman, N. and Poore, G.C.B. (1980). The distribution of *Callianassa* species (Crustacea, Decapoda) in Western Port, Victoria. *Proceedings of the Royal Society of Victoria* **91** 73-8.

Colin, P.L., Suchanek, T.H. and McMurty, G. (1986). Water pumping and particle resuspension by callianassids (Crustacea: Thalassinidea) at Enewetak and Bikini Atolls, Marshall Islands. *Bulletin of Marine Science* **38**, 19-24.

Davenport, J. (1988). The feeding mechanism of *Yoldia* (= *Aequiyoldia*) *eightsi* (Courthouy). *Proceedings of the Royal Society of London. Series B* **232**, 431-442.

Davis, W.R. (1993). The role of bioturbation in sediment resuspension and its interaction wtih physical shearing. *Journal of Experimental Marine Biology and Ecology* **171**, 187-200.

Day, J.H. (1967). *Polychaeta of Southern Africa. Part 2 Sedentaria*. Trustees of the British Museum (Natural History), London. 878pp.

De Ridder, C. (1982). Feeding and some aspects of the gut structure in the spatangoid echinoid, *Echinoderm cordatum* (Pennant). In. *International Echinoderms Conference, Tampa Bay*. (Ed. J.M. Lawrence) pp 5-9. A.A.Balkema, Rotterdam.

De Vaugelas, J. (1985). Sediment reworking by Callianassid mud-shrimp in tropical lagoons: a review with perspectives. In: *Proceedings of the Fifth International Coral Reef Symposium, Tahiti, 1985* **6,** 617-22.

De Vaugelas, J., Delesalle, B. and Monier, C. (1986). Aspects of the biology of *Callichirus armatus* (A. Milne Edwards, 1870) (Decapoda, Thalassinidea) from French Polynesia. *Crustaceana* **50**, 20416.

De Vaugelas, J. and Buscail, R., (1990). Organic matter distribution in burrows of the thalassinid crustacean *Callichirus laurae*, Gulf of Aqaba (Red Sea). *Hydrobiologia* **207,** 269-77.

Devine, C.E. (1966). Ecology of *Callianassa filholi* Milne-Edwards 1878 (Crustacea, Thalassinidea). *Transactions of the Royal Society of New Zealand. Zoo*logy **8,** 93-110.

Dobbs, F.C. and Gurket, J.B. (1988). *Callianassa trilobata* (Crustacea: Thalassinidea) influences abundance of meiofauna, and biomass, composition and physiologic state of microbial communities within its burrow. *Marine Ecology Progress Series* **45**, 65-79.

Dworschak, P.C. (1981). The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology* **52**, 25-35.

Dworschak, P.C. (1983). The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea). I. The burrows. *Marine Ecol*ogy **4**, 19-43.

Dworschak, P.C. (1987a). Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea). *Investigacion Pesquera, Barcelona* **51,** 421-9.

Dworschak, P.C. (1987b). The biology of *Upogebia pusilla* (Petagna)(Decapoda, Thalassinidea). II: Environments and zonation. *Marine Ecol*ogy **8**, 337-58.

Dworschak, P.C. and Pervesler, P. (1988). Burrows of *Callianassa bouvieri* Nobili 1904 from Safaga (Egypt, Red Sea) with some remarks on the biology of the species. *Senkenbergiana maritima* **20,** 1-17.

Farley, R.D. and Case, J.F. (1968). Perception of external oxygen by the burrowing shrimp *Callianassa californiensis* Dana and *C. affinis* Dana. *Biological Bulletin* **134**, 261-5.

Felder, D.L. (1979). Respiratory adaptations of the estuarine mud shrimp, *Callianassa jamaicense* (Schmitt, 1935) (Crustacea, Decapoda, Thalassinidea). *Biological Bulletin* **157,** 125-37.

Fenchel, T. (1970). Studies on the decomposition of organic detritus derived from the turtlegrass *Thalassia testudinum. Limnology and Oceanography* **15**, 14-20.

Fenchel, T., Kofoed, L.H. and Lappalainen, A. (1975). Particle size-selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*. *Marine Biology* **30,** 119-28.

Foster-Smith, R.L. (1978). An analysis of water flow in tube-living animals. *Journal of Experimental Marine Biology and Ecology* **32,** 73-95.

