

MAKING WAVES
THE EFFECTS OF BOAT-WASH ON MACROBENTHIC
ASSEMBLAGES OF ESTUARIES

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A thesis submitted in fulfillment of the requirements for the degree of
Doctor of Philosophy in the University of Sydney

April 2003

The work contained within this thesis, except where otherwise acknowledged, is the result of my own investigations

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ABSTRACT

Numerous studies have examined ecological impacts of boating resulting from scarring by propellers, the discharge of pollutants and sewage, noise, anchoring and the infrastructure associated with boating (e.g. marinas and wharves). Only recently have studies considered the impact of wash. This is the loose water produced by a vessel as it travels through the water. Most studies have focussed on wash produced by fast-ferry services. It is, however, known that wind-generated waves, which are typically smaller and of lesser energy than many boat-generated waves, are important in determining the distribution and abundance of organisms. Thus, wash from smaller vessels may also have an impact on estuarine organisms.

This thesis considered: (i) any impact of wash from RiverCat ferries - 35 m, low-wash vessels that operate on the Parramatta River, Sydney, Australia – on intertidal assemblages and (ii) the effect of wash on epifauna associated with seagrass blades.

The collapse of seawalls and the erosion of river-banks was observed following the introduction of RiverCat ferries to the Parramatta River, Sydney, Australia. Several strategies of management – establishing no-wash zones, where ferries must slow to minimize wash and planting mangroves, which may dissipate wave-energy – have consequently been implemented. These were used in mensurative experiments, examining the effects of wash on infauna. If the establishment of no-wash zones and planting of mangroves are both effective in minimizing any ecological impact of wash, there should be a greater difference between assemblages in wash zones (where speed is unrestricted) from those in no-wash zones when mudflats are sampled than when sampling is done amongst pneumatophores of mangroves. Along the upper Parramatta River, assemblages of infauna differed between the zones, regardless of whether sampling was done on mudflats or amongst pneumatophores. The difference was no greater for organisms in mudflats. Along the lower Parramatta River, where there is generally less compliance with wash restrictions, no difference was seen. Thus, while planting mangroves does not appear to be effective in minimizing the ecological impacts of wash on macro-invertebrates, the establishment of no-wash zones may be.

During the 2000 Sydney Olympic Games, ferry services were suspended for 5 weeks along the western section of the Parramatta River. This managerial decision provided the manipulation for an experiment to determine whether patterns between the wash and no-wash zones of the upper Parramatta River were due to differences in the intensity of wash. If

patterns are due to wash, it was hypothesized that, following the removal of the disturbing force: (i) the assemblages of the wash and the no-wash zones would become more similar and (ii) abundances of taxa in the wash zone would increase to match abundances in the no-wash zone. Results supported hypothesis (i) but not hypothesis (ii).

The impact of wash on infauna may be a result of increased rates of mortality of adults and/or decreased rates of colonization. Any effect of wash may be direct or indirect. Two experiments were done to determine whether patterns between wash and no-wash zones were due to a direct or an indirect effect of wash on colonization and/or mortality. The first, which involved the deployment of units of defaunated sediment, evaluated models attributing the impact to decreased rates of colonization in the wash zone. If wash directly affects colonization, differences should be seen between the assemblages accumulating in homogeneous sediment placed in the wash zone and those in the no-wash zone. If it indirectly affects colonization via changes to characteristics of the sediment, which, in turn, determine patterns of colonization, no difference will, however, be seen in the assemblages accumulating in homogeneous units. A difference will, instead, be seen between the wash zone and the no-wash zone in the colonization of site-specific sediments. Colonization of sediment was less spatially variable in the homogeneous than in the site-specific sediment. This indicates that characteristics of the sediment are important in structuring assemblages. A difference in the colonization of the wash and no-wash zone was, however, not evident in either of the treatments.

The second experiment, in which cores of sediment were transplanted within and between the zones *with* their associated assemblages, considered direct and indirect effects of wash on assemblages, resulting from the net effect of mortality of adults and of colonization. This experiment did not support a direct effect of wash on assemblages but, instead, indicated that characteristics of the sediment are of primary importance in structuring assemblages. Abundances of Capitellidae, Nereididae and Amphipoda did, however, increase when sediment was transplanted from the wash to the no-wash zone and decrease when the reciprocal transplant was done. This indicates that, while assemblages do not appear to be directly affected by wash, the abundances of individual taxa are affected.

The second section of this thesis examined the effect of wash on epifauna associated with seagrass blades through a series of experiments in North Carolina, USA and the Greater

Sydney Metropolitan Region. In North Carolina, assemblages of epifauna differed between places exposed to wash from vessels traveling along the Atlantic Intracoastal Waterway and places that were sheltered from this disturbance. Abundances of gastropods and amphipods were smaller in the exposed places.

A possible model for this pattern is that these animals are dislodged from seagrass by the flapping of the blades as waves propagate through the bed. In the case of mobile organisms, this model will only explain decreased abundances if the frequency of the disturbance is greater than the time taken to recolonize the blades, or if organisms are more susceptible to predation while displaced. If epifauna are indeed displaced by waves, the effect of wash should be immediate.

It was hypothesized that if a boat were driven past patches of seagrass that are not usually subject to wash, abundances of small crustaceans and gastropods would decrease immediately after exposure to wash. This hypothesis was tested at two locations - Narrabeen and the Georges River. At Narrabeen, results supported the hypothesis. At the Georges River, in contrast, no change was seen from before to after the disturbance. This may be because this second location was exposed to strong currents, which may be much more important in structuring assemblages than wash.

On their own, neither the large-scale mensurative experiments nor the small-scale manipulative experiments described above, provided much information on the role of wash in structuring assemblages. Together, however, they showed that, under certain conditions, wash can reduce the abundance of epifaunal taxa and, where this effect occurs, it is immediate. Thus, although it is often difficult or even impossible to manipulate large-scale disturbances directly, observations of these disturbances may be coupled with smaller-scale controlled manipulative experiments to identify processes that are important in determining the distribution and abundance of organisms. This study has demonstrated that the large scale of a disturbance is not a barrier to the experimental test of processes, but rather a unique ecological opportunity to be exploited.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank Gee Chapman and Tony Underwood for the considerable contribution they have made to my professional development and the many opportunities with which they have provided me during my time at the Centre. Without them this thesis would not be here. In fact, I am fairly certain I would be a plant cell physiologist. Through their immense enthusiasm they managed to convince me that Marine Ecology was not just a subject that gave me a good timetable in third year but also an interesting and challenging science. I am particularly grateful to Gee Chapman, my primary supervisor, for controlling her excitement when handed the umpteenth piece of paper to read and for managing to keep track of almost all of them!

I would also like to extend a special thank-you to Pete Peterson for allowing me to spend several months in his lab in North Carolina and providing me with invaluable advice and encouragement on that phase of my project. What with September 11, the pipe bomb at the boat ramp and the broken axel on the trailer...I am surprised he has invited me back. Thanks too to the other members of his lab for their Southern hospitality and to Hal Summerson and David Gaskill for their help in the field.

To members of the Centre, past and present – I am not even going to try to list everyone who has provided assistance or made my life in some way more pleasant – thank-you all! I would, however, like to single out the remaining members of ‘the cohort’ who, after the last four years, are almost like family to me and who I am going to particularly miss. There’s Katie, with whom I have shared an office (and the ups and downs of work and social lives) and whose mountain of crap deflected attention from my not insignificant mess. Brianna, my gym buddy, who is probably the main reason why, at the end of writing this thesis, I still fit into my jeans. David - always eager to help a damsel in distress and share a beer...or six. And finally Craig – I’m glad there’s someone else out there who appreciates real football...no, not league – AFL!!!

My ‘non-Marine’ friends have made sure I have always had a life outside of uni and to them I owe my sanity. Special thanks to Alex, who has come into my life at the wrong end of my PhD, for always being there, tolerating my moodiness and not calling me a nerd too many times when I have gone to uni on a Saturday.

Last, but certainly not least, thanks to my family for all their love and support, for always encouraging me to follow my dreams and for not booting me out of the family home. It’s amazing how far an APA can go when you don’t have to pay rent!

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CHAPTER 1

GENERAL INTRODUCTION

1.1 The estuarine environment

Estuaries are zones of transition between rivers and the sea. They share characteristics of both, but are identical to neither. The most universally cited definition of an estuary is “a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage” (Cameron and Pritchard, 1963). This, however, omits a number of habitats that may be considered estuarine. Hopkinson and Hoffman (1984) argued that estuarine influences can extend beyond enclosed waterways to near-shore coastal waters, where seawater is diluted by drainage from land. According to Hopkinson and Hoffman’s interpretation, the brackish waters of the Amazon and Mississippi Rivers, which are seaward of their respective river-mouths, are estuarine. In addition, the Cameron and Pritchard definition does not include coastal lakes and lagoons that are only intermittently open to the ocean. The salinity of these bodies of water can range from fresh, during times of heavy rainfall, to hypersaline at times of little rainfall, when evaporation exceeds the supply of freshwater. Hutchings and Collett (1977) included intermittently open coastal lakes and lagoons by defining estuaries as the tidal portions of river mouths, bays and coastal lagoons, irrespective of whether they are dominated by hypersaline, marine or freshwater conditions.

For the purposes of this thesis, “estuary” will be used to describe bodies of water where: (i) discharge and water-levels are influenced by tidal processes transmitted through a permanent or intermittent connection with the ocean and (ii) salinity is variable due to mixing of seawater with freshwater run-off from the land. This definition includes tidal sections of rivers, lagoons and sounds.

Regardless of the way in which they are defined, estuaries are generally perceived as areas of great environmental variability. Many are characterized by longitudinal gradients in physico-chemical variables such as salinity, temperature and the concentration of suspended particulate matter (Pritchard, 1967). Salinity may range from near 0 to over 35 ppt and sediments may range from colloids to sands and detritus. Environmental gradients are displaced by the unidirectional currents of streams and/or oscillating tidal currents (Bassindale, 1943), resulting in large fluctuations in variables at points within the estuary.

These fluctuations are believed to select against taxa that cannot live and reproduce over a wide range of environmental conditions (e.g. Sanders, 1969; McLusky, 1981), resulting in a smaller diversity of species within estuarine habitats than in marine and limnic environments

(Moverley and Hirst, 1999). Sessile organisms are particularly susceptible to large fluctuations at individual points in an estuary (Kinne, 1971). In many estuaries, the number of species decreases from the sea towards brackish parts, before increasing again in the direction of the river (Remane, 1934; Alexander *et al.*, 1935).

In contrast to taxonomic diversity at the scale of individual habitats, functional diversity at the scale of the estuary is great (Moverley and Hirst, 1999). This is primarily due to the large range of habitats that estuaries support, which include muddy and sandy beaches, marshes, mangroves, seagrass meadows, rocky reefs and artificial structures, such as seawalls, pontoons and pilings (see Ponder *et al.*, 2002). The large diversity at the scale of an estuary may also be attributed to the diversity of sources from which estuarine fauna are derived – estuaries contain species from limnic and marine environments, in addition to a unique component (e.g. Day, 1951).

Salt marshes and other wetlands in estuaries frequently export disproportionately large biomasses of fish and invertebrates, relative to their small area (Boesch and Turner, 1984). These habitats are often referred to as nursery grounds (e.g. Robertson and Duke, 1987; Laegdsgaard and Johnson, 1995). The importance of such habitats on the survival, growth and subsequent entry of juveniles into the adult population scales is, however, unclear. Many of the studies of fish in mangroves have used inconsistent sampling methods or inadequate sampling designs (Connolly, 1999, but see Nagelkerken *et al.*, 2000a, 2000b). Properly designed studies, with appropriate replication and where mangroves and other habitats are sampled at multiple spatial scales suggest that, at least in urban areas, mangroves may not be particularly important for fish (Clynick and Chapman, 2002). While unvegetated habitats may appear unproductive, their assemblages of infauna and epifauna can provide a significant food source for many species of fish (NSW Fisheries, 1998).

The productivity of estuaries, their location between the oceans and land-masses and their relatively protected waters, make them valuable resources. They support commercial and recreational fisheries (e.g. prawns, Broadhurst *et al.*, 1996), are often natural harbours (e.g. Sydney Harbour, Australia, on the Port Jackson estuary; Poole Harbour, U.K., fed by the Frome and Piddle Rivers) and/or routes for transportation (e.g. the Atlantic Intracoastal Waterway along the southeastern coast of the USA). They are also of great social value, being the preferred sites for human settlement. In New South Wales, Australia, 75% of the population live in towns and cities near estuaries (NSW DLWC, 2000a). Estuaries are often the cultural centres of coastal communities, serving as the focal point for local commerce, tourism and recreation. Boating,

fishing, swimming, surfing, and bird-watching are amongst the numerous recreational activities people enjoy in estuaries.

The high value that society has placed on estuaries for living, working and recreation has, however, made them one of the most heavily populated and used areas. This great level of development means that estuaries are subject to a large range of anthropogenic disturbances.

1.2 Disturbances

A disturbance is a process external to a population that causes environmental change (Underwood, 1989). Disturbances may, or may not, cause changes to the population(s) of interest. In the case that the disturbance does elicit a response (impact), the cause and effect are collectively termed a perturbation (Bender *et al.*, 1984).

Glasby and Underwood (1996) identified four types of perturbation according to the time-scale of the constituent disturbance and response. A perturbation is classified as a 'discrete pulse' when both the disturbance and the response are of short duration. When the disturbance is of short duration, but the effect is sustained, the perturbation is a 'protracted pulse'. Press disturbances are of longer duration and, like pulse disturbances, may give rise to responses of a short (discrete) or long (protracted) temporal scale. These perturbations are termed 'discrete presses' and 'protracted presses', respectively.

Disturbance is undisputedly an important factor in determining the structure of aquatic and terrestrial assemblages (e.g. Cooper, 1926; Watt, 1947; Dayton, 1971; Connell, 1978; Sousa, 1984; Pickett and White, 1985; McGuinness, 1987) and is a major source of temporal and spatial heterogeneity (reviewed by Sousa, 1984). The severity of a disturbance is determined by its intensity (physical force of the event per unit area per unit time), frequency (mean number of disturbing events in a set period of time), area and the nature of its periodicity (cyclic or stochastic) (Sousa, 1984; Huston, 1994; Townsend *et al.*, 1997). It is, however, unclear how these variables interact with one another to determine the impact of the disturbance (Death and Winterbourn, 1995). Most studies have considered the effect of these variables on the severity of the disturbance independently of one another (e.g. Thrush *et al.*, 1996; Phillips *et al.*, 1997; but see McCabe and Gotelli, 2000).

In any case, it appears that the relationship between these variables and the severity of the disturbance is not always linear (Pearson, 1981). For example, gradients of contaminants (i.e. intensity of disturbance) are often poorly matched with gradients of ecology (Keough and Black, 1996, Raimondi and Reed, 1996). Substrata in the immediate vicinity of industrial-waste and sewage outfalls are sometimes devoid of benthic macrofauna, with abundances peaking a short

distance from the point of discharge, before decreasing to 'background' levels with distance (e.g. Bellan and Bellan-Santini, 1972; Anger, 1975; Rosenberg, 1976; Bishop *et al.*, 2002). Non-linear relationships between the frequency of disturbance and diversity of organisms have also been reported (e.g. AuClair and Goff, 1971; Lubcheco and Menge, 1978; Collins *et al.*, 1995; Hiura, 1995). These studies found greatest diversity of organisms at intermediate frequencies of disturbance and small diversities at large and small frequencies, supporting the Intermediate Disturbance Hypothesis, proposed, historically, by Tansley and Adamson (1925) and, in a more recent context, by Connell (1978).

Characteristics of the environment, the initial structure of the affected assemblage and the biology of its constituent organisms may also determine the severity of a disturbance. For example, organisms living in cracks, crevices and rockpools should be less susceptible to the effects of waves than organisms on exposed substrata (Denny, 1985). The stage in an organism's life-cycle at which it is disturbed and the distance over which it can disperse will influence its susceptibility (see Underwood, 1989).

1.3 Boating as a disturbance

Boating, like most human activities, is a contributing cause to many disturbances in natural environments. The ecological impacts of boating are of increasing concern given that: (i) participation rates for recreational boating are on the rise (ii) vessels are becoming larger and engines more powerful and (iii) development of the coastal zone means that there is better access to more waterways (Total Environment Centre, 1996).

Boats constitute a potentially significant source of a number of contaminants. These include organic and inorganic chemicals (e.g. trace elements, tributyltin, polychlorinated biphenyls, chromated copper arsenate, petroleum hydrocarbons, polynuclear aromatic hydrocarbons), coliform bacteria and pathogens (e.g. McMahon, 1989; Lenihan *et al.*, 1990; Weis and Weis, 1992; McGee *et al.*, 1995), which have been found in elevated concentrations adjacent to marinas and in areas of boating-related activities (e.g. washing down, sanding and painting, draining bilge water, refuelling; Young *et al.*, 1979; Faust, 1982; Marcus and Stokes, 1985; Valkirs *et al.*, 1986; Langston *et al.*, 1987; McMahon, 1989; Clarisse and Alzieu, 1993; McGee *et al.*, 1995).

Many studies have examined the effects of contaminants on the biology and ecology of benthic organisms. Unfortunately, most have provided only circumstantial evidence of impacts. For example, Waldock *et al.* (1999) acknowledge that their study on the River Crouch provides only circumstantial evidence for an effect of tributyltin on assemblages of infauna. Between

1987 and 1992, they found an increase in the diversity of infauna, coincident with a decrease in the concentration of TBT in the sediment.

Until recently, TBT was added to paint to kill fouling organisms. Despite the paucity of properly controlled studies examining the impact of TBT on natural assemblages in estuaries, a large number of studies have reported the same deleterious effects, leaving little doubt as to its toxicity. TBT has been implicated in causing deformities in oysters (Alzieu *et al.*, 1980; Alzieu *et al.*, 1981; Waldock and Thain, 1983; Thain and Waldock, 1986) and decimating populations of dogwhelks (*Nucella lapillus*) (Bryan *et al.*, 1986; Davies and Bailey, 1991; Evans *et al.*, 1991), clams (*Scrobicularia plana*) and whelks (*Buccinum undatum*) (Ruiz *et al.*, 1996; ten Hallers-Tjabbes *et al.*, 1994).

Deleterious effects of polynuclear aromatic hydrocarbons (PAHs), found in petroleum products, on aquatic organisms have also been documented. PAHs are toxic to many benthic invertebrates (Sammut and Nickless, 1978; Lee *et al.*, 1981; Widdows *et al.*, 1995; Lee and Page, 1997) and, in places where the concentrations of PAHs are great, abundances and types of these organisms are reduced (Olsgard and Gray, 1995). At moderate concentrations, the environment is made suitable for opportunistic species, which take advantage of the increases in microflora in response to concentrations of PAHs (Sanders *et al.*, 1980; Bunch, 1987; Steichen *et al.*, 1996; Lee and Page, 1997).

There is also evidence for a direct physical impact of boating on flora and fauna. Anchors can cause damage to corals (Davis, 1977; Tilmant and Schmahl, 1981). Macrofauna in sediments may be displaced by propeller-scarring. Losses of seagrasses have resulted from scouring by boat-moorings, anchors and propellers (Zieman, 1976; Walker *et al.*, 1989; Hastings *et al.*, 1995; Creed and Amado Filho, 1999). Although losses are generally small, the scoured area results in an increase in the length of "edge" which is vulnerable to erosion during storms (Walker *et al.*, 1989). Regrowth of seagrass is often slow, with recovery rates of *Thalassia testudinum* in the Florida Keys requiring an average of 3.5 to 4.1 years (Dawes *et al.*, 1997). Propellers may also decrease cover of seagrass indirectly through the resuspension of sediment (Gucinski, 1981), although this is yet to be determined experimentally.

In addition to these disturbances associated with the boats themselves, disturbances related to facilities associated with boating appear to be important in structuring assemblages of benthic organisms. Probably the most studied of these is dredging of boating channels, which has been found to decrease the diversity of assemblages of macrobenthic invertebrates and the abundances of taxa (Gilmore and Trent, 1974; Kaplan *et al.*, 1974; Daiber *et al.*, 1975; Pfitzenmyer, 1975, 1978; Allen and Hardy, 1980; Van Dolah *et al.*, 1984).

Marinas have also received much attention. The large numbers of artificial substrata associated with these developments (e.g. pilings and floating pontoons) increase the area of vertical surface available to fouling organisms, shade hard and soft substrata and obstruct flow of water (e.g. McGee *et al.*, 1995; Turner *et al.*, 1997). Recent work in Sydney Harbour suggests that assemblages of sessile invertebrates colonizing these structures are quite different from those on nearby rocky reefs (Connell and Glasby, 1999; Glasby and Connell, 2001). In addition, the rooftops and paved surfaces (roads, parking-lots, pavements) associated with marinas and other boating facilities may increase the stormwater runoff entering estuarine waters. In developed areas, this run-off can contain contaminants that are toxic or carcinogenic to aquatic organisms and may affect nutrients, oxygen demand, fecal coliform bacteria, sediment and heat (US EPA, 1983).

Unfortunately, most of this research has been published only in the grey literature (but see Connell and Glasby, 1999; Glasby and Connell, 2001) and is relatively inaccessible. Not having been subject to the scrutiny of a formal process of peer-review, it is also of dubious quality. Much of this research has used experimental designs that lack sufficient temporal and spatial replication to be of use in the assessment of ecological impacts (e.g. Pfitzenmyer, 1975, 1978). Fortunately, with the growing realization that applied research is just as important as pure research, the number of studies on the ecological impacts of boating in scientific journals appears to be increasing and the quality of these is improving.

Perhaps the most urgently required research in the area of disturbances due to boating, then, is on the ecological impact of wash. Wash is the loose water left behind a vessel as it moves through the water. Despite numerous studies documenting the erosion of shorelines and the resuspension of sediment by wash (e.g. Anderson, 1976; Hilton and Phillips, 1982; Nanson *et al.*, 1994; Schoellhamer, 1996), it remains largely unknown whether it has any ecological impact. Boat wash may be expected to be important in determining the ecology of estuaries given that: (i) wash from a vessel is similar to wind-driven waves (Stumbo *et al.*, 1999) and (ii) the well-established role of naturally produced waves in structuring assemblages of soft and hard substrata.

1.4 Waves as a disturbance to organisms on rocky shores

Oceanic waves are widely documented to be a major force determining the biology and ecology of rocky shores. Water-motion, associated with the propagation and breaking of waves, can purportedly affect all stages of the life-history of a marine organism, for example, the fertilization of gametes (Pennington, 1985; Denny and Shibata, 1989; Levitan, 1991), settlement

of larvae onto hard substrata (Eckman *et al.*, 1990; Bertness *et al.*, 1992), growth (Palumbi, 1984; Koehl and Alberte, 1988) and mortality (Denny *et al.*, 1985; Witman and Suchanek, 1984; Carrington, 1990). Exposure may also be important in determining the morphology of organisms (e.g. Trussell *et al.*, 1993; Hobday, 1995; Blanchette, 1997; Ruuskanen, *et al.*, 1999), the composition of assemblages (Kautsky and Kautsky, 1989; Phillips *et al.*, 1997), patterns of horizontal and vertical distribution (Seapy and Littler, 1978; Underwood, 1981; McQuaid and Branch, 1985; Underwood and Jernakoff, 1984; Graham, 1997) and biomass (McQuaid and Branch, 1985; Ricciardi and Bourget, 1999).

The effects of wave-action on intertidal organisms can be a result of wetting by wash and spray, or a result of mechanical action of waves (see Southward, 1958; Jones and Demetropolous, 1968). Two main hydrodynamic forces act on organisms as a result of waves – drag, which acts in the direction of flow and lift, which is perpendicular to it. These are approximately proportional to the square of water-velocity (see Denny, 1998 for a more detailed discussion of drag and lift).

Most of the studies documenting waves to be important in structuring benthic assemblages have tested their hypotheses by comparing the biota of sheltered and exposed rocky shores (e.g. Seapy and Littler, 1978; McQuaid and Branch, 1984, 1985). While such comparisons may strongly suggest that wave-action is important in structuring assemblages of rocky shores, they do not unambiguously demonstrate that there is a causal effect of wave-action in structuring assemblages. Manipulative experiments are required to unconfound exposure from other differences among shores.

1.5 Waves as a disturbance to organisms in soft-sediments

As well as affecting the distribution and abundance of intertidal organisms living on rocky shores, wave action appears to be important in determining the composition of plants and animals in soft-sediments. This appears to be the case in the sheltered environments of estuaries as well as along open coasts.

Extreme events, such as storms, can produce sizable waves in estuarine habitats and along open coastlines, alike. Although such events are infrequent, they can have lasting effects on populations (see Gaines and Denny, 1993). During storms, adult infauna can be passively resuspended and transported over large distances (Dobbs and Vozarik, 1983; Emerson and Grant, 1991; Commito *et al.*, 1995a,b; Shull, 1997). In extreme cases, the sediment can be entirely defaunated (Yeo and Risk, 1979). The sabellid polychaete, *Phragmatopoma lapidosa*, appears to exhibit a spawning response to damage from intense storms (Barry, 1989).

Recruitment of this polychaete along the open coast of California was significantly correlated with the intensity of wave-disturbances during the previous 2-5 months.

Surprisingly, smaller waves appear to be important in structuring benthic assemblages in estuaries. This is despite the seemingly small forces generated by waves as opposed to tidal currents. Mean wind-wave conditions have been found to play an important role in contributing to variability in the structure of assemblages, probably as a result of the disturbance of sediment (Turner *et al.*, 1995).

Moreover, wave-action is considered one of the strongest factors influencing the horizontal and vertical distribution of plants within enclosed waterways (Hutchinson, 1975; Spence, 1982; Keddy, 1982, 1983, 1985; Kautsky, 1987; Chambers, 1987; Coops *et al.*, 1991; Fonseca and Bell, 1998). It may directly affect distribution by uprooting established individuals, displacing seedlings and washing out and/or burying seed-banks (Kimber and Barko, 1994; Madsen *et al.*, 1996; Fonseca and Kenworthy, 1987). Alternatively, waves may wash clays and silts from the sediment, leaving coarser material that is less favourable for growth (Spence, 1982; Wilson and Keddy, 1985; Keddy, 1985). This will increase the turbidity of the water and, consequently, the light available for photosynthesis. The aquatic macrophytes of estuaries may be more susceptible to disturbance by waves due to the generally small background levels to which they are exposed.

Landscape features of seagrass beds are strongly influenced by waves adjacent to the open mouths of estuaries. Cover, shape (perimeter:area ratio), the below-ground biomass, density of shoot and flowering of seagrasses all appear to be related to exposure (Fonseca and Bell, 1998).

1.6 Previous studies investigating ecological impacts of boat-wash

While boats have been operating in coastal waterways for centuries (Andrews, 1975), it is only since the advent of fast ferries that the environmental effects of boat-wash have been seriously considered (e.g. Danish Maritime Authority, 1997; Stumbo *et al.*, 1999). To date, most of the research done on wash has appeared only as unpublished reports for various authorities and management agencies.