Fukuhara, H. and Sakamoto, M. (1988). Ecological significance of bioturbation of zoobenthos community in nitrogen release from bottom sediments in a shallow eutrophic lake. *Archiv fuer Hydrobiologie* **113,** 425-45.

Gordon, D.C. Jr. (1966). The effects of the deposit feeding polychaete *Pectinaria gouldii* on the intertidal sediments of Barnstable Harbour. *Limnology and Oceanography* **11**: 327-32.

Griffis, R.B. and Chavez, F.L. (1988). Effects of sediment type on burrows of *Callianassa californesis* Dana and Callianassa gigas Dana. *Journal of Experimental Marine Biology and Ecology* **117,** 239-53.

Griffis, R.B. and Suchanek, T.H. (1991). A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea). *Marine Ecology Progress Series* **79**, 171-83.

Grundmanis, V. and Murray, J.W. (1977). Nitrification and denitrification in marine sediments from Puget Sound. *Limnology and Oc*eanography **22,** 804-13.

Hailstone, T.S. and Stephenson, W. (1961). The biology of *Callianassa* (Trypaea) *australiensis* Dana 1852 (Crustacea, Thalassinidea). *University of Queensland. Papers of the Department of Zoology* **1**, 261-85.

Henriksen, K., Rasmussen, M.B. and Jensen, A. (1983). Effect of bioturbation on microbial transformations in the sediment and fluxes of ammonium and nitrate to the overlying water. *Ecological Bulletin* **35,** 193-205.

Hill, B. (1981). Respiratory adaptations of three species of *Upogebia* (Thalassinidea, Crustacea) with special reference to low tide periods. *Biological Bulletin* **160,** 272-9.

Hopkinson, C.S. Jr. (1987). Nutrient regeneration in shallow-water sediments of the estuarine plume region of the nearshore Georgia Bight, USA. *Marine Biology* **94**, 127-42.

Hughes, R.N. (1969). A study of feeding in *Scrobicularia plana. Journal of the Marine Biological Association of the United Kingdom* **49**, 805-23.

Hüttel, M. (1990). Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sandflat sediments. *Marine Ecology Progress Series* **62,** 241-8.

Hylleberg, J. and Gallucci, V.F. (1975). Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta. Marine Biology* **32,** 167-78.

Jones, S.E. and Jago, C.F. (1993). *In situ* assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology* **115,** 133-42.

Koike, I. and Mukai, H. (1983). Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major. Marine Ecology Progress Series* **12**, 185-90.

Krantzberg, G. (1985). The influence of bioturbation on physical, chemical and biological parameters in aquatic environments: A review. *Environmental Pollution. Series A* **39,** 99-122.

Kristensen, E., Jensen, M.H. and Aller, R.C. (1991). Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual polychaete (*Nereis virens*) burrows. *Journal of Marine Research* **49,** 355-77.

Kudenov, J.D. (1982). Rates of seasonal sediment reworking in *Axiothella rubrocincta* (Polychaeta: Malanidae). *Marine Biology* **70**, 181-6.

Law, C.S., Rees, A.P. and Owens, N.J.P. (1991). Temporal variability of denitrification in estuarine sediments. *Estuarine and Coastal Shelf Science* **33**, 37-56.

McMurty, G.M., Schneider, R.C., Colin, P.L., Buddemeier, R.W. and Suchanek, T.H. (1985). Redistribution of fallout radionuclides in Enewetak Atoll lagoon sediments by callianassid bioturbation. *Nature* **313,** 674-7.

Meadows, P.S. and Tait, J. (1989). Modification of sediment permeability and shear strength by two burrowing invertebrates. *Marine Biology* **101**, 75-82.

Miller, M.F. (1984). Bioturbation of intertidal quartz-rich sands: a modern example and its sedimentologic and paleoecologic implications. *Journal of Geology* **92**, 201-16.

Mukai, H. and Koike, I. (1984). Behaviour and respiration of the burrowing shrimps *Upogebia major* (De Haan) and *Callianassa japonica* (De Haan). *Journal of Crustacean Biology* **4**, 191-200.

Murphy, R.C. and Kremer, J.N. (1992). Benthic community metabolism and the role of deposit-feeding callianassid shrimp. *Journal of Marine Research* **50**, 321-40.

Nash, R.D.M., Chapman, C.J., Atkinson, R.J.A. and Morgan, P.J. (1984). Observations on the burrows and burrowing behaviour of *Calocaris macandreae* (Crustacea: Decapoda: Thalassinoidea). *Journal of Zoology* **202**, 425-39.

Nichols, D., (1959). Changes in the chalk heart-urchin *Micraster* interpreted in relation to living forms. *Philosophical Transactions. Royal Society of London. Series B* **242**, 347-437.

Novitsky, J.A. and Karl, D.M. (1986). Characterisation of microbial activity in the surface layers of a coastal sub-tropical sediment. *Marine Ecology Progress Series* **28**, 49-55.

Officer, C.B. and Lynch, D.R. (1989). Bioturbation, sedimentation and sediment-water exchanges. *Estuarine and Coastal Shelf Science* **28**, 1-12.

Olafsson, E.B. (1986). Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal Ecology* **55**, 517-26.

Ott, J.A., Fuchs, B., Fuchs, R. and Malasek, A. (1976). Observations on the biology of *Callianassa stebbingi* Borrodaile and *Upogebia litoralis* Risso and their effect upon the sediment. *Senckenbergiana maritima* **8**, 61-79.

Pemberton, G.S., Risk, M.J. and Buckley, D.E. (1976). Supershrimp: deep bioturbation in the Strait of Causo, Nova Scotia. *Science* **192**, 790-1.

Pervesler, P. and Dworschak, P.C. (1985). Burrows of *Jaxea nocturna* Nardo in the Gulf of Trieste. *Senckenbergiana maritima* **17**, 33-53.

Pohl, M.E., (1946). Ecological observations on *Callianassa major* (Say) in Beaufort, North Carolina. *Ecol*ogy **27,** 71-80.

Poore, G.C.B. (1975). Systematics and distribution of *Callianassa* (Crustacea, Decapoda, Macrura) from Port Phillip Bay, Australia, with descriptions of two new species. *Pacific Sci*ence **29**, 197-209.

Poore, G.C.B. and Rainer, S. (1979). A three-year study of benthos of muddy environments in Port Phillip Bay, Victoria. *Estuarine and Coastal Shelf Science* **9**, 477-97.

Poore, G.C.B., Rainer, S.F., Spies, R.B. and Ward, E. (1975). The zoobenthos program in Port Phillip Bay, 1969-73. *Fisheries and Wildlife Paper, Victoria* **7**, 1-78.

Posey, M.H. (1986 a). Predation on a burrowing shrimp: distribution and community consequences. *Journal of Experimental Marine Biology and Ecology* **103**, 143-61.

Posey, M.H. (1986 b). Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis. Marine Ecology Progress Series* **31**, 15-22.

Posey, M.H., Dumbauld, B.R. and Armstrong, D.A. (1991). Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. *Journal of Experimental Marine Biology and Ecology* **148**, 283-94.

Rashid, M.A. (1985). *Geochemistry of marine humic compounds*. Springer-Verlag, Berlin 291pp.

Regnault, M., Boucher-Rodoni, R., Boucher, G. and Lasserrer, P. (1988). Effects of macrofauna excretion and turbulence on inorganic nitrogenous exchanges at the water-sediment interface. Experimental approach microcosms. *Cahiers de Biologie Marine* **29**, 427-44.

Reichardt, W. (1988). Impact of bioturbation by *Arenicola marina* on microbiological parameters in intertidal sediments. *Marine Ecology Progress Series* **44**, 149-58.

Rhoads, D.C. (1974). Organism-sediment relations on the muddy sea floor. *Oceanography and Marine Biology Annual Review* **12**, 263-300.

Rhoads, D.C. and Young, D.K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28**, 150-78.

Rhoads, D.C. and Boyer, L.F. (1982). The effects of marine benthos on physical properties of sediments. A sucessional perspective. In: *Animal-Sediment Relations.* (Eds P.L. McCall and M.J.S.Tevesz) pp. 3-52. Plenum Press, New York.

Riddle, M.J., Alongi, D.M., Dayton, P.K. Hansen, J.A. and Klumpp,D.W. (1990). Detrital pathways in a coral reef lagoon. Macrofaunal biomass and estimates of production. *Marine Biology* **104**, 109-18.