Fast ferries operate at speeds approaching 50 knots and produce longer waves than do conventional vessels. The production of wash is dependent on the depth and width of a body of water, the speed at which the vessel is traveling, the volume of water it displaces and its planing altitude. Thus, in confined waters, shoaling of wash from fast ferries results in waves of great height and energy. These waves are at the centre of a number of conflicts between ferry-operators and environmental and recreational interests (see Albright, 2000; Parnell and Kofoed-Hansen, 2001). Real or perceived problems caused by high-speed craft have been reported in the

confined waterways of San Francisco Bay, California (Austin, 1999); Puget Sound, Washington (Stumbo *et al.*, 1999); British Columbia, Canada (British Columbia Ferry Corporation, 2000); Ireland (Maritime and Coastguard Agency, 1998); Sweden (Ström and Ziegler, 1998); Denmark (Danish Hydraulic Institute, 1996; Danish Maritime Authority, 1997; Kofoed-Hansen and Mikkelsen, 1997; Kirkegaard *et al.*, 1998a,b); The Netherlands (Anon., 2000); England (Hamer, 1999) and New Zealand (Parnell, 1996; Kirk and Single, 2000).

One of the more publicized cases of conflict surrounding the introduction of fast ferries is that of the Marlborough Sounds, New Zealand. Fast ferries were introduced to the inter-island route, which crosses the Cook Strait and passes through the Tory Channel, the Inner Queen Charlotte Sound and the Marlborough Sounds, in summer 1994/1995. Shortly after the commencement of services, residents of the Tory Channel expressed concerns that wash from the ferries, which appeared considerably more powerful than that from conventional ferries, was having a deleterious effect on the artificial and natural structures of the sound and on its flora and fauna. These concerns culminated in a number of applications being filed against the operator (New Zealand Rail Limited and Sea Shuttles, NZ, Limited) for a permanent enforcement order to stop services from operating. These were heard before the Planning Tribunal in early 1995, but were rejected. The reasoning behind this decision was purportedly that the disturbance set a new “equilibrium of the ecosystem” and the maintenance of any equilibrium (existing or new) would be adequate for sustainable management (reviewed by Pardy, 1995).

The logic of this decision is of concern. Although the maintenance of any equilibrium may be acceptable in terms of sustainable management, it is not in terms of ecology. Although a depauperate assemblage, dominated by opportunistic species and a diverse assemblage, containing a number of rare species, might each vary in time and space about an equilibrium, these are clearly not equivalent in terms of their ecological “value”.

Several studies have been done in the Marlborough Sounds subsequent to the decision of the Planning Tribunal. These are, unfortunately, not without problems of their own. Davidson (1996, 1997) attempted to test for an ecological impact of ferry-wash by sampling a number of ecological variables in exposed (impact) and sheltered (control) sites, during on-seasons (summer) and off-seasons (remainder of the year). While a ‘beyond-BACI’ style analysis of data (*sensu* Underwood, 1991, 1992), testing for an interaction between the factors on-season vs off-season and control vs impact would have enabled the assessment of any impact, this was not done. Instead, pair-wise tests were done between control and impact sites in individual seasons and between seasons at control or impact sites. This confounds the operation of services with season - any change during off-seasons may be seasonal and not due to recovery following the

removal of the disturbing force. Moreover, through repeatedly analyzing the same data without the required Bonferroni adjustments, the author ran the risk of committing a Type I error (Ryan, 1959). In addition, some of the sampling involved the repeated sampling of fixed quadrats, introducing problems of non-independence (see Underwood, 1997).

The poor quality of studies addressing the question of ecological impacts due to boat-wash appears to be a universal problem. Asplund and Cook (1999) attempted to determine the effectiveness of no-wake zones in protecting the aquatic macrophytes of a lake in Wisconsin by comparing the cover of several species in wake, no-wake and no-motor zones. No-wake and no-motor zones were established on sections of the lake using regulatory buoys. Unfortunately, no-wake zones could easily be circumnavigated and rather than slowing to pass through these, most boaters simply avoided them. Increased covers of macrophytes in no-wake zones matched those in no-motor zones and may have been due to the absence of propeller scarring and unrelated to a reduction in boat-wash.

Another study, by Doyle (2001), attempted to determine the effect of boat-wash on the early growth of the macrophyte *Vallisneria americana* by dropping a concrete block, which produced a wave 0.15 m in height, into an experimental raceway containing seedlings. The block was dropped five times within a period of 3 min to simulate boat traffic. According to the author, the height of the waves produced in the experiment was at the low end of the range reported for boat-wash (Bhowmik *et al.*, 1982; Bhowmik *et al.*, 1991) and the intent was to determine whether or not smaller waves, not powerful enough to uproot plants, would affect their growth and development. Although growth of plants exposed to waves was compared to growth in a control raceway, neither was compared to growth-rates in the field. Given the highly contrived experimental procedures of this study, its value is questionable.

Well-designed studies assessing the putative impact of boat-generated waves are clearly required.

1.7 Approach used in this thesis

In this thesis, the affects of boat-wash on benthic assemblages on hard and in soft substrata are examined in a variety of estuarine habitats. I chose estuarine environments for two reasons. First, as previously discussed, boat-traffic is particularly concentrated in estuaries due to their proximity to human settlements and their location between the land-masses and the oceans. Second, the narrow width of estuaries means that the fetch over which wind-driven waves are generated is generally short and the size of naturally-produced waves is small. Presumably, assemblages in estuarine habitats will be more susceptible to the effects of wash than are

assemblages of the open coast-line because the former are not naturally exposed to great wave-action, whereas the latter are.

Assemblages of benthic macrofauna are used as indicators of environmental change. This is because many taxa are: (i) abundant over broad geographic distributions; (ii) relatively non-mobile and are therefore useful in studying local effects of disturbances; (iii) early colonizers which respond quickly to changes in environmental conditions (Rosenberg, 1973; Grassle and Grassle, 1974); (iv) easy to identify and including many different trophic levels (i.e. filter-feeders, deposit-feeders, predators; Clarke and Warwick, 2001) and (v) quantitatively sampleable using relatively simple methods. Moreover, benthic macrofauna are an integral part of the estuarine food-chain and may affect the productivity of fish and crabs (Diaz and Schaffner, 1990).

The benthic assemblages considered in this study come from a variety of intertidal and shallow subtidal habitats. Assemblages in deeper habitats have not been included because waves do not interact with the bottom until the depth is less than one-twentieth the wave-length. Assemblages on hard- and in soft-substrata were sampled because the processes structuring these appear to differ markedly (Peterson, 1979, 1991; Wilson, 1991) and they are likely therefore to differ in ways that are affected by wash. For example, Woodin (1991) pointed out that, on hard substrata, patterns of colonization are primarily determined by settlement due to the large number of sessile organisms that cannot relocate following attachment (although mussels and barnacles are a notable exception; Bayne, 1964; Crisp, 1974). In soft sediments, the relative importance of settlement is less due to the important contribution of post-settlement migration of adults and juveniles to colonization.

Hard substrata provide an essentially two-dimensional environment, while the soft-sediment environment is three-dimensional. Thus, organisms in soft-sediment habitats could conceivably avoid the effects of wash by burying into the third dimension while organisms on hard substrata must bear the full force.

An essentially multivariate approach is used in this thesis due to its sensitivity in detecting ecological change. Statistical methods are discussed in detail in Chapter 2. In many cases, data from prior to the commencement of boating activity are not available and, in some instances, suitable control locations, sheltered from boat-generated waves cannot be used. In these cases, hypotheses are tested regarding the success of strategies of management (e.g. no-wash zones, re-vegetation of river-banks) in minimizing the ecological impacts of wash. This study takes advantage of managerial decisions as manipulations of assemblages.

The thesis is divided into two sections. Section I (Chapters 2-6), “RiverCat ferries: low wash or big swash?”, considers the ecological impacts of wash from the supposedly “low-wash” RiverCat ferries, on assemblages of the Parramatta River, Sydney, Australia. Background to the RiverCat ferry service and general methods are described in Chapter 2. In Chapter 3, the potential impacts of RiverCat-wash on intertidal assemblages of seawalls are considered. Chapter 4 examines the putative impact of this disturbance on infaunal assemblages and the role of existing strategies of management in minimizing this. The role of RiverCat wash in structuring infaunal assemblages is further considered in Chapter 5, through a manipulative experiment arising from a managerial decision. Problems in distinguishing any impact of wash from a background of great temporal and spatial variability are addressed in Chapter 6 and direct and indirect effects of wash are considered.

Section II (Chapters 7-8), “Seagrasses: baffles or beaters?”, considers the effect of wash on assemblages associated with seagrass in a variety of estuarine waterways. Chapter 7 relates to mensurative studies done along the Atlantic Intracoastal Waterway, North Carolina USA. In Chapter 8, manipulative experiments on the epifaunal assemblages of seagrass are described. Chapter 9 is the General Discussion. There, findings from each of the two sections are synthesized and the role of science in management is discussed.

This study aims to determine the importance of wash in structuring estuarine assemblages and to evaluate critically the strategies of management designed to minimize any impact.

Section I.

RiverCat ferries: low wash or big swash?

CHAPTER 2

RIVERCAT FERRIES ON THE PARRAMATTA RIVER: BACKGROUND AND GENERAL METHODS

2.1 The Parramatta River

The Parramatta River (Fig. 2.1) is the largest river emptying into Port Jackson, Sydney, Australia (151°13'E 33°52'S). It has a length of 19 km from its source in western Sydney to Balmain, a width of 50-300 m and is up to 15 metres deep. The total area of the Parramatta River catchment is 130 km² and the waterway itself has an area of 12 km² (NSW DLWC, 2000b). The river is tidal to the Charles Street Weir in Parramatta, where it has a spring range that is 11% greater than at the Heads (approximately 2.0 m).

About 85% of the Parramatta River catchment is urbanized (Total Environment Centre, 1996). Historically, the upper reaches have been subject to a lot of eutrophication and heavy metal contamination due to the large number of industrial sites adjoining this section of river. The situation has improved since the introduction of licensing procedures for trade waste in 1976, under the Clean Waters Act and Regulations (SPCC, 1987). A large proportion of the catchment does, however, remain paved with impervious material or covered by buildings and during periods of rain, large volumes of run-off containing garbage, soil, bacteria and dissolved substances enter the river (Laxton, 1991).

The shores of the lower Parramatta River are dominated by hard substrata. Artificial structures such as sandstone and concrete seawalls, pontoons and pilings are common as is natural rocky reef, which is composed of Hawkesbury sandstone. Mangrove forests are reduced to small remnant patches; sediment is generally coarse and sandy. To the west of Meadowbank, there are large stretches of mangrove forest interspersed with unvegetated mudflat. The sediment of the upper Parramatta River is much finer and contains greater proportions of clay and silt. There has been extensive reclamation of land in the Homebush and Silverwater areas, with minor reclamation in the majority of the other embayments along the river.

Along the Parramatta River, wind speed and direction vary locally according to topography and distance from the sea. Winds may result from large-scale pressure patterns, nocturnal drainage flows down slopes and valleys or from coastal systems. Winds arising from pressure patterns are predominantly westerly from May to September and easterly from November to March. They are strongest in September and weakest in April (Smith, 1990). Nocturnal winds (katabatic drift) typically have speeds of less than 10km/h and are most frequent and of longest duration during

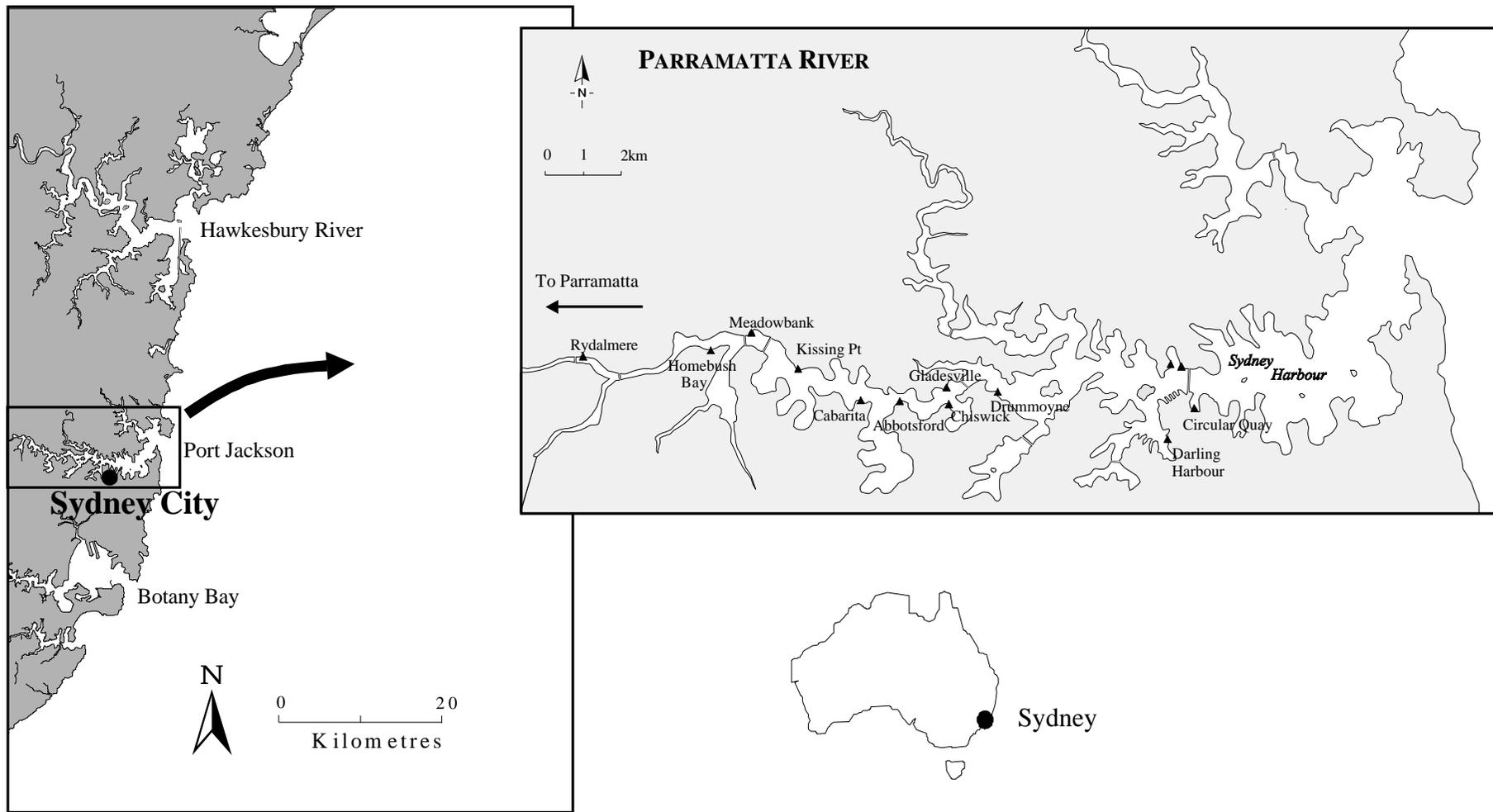


Figure 2.1 Map of the Sydney coastline showing the location of the Parramatta River. The inset shows the location of RiverCat wharves along the river.

winter (Hyde *et al.*, 1983). Onshore sea breezes usually have speeds of less than 30 km/h and are most prevalent during the afternoon and evening of the warmer months (Smith, 1990).

The Parramatta River is a popular location for recreational boating due to its proximity to Sydney city. Boat traffic is greatest on the lower Parramatta River and decreases with distance from Sydney Harbour (Patterson Britton, 2000b; Table 2.1). The majority of boating activity at Silverwater can be attributed to the RiverCat ferries (70-74%, Table 2.1).

2.2 History of boating on the Parramatta River

Since European settlement, the Parramatta River has been an important transport link between Sydney city and Parramatta. Initially, row-boats were used to transport goods between the colony at Sydney Cove and the farming outpost of Rose Hill, but, in October, 1789, the first ferry was commissioned (Andrews, 1975).

Only vessels of shallow draught, traveling at high tide, were able to navigate the last few kilometres of channel to Parramatta. When deeper-draught, propeller-driven ferries replaced paddle-wheelers in the late 1870s, the terminus had to be moved back to Duck Creek, Silverwater, with passengers transported the remaining 4.5 km by steam tram (Andrews, 1975). This change marked the beginning of the demise of the ferries. In 1928, services were cut back to Gladesville and in the early 1950s, services ceased altogether as commuters turned to road and rail (Prescott, 1984).

In 1987, ferries were re-introduced to the river between Meadowbank and Sydney. Wharves were opened at Meadowbank, Abbotsford, Gladesville, Drummoyne, Hunters Hill, Balmain, McMahon's Point and Circular Quay (State Transit, 1993). This service proved popular and it was proposed to extend the services to Raven Point/Putney Point, Cabarita Point and Chiswick. In 1988, the State Government directed the (then) Urban Transport Authority to facilitate the introduction of a high-speed ferry service linking Parramatta and Sydney (Smith, 1990).

There were two main criteria for the design of the ferries. First, the travel-time between Parramatta and Sydney was required to be equivalent to or shorter than that along road and rail links. This translates to an average speed of 21 knots. Second, the wash produced by the ferries must not impact the natural habitats and artificial structures of the river (Smith, 1990).

Table 2.1 Total boat-traffic over a randomly chosen period of seven consecutive days between *a.* 5th May and 8th June, 1988 and *b.* 26th May and 9th June, 2000 at four locations along the Parramatta River. Counts are as determined by Patterson Britton and Partners Pty Ltd (2000b) using time-lapse video.

a.

| | Powercraft | Monohull Charter | Catamaran Charter | Work Boat Fishing Boat | RiverCat | Jet Ski | Total | Total (less RiverCats) | % RiverCats (of Total) |
|--------------------|------------|---------------------|----------------------|---------------------------|----------|---------|-------|---------------------------|---------------------------|
| Gladesville Bridge | 1095 | 30 | 9 | 60 | 271 | 11 | 1476 | 1205 | 18 |
| Abbotsford | 916 | 11 | 14 | 60 | 292 | 43 | 1336 | 1044 | 22 |
| Meadowbank | 323 | 0 | 3 | 26 | 239 | 16 | 607 | 368 | 39 |
| Silverwater | 36 | 0 | 0 | 29 | 181 | 14 | 260 | 79 | 70 |

b.

| | Powercraft | Monohull Charter | Catamaran Charter | Work Boat Fishing Boat | RiverCat | HarbourCat | Jet Ski | Total | Total (less RiverCats/ HarbourCats) | % RiverCats/ HarbourCats (of Total) |
|--------------------|------------|---------------------|----------------------|---------------------------|----------|------------|---------|-------|---|---|
| Gladesville Bridge | 995 | 4 | 17 | 27 | 183 | 142 | 6 | 1374 | 1049 | 24 |
| Abbotsford | 871 | 4 | 14 | 35 | 186 | 145 | 23 | 1278 | 947 | 26 |
| Meadowbank | 150 | 8 | 0 | 21 | 161 | 132 | 23 | 495 | 202 | 59 |
| Silverwater | 36 | 0 | 0 | 18 | 143 | 119 | 39 | 355 | 93 | 74 |

Source: adapted from p 17 Patterson Britton, 2000b.

2.3 RiverCat ferries

Following a lengthy period of design and planning and the dredging of the upper reaches of the river, the 35 m long, low-wash RiverCat ferries were introduced to the Parramatta River in 1993. To this date, these catamarans operate along a 24 km stretch of river between Circular Quay and Parramatta (Fig. 2.1).

Despite being designed specifically for the Parramatta River, damage to the natural and artificial structures of the river has been reported following their introduction. This includes erosion and accretion of beaches, uprooting of mangroves and the collapse of seawalls (Wilson, 1994).

The wash produced by RiverCat ferries is of fairly small amplitude compared to the older “Lady Class” ferries previously used on the Parramatta River. It has been proposed that the deleterious effects of wash are due to “blockage” rather than the amplitude of the waves *per se* (Patterson Britton, 2000c). Blockage results when vessels are operated in channels of restricted width and/or depth. The effects of blockage include:

- (i) surge – the rise in surrounding water-level preceding an approaching vessel;
- (ii) draw-down – the lowering of the water level abreast of a passing vessel, often appearing as a recession of water from a beach or bank as a vessel passes close offshore;
- (iii) backwater flow – the acceleration of water across a shallow seabed as a vessel passes above.

Blockage is typically a function of the dimensions of the channel, the dimensions of the vessel, the vessel’s speed and the distance of the sailing-line from the shore (Dand, 1982).

Blockage and other effects of wash from RiverCat ferries are being considered in detail in a long-term study of the shorelines of the Parramatta River commissioned by the NSW Waterways Authority. This study, by Patterson Britton and Partners Pty Ltd, is on the effects of wash at four sites along the upper Parramatta River between Rydalmere and Parramatta. These sites were chosen because the river is very narrow at these places and the shoreline is particularly susceptible to the effects of wash.

Results to date indicate that there is a critical speed of RiverCats at which erosion of riverbanks occurs (Patterson Britton, 1999a). At Parramatta, this speed is 8-12 knots and at Rydalmere it is 10-14 knots. These speeds are commonly associated with near-bed velocities of 1 $\text{m}\cdot\text{s}^{-1}$, although this varies with tide. Above the critical speed, vessels produce waves of reduced height and shorter period. These can still cause significant increases in turbidity and bed velocities of up to 0.7 $\text{m}\cdot\text{s}^{-1}$ from breaking on the shore.

The observation of a non-linear relationship between speed of the ferries and near-bed flow is as predicted from calculations of depth Froude (F_d) numbers (a unit-less number which relates the velocity of a fluid to the velocity of waves in an open channel):

$$F_d = V.(gd)^{-0.5}$$

where V is the speed of the vessel, g is the acceleration due to gravity and d is water-depth. At relatively low values of F_d (0.6), wave heights are small and both transverse and divergent waves are produced (Patterson Britton, 2000c). Surge and draw-down appear to peak at depth Froude numbers around 0.7; at higher and lower depth Froude numbers they are negligible. As F_d approaches 1.0, waves converge to form a single, large transverse wave. This may be followed by a series of smaller waves of shorter period. The magnitude of the initial wave decreases beyond depth Froude numbers of 1.0. As a general rule, depth Froude numbers in the range of 0.6 - 1.0 produce waves of greatest height and energy, so should be avoided by ferry captains (Patterson Britton, 1999a).

2.4 Present strategies of management

A number of strategies of management have been adopted along the Parramatta River in response to the perceived effects of RiverCat wash.

The first of these is the establishment of a no-wash zone on the upper Parramatta River, between the Silverwater Bridge and the western terminus of services at Parramatta. Within this zone, RiverCats are legally required to travel at speeds less than or equal to 7 knots (15 km/h). Adherence to this regulation is sporadically monitored by NSW Waterways. There is another no-wash zone along the Parramatta River, between the Gladesville Bridge and Five Dock Point, which pre dates the RiverCat ferry service. Along other sections of the river, speed is unrestricted and ferries commonly travel at up to 30 knots.

The second is the planting of mangrove seedlings along unvegetated river banks in an attempt to stabilize the sediment and reduce erosion.

Finally, in 1998, two smaller HarbourCat ferries were added to the RiverCat fleet. These are 24 m in length so should, presumably, cause less blockage than the larger RiverCat ferries. Patterson Britton and Partners (1999b) have examined the relationship between the speed of these vessels and depth Froude number, current-velocity and wave-height. Their results suggest that there is a greater “buffer-zone” above the 7 knot speed limit for HarbourCat than RiverCat ferries, before wash starts to affect deleteriously the river’s foreshores. The HarbourCats do,

however, have a greater displacement-to-length ratio (2.5×10^{-3} tonnes.m⁻³) than do RiverCats (1.4×10^{-3} tonnes.m⁻³; Patterson Britton, 2000c). This ratio is purportedly correlated with the erosive capacity of wash (see Stumbo *et al.* 1999).

There is no distinction between RiverCats and HarbourCats on timetables for the ferry service – they are used interchangeably. Thus, for the purposes of this thesis, RiverCats *and* HarbourCats will be collectively referred to as RiverCat ferries.

2.5 General Methods

In the subsequent chapters, a number of experiments investigating the effects of wash from RiverCat ferries on assemblages on hard- and in soft-substrata are described. Here, the general methodology of these experiments is outlined.

All sampling of hard and soft substrata was done during low tide.

2.5.1 Sampling of hard substrata (seawalls)

To ensure that assemblages sampled on different seawalls could be compared, it was necessary to sample them at the same tidal height. This was done by inserting screws into the seawall at a single height and measuring the distance between these and the waterline at an arbitrary level of the tide (as per Blockley, 1999; Chapman and Bulleri, 2003). The tidal height at the time of measurement was obtained from Sydney Ports Corporation and the height of the screws above MLWS thus calculated.

Two tidal heights were sampled. These are referred to as mid- and high-shore and were 0.9 m and 1.4 m above MLWS, respectively. It was not possible to sample any lower because of the rubble adjacent to many of the seawalls that may shelter low-shore assemblages from the effects of wash.

Sampling was done using quadrats (described in Section 3.2) placed on the seawall so that their centre was at the required height. Abundances of algae and sessile animals were recorded as percentage covers; mobile organisms were counted within the quadrats. Cover was recorded as primary if the organism was directly attached to the substratum and secondary if it was attached to the primary cover.

2.5.2 Soft sediment

Sampling of sediment and associated fauna was done using corers, 10 cm in diameter and constructed of PVC pipe, following Morrisey *et al.* (1992). These were inserted into the sediment to a depth of 10 cm and carefully dug out. Cores were emptied into individually labeled plastic

bags and transported back to the laboratory, where they were either immediately preserved or stored overnight at 4°C. Preservation was with 7% formalin in seawater. Animals were stained using Biebrich Scarlet.

Samples were sieved through a 500 µm mesh. This size of mesh has been found to allow accurate and cost-efficient sampling of spatial variation of assemblages of macrofauna in soft sediments (Lewis and Stoner, 1981; Eleftheriou and Holme, 1984; Hartley and Dicks, 1987; James *et al.*, 1995). Animals retained on the sieve were kept for identification and enumeration. In the case that the sediment was coarse and did not fall through the sieve, animals were separated from the sediment by elutriating each core ten times. Before disposing of the sediment, it was quickly checked under a hand-lens to ensure that all animals had been removed.

All fauna retained by the sieve were identified and counted under a dissecting microscope. In the case of fragmented organisms, only anterior pieces (i.e. heads) were counted, so as not to over-estimate their number. Where only the posterior end was present (i.e. no anterior end was found for that taxon), the animal was given a count of one.

2.5.3 Taxonomic resolution

The analysis of assemblages is generally regarded as expensive due to the time involved in identifying and sorting animals to the level of species (Clarke and Warwick, 2001). In places such as Australia, this is not aided by the paucity of taxonomic information available and the great uncertainty that may be associated with classification. The identification of organisms to broader taxonomic groups (i.e. genus, family, phylum) saves time and money and, in most instances, does not result in the significant loss of ecological information (e.g. James *et al.*, 1995; Chapman, 1998). The use of a coarser taxonomic resolution may, in fact, be more appropriate for assessments of environmental impacts because natural variation at the level of species is often great and may preclude detection of an impact (Clarke and Warwick, 2001).

The taxonomic resolution used in this study varied among types of fauna according to their abundance, their morphological complexity and the taxonomic information available. In general, groups of infauna were kept broad to minimize sorting time. For example, polychaetes were sorted to family, crustaceans, in most cases, were sorted to order and bivalves and gastropods were sorted to species.

Taxa comprising assemblages of hard substrata are generally much quicker and easier to identify. In this study, they were identified to the finest taxonomic resolution possible, which was usually species or genus.

2.6 Analyses

This thesis uses a predominantly multivariate approach to assess the impact of boat-wash on assemblages of benthic marine organisms. Univariate analyses were used to examine patterns of abundance of individual taxa and environmental variables.

2.6.1 Multivariate analyses

A combination of measures of dissimilarity, ordination techniques and non-parametric statistical analyses were used to examine differences in assemblages.

Unless otherwise indicated, all ordinations and analyses were done using Bray-Curtis coefficients of dissimilarity (Bray and Curtis, 1957). This measure has been recommended for ecological data because it takes the value 0 when two samples are identical and 100 when they have no species in common, is independent of the scale of measurement, is not affected by joint absences or the inclusion of additional samples within a matrix and registers differences in total abundance of two samples as a less-than-perfect similarity, even when the relative abundances of all species are identical (Clarke, 1993).

Unlike univariate analyses, some multivariate analyses do not require assumptions of homogeneity of variances. In many multivariate analyses, the role of transformation is to down-weight the contribution of common species so that the outcome is not overly dependent on patterns in abundant species (Clarke, 1993; Clarke and Warwick, 2001). There does not, however, appear to be any biological reason why less abundant taxa should be forced to contribute relatively more to measures of dissimilarity than do more abundant taxa. Analyses of untransformed data consequently formed the basis for the interpretation of experiments in this thesis. These analyses took into consideration the species present, their frequencies of occurrence in samples, their relative abundances and the total abundance of organisms within a sample (see Tabachnick and Fidel, 1989).

Analyses were also done on presence-absence data to determine whether patterns evident in the original data were driven by the species present in the samples or their abundances. Presence-absence data has the effect of giving equal weight to all species, regardless of whether they are rare or abundant. Presence-absence analyses are still, however, affected by frequency of occurrence, which is often correlated with abundance.

Multivariate data were ordinated on two-dimensional plots using non-metric multi-dimensional scaling (nMDS; Shephard, 1962; Kruskal, 1964). nMDS uses the rank order of dissimilarity coefficients to produce a 'map' of the data. The distances between points on the plot have the same rank order as the corresponding dissimilarities between samples - the closer

together the points, the more similar the samples they represent. The extent to which the representation agrees with the original data is reflected in its *stress*. A plot with a stress of less than 0.1 is generally considered to be a good representation of the data and the risk of misinterpretation is minimal. Plots with a stress of 0.1-0.2 are also potentially useful, but it is recommended that any conclusions drawn from these be cross-checked with those from alternative techniques (Field *et al.*, 1982; Clarke, 1993).

Non-parametric multivariate analysis of variance (NP-MANOVA; Anderson, 2001) and analysis of similarities (ANOSIM; Clarke, 1993) were used to test hypotheses about multivariate differences among assemblages. Both methods were used to analyse data collected from simple, mensurative experiments because NP-MANOVAs test hypotheses regarding multivariate distances (measures of dissimilarity) whereas ANOSIMs test hypotheses regarding rank dissimilarities. Data collected from more complex manipulative experiments were analysed using NP-MANOVA only, because, unlike ANOSIM, it can be used to test for interactions. NP-MANOVA compares within-group to between-group sums of squared dissimilarities, using a permutation test to obtain a *P*-value.

ANOSIM is based on rank similarities between samples. Between-group ranks are compared to the within-group ranks giving a test statistic, *R*. The test statistic may lie between 1 and -1 and is approximately zero when the null hypothesis is true. The statistical significance of *R*-observed is determined by comparing it to the distribution of the *R* statistic obtained by recalculating it under permutations of the sample labels. One of the limitations of ANOSIM is that any samples that are totally devoid of animals must be removed from the data matrix before the analysis can be done. While it may be argued that these samples are ecologically irrelevant since they do not contain an assemblage, they may be important in the analysis of impacts that decrease the types and numbers of organisms. This problem was eliminated by inserting a dummy variable that had a uniform value across samples into the data matrix. This ensured that all samples had at least one organism without interfering with measures of dissimilarity.

Each of these methods can only analyse a maximum of two factors at a time. Experimental designs used in this thesis commonly had three factors – exposure (wash/no-wash), locations within exposure groups and sites within locations. Consequently, the spatial scale of location was often omitted from multivariate analyses so that patterns on the scale of exposure group and site could be examined.

Unless otherwise indicated, the *F*-distributions of null hypotheses, tested using NP-MANOVA, were calculated using 4999 permutations of residuals under the full model (ter Braak, 1992, Anderson and Legendre, 1999). This type of permutation was used because: (i) the

number of levels of nested factors was often sufficiently small to preclude a meaningful test if restricted permutations of raw data (Anderson, 2001) were used and (ii) it can be used to rapidly test orthogonal designs where the number of replicates is at least 5 (Anderson, 2001).

In the case that NP-MANOVA or ANOSIM detected a statistically significant difference ($P = 0.05$) among levels of a term of interest, relevant *a posteriori* pair-wise comparisons were done. Species contributing most to multivariate differences between samples were identified using SIMPER (Clarke, 1993).

2.6.2 Univariate analyses

Multi-factorial analyses of variance (ANOVA) were used to test hypotheses concerning differences in the abundance of individual taxa. Multivariate patterns may be explained by several univariate patterns if a few species are controlling the structure of assemblages.

ANOVA assumes homogeneity of variance and this was tested for using Cochran's *C*-test. Many taxa of infauna from the Parramatta River had log-normal distributions and Cochran's *C*-test was consistently significant. These data were transformed using $\ln(x + 1)$ (see Underwood, 1997). In some analyses, heterogeneous variances could not be stabilised by transformation. Given that analysis of variance is relatively robust to heterogeneous variances (Box 1953, Underwood 1997), particularly if there are many independent estimates of variance, data were analysed regardless. Significant results were interpreted with caution due to the increased probability of Type I error associated with the analysis of such data.

Non-significant terms were pooled with the residual using the criterion $P > 0.25$ (Winer *et al.*, 1991) where this resulted in a more powerful test for the main effects of interest.

Analyses of variance were followed by *a posteriori* Student-Newman-Keul tests (SNK tests) to identify significant differences among appropriate means (Winer *et al.*, 1991; Underwood, 1997).

CHAPTER 3

PATTERNS IN THE DISTRIBUTION AND ABUNDANCE OF INTERTIDAL ORGANISMS ON SEAWALLS SHELTERED FROM AND EXPOSED TO THE WASH OF RIVERCAT FERRIES

3.1 Introduction

Wave-exposure along rocky shores is known to have direct effects on biota and to modify ecological interactions (e.g. Dayton, 1975; Menge, 1978a; Seapy and Littler, 1978; Underwood, 1981; McQuaid and Branch, 1984; Underwood and Jernakoff, 1984; Bell and Denny, 1994; Viejo *et al.*, 1995). Intertidal assemblages exposed to great wave-energy may have an increased vertical distribution of sessile organisms, such as barnacles (Seapy and Littler, 1978; Underwood, 1981; McQuaid and Branch, 1985) and algae (Underwood and Jernakoff, 1984), a greater abundance of macro-algae (Underwood, 1981; Underwood and Jernakoff, 1984, McQuaid and Branch, 1984, 1985; Bustamante and Branch, 1996) and filter-feeders (McQuaid and Branch, 1985), or a greater total biomass (McQuaid and Branch, 1985; Ricciardi and Bourget, 1999) than assemblages on sheltered shores. The species comprising intertidal assemblages may also differ between sheltered and exposed shores. For example, on exposed shores, foliose algae may be replaced by calcareous and leathery macrophytes (Phillips *et al.*, 1997) or small, finely branched species (Kautsky and Kautsky, 1989).

The effect of wave-action on intertidal organisms may be a result of wetting by wash or splash, or a result of mechanical action due to the movement or energy of waves (see Southward, 1958; Jones and Demetropoulos, 1968). On wave-exposed shores, the wetting of the substratum to a greater height may allow organisms which have upper vertical limits determined by physical factors to occupy higher levels than they would in places sheltered from wave-action (e.g. Underwood and Jernakoff, 1984). Such wetting may also increase the period over which a substratum is immersed, potentially increasing the proportion of time during which planktonic larvae can settle, filter-feeders can feed and wastes are released into the aquatic environment, but potentially reducing the period over which algae can photosynthesise (see Menge, 1978a; Koehl, 1986). The mechanical action of waves results in greater friction and dynamic pressure on organisms and may act to dislodge organisms from the substratum or result in changes to their behaviour and morphology (Menge, 1974; Menge, 1978a,b; Denny *et al.*, 1985; Brown and Quinn, 1988; Trussel *et al.*, 1993; Hobday, 1995; Etter, 1996; Blanchette, 1997). As most waves break at low to mid-tidal heights, the mechanical action of waves should be greater at these than

at higher levels. Wetting by splash and spray may, however, affect all levels on the shore. Thus, it may be hypothesised that the effect of wave-action on assemblages will differ among tidal heights.

A similar suite of species is found on seawalls as on rocky shores (Blockley, 1999; Chapman and Bulleri, 2003). Patterns in the distribution and abundance of these species may therefore be modified by similar processes on seawalls and rocky shores. Seawalls along the Parramatta River are exposed to the wash of passing RiverCat ferries. While RiverCat wash is generally smaller than the waves of the open coast, many of their effects, such as increasing the height to which the substratum is wet, are analogous. If the ecology of seawalls is indeed modified by the same processes as on rocky shores, the wash of RiverCat ferries should have a similar affect on the intertidal assemblages of seawalls as oceanic waves have on intertidal assemblages on rocky shores. If this model is correct, the distribution and abundance of organisms will differ between seawalls that are exposed to and sheltered from wash.

RiverCats travel along the entire navigable length of the Parramatta River, making it impossible to compare the assemblages on seawalls exposed to wash with those completely sheltered from wash, without the possibility of confounding with other factors. Seawalls located in large bays along the river, which are sheltered from the wash of RiverCat ferries, are also sheltered from wind-waves and much of the wash produced by other commercial and recreational vessels. They are also likely to be subject to different small-scale hydrodynamic processes because they are at the heads of bays. Sandstone seawalls, of similar construction to those along the Parramatta River are absent from adjacent estuaries (i.e. Georges River, Port Hacking and Pittwater). A comparison may, however, be made between seawalls along the Parramatta River that are more or less exposed to the wash of RiverCat ferries.

The energy and height of boat-generated waves decreases with distance from the sailing line (Das and Johnson, 1970; Bhowmik, 1975). Thus, seawalls located closer to the main RiverCat ferry route (on points) should be more exposed to the wash of RiverCat ferries than those located further away (in small bays along the main river channel).

In this chapter, two hypotheses were tested: (i) assemblages found at mid- or high tidal heights on seawalls close to the RiverCat ferry route will differ from those on seawalls further away and (ii) the mean maximal height at which barnacles or algae are found will be greater on seawalls close to the ferry route than on those further away. These hypotheses are very general because the structure of assemblages on seawalls along the Parramatta River had not previously been determined and more specific predictions about the effect of wave-action could not therefore

be made. During sampling, however, more observations were made, more specific models developed and tests of the corresponding hypotheses described.

3.2 Materials and Methods

In order to test the hypothesis that the assemblages found on seawalls close to the RiverCat ferry route will differ from those found on seawalls further away, vertical sandstone seawalls were sampled at two locations close to the ferry route (Abbotsford Point [N1] and Henley [N2]) and two locations further from the ferry route (Looking Glass Bay [F1] and Abbotsford Bay [F2]) on the 19th and 20th May, 2000 (Figure 3.1). At each location, two 5 m-long sections of wall were haphazardly selected as sites. These were separated by at least 5 m so that spatial independence of sampling would be maintained. Estimates of the abundance of species were determined using 25 points of intersection of a 15 x 15 cm quadrat strung with a grid of nylon strings at 2.5 cm intervals. Five quadrats were randomly placed at mid- and high tidal heights (see Section 2.5.1) and the abundance of all sessile and mobile species in each quadrat was determined using the method described in Section 2.5.1. This size of quadrat was chosen so that less than 16 % of the total area of the sites would be sampled at any one time and sampling could consequently be temporally independent (see Banwell, 1996).

The maximal height above MLWS at which (i) barnacles and (ii) algae were found was also determined at 10 places within each site to test the hypotheses that the maximal height at which barnacles or algae would be found will be greater on seawalls close to the RiverCat ferry route than on walls further away. Ten horizontal distances along the wall were selected using random numbers. At each horizontal distance, the maximal height above MLWS at which barnacles or algae were found was recorded. Heights were measured relative to points of known elevation.

During this initial sampling, the observation was made that seawalls orientated perpendicular to the direction of propagation of waves appeared more exposed to the wash of RiverCat ferries than seawalls orientated parallel to the direction of propagation. The abundance of macro-algae and the cover of *Mytilus* sp. were greater on seawalls exposed to the wash of RiverCat ferries than on walls sheltered from wash, while the abundance of the barnacle, *Hexaminius foliorum*, showed the opposite pattern. The mussel, *Xenostrobus securis*, was only found in areas that were most sheltered from wash (i.e. further from the RiverCat ferry route).

It was hence predicted that further sampling of seawalls close to or further from the RiverCat ferry route and oriented perpendicular or parallel to the direction of propagation of wash would find that:

1. Walls located close to the RiverCat ferry route and orientated perpendicular to the direction of propagation of wash would be the most exposed and walls located further from the RiverCat route and parallel to the direction of propagation of waves the least exposed to the wash of RiverCat ferries.
2. The total cover of algae would be greater on seawalls close to the RiverCat ferry route than on seawalls further away and would be greater on seawalls orientated perpendicular to the direction of propagation of wash than on those orientated parallel.
3. The abundance of *Mytilus* sp. would follow the patterns described above for algae.
4. The percentage cover of *H. foliorum* would be less on seawalls close to the ferry route than on those further away and on walls perpendicular to the direction of propagation of waves than those that are parallel.
5. *X. securis* would only be present on sheltered seawalls (i.e. those that are further from the RiverCat ferry route and are orientated perpendicular to incoming wash).

In order to test these hypotheses, seawalls close to the ferry route and orientated perpendicular to the direction of propagation of wash (Abbotsford Point, Henley, Parramatta River Sailing Club), close to the ferry route and parallel to incoming wash (Abbotsford Point, Bedlam Bay 1, Bedlam Bay 2), further from the ferry route and perpendicular to wash (Abbotsford Bay, Gladesville Hospital, Putney Park) and further from the ferry route and parallel to wash (Abbotsford Bay, Looking Glass Bay and Putney Park) were sampled on the 9th and 10th August, 2000 (Fig. 3.2). Only one 5 m-long site was sampled on each wall due to the limited length of wall with the required orientation. As with the initial sampling, five 15 x 15 cm quadrats were randomly positioned at each tidal height and the abundances of macro-algae, *H. foliorum*, *Mytilus* sp. and *X. securis* determined.

The upper limits of (i) algae and (ii) barnacles were also determined at ten positions within each site at this second time of sampling, using the same method outlined above. This was to test the hypothesis that the mean maximal vertical height of each will be greater on exposed seawalls (located close to the ferry route and orientated perpendicular to incoming wash) than on sheltered walls (located further from the ferry route and parallel to incoming wash).

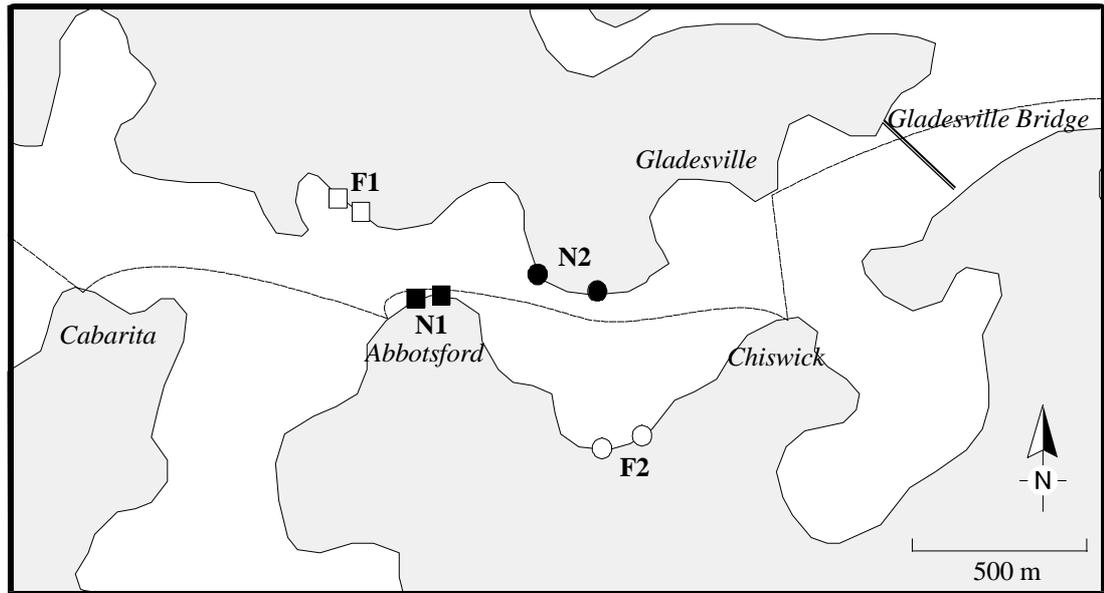


Figure 3.1 Map of the Parramatta River showing the location of seawalls close to (black: N1, N2) and further from (white: F1, F2) the RiverCat Ferry route that were sampled on 19th - 20th May, 2000.

N1: Abbotsford Point, N2: Henley, F1: Looking Glass Bay, F2: Abbotsford Bay
 ----- RiverCat ferry route

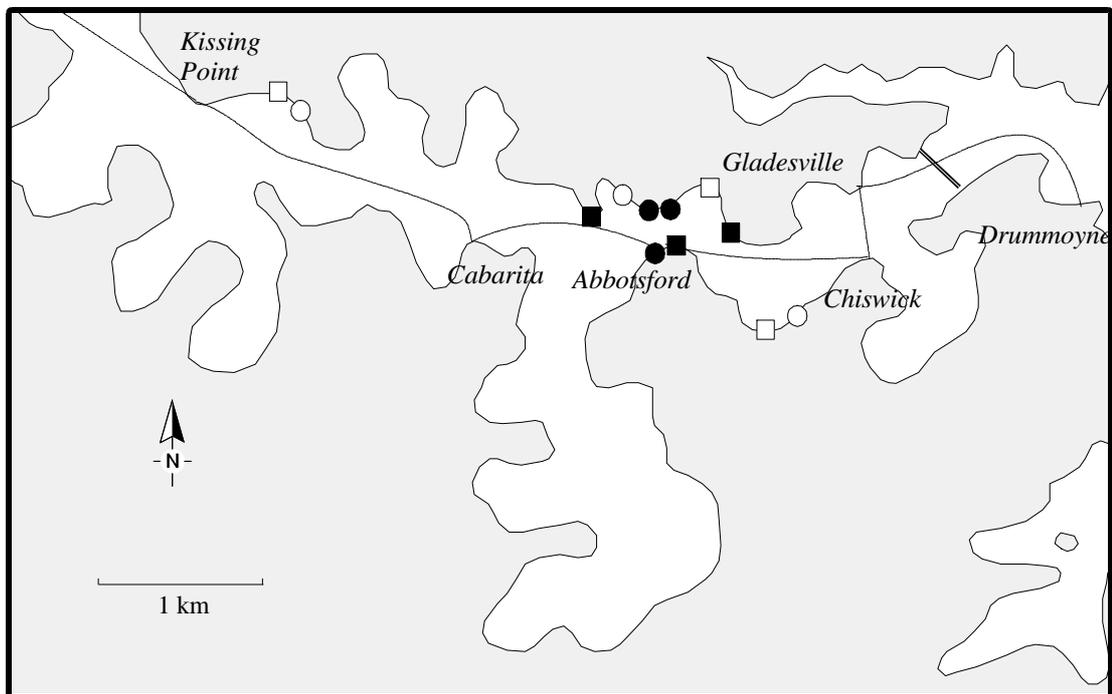


Figure 3.2 Map of the Parramatta River showing the location of seawalls close to (black) and further from (white) the RiverCat Ferry route and orientated perpendicular (squares) and parallel (circles) to the direction of propagation of wash that were sampled on the 9th - 10th August, 2000.

■ = close, perpendicular; ● = close, parallel; □ = far, perpendicular; ○ = far, parallel
 ----- RiverCat Ferry route

Differences between assemblages on seawalls close to or further from the RiverCat ferry route were examined using nMDS ordinations of centroids representing sites and NP-MANOVA (Anderson, 2001) and ANOSIM (Clarke, 1993) of untransformed data and measures of presence-absence. Data for mid- and high tidal heights were analysed separately because assemblages differ markedly between these. Only the factors, proximity and sites, were analysed because NP-MANOVA and ANOSIM can only handle two factors at a time (see Section 2.6.1). The factor location was omitted because spatial variability was greater at the scale of sites. Centroids were used in nMDS ordinations because of the large stress of plots using individual quadrats. Both NP-MANOVAs and ANOSIMs were done because they use different methods to calculate test statistics and therefore test different hypotheses (see Section 2.6.1). Both untransformed and presence-absence data were analysed because a comparison of their results enable separation of the contribution of differences in the abundances of species and differences in the types of species present in determining patterns. Any difference found when untransformed data is analysed may be due to differences in the species present, their abundance and frequency among replicates. Analysis of presence-absence data does not consider abundances.

SIMPER (Clarke, 1993) analyses were done to identify the species contributing most to differences between treatments. Differences in the abundance of these species between treatments were then tested for using ANOVAs (see Section 2.6.6).

3.3 Results

Sixteen taxa of algae and 15 taxa of invertebrates were identified during this study (Table 3.1). Many algae were only identified to genus because of the similar appearance of individual species in the field. In some cases, where algae were very small or present in complex mats, they could not be assigned to a genus and were classified as green filaments or green film. “Scuzz” refers to a brown scum found on surfaces; it may have been composed of detritus and/or a micro-algal film.

3.3.1 Initial sampling of assemblages on seawalls close to or further from the RiverCat ferry route

At a mid-tidal height, assemblages differed between seawalls close to or further from the RiverCat ferry route. This was evident by a separation of centroids into two groups corresponding to these proximities on nMDS plots of untransformed (Fig. 3.3(i)a) and presence-absence (Fig. 3.3(ii)a) data. The analysis of untransformed data using NP-MANOVA and

ANOSIM showed the difference between treatments (proximity to wash) to be statistically significant ($p < 0.05$, Tables 3.2a, 3.3a). An ANOSIM using the presence-absence data did not, however, find any significant difference between the two groups ($p > 0.05$, Table 3.3a) despite the significant result of the NP-MANOVA ($p < 0.05$, Table 3.2a). Given the small number of possible permutations (35) that could be used for the ANOSIM and the small significance level (6 %) obtained for the test, it is, however, safe to consider the composition of assemblages different between walls close to or further from the RiverCat route.

At the higher tidal level, the assemblage found in one of the sites at Henley appeared considerably different from the other assemblages (Fig. 3.3(i)b). This appeared to be due to greater abundance of the encrusting alga, *Hildenbrandia rubra*, at this site than at other places. The ordination was repeated without this site in order to determine whether any pattern was evident among the remainder of sites. No separation of points into ‘near’ and ‘far’ treatments was evident (Fig 3.3(i)c) and no significant difference was found between these two treatments using either NP-MANOVA ($p > 0.05$, Table 3.2b) or ANOSIM ($p > 0.05$, Table 3.3b). In contrast, centroids of presence-absence data appeared to separate into ‘near’ and ‘far’ groups on nMDS plots including or excluding the site at Henley (Fig. 3.3(ii)b,c). These differences were, however, non-significant for untransformed and for presence-absence data using NP-MANOVA ($p > 0.05$, Table 3.2b) and ANOSIM ($p > 0.05$, Table 3.3b).

Significant spatial variability was found among assemblages at the scale of sites at each of the heights when untransformed or presence-absence data were analysed using NP-MANOVA ($p < 0.001$, Table 3.2a,b). At the mid tidal height, Bray-Curtis measures of dissimilarity were larger between sites of the ‘near’ proximity treatment than between sites of the ‘far’ treatment (Fig. 3.4, Table 3.4). At the high tidal height, the opposite pattern was seen – assemblages were more similar between sites near to the ferry route than between those further away (Fig. 3.4, Table 3.4). No pattern was seen in measures of within-site variability between places near and far from the ferry route (Fig. 3.5, Table 3.5) at either tidal height.

Many species contributed to the dissimilarity between the assemblages on seawalls close to or further from the Rivercat route at the mid-tidal height (Table 3.6). In all cases, however, the contribution of these species to the dissimilarity between treatments was no greater than their contribution to among-site differences in one or more of the treatments. Based on these results, it could not be concluded that any of the species were more important than the others in contributing to the difference between the treatments.