Rowden, A.A., Jones, M.B. and Morris, A.W. (1992). Sediment turnover estimates for the mud shrimp *Callianassa subterranea* (Montagu)(Thalassinidea) and its influence upon sediment resuspension in the North Sea. In: *First European Crustacean Conference, Paris, August 31-September 5, 1992*, **Abstracts**, 130-1.

Sayama, M. and Kurihara, Y. (1983). Relationship between burrowing activity of the polychaetous annelid, *Neanthes japonica* (Izuka) and nitrification-denitrification processes in the sediments. *Journal of Experimental Marine Biology and Ecology* **72**, 233-41.

Self, R.F.L. and Jumars, P.A. (1988). Cross-phyletic patterns of particle selection by deposit feeders. *Journal of Marine Research* **46**, 119-43.

Shinn, E.A. (1968). Burrowing in recent lime sediments of Florida and the Bahamas. *Journal of Paleontology* **42**, 879-94.

Specht. D.T. and Lee, H. II. (1989). Direct measurement technique for determining ventilation rate in the deposit feeding clam *Macoma nasuta* (Bivalvia, Tellinaceae) *Marine Biology* **101**, 211-18.

Stamhuis, E.J. (1992). Optimal deposit foraging in the benthic shrimp *Callianassa subterranea*: improving food quality by mechanical selection on grain size. In: *First European Crustacean Conference, Paris, August 31-September 5, 1992*, **Abstracts**, 153-4.

Suchanek, T.H. (1983). Control of seagrass communities and sediment disribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *Journal of Marine Research* **41**, 281-98.

Suchanek, T.H. (1985). Thalassinid shrimp burrows: ecological significance of species-specific architecture. In: *Proceedings. Fifth International Coral Reef Symposium, Tahiti, 1985* **5**, 205-10.

Suchanek, T.H. and Colin, P.L. (1986). Rates and effects of bioturbation by invertebrates and fishes at Enewetak and Bikini Atolls. *Bulletin of Marine Science* **38**, 25-34.

Suchanek, T.H., Colin, P.L., McMurty, G.M. and Suchanek, C.S. (1986). Bioturbation and redistribution of sediment radionuclides in Enewetak Atoll lagoon by callianassid shrimp: biological aspects. *Bulletin of Marine Science* **38**, 144-54.

Swift, D.J. (1993). The macrobenthic infauna off Sellafield (North-eastern Irish Sea) with special reference to bioturbation. *Journal of the Marine Biological Association of the United Kingdom* **73**, 143-62.

Tamaki, A. (1988). Effects of the bioturbating activity of the ghost shrimp *Callianassa japonica* Ortmann on migration of mobile polychaete. *Journal of Experimental Marine Biology and Ecology* **120**, 81-95.

Tudhope, A.W. and Scoffin, T.P. (1984). The effects of *Callianassa* bioturbation on the preservation of carbonate grains in Davies reef lagoon, Great Barrier Reef, Australia. *Journal of Sedimentary Petrology* **54**, 1091-6.

Tunberg, B. (1986). Studies on the population ecology of *Upogebia deltaura* (Leach)(Crustacea,Thalassinidea). *Estuarine and Coastal Shelf Science* **22**, 753-65.

Waslenchuk, D.G., Matson, E.A., Zajac, R.N., Dobbs, F.C. and Tramontano, J.M. (1983). Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudian sediments. *Marine Biology* **72**, 219-25.

Witbaard, R. and Duineveld, G.C.A. (1989). Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu) (Thalassinidea) from the southern North Sea. *Sarsia* **72**, 209-19.

Wilson, R.S., Cohen, B.F. and Poore, G.C.B. (1993). The role of suspension-feeding and deposit-feeding benthic macroinvertebrates in nutrient cycling in Port Phillip Bay. Technical Report No.10, CSIRO Port Phillip Bay Environmental Study, Melbourne.

Wisniewski, R.N. (1993). The release of phosphorous during sediment resuspension. *Hydrobiologia* **253**, 321.

Yamada, H. and Kayama, M. (1987). Liberation of nitrogenous compounds from bottom sediment and effect of bioturbation by small bivalve, *Theora lata* (Hinds). *Estuarine and Coastal Shelf Science* **24,** 539-55.

Zwarts, L. and Wanink, J. (1989). Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Marine Biology* **100**, 227-40.