Table 3.1 Taxa found on seawalls close to and further from the RiverCat ferry route.

| | | | | |
|-----------------------|----------------|-------------------------------|--|--|
| Algae: | Chlorophyta | Cladopheraceae | <i>Chaetomorpha</i> sp. <i>Cladophora</i> sp. <i>Rhizoclonium implexum</i> | |
| | | Ulviceae | <i>Enteromorpha</i> sp. <i>Ulva</i> sp. Green filaments Green film | |
| | | Phaeophyta | Ralfsiaceae | <i>Ralfsia verrucosa</i> |
| | | | Scytosiphonaceae | <i>Endarachne binghamiae</i> |
| | Rhodophyta | Corallinaceae | <i>Corallina officinalis</i> | |
| | | Gelidiaceae | <i>Gelidium pusillum</i> <i>Pterocladia</i> sp. | |
| | | Hildenbrandiaceae | <i>Hildenbrandia rubra</i> Unidentified red leafy | |
| | | Unidentified blue-green algae | | |
| | Scuzz | | | |
| | Invertebrates: | Annelida | Serpulidae | <i>Hydroides</i> sp. |
| | | | Spirorbidae | |
| | | Bryozoa | Membraniporidae | <i>Conopeum seurati</i> |
| | | Porifera | Unidentified orange sponge | |
| | | Crustacea | Archaeobalanidae | <i>Elminius covertus</i> |
| Balanidae | | | <i>Balanus amphitrite</i> <i>Balanus variegatus</i> | |
| | | | Tetraclitidae | <i>Hexaminus foliorum</i> |
| | | | Crab | |
| Mollusca (Bivalvia) | | | Mytilidae | <i>Mytilus</i> sp. <i>Xenostrobus securis</i> |
| | | Ostreidae | <i>Crassostrea gigas</i> <i>Saccostrea commercialis</i> | |
| | | | Littorinidae | <i>Bembicium auratum</i> |
| Mollusca (Gastropoda) | | Siphonariidae | <i>Siphonaria denticulata</i> | |

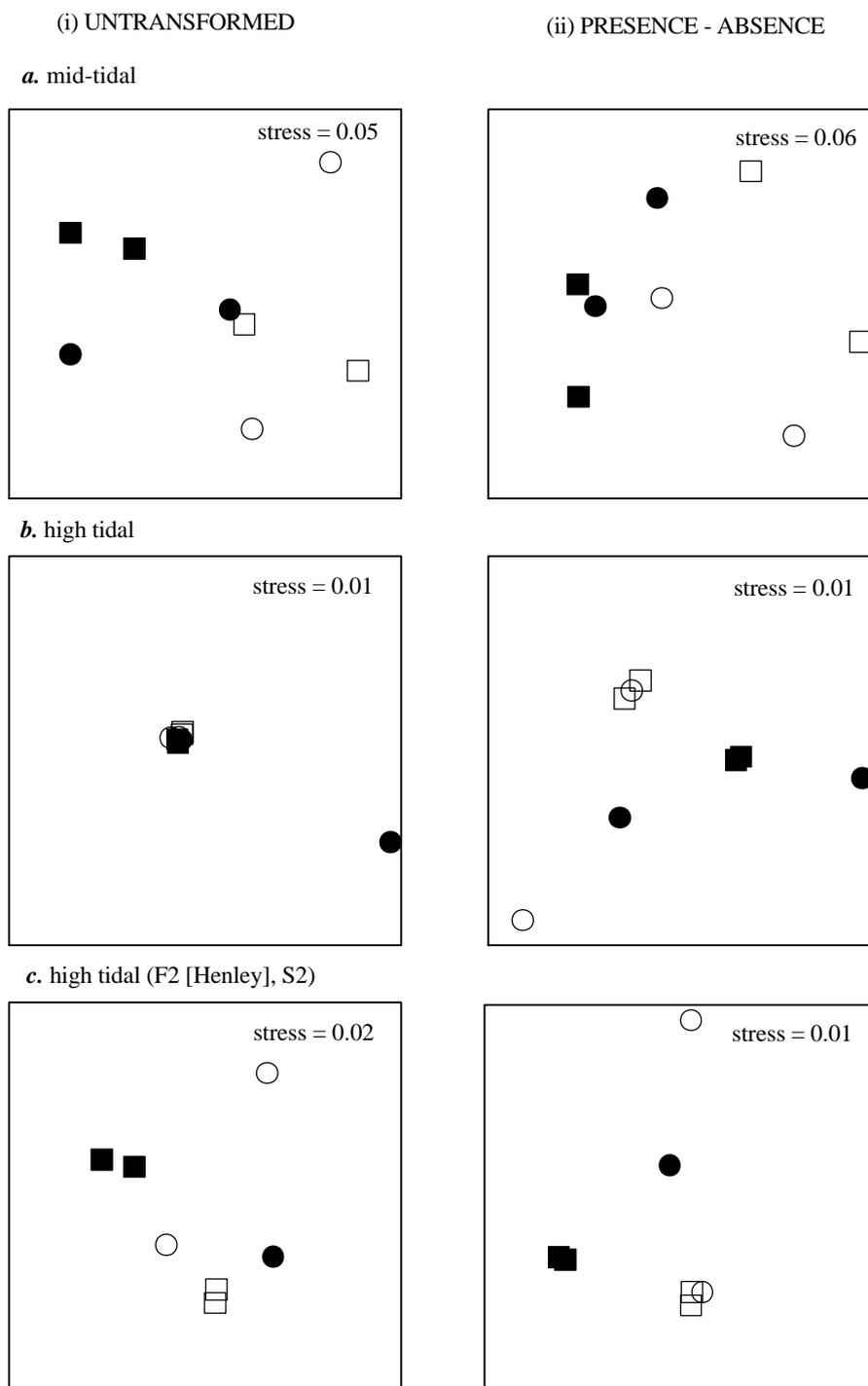


Figure 3.3 nMDS ordinations of intertidal assemblages on seawalls close to (black; squares = N1, circles = N2) and further from (white; squares = F1, circles = F2) the RiverCat ferry route at *a.* mid- and *b, c* high tidal heights (*b*: all data, *c*: excluding data from one site at Henley [F2]) at Time 1 (19-20th May, 2000). Points represent centroids of untransformed data (i) and presence-absence data (ii) from each site. $n = 5$.

Table 3.2 Summaries of NP-MANOVAs comparing spatial variation in assemblages of sessile species on seawalls close to or further from the RiverCat ferry route at *a.* a mid tidal height and *b.* a high tidal height. pr = proximity (2 levels: near, far; fixed), si(pr) = sites (8 levels, random). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a. Mid-tidal height

| source | df | untransformed | | pres-abs | |
|---------|----|---------------|-----|----------|-----|
| | | <i>p</i> | Sig | <i>p</i> | Sig |
| pr | 1 | 0.0106 | * | 0.0162 | * |
| si (pr) | 6 | 0.0002 | *** | 0.0002 | *** |
| res | 32 | | | | |

b. High tidal height

| source | df | untransformed | | pres-abs | |
|---------|----|---------------|-----|----------|-----|
| | | <i>p</i> | Sig | <i>p</i> | Sig |
| pr | 1 | 0.2112 | NS | 0.1956 | NS |
| si (pr) | 6 | 0.0002 | *** | 0.0002 | *** |
| res | 32 | | | | |

Table 3.3 Summaries of ANOSIMs testing for differences between assemblages on seawalls close to and further from the RiverCat ferry route at *a.* a mid tidal height and *b.* a high tidal height. pr = proximity (2 levels: near, far; fixed) si (pr) = sites (8 levels, random). $n = 5$.

a. Mid-tidal height

| source | no. permutations | untransformed | | pres-abs | |
|---------|------------------|-------------------------------|-----------|-------------------------------|-----------|
| | | sample statistic (<i>R</i>) | prob. (%) | sample statistic (<i>R</i>) | prob. (%) |
| pr | 35 | 0.57 | 3 | 0.45 | 6 |
| si (pr) | 500 | 0.50 | 0 | 0.64 | 0 |

b. High tidal height

| source | no. permutations | untransformed | | pres-abs | |
|---------|------------------|-------------------------------|-----------|-------------------------------|-----------|
| | | sample statistic (<i>R</i>) | prob. (%) | sample statistic (<i>R</i>) | prob. (%) |
| pr | 35 | 0.25 | 9 | 0.14 | 26 |
| si (pr) | 5000 | 0.74 | 0 | 0.76 | 0 |

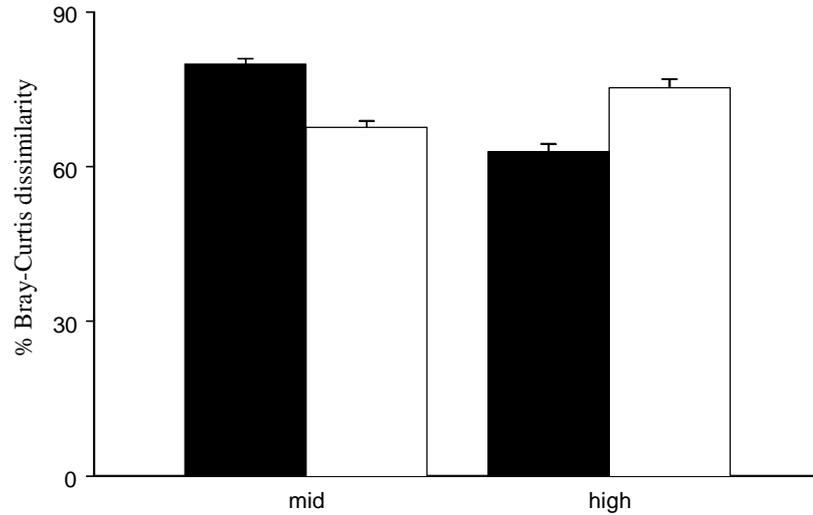


Figure 3.4 Mean (+S.E.) Bray-Curtis dissimilarity for among-site comparisons in assemblages on seawalls near (black) or far (white) from the RiverCat ferry route, at mid- or high tidal heights. $n = 150$.

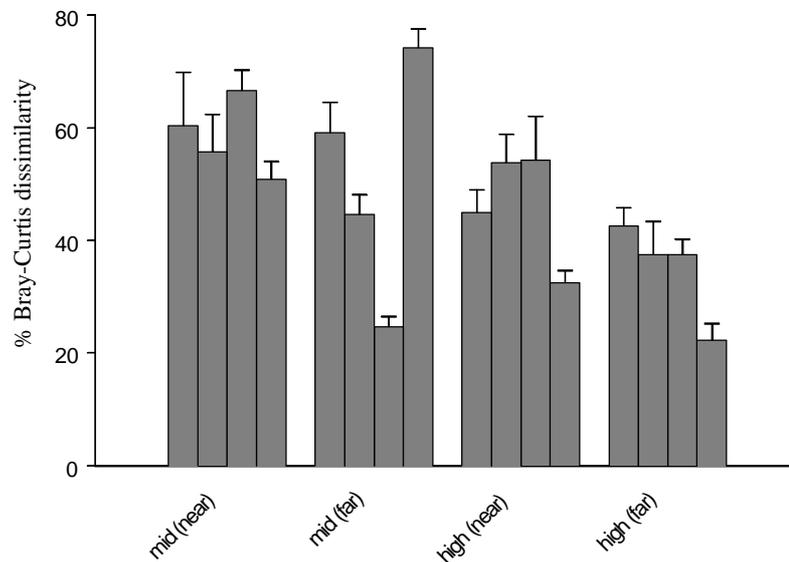


Figure 3.5 Mean (+S.E.) Bray-Curtis dissimilarity for within-site comparisons in assemblages on seawalls near or far from the RiverCat ferry route, at mid- or high tidal heights. $n = 10$ for each site.

Table 3.4 Summaries of analyses comparing Bray-Curtis measures of among-site variability between places near (N) and far (F) from the RiverCat ferry route, at two tidal heights. pr = proximity (2 levels: near, far). $n = 150$.

| Source of variation | df | mid | | | high | | |
|---------------------|-----|-------------|------|------|-------------|-------|------|
| | | MS | F | sig. | MS | F | sig. |
| pr | 1 | 0.69 | 8.08 | ** | 2.34 | 25.82 | *** |
| res | 298 | 0.09 | | | 0.09 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.54 NS | | | C = 0.51 NS | | |
| SNK | | N > F | | | N < F | | |

Table 3.5 Summaries of analyses comparing Bray-Curtis measures of within-site variability between places near (N) and far (F) from the RiverCat ferry route, at two tidal heights. pr = proximity (2 levels: near, far), lo (pr) = location (4 levels: random), si (lo (pr)) = site (8 levels, random). $n = 10$.

| Source of variation | df | mid | | | high | | |
|---------------------|----|------------|------|------|-------------|------|------|
| | | MS | F | sig. | MS | F | sig. |
| pr | 1 | 1.01 | 4.51 | NS | 1.82 | 3.58 | NS |
| lo (pr) | 2 | 0.22 | 0.67 | NS | 0.51 | 0.72 | NS |
| si (lo (pr)) | 4 | 0.33 | 2.05 | NS | 0.70 | 4.29 | ** |
| res | 72 | 0.16 | | | 0.16 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.31 * | | | C = 0.35 ** | | |

Table 3.6 Percentage dissimilarity between 'near' and 'far' treatments and among sites within 'near' or 'far' treatments in the taxa contributing most to differences between assemblages close to or further away from the RiverCat ferry route at a mid tidal height.

| species | % dissimilarity | | |
|---------------------------|-----------------|-------------|------------|
| | near-far | within near | within far |
| <i>Gelidium pusillum</i> | 13 | 3 | 17 |
| <i>Mytilus</i> sp. | 11 | 0 | 18 |
| <i>Enteromorpha</i> sp. | 11 | 18 | 8 |
| Scuzz | 10 | 13 | 8 |
| <i>Hexaminus foliorum</i> | 9 | 13 | 6 |
| <i>Ulva</i> sp. | 6 | 5 | 5 |

Univariate analyses were done on individual taxa to test the hypothesis that abundances of these would differ between seawalls close to or further from the RiverCat ferry route. All species that appeared to be present in a majority of quadrats within at least one of the two treatments were analysed. Rare or very patchy species were not examined. Species fulfilling this criterion were *Enteromorpha* sp., *Ulva* sp., *Gelidium pusillum*, *Balanus amphitrite* and *Hexaminus foliorum* at both heights, *Mytilus* sp. at the mid-tidal height and *Eliminius covertus* at the high tidal height. Univariate analyses were also done on the total abundances of macro-algae and barnacles because previous studies suggested that the effects of wave-action on species were consistent across these broad taxonomic groups (e.g. Seapy and Littler, 1978; Underwood, 1981; Underwood and Jernakoff, 1984).

At the mid-tidal height, the mean abundances of *Ulva* sp., *G. pusillum* and *Mytilus* sp. were significantly greater in sites close to the RiverCat ferry route than in sites further away ($p < 0.05$, Table 3.7a, Fig. 3.6b,c,h). No significant difference between the two treatments was found in the mean abundances of *Enteromorpha* sp. or *B. amphitrite* ($p > 0.05$, Table 3.7a, Fig. 3.6a,e). The total abundance of algae appeared greater close to the ferry route than further away (Fig. 3.6d) and the abundance of *H. foliorum* and the total cover of barnacles appeared greater in sites further from the ferry route (Fig. 3.6f,g). These differences were, however, not statistically significant because of the large variability found among sites in each treatment ($p > 0.05$, Table 3.7a).

At the high tidal height, a statistically significant difference was found between proximity-treatments in the abundance of total macro-algae only (near > far, $p < 0.05$, Table 3.7b; Fig 3.7d). The abundances of *Ulva* sp. and *G. pusillum* were greater on seawalls close to the ferry route (Fig. 3.7b,c) and the abundance of *E. covertus* were greater on seawalls further away (Fig 3.7e). These differences were, however, not statistically significant (Table 3.7b).

The lack of statistically significant results can be attributed to the great spatial variability of abundances from site to site with proximity-treatments for almost all taxa (Table 3.7a,b).

Table 3.7 Summaries of analyses comparing spatial variation in the abundance of intertidal organisms on seawalls close to or further from the RiverCat ferry route at **a.** a mid-tidal height and **b.** a high tidal height. pr = proximity (2 levels: close, far; fixed), lo (pr) = location (4 levels, random), si (pr x lo) = sites (8 levels, random). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a.

| Source of variation | df | <i>Enteromorpha</i> sp. | | | <i>Ulva</i> sp. | | | <i>Gelidium pusillum</i> | | | total algae | | |
|---------------------|----|-------------------------|-------|------|-----------------|-------|------|--------------------------|-------|------|-------------|------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pr | 1 | 0.1 | 0.00 | NS | 372 | 20.11 | * | 53.6 | 40.87 | * | 3960 | 2.47 | NS |
| lo (pr) | 2 | 18.1 | 1.74 | NS | 19 | 0.18 | NS | 1.3 | 0.49 | NS | 1606 | 0.48 | NS |
| si (lo (pr)) | 4 | 10.4 | 15.53 | *** | 104 | 1.31 | NS | 2.7 | 2.75 | * | 3362 | 5.50 | ** |
| res | 32 | 0.7 | | | 80 | | | 1.0 | | | 611 | | |
| Cochran's test | | C = 0.34 NS | | | C = 0.39 NS | | | C = 0.36 NS | | | C = 0.29 NS | | |
| SNK | | | | | N > F | | | N > F | | | | | |

| Source of variation | df | <i>Balanus amphitrite</i> | | | <i>Hexaminius foliorum</i> | | | total barnacles | | | <i>Mytilus</i> sp. | | |
|---------------------|----|---------------------------|------|------|----------------------------|------|------|-----------------|-------|------|--------------------|-------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pr | 1 | 109 | 0.44 | NS | 9.98 | 1.63 | NS | 3920 | 17.35 | NS | 5476 | 56.92 | * |
| lo (pr) | 2 | 247 | 0.98 | NS | 6.14 | 0.98 | NS | 226 | 0.15 | NS | 96 | 0.23 | NS |
| si (lo (pr)) | 4 | 251 | 5.42 | ** | 6.26 | 5.08 | ** | 1544 | 5.80 | ** | 414 | 1.21 | NS |
| res | 32 | 46 | | | 1.23 | | | 266 | | | 341 | | |
| Cochran's test | | C = 0.97 ** | | | C = 0.34 NS | | | C = 0.47 ** | | | C = 0.48 ** | | |
| SNK | | | | | | | | | | | N > F | | |

b.

| Source of variation | df | <i>Enteromorpha</i> sp. | | | <i>Ulva</i> sp. | | | <i>Gelidium pusillum</i> | | | total algae | | |
|---------------------|----|-------------------------|-------|------|-----------------|------|------|--------------------------|------|------|-------------------|-------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pr | 1 | 1145 | 1.19 | NS | 4.88 | 1.80 | NS | 667 | 3.84 | NS | 20070 | 7.01 | * |
| lo (pr) | 2 | 961 | 25.48 | ** | 2.71 | 0.92 | NS | 174 | 0.43 | NS | 2865 ^a | 11.07 | NS |
| si (lo (pr)) | 4 | 38 | 0.25 | NS | 2.96 | 5.90 | ** | 400 | 3.24 | * | | | |
| res | 32 | 150 | | | 0.50 | | | 123 | | | 259 | | |
| Cochran's test | | C = 0.74 ** | | | C = 0.32 NS | | | C = 0.89 ** | | | C = 0.63 ** | | |
| SNK | | | | | | | | | | | N > F | | |

| Source of variation | df | <i>Elminius covertus</i> | | | <i>Hexaminius foliorum</i> | | | total barnacles | | |
|---------------------|----|--------------------------|------|------|----------------------------|------|------|-----------------|------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pr | 1 | 221 | 6.63 | NS | 2756 | 1.02 | NS | 4580 | 1.31 | NS |
| lo (pr) | 2 | 33 | 0.38 | NS | 2703 | 2.45 | NS | 3495 | 2.65 | NS |
| si (lo (pr)) | 4 | 88 | 6.36 | *** | 1102 | 6.95 | *** | 1317 | 9.35 | *** |
| res | 32 | 14 | | | 159 | | | 141 | | |
| Cochran's test | | C = 0.65 ** | | | C = 0.26 NS | | | C = 0.28 NS | | |

^aSS_{location}/SS_{site} was not significant at $p = 0.25$, allowing MS_{location} to be pooled with MS_{site} (Underwood, 1997).

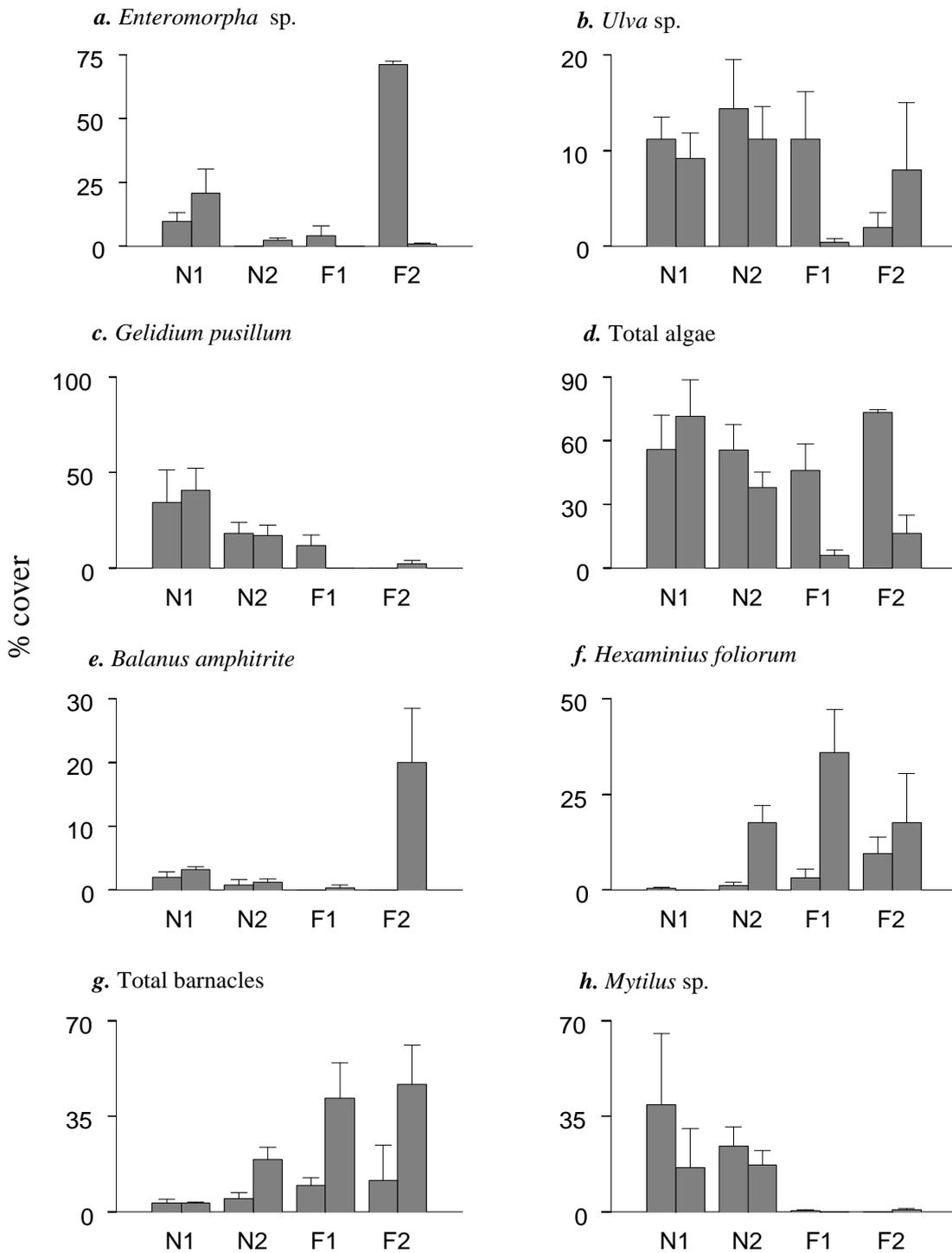


Figure 3.6 Mean (+ S.E.) percentage cover of sessile organisms found at a mid-tidal height on seawalls located close to (N1 and N2) and further from (F1 and F2) the RiverCat ferry route. $n = 5$ in two sites at each location.

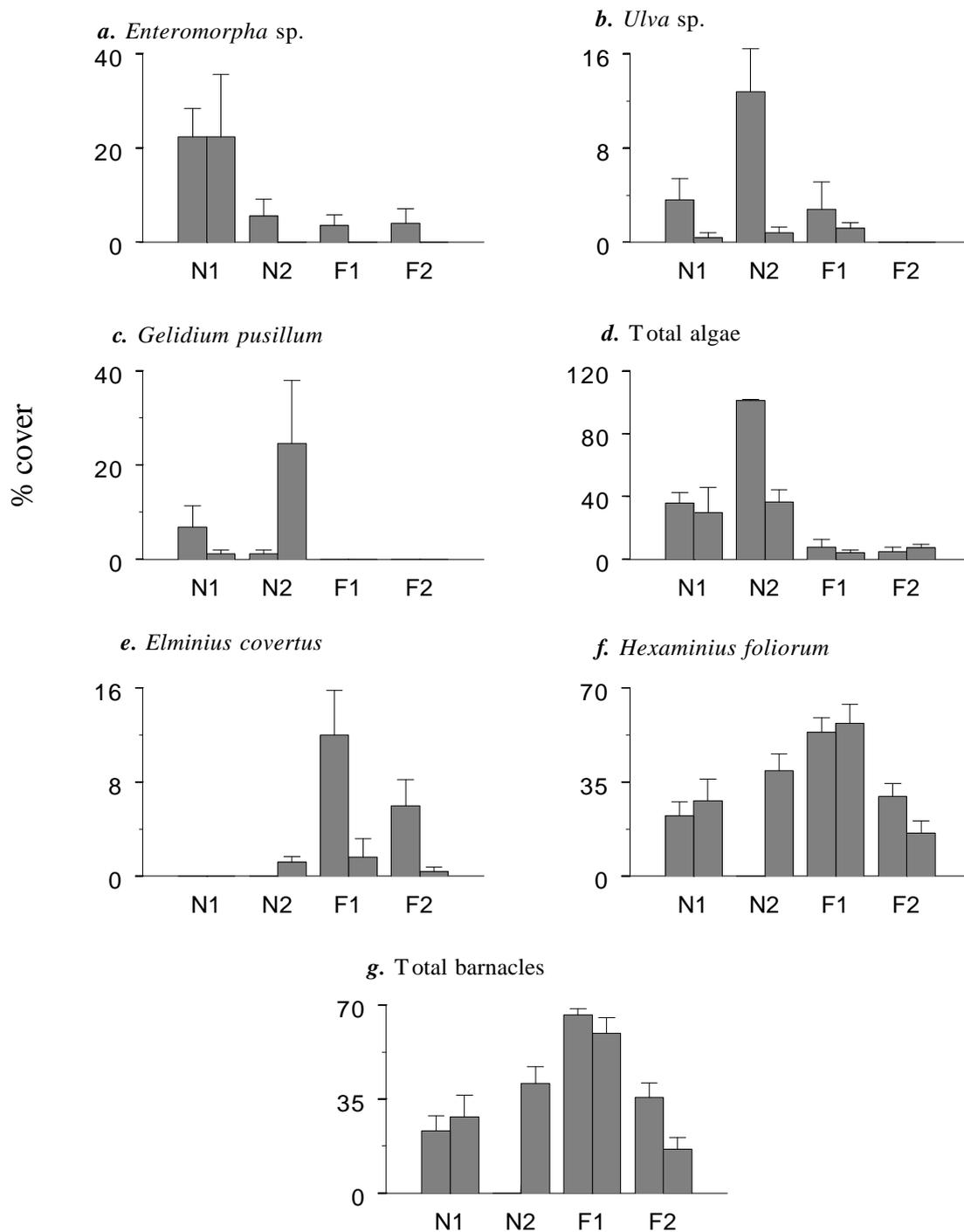


Figure 3.7 Mean percentage cover (+ S.E.) of sessile organisms found at a high tidal height on seawalls located close to (N1 and N2) and further from (F1 and F2) the RiverCat ferry route. $n = 5$ in two sites at each location.

3.3.2 Abundances of organisms on seawalls close to or further from the RiverCat ferry route and orientated perpendicular and parallel to the direction of propagation of wash.

No significant difference was found in the abundance of macro-algae, *H. foliorum* or *X. securis* between proximity or orientation treatments on seawalls at either high or mid tidal heights ($p > 0.05$, Table 3.8a,b; Fig. 3.8a,b; Fig. 3.9a,b). At the mid-tidal height, however, *X. securis* was only found on the most sheltered seawalls sampled (i.e. those further from the ferry route and orientated parallel to the direction of propagation of wash, Fig. 3.8d), as predicted. A significant proximity by orientation interaction was found in the cover of *Mytilus* sp. at the mid-tidal height ($p < 0.01$, Table 3.8a, Fig 3.8c). Post-hoc SNK tests showed this interaction to be due to a greater cover of *Mytilus* sp. on seawalls close to the ferry route and orientated perpendicular to the direction of propagation of wash than on seawalls close to the ferry route but orientated parallel to wash or on seawalls located further away. At the higher level, no pattern was found between treatments in cover of this species (Table 3.8b, Fig. 3.9c).

3.3.3 The vertical distribution of sessile organisms on seawalls exposed to and more sheltered from ferry wash

No pattern was found in the mean height of the upper limit of barnacles or algae on seawalls exposed to and more sheltered from wash at either time of sampling ($p > 0.05$, Table 3.9a,b, Fig. 3.10, 3.11).

Table 3.8 Summaries of analyses comparing spatial variation in the abundance of intertidal organisms on seawalls close to and further from the RiverCat ferry route and orientated perpendicular and parallel to the direction of propagation of wash at **a.** a mid-tidal height and **b.** a high tidal height. pr = proximity (2 levels: close, far; fixed), or = orientation (2 levels: perpendicular, parallel; fixed), si (pr x or) = sites (12 levels, random). $n = 5$. **NS** $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a.

| Source of variation | df | total algae | | | <i>Hexaminius foliorum</i> | | | <i>Mytilus</i> sp. | | | <i>Xenostrobus securis</i> | | |
|---------------------|----|---|------|------|----------------------------|------|------|--------------------|-------|------|----------------------------|------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pr | 1 | 8 | 0.21 | NS | 91.3 | 4.10 | NS | 131 | 17.20 | ** | 0.07 | 4.00 | NS |
| or | 1 | 4 | 0.10 | NS | 41.7 | 1.87 | NS | 111 | 14.59 | ** | 0.07 | 4.00 | NS |
| pr x or | 1 | 144 | 3.73 | NS | 22.3 | 5.64 | NS | 93 | 12.19 | ** | 0.07 | 4.00 | NS |
| si (pr x or) | 8 | 39 | 2.80 | * | 70.4 | 3.16 | *** | 8 | 0.67 | NS | 0.02 | 0.73 | NS |
| res | 48 | 14 | | | 4.0 | | | 11 | | | 0.02 | | |
| Cochran's test | | C = 0.23 NS | | | C = 0.33 * | | | C = 0.42 ** | | | C = 0.73 ** | | |
| SNK | | NP > NP _a = FP = FP _a | | | | | | | | | | | |

b.

| Source of variation | df | total algae | | | <i>Hexaminius foliorum</i> | | | <i>Mytilus</i> sp. | | |
|---------------------|----|-------------|-------|------|----------------------------|-------|------|--------------------|------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pr | 1 | 168 | 0.61 | NS | 269 | 2.50 | NS | 0.00 | 0.09 | NS |
| or | 1 | 334 | 1.21 | NS | 5 | 0.04 | NS | 0.04 | 0.82 | NS |
| pr x or | 1 | 175 | 0.64 | NS | 198 | 1.84 | NS | 0.04 | 0.82 | NS |
| si (pr x or) | 8 | 275 | 16.96 | *** | 108 | 13.13 | *** | 0.05 | 3.14 | ** |
| res | 48 | 16 | | | 8 | | | 0.01 | | |
| Cochran's test | | C = 0.25 NS | | | C = 0.15 NS | | | C = 0.43 ** | | |

NP = close to ferry route, perpendicular orientation, NP_a = close to ferry route, parallel orientation, FP = further from ferry route, perpendicular orientation, FP_a = further from ferry route, parallel orientation

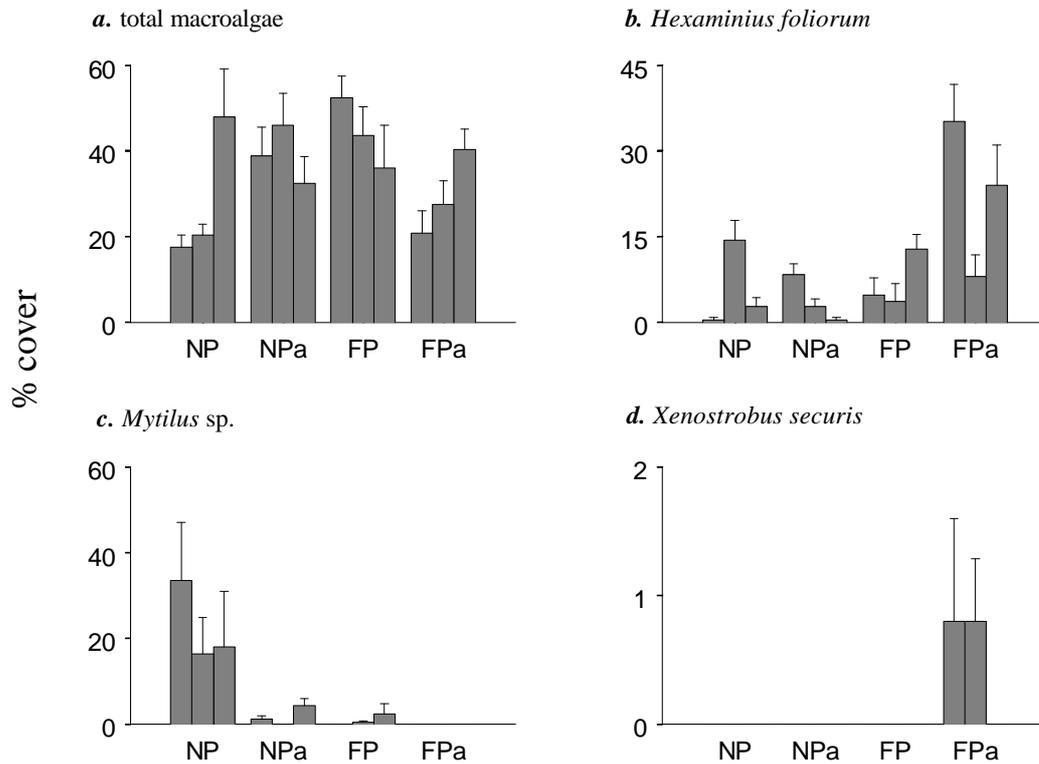


Figure 3.8 Mean (+ S.E.) percentage cover of sessile organisms found at a mid-tidal height on seawalls located close to (N) and further from (F) the RiverCat ferry route and orientated perpendicular (P) and parallel (Pa) to the direction of propagation of wash ($n = 5$).

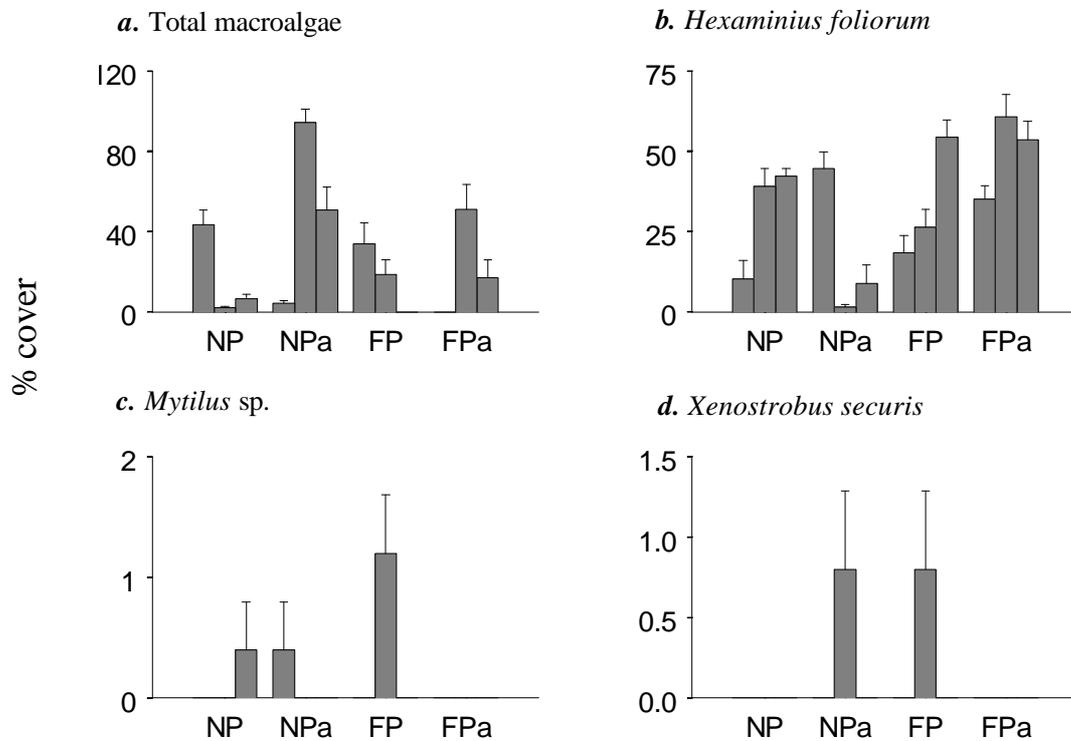


Figure 3.9 Mean (+ S.E.) percentage cover of sessile organisms found at a high tidal height on seawalls located close to (N) and further from (F) the RiverCat ferry route and orientated perpendicular (P) and parallel (Pa) to the direction of propagation of wash ($n = 5$).

Table 3.9 Summaries of ANOVAs comparing spatial variation in the mean upper vertical limit of the distributions of macro-algae and barnacles on **a.** seawalls close to and further from the RiverCat ferry route and **b.** seawalls close to and further from the ferry route and perpendicular and parallel to the direction of propagation of wash. pr = proximity (2 levels: close, far; fixed), or = orientation (2 levels: perpendicular, parallel; fixed), lo (pr) = location (4 levels, random), si (lo (pr)) = sites (8 levels, random), si (pr x or) = sites (12 levels random) $n = 10$. NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| a. | | | | | | | |
|---------------------|-----|---------------|-------|-----------|---------------|-------|------|
| algae | | | | barnacles | | | |
| source of variation | df | MS | F | sig. | MS | F | sig. |
| pr | 1 | 0.88 | 15.73 | NS | 0.05 | 0.67 | NS |
| lo (pr) | 2 | 0.06 | 0.17 | NS | 0.08 | 1.82 | NS |
| si (lo (pr)) | 4 | 0.33 | 70.05 | *** | 0.04 | 30.83 | *** |
| res | 72 | 0.00 | | | 0.00 | | |
| Transformation | | | | | | | |
| Cochran's test | | $C = 0.56$ ** | | | $C = 0.34$ ** | | |
| b. | | | | | | | |
| algae | | | | barnacles | | | |
| source of variation | df | MS | F | sig. | MS | F | sig. |
| pr | 1 | 0.25 | 0.9 | NS | 0.00 | 0.01 | NS |
| or | 1 | 0.01 | 0.04 | NS | 0.00 | 0.01 | NS |
| pr x or | 1 | 0.05 | 0.19 | NS | 0.02 | 0.2 | NS |
| si (pr x or) | 8 | 0.27 | 55.14 | *** | 0.08 | 64.55 | *** |
| res | 108 | 0.01 | | | 0.00 | | |
| Transformation | | | | | | | |
| Cochran's test | | $C = 0.31$ ** | | | $C = 0.15$ NS | | |

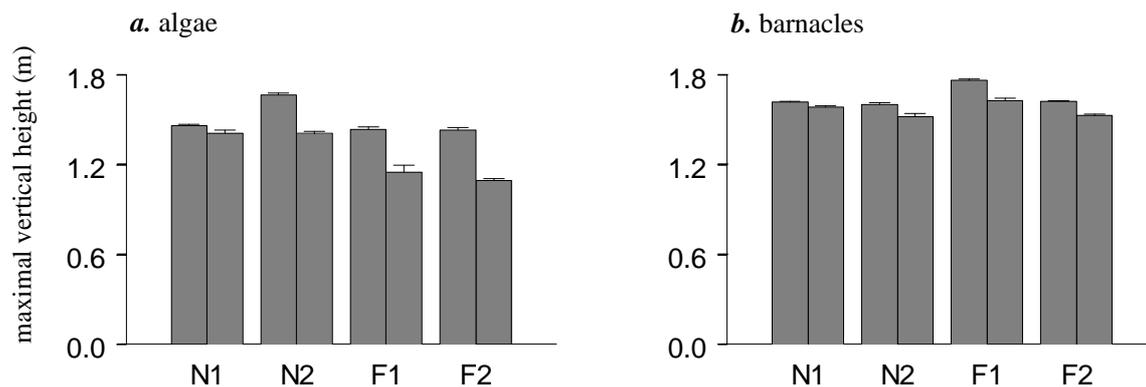


Figure 3.10 The mean (+S.E.) height of the upper limit of *a.* macro-algae and *b.* barnacles above MLWS within sites of seawalls located close to (N1 and N2) and further from (F1 and F2) the RiverCat ferry route ($n = 10$).

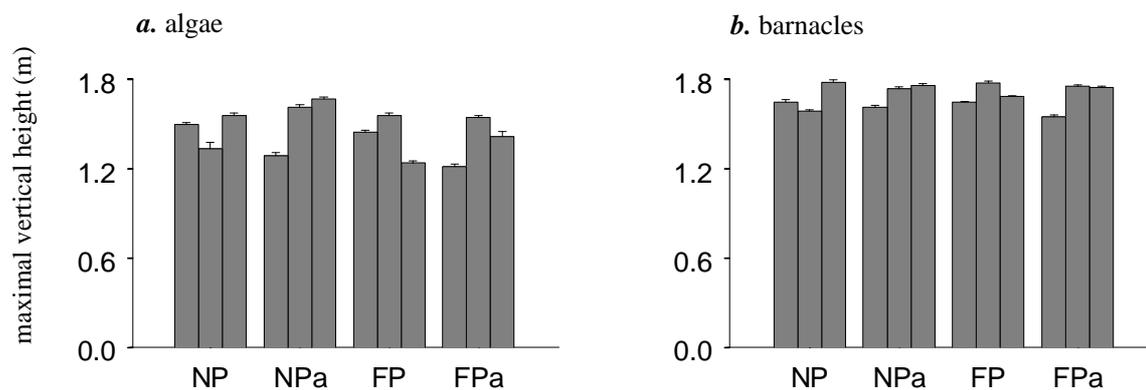


Figure 3.11 The mean (+S.E.) height of the upper limit of *a.* macro-algae and *b.* barnacles above MLWS on seawalls located close to (N) and further from (F) the RiverCat ferry route and orientated perpendicular (P) and parallel (Pa) to the direction of propagation of wash ($n = 10$).

3.4 Discussion

At the mid-tidal height, assemblages were found to differ between seawalls close to or further from the RiverCat ferry route. This difference appeared to be primarily due to a greater total cover of macro-algae on seawalls close to the ferry route, in particular greater abundances of *Ulva* sp. and *Gelidium pusillum*. It has been widely observed that the abundance of algae is greater on wave-exposed than on sheltered shores (e.g. Underwood, 1981; Underwood and Jernakoff, 1984; McQuaid and Branch, 1984, 1985; Bustamante and Branch, 1996) and various models have been proposed to explain this pattern, in terms of both direct and indirect effects of wave-action (see Underwood and Jernakoff, 1984; Koehl, 1986; Leigh *et al.*, 1987; Brown and Quinn, 1988 for various models). This pattern of macro-algal abundance was, however, not persistent - no difference was found between seawalls close to or further from the ferry route at a second sampling time when the orientation of the walls was also taken into consideration – and the significant pattern at the first time of sampling may therefore have been due to some factor other than exposure to wash.

A persistent difference in the abundance of *Mytilus* sp. was, however, found between seawalls close to or further from the ferry route and contributed to the above pattern in assemblages at the mid-tidal height. When the orientation of seawalls was also considered, the abundance of *Mytilus* sp. was found to be greatest on walls close to the ferry route that were perpendicular to the direction of propagation of wash. The observation that *Mytilus* sp. is present in greatest abundance on the seawalls most exposed to the wash of RiverCats is consistent with previous studies that have shown mussels to be one of the key competitors for space in wave-stressed rocky intertidal environments (e.g. Paine, 1974; Suchanek, 1978; Seed and Suchanek, 1992).

No significant difference was found in the abundance of any other taxa between seawalls exposed to or sheltered from the wash of RiverCat ferries at this tidal height, although the abundance of *Hexaminius foliorum* was greater further away from the ferry route and the mussel *Xenostrobus securis* was only present on the most sheltered seawalls. These results are in contrast to previous studies that have observed the abundance of filter feeders, such as barnacles, to be greater on exposed shores (e.g. Underwood *et al.*, 1983). A possible explanation for the pattern observed in *H. foliorum* is that the large cover of macro-algae close to the ferry route limited the space available for barnacle cyprids to settle (see Denley and Underwood, 1979; Denley, 1981). The greater water-velocities associated with exposed seawalls may have prevented recruitment of *X. securis* in these places.

At the higher level, no significant difference was found between assemblages or the abundances of individual species close to or further from the RiverCat route. Moreover, no difference was found in the mean height of the upper limit at which barnacles or algae were found between these two treatments, nor between seawalls orientated perpendicular or parallel to incoming wash, despite the widely-documented observation that the upper boundaries in the distribution of intertidal organisms are higher in areas exposed to wave-action than in areas that are sheltered (e.g. Underwood and Jernakoff, 1984).

A number of models may explain the lack of pattern found at the higher level. First, exposure to waves may be unimportant in determining the ecology of organisms found at a high level on seawalls. Second, exposure to waves may be important, but the effects might not have been sufficient for a significant difference to be seen. Third, exposure to waves may be important in determining the ecology at this height, but wash from RiverCats is unimportant because splash and spray from other vessels and wind-driven waves wet seawalls to a greater height than does wash from RiverCats. During this study, it was observed that on very windy days, wind-driven waves hitting all seawalls were much greater in height than the wash produced by the RiverCat ferries. Such “extreme” events may be more important in structuring assemblages than regular events, as suggested by Gaines and Denny (1993).

Significant variability was observed among seawalls close to or further from the ferry route and perpendicular or parallel to the direction of propagation of wash at the two times of sampling. The consistency of this variability across treatments suggests that it is due to smaller-scale processes and is not related to the disturbance caused by RiverCat ferries. Seawalls along the Parramatta River differ in their small-scale topographic heterogeneity (e.g. the number and size of cracks and crevices between sandstone blocks and the degree to which the surfaces of blocks have been abraded) and the depth and topography of the adjacent river-bed. Small-scale topographic heterogeneity of substrata has been shown to be important in determining the abundance of individual species and the diversity of assemblages (e.g. Emson and Faller-Fritsch, 1976; Harlin and Lindburgh, 1977; Woodin, 1978; Menge *et al.*, 1983; Watanuki and Yamamoto, 1990). For example, many species of algae are more abundant on substrata with coarser particles (Harlin and Lindburgh, 1977; Watanuki and Yamamoto, 1990), perhaps because such substrata have a greater area on which to settle, and the abundance of the Littorinid *Littorina rudis* appears to be positively affected by the availability of crevices (Emson and Faller-Fritsch, 1976).

Differences in the ages of the seawalls may contribute to spatial variability because seawalls of different ages will have had different histories of disturbance, which can be important in determining the structure of intertidal assemblages (see Underwood, 1989).

The apparent unimportance of wash from RiverCat ferries in determining the structure of intertidal assemblages is in contrast to the findings of Blockley (1999). His study, in Sydney Harbour, found assemblages to differ between seawalls exposed to or sheltered from oceanic swell, boat-wash and wind-waves. He also found spatial variability to be greater among wave-exposed seawalls than among sheltered seawalls. The apparent difference in effect of RiverCat-wash and other waves on the assemblages of seawalls may be a function of the frequency of waves. In contrast to oceanic swell that constantly hits a shore, the waves resulting from passing RiverCat ferries are relatively infrequent, occurring around once every fifteen minutes during daylight hours only. Alternatively, the height of wash from RiverCat ferries may not be great enough to extend the vertical height to which seawalls are wetted.

At no stage of this study was the energy or height of waves produced by RiverCats quantified at seawalls close to or further from the ferry route or at seawalls orientated perpendicular and parallel to incoming wash. It is possible that there was, in fact, no significant difference in these variables between treatments and that if the assemblages of seawalls that are completely sheltered from wash were compared with those exposed to wash a difference would be seen.

CHAPTER 4

INITIAL PATTERNS IN THE DISTRIBUTION AND ABUNDANCE OF MACROBENTHIC INFAUNA BETWEEN WASH AND NO-WASH ZONES OF THE PARRAMATTA RIVER

4.1 Introduction

In addition to affecting the distribution and abundance of intertidal organisms on hard substrata (see Section 3.1), wave-action appears to be important in determining the composition of assemblages of soft-sediment habitats. Temporal variability in assemblages has been found to correspond to periods of storms (Eagle, 1975; McCall, 1977, 1978; Rachor and Gerlach, 1978; Yeo and Risk, 1979; Dobbs and Vozarik, 1983; Barry, 1989; Posey *et al.*, 1996) and there is growing evidence to suggest that waves generated by less extreme events, such as wind, are also important in determining the composition of assemblages (Tamaki, 1987; Emerson and Grant, 1991; Commito *et al.*, 1995a,b; Turner *et al.*, 1999).

Waves produced by boats may play a similar role in determining the structure of assemblages of soft-sediment habitats as waves produced by natural processes. It is, however, unknown whether the ecological impact of boat-generated waves on assemblages of macrobenthic infauna is greater or less than that of wind-driven waves. The majority of studies on boat-generated waves have focused on their impact on the morphology of riverbanks and mudflats (e.g. Hay, 1968; Scholer, 1974; Nanson *et al.*, 1994; Kirk and Single, 2000) and have not considered whether they affect the ecology of the benthos.

Ideally, experiments to assess the ecological impacts of boat-wash should involve sampling assemblages in places with (impact) and without (control) boat-traffic. In many estuaries this is, however, not possible because there is unrestricted access to the waterway. Strategies of management, implemented in an attempt to reduce the impact of boat-generated waves on the morphology of banks, may, however, be viewed as experiments (see Underwood, 1989, 1995) that can provide an opportunity to study this disturbance. If boat-wash does have an effect on assemblages of soft-sediment habitats, such strategies may reduce the ecological and the physical impact of this disturbance.

Along the Parramatta River, such strategies of management have included the establishment of no-wash zones and the re-vegetation of banks with mangroves. Upon entering no-wash zones, vessels must slow down to reduce wash. Thus, the intensity of disturbances from wash should be less in no-wash zones than in similar sections of a body of water where vessels travel at greater speeds. The intensity of a disturbance is widely documented to be important in determining the resulting impact (e.g. Malanson, 1984; Sousa, 1984; McCabe and Gotelli, 2000).

If this were the case with boat-wash, assemblages found within no-wash zones should be less disturbed than those found in places with greater wash. Asplund and Cook (1999) attempted to evaluate the role of no-wash zones in protecting aquatic macrophytes. The effects of wash were, however, confounded with other impacts of boating (e.g. scouring by propellers) because fewer boats entered no-wash zones than were found in adjacent areas.

Planting mangroves along unvegetated banks effectively changes the type of habitat available to soft-sediment assemblages and is therefore likely to change an assemblage (see Plazait, 1975; Wells, 1986; Sheridan, 1997 for examples of studies that have examined differences in assemblages between these two habitats). Stabilisation of sediment by seagrass beds is believed to reduce the impact of disturbances from waves on infauna by increasing settlement of larvae and reducing the number of adults that are resuspended and transported away (Orth, 1975, 1977). Stabilisation of sediment by the tubes of polychaetes and crustaceans results in increased diversity of infauna (Buchanan, 1963; Fager, 1964; Mills, 1967; Young and Rhoads, 1971). Assemblages that become established in vegetated habitats may be less susceptible to the effects of wash than are assemblages in unvegetated habitats because the roots and rhizomes of mangroves are believed to be important in stabilizing shorelines (e.g. Bennett and Reynolds, 1993) and may dissipate the energy of surface waves in shallow water (e.g. Kobayashi *et al.*, 1992; Massel *et al.*, 1999). Unvegetated mudflats and mangrove forests are found in the wash and no-wash zones of the Parramatta River.

For the reasons outlined in Chapter 3, it is not possible to compare assemblages among places along the Parramatta River that are exposed to or completely sheltered from the wash of RiverCat ferries. Instead, in this chapter, the hypothesis that assemblages of intertidal macrofauna will differ between wash and no-wash zones of the Parramatta River is tested. It is also predicted that any difference in assemblages between wash and no-wash zones will be greater in unvegetated habitat (intertidal mud- and sand-flats) than in vegetated habitat (amongst the pneumatophores of mangrove forests). By testing these hypotheses, the importance of the establishment of no-wash zones and the revegetation of river-banks, strategies of management commonly used to reduce the *physical* effects of wash, are evaluated in terms of the minimisation of the *ecological* effects of wash.

4.2 Materials and Methods

In order to test the above hypotheses, assemblages of macrobenthic infauna were sampled in unvegetated and in vegetated habitat of two no-wash zones of the Parramatta River and in adjacent sections of the river where the production of wash is allowed (subsequently referred to

as wash zones). The no-wash zones were located between the Gladesville Bridge and Five Dock Point (downstream no-wash zone) and to the west of the Silverwater Bridge (upstream no-wash zone; Fig. 4.1). In the former no-wash zone, the speed at which vessels must travel was not specified; in the latter, boat-traffic was restricted to RiverCat ferries which were legally required to travel slower than 7 knots. Unvegetated habitat was predominantly mudflat in the upstream area and sandy beach in the downstream area. Vegetated habitat was sediment amongst the pneumatophores.

It was originally intended that sediment would be collected from wash zones to the east and west of no-wash zones so that any difference in assemblages due to wash would not be confounded by differences due to gradients in physical variables along the river. Sampling was, however, not possible to the west of the upstream no-wash zone because this zone extends to Parramatta, the western terminus of ferry services. While ferries travel to the east and west of the downstream no-wash zone, sampling could not be done to the east because of the absence of suitable habitat close to the no-wash zone. Locations within wash or no-wash zones were separated by less than 1.5 km.

Benthic macrofauna were collected from the upstream no-wash zone and the adjacent wash zone on the 28th April (Time 1) and the 30th May (Time 2), 2000; macrofauna from wash and no-wash zones situated downstream were collected on the 30th May (Time 1) and the 19th July (Time 2), 2000. Unvegetated or vegetated habitats were sampled in the upstream locations. Only the unvegetated habitat could be sampled in the downstream locations because of the absence of mangroves along this section of the river.

At time 1, sediment from upstream was collected from one location within the no-wash zone (500 m east of Rydalmere Wharf [NW/NW3]) and from two locations within the wash zone immediately to the east (George Kendall Riverside Park, Ermington [W1] and at Wilson Park, Silverwater [W2]; Fig. 4.1). This sampling served as a pilot study and for this reason only one location within the no-wash zone was sampled, so that, in the absence of any pattern, not too much time and effort would have been wasted. The location within the no-wash zone was situated upstream of the Duck River, a major tributary of the Parramatta River, while the two wash zone locations were situated downstream of this river. Thus, any difference found in assemblages between treatments may be due to the Duck River and could not necessarily be attributed to differences in wash. An additional two locations were therefore sampled within the no-wash zone at time 2 at Eric Primrose Reserve, Rydalmere (NW1) and Silverwater Park, Silverwater (NW2; Fig. 4.1).

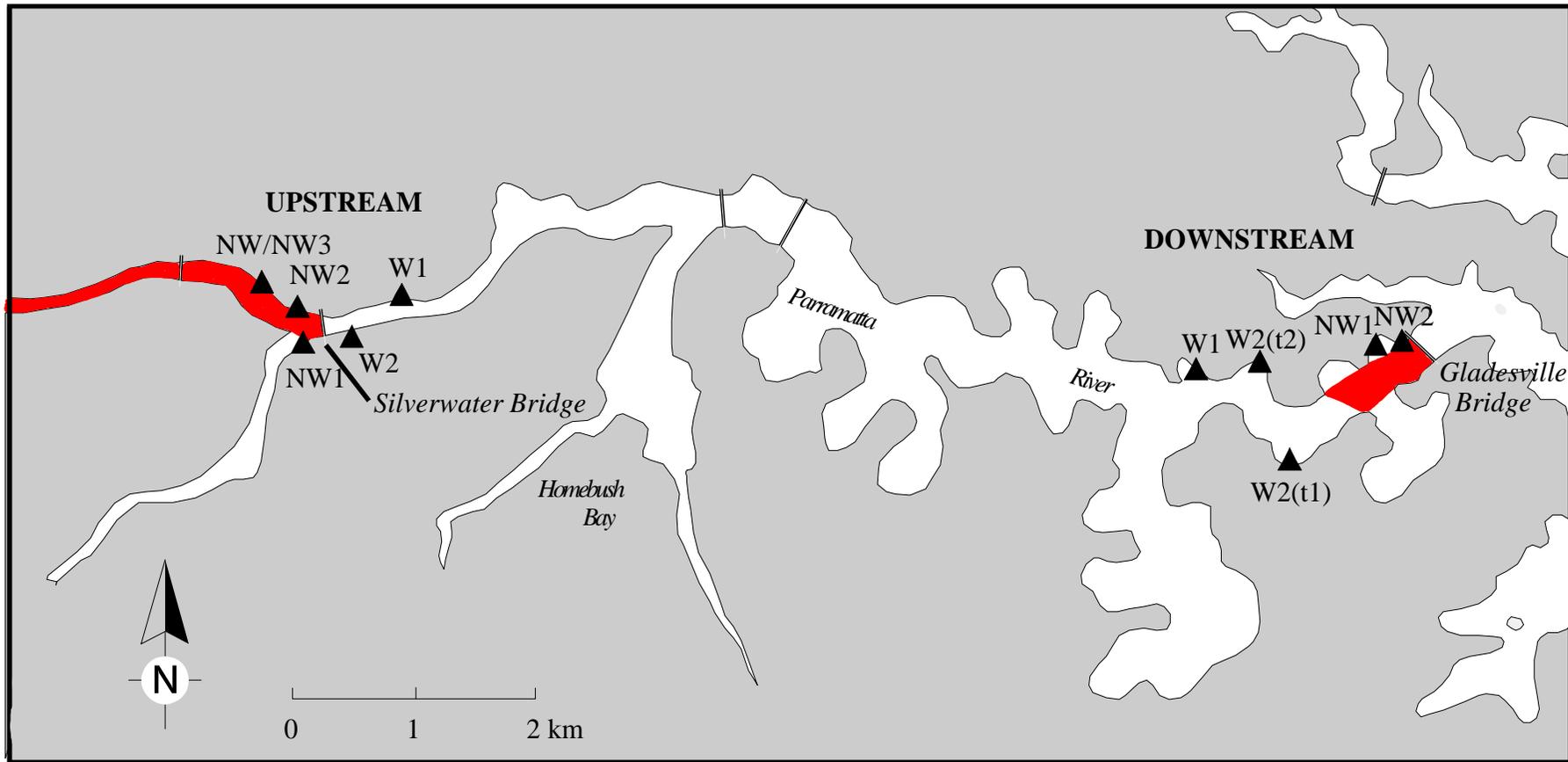


Figure 4.1 Map of the Parramatta River showing upstream and downstream no-wash zones █ and the locations within wash (W) and no-wash zones (NW) sampled.

UPSTREAM - W1: George Kendall Riverside Park, Ermington; W2: Wilson Park, Silverwater; NW1: Silverwater Park, Silverwater; NW2: Eric Primrose Reserve, Rydalmere; NW/NW3: 500 m east of Rydalmere Wharf

DOWNSTREAM – W1: Banjo Patterson Park, Gladesville; W2(t1): Abbotsford Bay; W2(t2); Gladesville Hospital; NW1: Betts Park, Huntley’s Point; NW2: Gladesville Bridge

Within the downstream no-wash zone, sediment was collected from Betts Park, Huntley's Point (NW1) and 100 m west of the Gladesville Bridge (NW2) at times 1 and 2. Sediment was collected from the wash zone to the east at Banjo Patterson Park, Gladesville (W1) and Abbotsford Bay (W2(t1)) at Time 1. At time 2, sediment was collected from Gladesville Hospital (W2(t2)) instead of Abbotsford Bay so that all locations, within wash or no-wash zones, would be situated on the northern bank of the river (Fig. 4.1). In the no-wash zone, it was not possible to sample on the southern side of the river because of the absence of suitable habitat.

Within each location, two sites, approximately 15 m long were randomly selected, 10s of metres apart. In the upstream locations, these sites contained unvegetated and vegetated habitats which were, wherever possible, at roughly the same tidal height and distance from the centre of the river. Five cores of sediment were haphazardly collected from each of the types of habitat within each site and transported back to the laboratory for processing and sorting (see Section 2.5.2 for a full description of the sampling method).

Differences between the assemblages in wash and no-wash zones were examined using nMDS ordinations of centroids representing sites and NP-MANOVAs (Anderson, 2001) and ANOSIMs (Clarke, 1993) of untransformed data. NP-MANOVAs and ANOSIMs were done because NP-MANOVAs test hypotheses regarding multivariate distances (measures of dissimilarity) whereas ANOSIMs test hypotheses regarding rank-dissimilarities. Presence-absence data were also analysed to test the hypothesis that differences in assemblages would be primarily due to differences in the types of organisms present and their distribution among samples.

Only two factors can be included in ANOSIMs and NP-MANOVAs. The factor, location, was omitted from ANOSIMs testing for differences between zones within each of the habitats because nMDS plots indicated great variability at the scale of sites. NP-MANOVAs for data collected from the upper Parramatta River at time 2 and the lower Parramatta River at each of the times also included the factors, zone and site. In the case of the data collected from the upper Parramatta River at time 1, the two factors analysed were locations and sites because different numbers of sites were sampled in each of the zones and NP-MANOVAs cannot handle unbalanced sampling designs. The hypothesised interaction between zone and habitat was tested for using NP-MANOVAs with the factors habitat and site.

Increased variability among samples has been hypothesized to be a general feature of stressed environments (Warwick and Clarke, 1993; but see Chapman *et al.*, 1995 for an example where this is not the case). Therefore, Bray-Curtis measures of within-site variability, calculated in the above analyses, were compared among sites of the upper Parramatta River to test the

hypotheses that, within each of the habitats, variability among: (i) cores and (ii) sites would be greater in the wash than in the no-wash zone.

ANOVAs were done to test the hypothesis that abundances of individual taxa would be smaller in the wash zone than the no-wash zone. Because assemblages were fairly depauperate, ANOVAs were done using the taxa present in a majority of sites in either the wash or no-wash zone. Two-tailed *F*-tests of variances, (i) among cores in the wash zone versus among cores in the no-wash zone and (ii) among sites in the wash zone versus among sites in the no-wash zone, were done to test the hypothesis that spatial variability at each of these scales would be greater in the wash than in the no-wash zones.

4.3 Results

Assemblages of the upper Parramatta River were dominated by polychaetes of the families Capitellidae and Nereididae (Table 4.1). Assemblages further downstream were dominated by syllids.

4.3.1 Upper Parramatta River

At each time of sampling, untransformed data appeared to separate into two groups corresponding to wash and no-wash zones (Fig. 4.2). At time 1, this separation of points appeared to be greater within the unvegetated habitat than the vegetated habitat. No such difference was, however, evident at time 2. On the plots of presence-absence data, some separation of points into groups corresponding to wash and no-wash zones was evident for each habitat, although patterns were less clear than on plots of untransformed data. At time 2, the taxa present in the unvegetated habitat of W1(S2) differed from those in all other sites. This pattern appeared to be driven by the absence of Nereididae from W1(S2). The persistent difference in the assemblages of wash and no-wash zones across both times of sampling indicates that the sampling done at time 1 was not confounded by the situation of sites relative to the Duck River.

At time 1, only 15 permutations of data were possible for ANOSIM tests for differences between the zones because of the small number of sites sampled in the wash or no-wash zone. Thus, tests could only be significant if all of the permutations produced a test statistic less than *R*. It was not surprising, then, that all of the tests for differences between zones at time 1 were non-significant (Table 4.2a). The large (0.93) sample statistic, *R*, calculated for the untransformed data from the unvegetated sediment does, however, indicate that assemblages differed between wash and no-wash zones (Table 4.2a(i)), as indicated by the nMDS (Fig. 4.2a(i)). At time 2, more permutations were possible due to the larger number of sites sampled.

Significant differences were found between wash and no-wash zones when untransformed or presence-absence data were analysed, from unvegetated or vegetated sediment (Table 4.2b). These differences are consistent with the patterns shown on the nMDS plots (Fig. 4.2b).

Table 4.1 Taxa of macrobenthic infauna present (*) in vegetated and unvegetated sediment of the upper Parramatta River and unvegetated sediment of the lower Parramatta River, at two times of sampling.

| | | | UPSTREAM | | | | DOWN-STREAM | |
|-----------|-------------|---------------------------------|----------|----|-----|----|-------------|----|
| | | | unveg | | veg | | t1 | t2 |
| | | | t1 | t2 | t1 | t2 | | |
| Annelida | Oligochaeta | | * | * | * | * | * | * |
| | Polychaeta | Capitellidae | * | * | * | * | * | * |
| | | Cirratulidae | | | | | * | |
| | | Eunicidae | | * | | * | | |
| | | Hesionidae | | | | * | * | * |
| | | Nephtyidae | | * | | * | | * |
| | | Nerididae | * | * | * | * | * | |
| | | Orbiniidae | | | | * | | * |
| | | Paraonidae | | | | | * | |
| | | Sabellidae | | * | | * | | * |
| | | Spionidae | | * | * | * | | * |
| | | Spirorbidae | | | | | | * |
| | | Syllidae | | * | | | * | * |
| | | Terebellidae | | | | | * | |
| Crustacea | | Amphipoda | * | * | * | * | * | * |
| | | Isopoda | * | * | * | * | * | * |
| | | Tanaidacea | * | * | * | * | * | * |
| Mollusca | Bivalvia | <i>Artheritica helmsii</i> | * | * | * | * | * | * |
| | | <i>Laternula</i> sp. | | * | | * | | |
| | | <i>Spisula trigonella</i> | * | * | | | | |
| | | <i>Soletellina donacoidales</i> | | | | | | * |
| | | <i>Tellina delatoidales</i> | * | * | * | * | | * |
| | | <i>Xenostrobus securis</i> | | * | * | * | | * |
| | Gastropoda | <i>Velacumantis australis</i> | | | * | | | |
| Nematoda | | | | * | | * | * | * |
| Nemertea | | | | * | | * | * | * |
| Sipuncula | | | | | | | | * |
| Other | | Insect larvae | * | * | * | * | * | * |

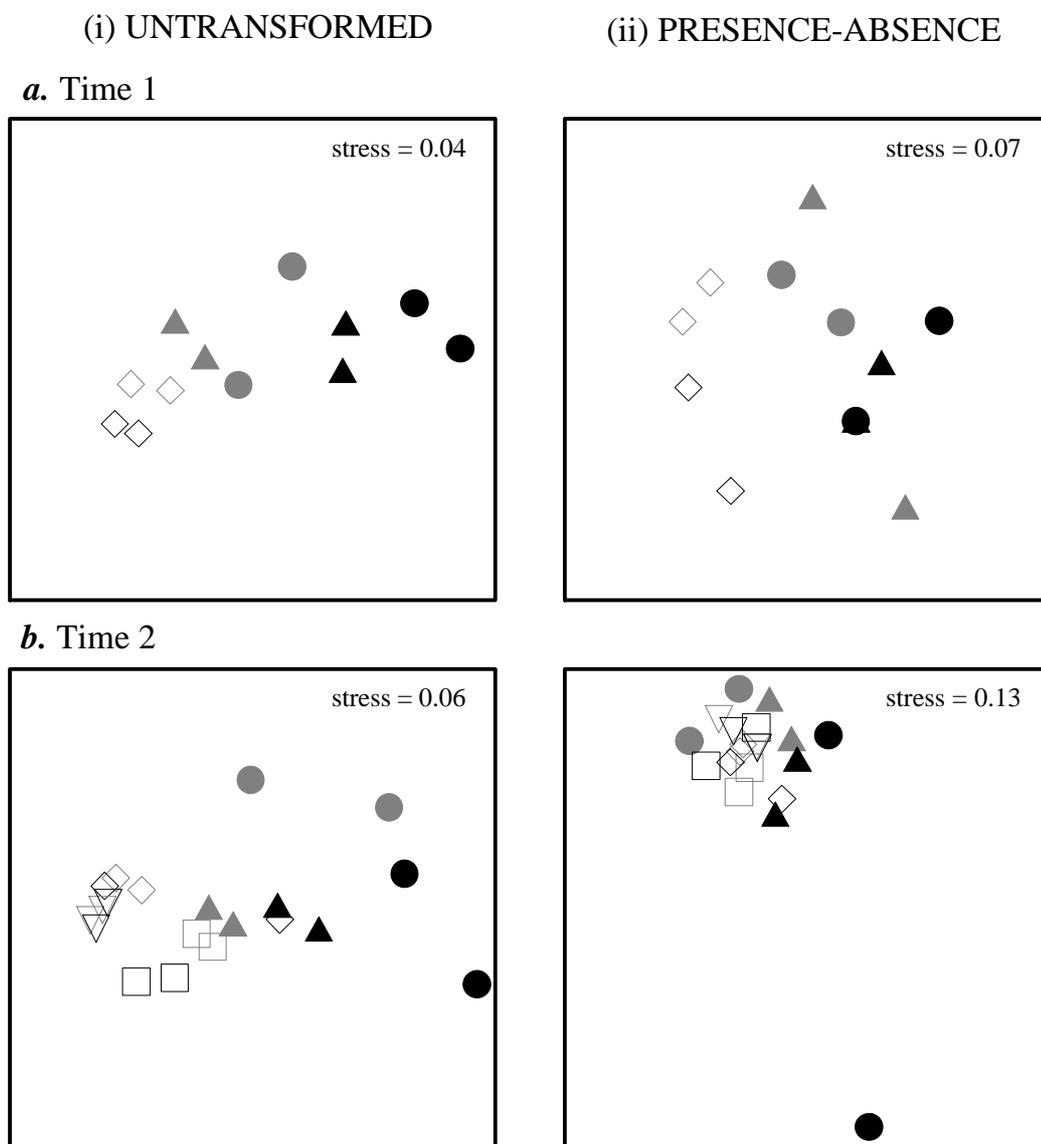


Figure 4.2 nMDS ordinations of assemblages of benthic macrofauna found within vegetated (grey) and unvegetated (black) sediment of wash (filled symbols; W1: circles, W2: triangles) and no-wash (unfilled symbols; NW1: squares, NW2: inverted triangles, NW/NW3: diamonds) zones of the upper Parramatta River. Points represent centroids of (i) untransformed data and (ii) presence-absence data from each site. $n = 5$.

Table 4.2 Summaries of ANOSIMs testing for differences in assemblages of macrobenthic infauna between wash and no-wash zones of the upper Parramatta River at **a.** Time 1 (28/04/00) and **b.** Time 2 (30/05/00), in (i) unvegetated and (ii) vegetated sediment. zo = zone (2 levels: wash, no-wash; fixed); si (zo) = sites (6 levels at time 1, 10 levels at time 2; random).

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a. Time 1

| source | No. possible permutations | untransformed | | presence-absence | |
|---------|---------------------------|-------------------------------|-----|-------------------------------|-----|
| | | Sample statistic (<i>R</i>) | Sig | Sample statistic (<i>R</i>) | Sig |
| zo | 15 | 0.93 | NS | 0.18 | NS |
| si (zo) | 5000 | 0.22 | ** | 0.09 | NS |

(i) unvegetated sediment

| source | No. possible permutations | untransformed | | presence-absence | |
|---------|---------------------------|-------------------------------|-----|-------------------------------|-----|
| | | Sample statistic (<i>R</i>) | Sig | Sample statistic (<i>R</i>) | Sig |
| zo | 15 | 0.14 | NS | 0.46 | NS |
| si (zo) | 5000 | 0.16 | * | 0.21 | ** |

(ii) vegetated sediment

b. Time 2

(i) unvegetated sediment

| source | No. possible permutations | untransformed | | presence-absence | |
|---------|---------------------------|-------------------------------|-----|-------------------------------|-----|
| | | Sample statistic (<i>R</i>) | Sig | Sample statistic (<i>R</i>) | Sig |
| zo | 210 | 0.72 | ** | 0.50 | ** |
| si (zo) | 5000 | 0.61 | *** | 0.31 | *** |

(ii) vegetated sediment

| source | No. possible permutations | untransformed | | presence-absence | |
|---------|---------------------------|-------------------------------|-----|-------------------------------|-----|
| | | Sample statistic (<i>R</i>) | Sig | Sample statistic (<i>R</i>) | Sig |
| zo | 210 | 0.51 | *** | 0.54 | ** |
| si (zo) | 5000 | 0.41 | *** | 0.28 | *** |

At time 1, an NP-MANOVA, done on untransformed data, showed assemblages to differ between the location in the no-wash zone and those in the wash zone (Table 4.3a(i)). In the vegetated habitat, however, assemblages differed between the two locations in the wash zone, but were similar at W2 (Wilson Park) and in the no-wash zone (Table 4.3a(ii)). The analysis of presence-absence data indicated no difference in taxa or their distribution among cores between the wash and no-wash zone (NP-MANOVA; Table 4.3a). At time 2, assemblages in unvegetated sediment differed significantly among locations when untransformed data were analysed (Table 4.3b(i)), as did assemblages in the vegetated habitat when untransformed or presence-absence data were analysed (Table 4.3b(ii)). *A posteriori* tests examining these differences were, however, not consistent with an effect of wash.

A significant interaction between the factors habitat and site was found in the untransformed data, at each time of sampling, and in the presence-absence data at time 2 (NP-MANOVA; Table 4.4). *A posteriori* tests, examining the differing patterns in unvegetated and vegetated habitats, are shown in the table.

Assemblages within each habitat, at each time, were more variable in sites of the wash zone than sites of the no-wash zone (Fig. 4.3a,b). Differences between the assemblages of unvegetated and vegetated sediment were also greater in the wash zone (Fig. 4.3c). Dissimilarities were not analysed statistically because they are non-independent and hence violate the assumptions of most tests (e.g. ANOVA; Underwood, 1997).

At Time 1, the abundances of capitellids, nereids and amphipods were greater in the unvegetated habitat of the no-wash zone than the wash zone (Fig. 4.4(i)). Within the vegetated habitat, the abundances of capitellids and nereids were greater in the no-wash zone (Fig. 4.4(ii)a,b). These differences were, however, not significant statistically (ANOVA; Table 4.5) due to great spatial variability at the scale of replicates (metres), sites within locations (10s of metres) and locations (100s of metres). Other differences between wash and no-wash zones at Time 1 were the absence of *Arthritica helmsii* from wash zones of both habitats, *Spisula trigonella* from all places except for the no-wash zone of unvegetated habitat and isopods from the unvegetated habitat of the wash zone.

At time 2, the difference in assemblages between wash and no-wash zones of each of the habitats appeared to be due to greater abundances of capitellids, nereids, sabellids, spionids, amphipods, isopods and *Xenostrobos securis* in the no-wash zone (Fig. 4.5). Nephytiidae, in contrast, were only present in the wash zone. Of these taxa, only sabellids in the vegetated habitat and amphipods and *X. securis* in the unvegetated habitat differed significantly in abundance between the wash and no-wash zone (Table 4.6). In the case of each of these

analyses, heterogeneity of variances was more significant than the difference between zones, such that the analyses could only be interpreted in conjunction with graphical representations.

Many taxa in unvegetated or vegetated habitat appeared more variable, at the scale of cores, in the no-wash zone than in the wash zone (two-tailed *F*-tests; Table 4.7). Several were also more variable in the no-wash zone at the scale of sites (Table 4.7).

Table 4.3 Summaries of NP-MANOVAs comparing spatial variation in the abundance of taxa of macrobenthic infauna among locations and sites of the upper Parramatta River at **a.** Time 1 (28/04/00) and **b.** Time 2 (30/05/00), in (i) unvegetated and (ii) vegetated habitat. lo = location (3 levels at time 1: W1, W2, NW; 5 levels at time 2: W1, W2, NW1, NW2, NW3); si (lo) = sites (2 levels within each location, random). *n* = 5. NS *p* > 0.05, * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

a. Time 1

(i) unvegetated sediment

| | untransformed | | | pres-abs | |
|--------------------|---------------|----------|------|----------|------|
| | <i>df</i> | <i>p</i> | sig. | <i>p</i> | sig. |
| lo | 2 | 0.0006 | *** | 0.4348 | NS |
| si(lo) | 3 | 0.0800 | NS | 0.0874 | NS |
| res | 24 | | | | |
| lo: (W1 = W2) ? NW | | | | | |

(ii) vegetated sediment

| | untransformed | | | pres-abs | |
|--------------------|---------------|----------|------|----------|------|
| | <i>df</i> | <i>p</i> | sig. | <i>p</i> | sig. |
| lo | 2 | 0.0008 | *** | 0.0836 | NS |
| si(lo) | 3 | 0.2218 | NS | 0.0596 | NS |
| res | 24 | | | | |
| lo: W1 ? (W2 = NW) | | | | | |

b. Time 2

i) unvegetated sediment

| | untransformed | | | pres-abs | |
|------------------------------------|---------------|----------|------|----------|------|
| | <i>df</i> | <i>p</i> | sig. | <i>p</i> | sig. |
| lo | 4 | 0.0006 | *** | 0.0694 | NS |
| si (lo) | 5 | 0.0002 | *** | 0.0022 | ** |
| res | 40 | | | | |
| lo: (W1 = W2 = NW2) ? NW1 ? NW3 | | | | | |

(ii) vegetated sediment

| | untransformed | | | pres-abs | |
|--|---------------|----------|------|----------|------|
| | <i>df</i> | <i>p</i> | sig. | <i>p</i> | sig. |
| lo | 4 | 0.0002 | *** | 0.0052 | ** |
| si (lo) | 5 | 0.5864 | NS | 0.3382 | NS |
| res | 40 | | | | |
| lo: W1 ? W2 ? NW1 (W1 = W2 = NW1) ? NW1 ? NW3 ? (NW2 = NW3) | | | | | |

Table 4.4 Summaries of non-parametric MANOVAs comparing spatial variation in assemblages of macrobenthic infauna between habitats and among sites within wash (W) and no-wash (NW) zones of the upper Parramatta River at *a.* time 1 (28/04/00) and *b.* time 2 (30/05/00). ha = habitat (2 levels: unvegetated [U], vegetated [V]; fixed) si = sites (6 levels at time 1, 10 levels at time 2; random). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a. Time 1

| source | untransformed | | | pres-abs | |
|---------------------------|--------------------------------|--------|-----|--------------------------------|-----|
| | df | p | Sig | p | Sig |
| ha | 1 | 0.0232 | * | 0.0952 | NS |
| si | 5 | 0.0002 | *** | 0.0002 | *** |
| ha x si | 5 | 0.0002 | *** | 0.0306 | * |
| res | 48 | | | | |
| <i>a posteriori</i> tests | U: (W1S1 = W1S2 = W2S1 = W2S2) | | | U: (W1S1 = W1S2 = W2S1 = W2S2) | |
| ha x si: | ≠ NWS1 ≠ NWS2 | | | = NWS1) ≠ NWS2 | |
| | V: (W1S1 = W1S2 = W2S1) ≠ W2S2 | | | V: (W1S1 = W1S2 = W2S1) ≠ W2S2 | |
| | ≠ NWS1 ≠ NWS2 | | | ≠ NWS1 ≠ NWS2 | |

b. Time 2

| source | untransformed | | | pres-abs | |
|---------------------------|--------------------|--------|-----|--------------------|-----|
| | df | p | Sig | p | Sig |
| ha | 1 | 0.1572 | NS | 0.1446 | NS |
| si | 9 | 0.0002 | *** | 0.0002 | *** |
| ha x si | 9 | 0.0002 | *** | 0.0040 | ** |
| res | 80 | | | | |
| <i>a posteriori</i> tests | U: uninterpretable | | | U: uninterpretable | |
| ha x si: | V: uninterpretable | | | V: uninterpretable | |

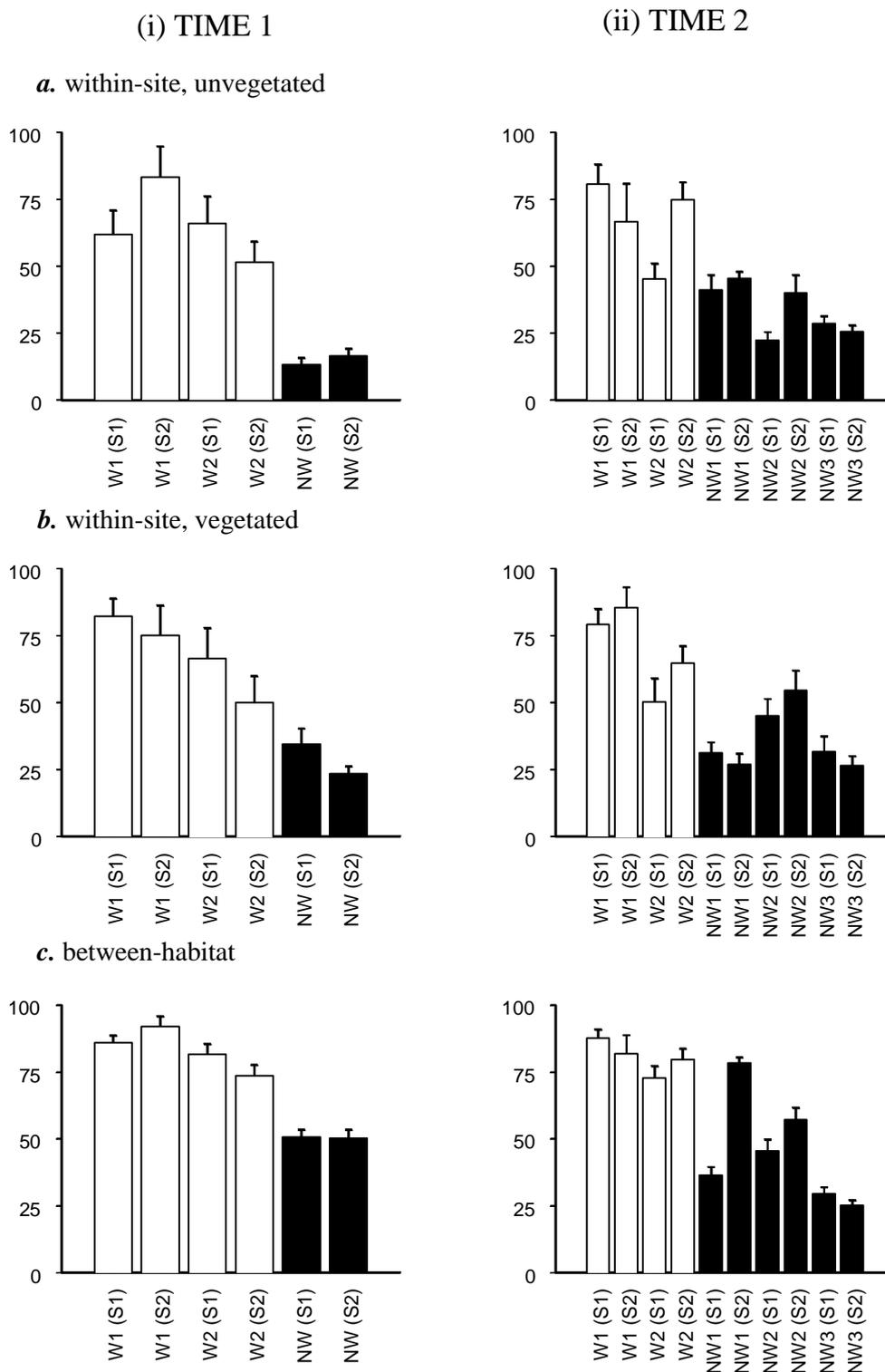


Figure 4.3 Bray-Curtis measures of within-site variability in assemblages of macrobenthic infauna in *a.* unvegetated sediment and *b.* vegetated sediment, of wash (white) and no-wash (black) zones along the upper Parramatta River ($n = 10$). Measures of dissimilarity between the assemblages of unvegetated and vegetated sediment, within each site, are also shown (*c.*; $n = 25$).

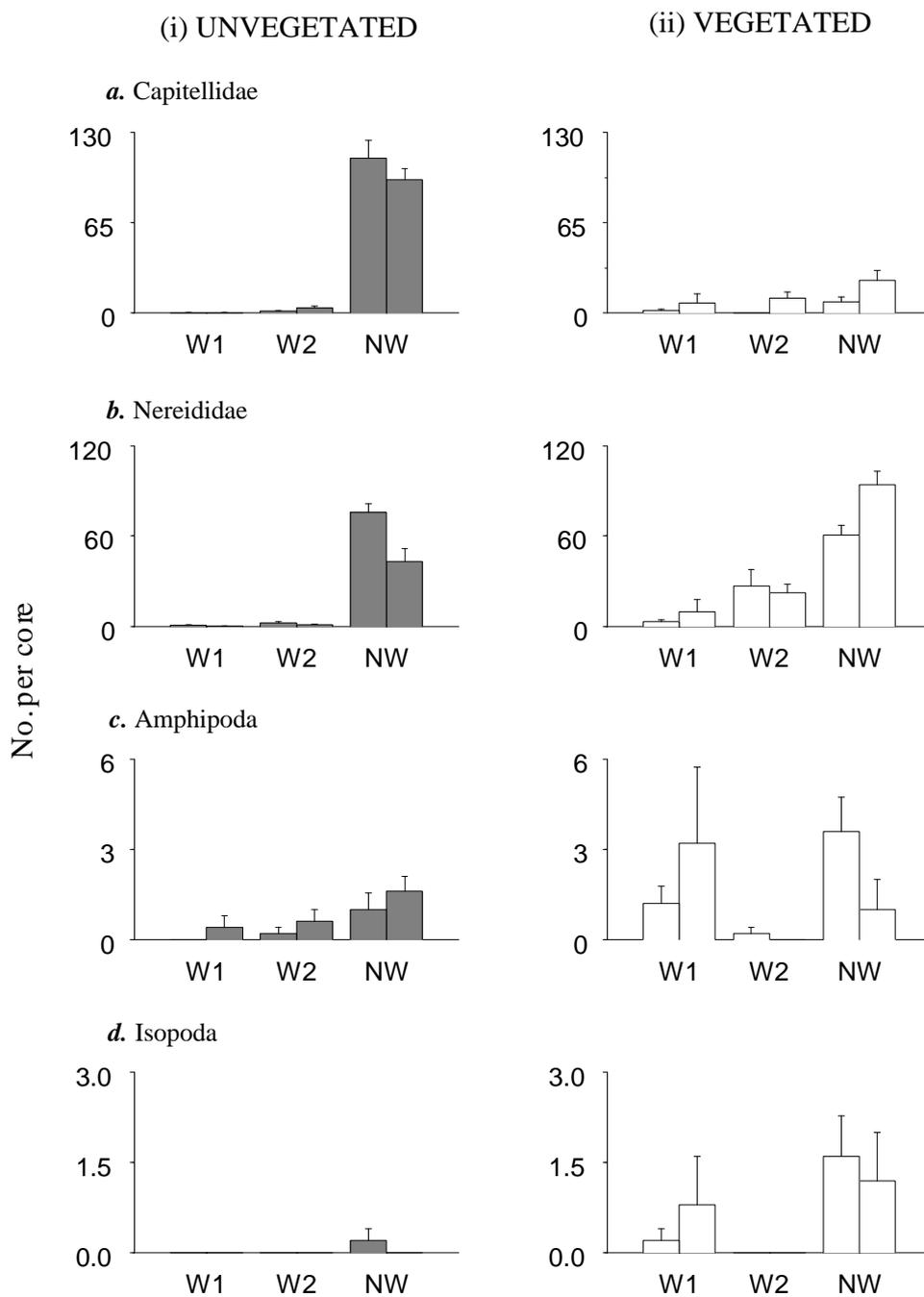


Figure 4.4 Mean (+ S.E.) abundance (per core) of taxa of macrobenthic infauna in unvegetated (grey) and vegetated (white) sediment of wash (W) or no-wash (NW) zones, along the upper Parramatta River, at Time 1 (28/04/00). $n = 5$, with two sites at each location.

Table 4.5 Summaries of asymmetrical analyses comparing spatial variation in the abundance of macrobenthic infauna, in unvegetated or vegetated sediment, between wash and no-wash zones of the upper Parramatta River at Time 1 (28/04/00).

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | df | Capitellidae | | | Nereididae | | | Amphipoda | | | Isopoda | | | | | | | | | | | | | | |
|--------------------|----|--------------|-----------|------|-------------|-----------|------|-------------|-----------|------|-------------|-----------|------|-------------|------|------|------------|------|----|-------------|---|---|-------------|------|----|
| | | Unvegetated | Vegetated | | Unvegetated | Vegetated | | Unvegetated | Vegetated | | Unvegetated | Vegetated | | | | | | | | | | | | | |
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | | | | | | | | | |
| location | 2 | | | | | | | | | | | | | | | | | | | | | | | | |
| wash vs no-wash | 1 | 102.24 | 27 | NS | 17.4 | 25 | NS | 78.7 | 67 | NS | 35.4 | 4 | NS | 1.84 | 19.2 | NS | 1.37 | 0.81 | NS | 0.03 | X | X | 2.13 | 8.03 | NS |
| wash | 1 | 3.79 | | | 0.7 | | | 1.2 | | | 9.8 | | | 0.10 | | | 1.69 | | | 0.00 | | | 0.27 | | |
| site (location) | 3 | | | | | | | | | | | | | | | | | | | | | | | | |
| site (wash) | 2 | 0.43 | | | 5.5 | | | 0.3 | | | 0.1 | | | 0.12 | | | 0.14 | | | 0.00 | | | 0.04 | | |
| site (no-wash) | 1 | 0.05 | | | 2.9 | | | 0.9 | | | 0.5 | | | 0.23 | | | 2.89 | | | 0.05 | | | 0.2 | | |
| residual | 24 | | | | | | | | | | | | | | | | | | | | | | | | |
| residual (wash) | 16 | 0.26 | | | 1.1 | | | 0.2 | | | 1.7 | | | 0.15 | | | 0.50 | | | 0.00 | | | 0.15 | | |
| residual (no-wash) | 8 | 0.05 | | | 0.7 | | | 0.1 | | | 0.1 | | | 0.31 | | | 0.42 | | | 0.05 | | | 0.47 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | | | |
| Cochran's test | | C = 0.41 NS | | | C = 0.43 NS | | | C = 0.50 * | | | C = 0.38 NS | | | C = 0.27 NS | | | C = 0.50 * | | | C = 1.00 ** | | | C = 0.38 NS | | |

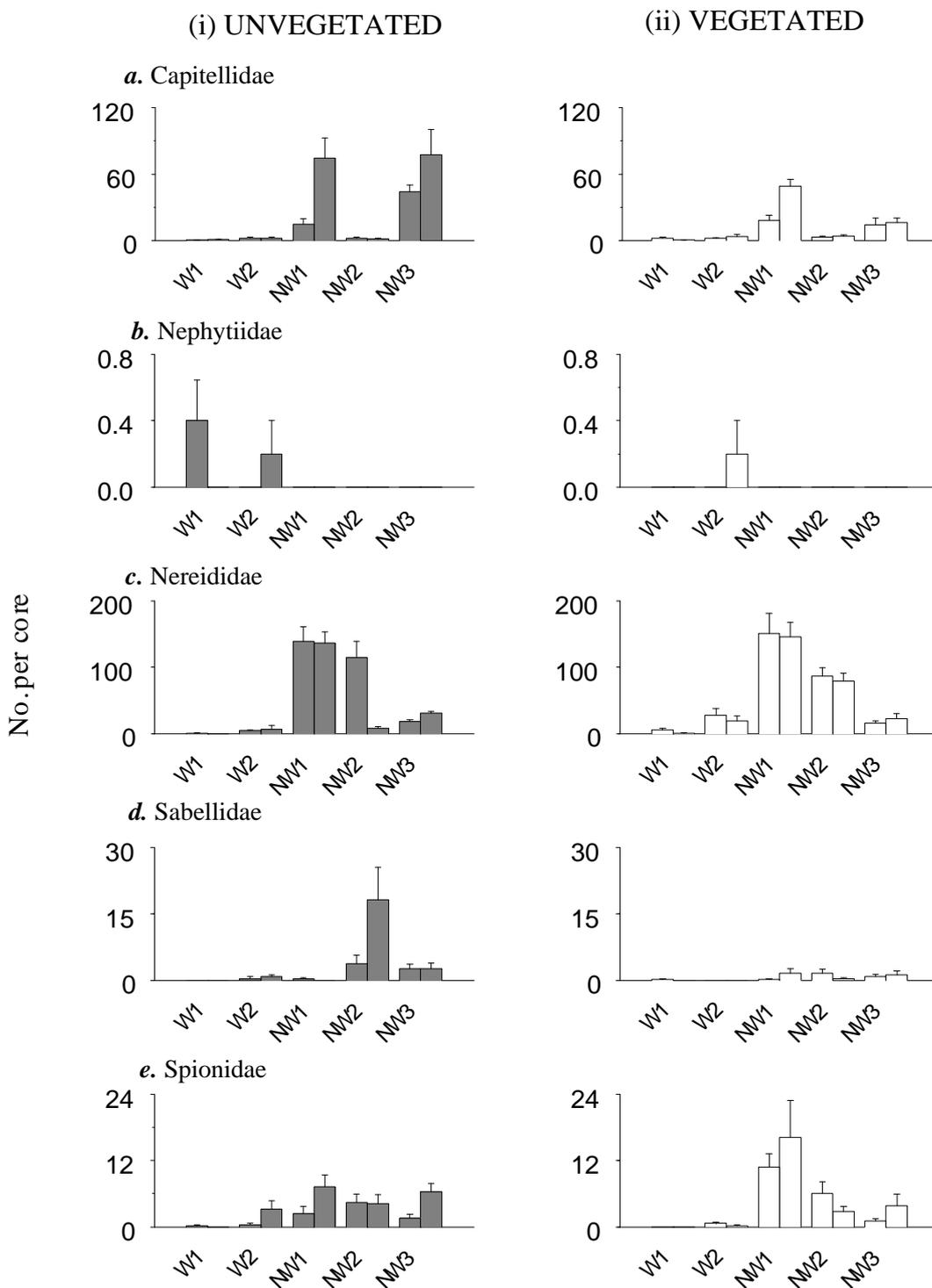


Figure 4.5 Mean (+ S.E.) abundance (per core) of taxa of macrobenthic infauna in unvegetated (grey) and vegetated (white) sediment of wash (W) or no-wash (NW) zones, along the upper Parramatta River, at Time 2 (30/05/00). $n = 5$, with two sites at each location.

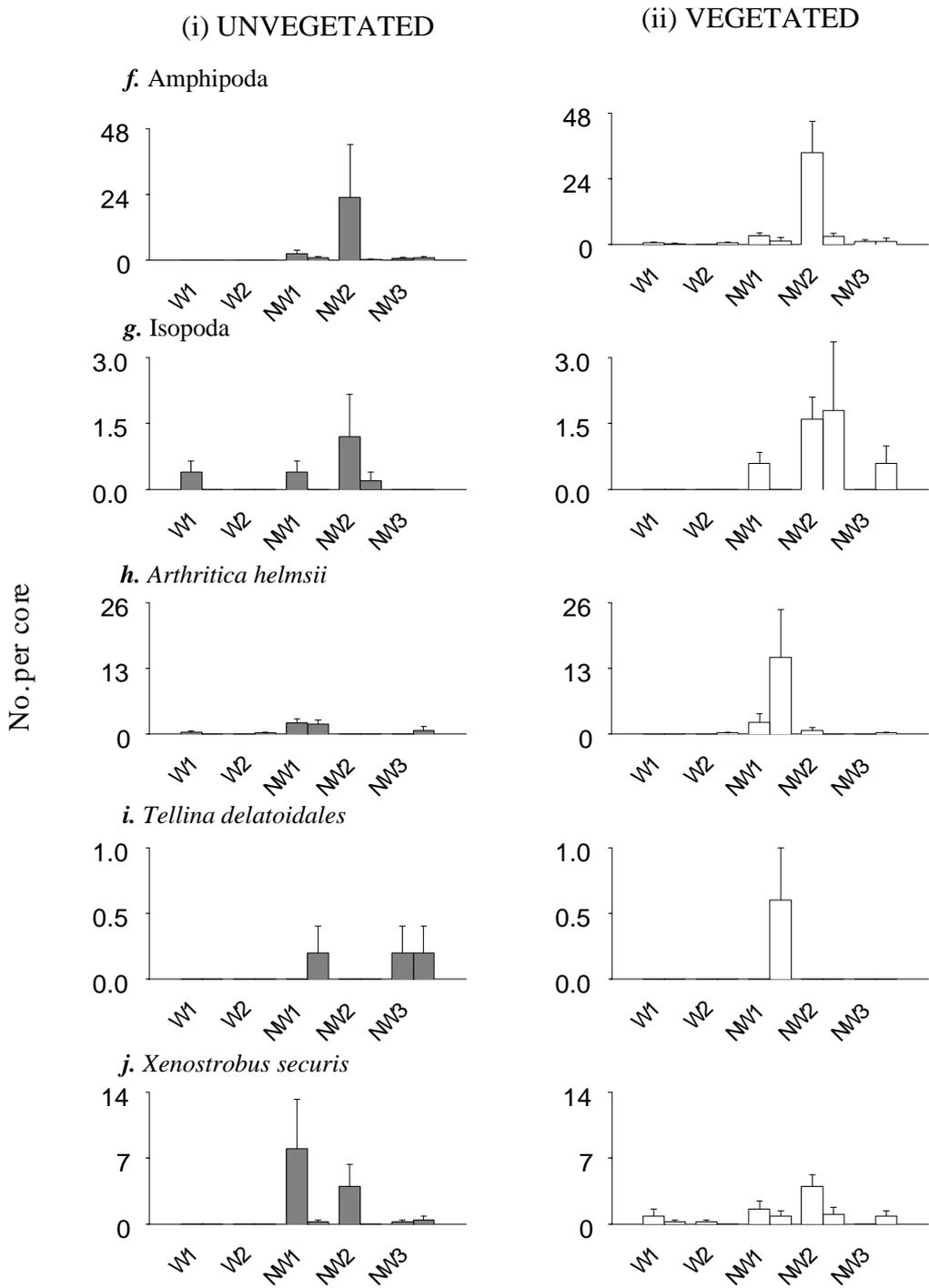


Figure 4.5 continued.

Table 4.6 Summaries of analyses comparing spatial variation in the abundance of macrobenthic infauna, in unvegetated or vegetated sediment, between wash and no-wash zones of the upper Parramatta River at Time 2 (30/05/00).

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | df | Capitellidae | | | Nereididae | | | Sabellidae | | | Spionidae | | | | | | | | | | | | | | |
|--------------------|----|--------------|-----------|------|-------------|-----------|------|-------------|-----------|------|-------------|-----------|------|------------|------|------|------------|------|------|-------------|-------|----|-------------|------|----|
| | | unvegetated | vegetated | | unvegetated | vegetated | | unvegetated | vegetated | | unvegetated | vegetated | | | | | | | | | | | | | |
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | | | | | | |
| zone | 1 | 16.76 | 1.0 | NS | 25.01 | 2.4 | NS | 109.38 | 11.6 | NS | 76.27 | 7.99 | NS | 1.62 | 0.7 | NS | 1.54 | 54.3 | * | 11.10 | 10.32 | NS | 31.07 | 11.2 | NS |
| location (zone) | 2 | 16.81 | 7.2 | * | 10.53 | 10.5 | * | 9.44 | 2.2 | NS | 9.55 | 13.94 | * | 2.28 | 21.9 | ** | 0.03 | 0.2 | NS | 1.08 | 0.93 | NS | 2.79 | 14.4 | * |
| location (wash) | 1 | 1.65 | | | 0.64 | | | 7.11 | | | 17.58 | | | 0.64 | | | 0.02 | | | 2.09 | | | 0.38 | | |
| location (no-wash) | 1 | 15.16 | | | 20.42 | | | 11.78 | | | 1.52 | | | 3.93 | | | 0.03 | | | 0.06 | | | 5.19 | | |
| site (location) | 4 | 2.35 | 3.3 | * | 1.00 | 2.7 | * | 4.32 | 11.2 | *** | 0.69 | 1.31 | NS | 0.10 | 0.4 | NS | 0.17 | 0.7 | NS | 1.15 | 2.79 | NS | 0.19 | 0.5 | NS |
| site (wash) | 2 | 0.06 | | | 0.52 | | | 0.45 | | | 1.36 | | | 0.10 | | | 0.02 | | | 0.98 | | | 0.10 | | |
| site (no-wash) | 2 | 4.64 | | | 1.49 | | | 8.18 | | | 0.01 | | | 0.11 | | | 0.31 | | | 1.32 | | | 0.29 | | |
| residual | 32 | 0.71 | | | 0.37 | | | 0.38 | | | 0.52 | | | 0.26 | | | 0.24 | | | 0.41 | | | 0.42 | | |
| residual (wash) | 16 | 0.59 | | | 0.45 | | | 0.59 | | | 0.89 | | | 0.12 | | | 0.02 | | | 0.25 | | | 0.06 | | |
| residual (no-wash) | 16 | 0.82 | | | 0.29 | | | 0.18 | | | 0.16 | | | 0.40 | | | 0.46 | | | 0.58 | | | 0.78 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | |
| Cochran's test | | C = 0.34 NS | | | C = 0.30 NS | | | C = 0.54 ** | | | C = 0.30 NS | | | C = 0.43 * | | | C = 0.40 * | | | C = 0.27 NS | | | C = 0.37 NS | | |
| SNK | | | | | | | | | | | | | | W < NW | | | | | | | | | | | |

| | df | Amphipoda | | | Isopoda | | | <i>Arthritica helmsii</i> | | | <i>Xenostrobus securis</i> | | | | | | | | | | | | | | |
|--------------------|----|-------------|-----------|------|-------------|-----------|------|---------------------------|-----------|------|----------------------------|-----------|------|-------------|------|------|-------------|-----|------|-------------|------|----|-------------|-------|----|
| | | unvegetated | vegetated | | unvegetated | vegetated | | unvegetated | vegetated | | unvegetated | vegetated | | | | | | | | | | | | | |
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | | | | | | |
| zone | 1 | 6.5 | 30.5 | * | 17.67 | 3.9 | NS | 0.25 | 2.0 | NS | 2.14 | 3.30 | NS | 1.32 | 0.6 | NS | 6.72 | 1.6 | NS | 5.08 | 48.4 | * | 3.77 | 10.79 | NS |
| location (zone) | 2 | 0.2 | 0.1 | NS | 4.57 | 1.6 | NS | 0.13 | 0.7 | NS | 0.65 | 4.14 | NS | 2.20 | 32.0 | ** | 4.19 | 3.8 | NS | 0.11 | 0.1 | NS | 0.35 | 0.52 | NS |
| location (wash) | 1 | 0.0 | | | 0.02 | | | 0.10 | | | 0.02 | | | 0.00 | | | 0.02 | | | 0.00 | | | 0.13 | | |
| location (no-wash) | 1 | 0.4 | | | 9.11 | | | 0.16 | | | 1.27 | | | 4.40 | | | 8.36 | | | 0.21 | | | 0.57 | | |
| site (location) | 4 | 1.8 | 2.9 | * | 2.88 | 7.8 | *** | 0.18 | 1.4 | NS | 0.16 | 0.93 | NS | 0.07 | 0.4 | NS | 1.10 | 3.0 | * | 2.08 | 5.8 | ** | 0.67 | 1.98 | NS |
| site (wash) | 2 | 0.0 | | | 0.31 | | | 0.10 | | | 0.12 | | | 0.00 | | | 0.02 | | | 0.00 | | | 0.07 | | |
| site (no-wash) | 2 | 3.6 | | | 5.44 | | | 0.26 | | | 0.19 | | | 0.14 | | | 2.17 | | | 4.15 | | | 1.27 | | |
| residual | 32 | 0.6 | | | 0.37 | | | 0.12 | | | 0.17 | | | 0.17 | | | 0.36 | | | 0.36 | | | 0.34 | | |
| residual (wash) | 16 | 0.0 | | | 0.10 | | | 0.04 | | | 0.06 | | | 0.00 | | | 0.02 | | | 0.00 | | | 0.18 | | |
| residual (no-wash) | 16 | 1.3 | | | 0.65 | | | 0.21 | | | 0.28 | | | 0.34 | | | 0.70 | | | 0.71 | | | 0.50 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | | | |
| Cochran's test | | C = 0.73 ** | | | C = 0.35 NS | | | C = 0.62 ** | | | C = 0.68 ** | | | C = 0.48 ** | | | C = 0.58 ** | | | C = 0.63 ** | | | C = 0.26 NS | | |
| SNK | | W < NW | | | | | | | | | | | | | | | W < NW | | | | | | | | |

Table 4.7 Two-tailed *F*-tests of variances, among cores in the wash zone (W) versus among cores in the no-wash zone (NW) and among sites in the wash zone versus among sites in the no-wash zone, along the upper Parramatta River. Degrees of freedom and mean squares are as given in Tables 4.5 and 4.6. X: comparison was not made due to absence of taxon from the wash zone. NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Taxon | Time | Unvegetated | | Vegetated | |
|----------------------------|------|--|--------------------------------|--|--------------------------------|
| | | Among cores (= Residual) wash vs no-wash | Among sites wash vs no-wash | Among cores (= Residual) wash vs no-wash | Among sites wash vs no-wash |
| Capitellidae | 1 | * W > NW | NS | NS | NS |
| | 2 | NS | * W < NW | NS | NS |
| Nereididae | 1 | NS | NS | NS | *** W > NW |
| | 2 | * W > NW | NS | *** W > NW | ** W > NW |
| Sabellidae | 2 | * W < NW | NS | *** W < NW | NS |
| Spionidae | 2 | * W < NW | NS | *** W < NW | NS |
| Amphipoda | 1 | NS | NS | * W < NW | NS |
| | 2 | X | X | *** W < NW | NS |
| Isopoda | 1 | X | X | NS | ** W < NW |
| | 2 | *** W < NW | NS | ** W < NW | NS |
| <i>Arthritica helmsii</i> | 2 | X | X | *** W < NW | ** W < NW |
| <i>Xenostrobos securis</i> | 2 | X | X | * W < NW | NS |

4.3.2 Lower Parramatta River

nMDS plots of untransformed or presence-absence data from the lower Parramatta River showed no separation of points into wash and no-wash zones at either time of sampling (Fig. 4.6). This result was confirmed by ANOSIMs and NP-MANOVAs, which did not find any difference between assemblages of wash and no-wash zones (Table 4.8, 4.9). Significant spatial variation in assemblages at the scale of sites was evident at times 1 and 2 (Table 4.8, 4.9).

Spionidae, which were more abundant in the wash than the no-wash zone at time 2, were the only invertebrates that differed significantly in abundance between the wash and no-wash zone (ANOVA; Table 4.10b; Fig. 4.7e). The abundance of oligochaetes did, however, also appear greater in the wash than the no-wash zone at Time 2 (Fig. 4.7a). Abundances of taxa were highly variable, both temporally and spatially (Fig. 4.7). Two-tailed *F*-tests showed that several taxa were more variable in the wash than in the no-wash zone, at the scale of cores (Table 4.11). Spionids, at time 1 did, however, show the reverse pattern (i.e. greater variability among cores in the no-wash zone). Few taxa displayed a difference in variability at the scale of sites between the wash and the no-wash zone (Table 4.11) and in no case was the difference persistent over time. The pattern of difference did not appear consistent across taxa either - some were more variable in the wash zone and others, more variable in the no-wash zone.

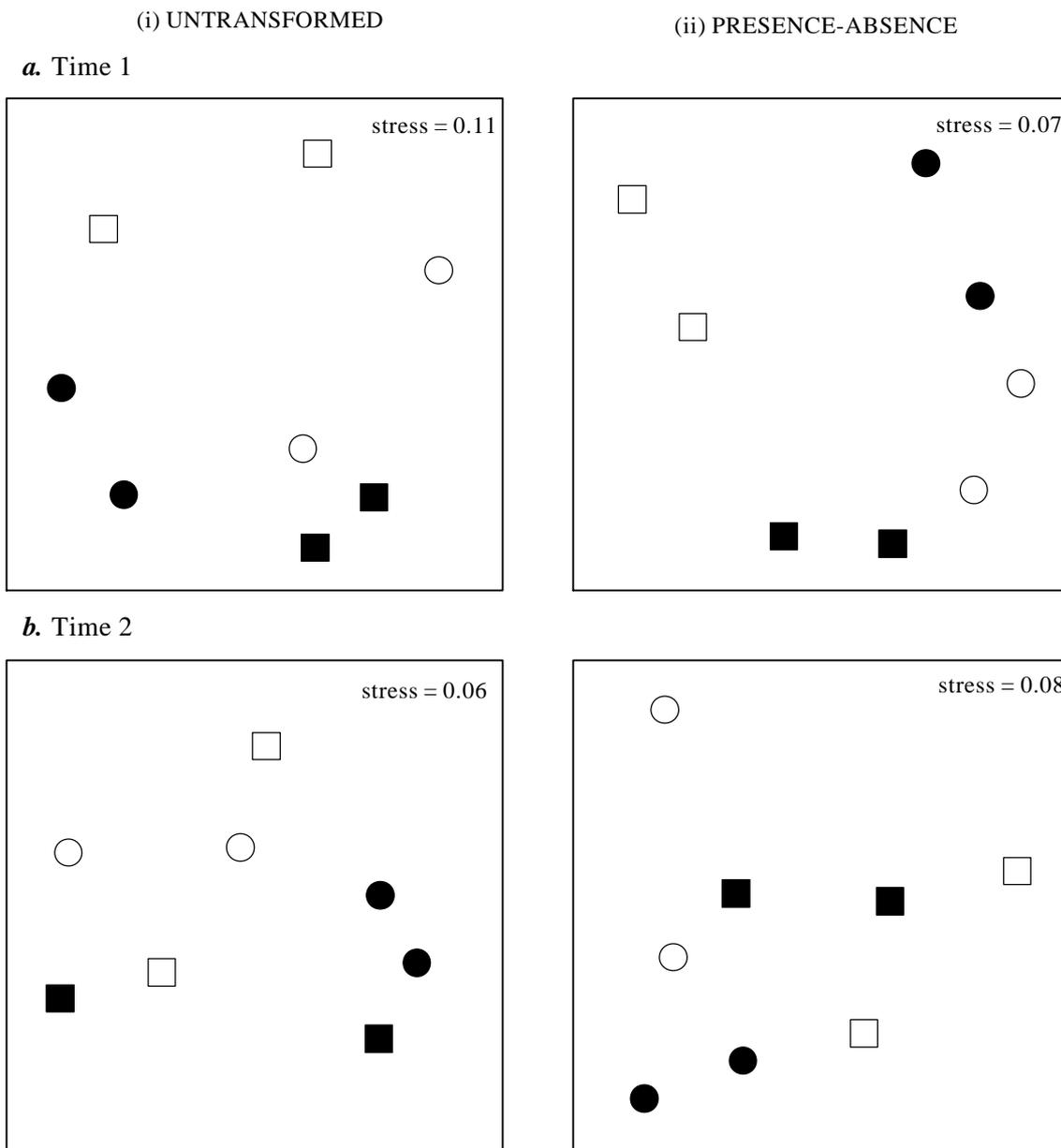


Figure 4.6 nMDS ordinations of assemblages of macrobenthic infauna in wash (black: circles – W1, squares – W2) and no-wash (white: circles – NW1, squares – NW2) zones of the lower Parramatta River at **a. Time 1** (30/05/00) and **b. Time 2** (19/07/00). Points represent centroids of (i) untransformed data and (ii) presence-absence data from each site. $n = 5$.

Table 4.8 Summaries of ANOSIMs testing for differences in assemblages of macrobenthic infauna between wash and no-wash zones at **a.** Time 1 (30/05/00) and **b.** Time 2 (19/07/00). zo = zones (2 levels: wash, no-wash; fixed); si (zo) = sites (8 levels; random). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a. Time 1

| source | untransformed | | | pres-abs | |
|---------|------------------|--------------------------|-----|--------------------------|-----|
| | No. permutations | Sample statistic (R) | Sig | Sample statistic (R) | Sig |
| zo | 35 | 0.17 | NS | -0.12 | NS |
| si (zo) | 5000 | 0.55 | *** | 0.61 | *** |

b. Time 2

| source | untransformed | | | pres-abs | |
|---------|------------------|--------------------------|-----|--------------------------|-----|
| | No. permutations | Sample statistic (R) | Sig | Sample statistic (R) | Sig |
| zo | 35 | 0.28 | NS | 0.27 | NS |
| si (zo) | 5000 | 0.64 | *** | 0.50 | *** |

Table 4.9 Summaries of NP-MANOVAs comparing spatial variation in the abundance of taxa of macrobenthic infauna between wash and no-wash zones of the lower Parramatta River at **a.** time 1 (30/05/00) and **b.** time 2 (19/07/00). zo = zone (2 levels: wash, no-wash; fixed) si (zo) = sites (8 levels, random). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a. Time 1

| source | untransformed | | | pres-abs | |
|---------|---------------|--------|-----|----------|-----|
| | df | p | Sig | p | Sig |
| zo | 1 | 0.2554 | NS | 0.4794 | NS |
| si (zo) | 6 | 0.0002 | *** | 0.0002 | *** |
| res | 32 | | | | |

b. Time 2

| source | untransformed | | | pres-abs | |
|---------|---------------|--------|-----|----------|-----|
| | df | p | Sig | p | Sig |
| zo | 1 | 0.1458 | NS | 0.0574 | NS |
| si (zo) | 6 | 0.0002 | *** | 0.0002 | *** |
| res | 32 | | | | |

Table 4.10 Summaries of analyses comparing spatial variation in the abundance of macrobenthic infauna between wash and no-wash zones of the lower Parramatta River at **a.** Time 1 (30/05/00) and **b.** Time 2 (19/07/00). **NS** $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a.

| source of variation | df | Oligochaeta | | | Capitellidae | | | Hesionidae | | | Nereididae | | | Spionidae | | |
|---------------------|----|-------------|-------|------|--------------|-------|------|-------------|-------|------|-------------|------|------|-------------|------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| zone | 1 | 1.02 | 0.03 | NS | 10.56 | 1.25 | NS | 10.8 | 0.84 | NS | 0.10 | 0.01 | NS | 0.02 | 0.02 | NS |
| location (zone) | 2 | 37.80 | 84.82 | *** | 8.43 | 34.83 | ** | 12.8 | 17.19 | * | 7.70 | 4.93 | NS | 0.88 | 1.00 | NS |
| location (wash) | 1 | 72.58 | | | 16.85 | | | 21.7 | | | 8.92 | | | 1.04 | | |
| location (no-wash) | 1 | 3.02 | | | 0.00 | | | 3.9 | | | 6.48 | | | 0.72 | | |
| site (location) | 4 | 0.45 | 0.40 | NS | 0.24 | 0.87 | NS | 0.7 | 1.47 | NS | 1.56 | 2.88 | * | 0.88 | 3.71 | * |
| site (wash) | 2 | 0.19 | | | 0.48 | | | 0.4 | | | 0.51 | | | 1.04 | | |
| site (no-wash) | 2 | 0.70 | | | 0.00 | | | 1.1 | | | 2.61 | | | 0.72 | | |
| residual | 32 | 1.12 | | | 0.28 | | | 0.5 | | | 0.54 | | | 0.24 | | |
| residual (wash) | 16 | 1.26 | | | 0.55 | | | 0.5 | | | 0.90 | | | 0.03 | | |
| residual (no-wash) | 16 | 0.97 | | | 0.00 | | | 0.5 | | | 0.18 | | | 0.45 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | |
| Cochran's test | | C = 0.27 NS | | | C = 0.84 ** | | | C = 0.39 NS | | | C = 0.60 ** | | | C = 0.95 ** | | |

| source of variation | df | Syllidae | | | Amphipoda | | | Isopoda | | | Nematoda | | | Nemertea | | |
|---------------------|----|-------------|------|------|------------|------|------|-------------|------|------|-------------|--------|------|-------------|------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| zone | 1 | 10.03 | 1.31 | NS | 0.06 | 0.00 | NS | 1.65 | 0.19 | NS | 0.48 | 0.03 | NS | 0.56 | 0.50 | NS |
| location (zone) | 2 | 7.68 | 0.55 | NS | 14.62 | 4.86 | NS | 8.73 | 8.34 | * | 14.32 | 162.52 | *** | 1.12 | 0.78 | NS |
| location (wash) | 1 | 0.00 | | | 14.78 | | | 15.18 | | | 24.76 | | | 2.23 | | |
| location (no-wash) | 1 | 15.35 | | | 14.46 | | | 2.28 | | | 3.89 | | | 0.01 | | |
| site (location) | 4 | 13.91 | 9.86 | *** | 3.01 | 8.81 | *** | 1.05 | 4.16 | ** | 0.09 | 0.13 | NS | 1.44 | 2.18 | NS |
| site (wash) | 2 | 1.85 | | | 5.76 | | | 0.17 | | | 0.02 | | | 0.71 | | |
| site (no-wash) | 2 | 25.97 | | | 0.25 | | | 1.92 | | | 0.31 | | | 2.17 | | |
| residual | 32 | 1.41 | | | 0.34 | | | 0.25 | | | 0.68 | | | 0.66 | | |
| residual (wash) | 16 | 1.50 | | | 0.22 | | | 0.25 | | | 0.55 | | | 0.88 | | |
| residual (no-wash) | 16 | 1.32 | | | 0.46 | | | 0.18 | | | 0.81 | | | 0.44 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | |
| Cochran's test | | C = 0.29 NS | | | C = 0.43 * | | | C = 0.29 NS | | | C = 0.23 NS | | | C = 0.35 NS | | |

Table 4.10 cont.

b.

| source of variation | df | Oligochaeta | | | Capitellidae | | | Hesionidae | | | Nereididae | | | Spionidae | | |
|---------------------|----|-------------|-------|------|--------------|-------|------|-------------|-------|------|-------------|-------|------|-------------|-------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| zone | 1 | 44.72 | 11.43 | NS | 34.29 | 1.75 | NS | 9.30 | 0.87 | NS | 1.30 | 0.11 | NS | 4.40 | 78.81 | * |
| location (zone) | 2 | 3.91 | 0.36 | NS | 19.64 | 3.77 | NS | 10.68 | 61.65 | *** | 11.60 | 1.52 | NS | 0.06 | 1.14 | NS |
| location (wash) | 1 | 7.82 | | | 39.26 | | | 21.36 | | | 16.94 | | | 0.02 | | |
| location (no-wash) | 1 | 0.00 | | | 0.02 | | | 0.00 | | | 6.25 | | | 0.10 | | |
| site (location) | 4 | 10.97 | 11.43 | *** | 5.21 | 20.99 | *** | 0.17 | 0.49 | NS | 7.64 | 29.08 | *** | 0.05 | 0.18 | NS |
| site (wash) | 2 | 11.40 | | | 10.40 | | | 0.30 | | | 9.03 | | | 0.00 | | |
| site (no-wash) | 2 | 10.54 | | | 0.02 | | | 0.05 | | | 6.25 | | | 0.10 | | |
| residual | 32 | 0.96 | | | 0.25 | | | 0.35 | | | 0.26 | | | 0.27 | | |
| residual (wash) | 16 | 0.94 | | | 0.47 | | | 0.65 | | | 0.50 | | | 0.50 | | |
| residual (no-wash) | 16 | 0.98 | | | 0.02 | | | 0.05 | | | 0.03 | | | 0.04 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | |
| Cochran's test | | C = 0.23 NS | | | C = 0.32 NS | | | C = 0.58 ** | | | C = 0.65 ** | | | C = 0.31 NS | | |

| source of variation | df | Syllidae | | | Amphipoda | | | Isopoda | | | Nematoda | | | Nemertea | | |
|---------------------|----|-------------|------|------|------------|-------|------|-------------|-------|------|-------------|------|------|------------|-------|------|
| | | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| zone | 1 | 1.70 | 0.11 | NS | 0.54 | 0.03 | NS | 6.63 | 1.51 | NS | 0.03 | 0.00 | NS | 5.65 | 1.05 | NS |
| location (zone) | 2 | 16.07 | 5.71 | NS | 15.79 | 15.36 | * | 4.40 | 15.35 | * | 7.33 | 3.32 | NS | 5.39 | 0.56 | NS |
| location (wash) | 1 | 25.77 | | | 12.32 | | | 0.11 | | | 14.64 | | | 6.33 | | |
| location (no-wash) | 1 | 6.38 | | | 19.26 | | | 8.69 | | | 0.02 | | | 4.46 | | |
| site (location) | 4 | 2.81 | 4.54 | ** | 1.03 | 3.95 | * | 0.29 | 1.20 | NS | 2.21 | 2.78 | * | 9.63 | 14.74 | *** |
| site (wash) | 2 | 0.11 | | | 1.04 | | | 0.11 | | | 0.98 | | | 9.37 | | |
| site (no-wash) | 2 | 5.51 | | | 1.01 | | | 0.46 | | | 3.44 | | | 9.89 | | |
| residual | 32 | 0.62 | | | 0.26 | | | 0.24 | | | 0.79 | | | 0.65 | | |
| residual (wash) | 16 | 0.58 | | | 0.47 | | | 0.16 | | | 0.70 | | | 0.94 | | |
| residual (no-wash) | 16 | 0.66 | | | 0.05 | | | 0.31 | | | 0.89 | | | 0.37 | | |
| Transformation | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | | ln (X + 1) | | |
| Cochran's test | | C = 0.24 NS | | | C = 0.44 * | | | C = 0.37 NS | | | C = 0.21 NS | | | C = 0.42 * | | |

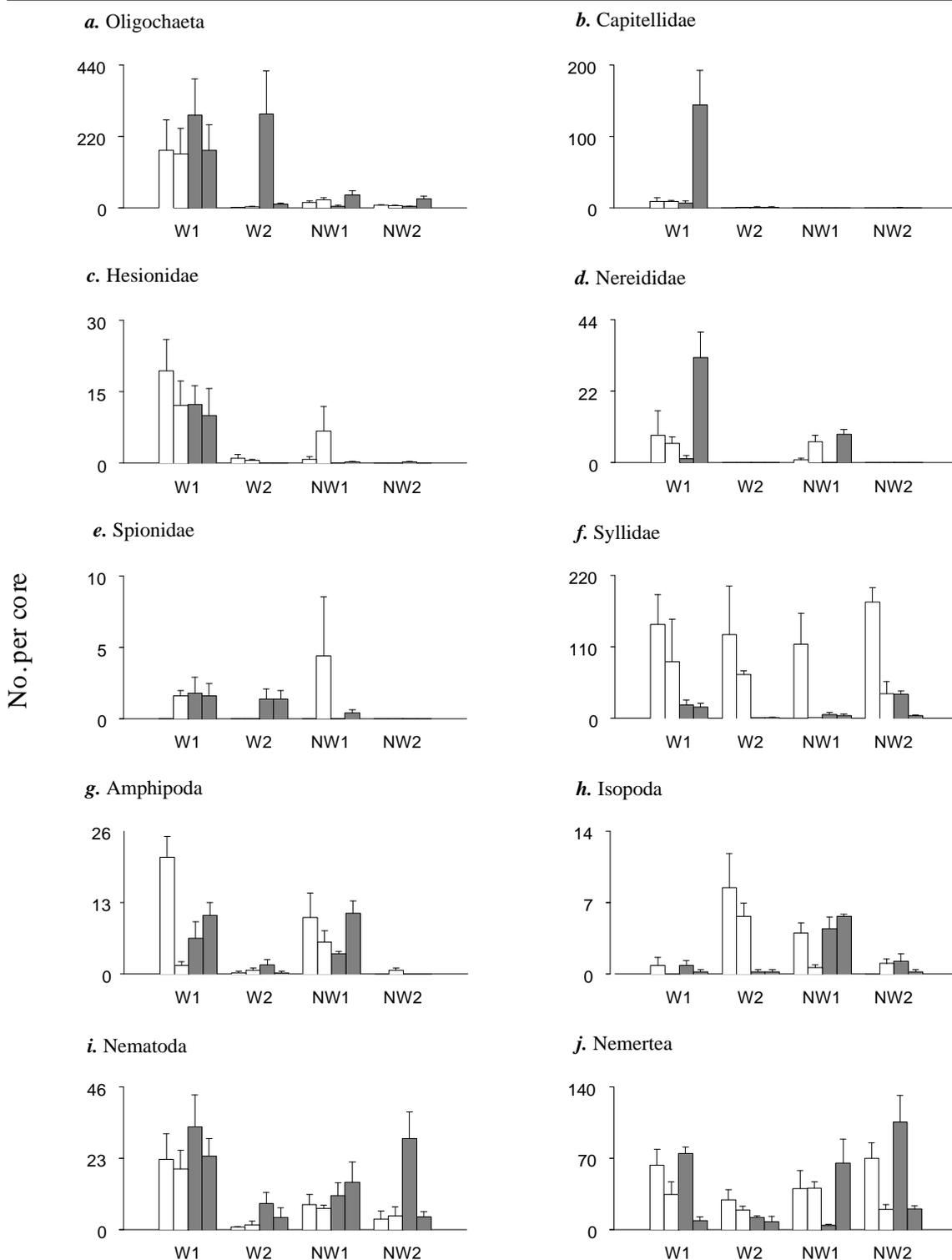


Figure 4.7 Mean (+ S.E.) abundance per core of taxa of macrobenthic infauna found in sites in the intertidal zone of sandy beaches in wash (W1 and W2) and no-wash (NW1 and NW2) zones of the lower Parramatta River. $n = 5$, at 2 sites in each location.

□ Time 1 (30/05/00) ■ Time 2 (19/07/00)

Table 4.11 Two-tailed *F*-tests of variances, among cores in the wash zone (W) versus among cores in the no-wash zone (NW) and among sites in the wash zone versus among sites in the no-wash zone, along the lower Parramatta River. Degrees of freedom and mean squares are as given in Table 4.10. X: comparison was not made due to absence of taxon from the no-wash zone.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Taxon | Time | Among cores (= Residual) wash vs no-wash | Among sites wash vs no-wash |
|--------------|------|--|--------------------------------|
| Oligochaeta | 1 | NS | NS |
| | 2 | NS | NS |
| Capitellidae | 1 | X | X |
| | 2 | *** W > NW | *** W > NW |
| Hesionidae | 1 | NS | NS |
| | 2 | *** W > NW | NS |
| Nereididae | 1 | ** W > NW | NS |
| | 2 | *** W > NW | NS |
| Spionidae | 1 | *** W < NW | NS |
| | 2 | *** W > NW | * W < NW |
| Syllidae | 1 | NS | NS |
| | 2 | NS | * W < NW |
| Amphipoda | 1 | NS | * W > NW |
| | 2 | ** W > NW | NS |
| Isopoda | 1 | NS | NS |
| | 2 | NS | NS |
| Nematoda | 1 | NS | NS |
| | 2 | NS | NS |
| Nemertea | 1 | NS | NS |
| | 2 | * W > NW | NS |

4.4 Discussion

Previous studies have reported the density and diversity of assemblages in sediments to be smaller in wave-exposed environments than in sheltered habitats (e.g. Brown and McLachlan, 1990; Dexter, 1992). In this study, assemblages of macrobenthic infauna differed between wash and no-wash zones of the upper Parramatta River, in unvegetated and vegetated habitats. This difference appeared to be primarily due to greater abundances of taxa in the no-wash zone than in the wash zone. Analyses of presence-absence data did not consistently find differences between wash and no-wash zones, suggesting that differences in the taxa present and their frequency of occurrence were of lesser importance in determining differences in assemblages.

The effect of wash on infaunal assemblages did not, however, appear general. In the lower Parramatta River, no difference was found between the assemblages of wash and no-wash zones.

The difference between assemblages in wash and no-wash zones of the upper Parramatta River was smaller in the vegetated than in the unvegetated habitat at the first time of sampling. At time 2, however, a similar difference was seen between the wash and the no-wash zone in each of the habitats. Bray-Curtis dissimilarities between the assemblages of the unvegetated and vegetated habitats were greater for sites in the wash zone than in the no-wash zone at each time. This may, however, be attributed to the greater within-site variability in assemblages in the no-wash, in each of the habitats. Thus, it remains unclear whether the root structure of mangroves indeed reduces the impact of boat-generated waves on infaunal assemblages.

In contrast to previous studies (e.g. Plazait, 1975; Wells, 1986; Sheridan, 1997) no obvious difference in the abundance and number of taxa present in the unvegetated and vegetated habitat was evident. Assemblages in the upper Parramatta River were fairly depauperate and were dominated by the opportunistic families of polychaetes, Capitellidae, Nereididae and Spionidae. The greater abundance of these three taxa and of Amphipoda, Isopoda and *Xenostrobus securis* in the no-wash than in the wash zone of the upper Parramatta River were primarily responsible for the difference detected between the assemblages of these two places. At time 2, smaller numbers of Nephytiidae in the no-wash zone than the wash zone may also have contributed to this pattern.

It has been hypothesised that disturbances, such as wind-stresses, that decrease the stability of the sediment, result in assemblages dominated by deposit-feeders and in which filter-feeders have a proportionally small abundance (Rhoads, 1974; Wildish and Peer, 1983; Wildish and Kristmanson, 1997). The preponderance of deposit-feeders in assemblages of the upper Parramatta River, however, is probably unrelated to the disturbance of sediment by RiverCat wash. Previous studies have found opportunistic deposit-feeders to dominate estuarine waters (e.g. Pearson and Rosenberg, 1978; Schaffner *et al.*, 1987) and muddy sediments such as those found along the upper Parramatta River (e.g. Rhoads, 1974; Rhoads and Young, 1970). The great abundance of suspension-feeders along the lower Parramatta River, also exposed to wash but with sandy sediment and a greater salinity, suggests that this is the case.

Underwood (1991, 1992, 1993, 1994) has drawn attention to the fact that, rather than simply altering abundances, impacts may alter temporal and spatial variability in impacted locations compared with control locations. Assemblages in wash or no-wash zones of the upper and lower Parramatta River were highly variable, spatially and temporally. In the upper Parramatta River, within-site variability in assemblages was generally smaller for sites in the no-

wash zone than for sites in the wash zone in unvegetated and vegetated habitat. This supports Warwick and Clarke's (1993) model that increased variability is a symptom of stressed environments. When spatial variability was examined for individual taxa, however, the reverse pattern was generally seen. The greater variability in the abundance of individual taxa in no-wash may be a function of the greater mean abundances found there.

The different patterns found between wash and no-wash zones of the upper and lower Parramatta River are not surprising considering the many differences found between these two sections of the river. While the number of RiverCats travelling on each of these sections of river was very similar, the main river channel is 2-3 times wider near the Gladesville Bridge than adjacent to the Silverwater Bridge. Thus, the intensity of wash from RiverCats reaching the shore should be smaller along the lower Parramatta River than along its upper reaches (see Das and Johnson, 1970; Bhowmik, 1975). The width of the lower Parramatta River also means that there is a greater available fetch for the generation of wind-driven waves. Coupled with the great recreational boat-traffic at the Gladesville Bridge, which is more than four times that at Silverwater (Patterson Britton, 2000b), these waves may swamp any effect of wash from RiverCat ferries along the lower Parramatta River.

It also appears that compliance with the no-wash regulation is greater at the upstream no-wash zone than at the downstream zone. Data collected by NSW Waterways on the speed of RiverCat ferries at various points along the river indicate that, while the majority of ferries slow to within the 7 knot speed-limit upon entering the upstream no-wash zone, most vessels maintain their speed (which may be as great as 30 knots) upon entering the downstream no-wash zone (Patterson Britton, 2000a). This is not surprising considering drivers may be fined for exceeding the speed limit in the upper no-wash zone, but are not given a suggested speed limit for the downstream no-wash zone.

Although the no-wash zone located to the west of the Silverwater Bridge appears to be important in reducing the impact of ferry-wash on macrobenthic infauna, the experimental design used to examine differences between the assemblages of the wash and no-wash zone is potentially confounded. Potential sources of confounding include: (i) gradients in variables, such as salinity, which occur along rivers with distance from the sea, (ii) differences in the concentration of contaminants in the sediment adjacent to locations differing in their historic land-use, (iii) the exclusion of recreational boat traffic from the section of the Parramatta River to the west of the Silverwater Bridge and (iv) intrinsic differences between the two sections of river.

Gradients in salinity and nutrients are important in determining the distribution and abundance of macrobenthic infauna (Boesch, 1977; Zajac and Whitlatch, 1982a; Schaffner *et al.*, 1987; de Decker and Bally, 1985; Castel *et al.*, 1989; Junoy and Vieitez, 1990). The results of this study do not, however, appear to be confounded by gradients along the river. As shown by Figure 4.5, in which locations are ordered in terms of their geographical location, patterns in the abundance of taxa do not follow a gradient with distance.

Similarly, patterns in the abundance of taxa do not appear to follow the likely pattern of contaminants. Numerous studies have shown the abundance of deposit-feeding polychaetes to be greater in places exposed to large concentrations of organic and toxic contaminants than places where the concentration of these is less (e.g. Gray *et al.*, 1988; Gray *et al.*, 1990; Warwick and Clarke, 1993; Braddock *et al.*, 1995). The abundances of small crustaceans, such as amphipods and isopods are negatively correlated with the concentration of toxic chemicals (e.g. Stander and Venter, 1968; Notini, 1978; Lenihan and Oliver, 1995). Amphipods and isopods were less abundant at the location situated adjacent to Wilson Park, a site formally occupied by the Petroleum and Chemical Corporation Australia Ltd. (1954-1974), and, hence, conformed to the above pattern. The abundance of deposit-feeding polychaetes (Capitellidae) was, however, also less at this location and, hence, followed the reverse pattern to that which would be expected from previous observations.

The remaining two potential sources of confounding cannot, unfortunately, be ruled out. The coincident location of the no-wash zone and the section of the river closed to recreational boating means that the difference observed between wash and no-wash zones may have been due to a difference in the volume of boat traffic between the two areas and not due to any difference in the intensity of wash from the RiverCats. During sampling, few boats were, however, observed adjacent to the places sampled in the wash zone, they were generally small and produced negligible amounts of wash compared to the RiverCats.

The fact that it was decided to establish a no-wash zone to the west of the Silverwater Bridge suggests that differences exist between the two sections of the river making the section to the west of the Silverwater Bridge more susceptible to the effects of wash and the section to the east less susceptible. A sampling design where assemblages are compared between times when the ferries are in operation and times when the ferries are stopped is required for causation to be established. Such a sampling regime is described in Chapter 5.

Thus, it appears that no-wash zones may be effective in reducing the impact of wash on the ecology of intertidal macrobenthic infauna and the morphology of river banks in places in places where compliance with this regulation is great. A few violations may, however, result in a

significant impact on the intertidal zone. The difference between assemblages in wash and no-wash zones does not appear to be smaller in pneumatophore than unvegetated habitat. Mangroves may, however, be found to be important in reducing the effects of boat-wash on macrobenthic infauna in places where the impact is greater (i.e. when places completely sheltered from wash and places that are very exposed are compared).

CHAPTER 5

THE 2000 SYDNEY OLYMPIC GAMES: GOOD FOR SPORT AND MACROFAUNA?

5.1 Introduction

Despite the plethora of studies that have invoked wave-action to explain patterns in the distribution and abundance of taxa of macrobenthic infauna (discussed in Section 4.1), few have attempted to demonstrate unambiguously a causal relationship between these variables. Surveying the plants and animals present in sheltered or exposed sites provides little insight into the processes causing any difference in assemblages between the two exposures. A difference between assemblages could be due to factors other than wave-action.

Manipulative experiments are the best way to determine the processes that cause spatial and temporal patterns of variation (see Underwood, 1990). In the case of environmental impacts, these usually take the form of a before-after study (see Underwood 1992, 1993, 1994), the manipulation being the disturbance itself. There are many instances where it is, however, impossible to obtain sufficient 'before' data to do a BACI or beyond-BACI style analysis. For example, oil-spills usually occur without any prior indication and there is usually insufficient time to collect samples between weather warnings and major storms.

A number of strategies has been used to demonstrate causation where there are no 'before' data. The first of these involves introducing artificial substrata (e.g. settlement panels, defaunated sediment) to the putatively impacted site and control sites to test for any difference in the assemblages that recolonise the substrata between the two types of area (Glasby and Underwood, 1996). This method assumes that the effect of the disturbance is sustained over time (i.e. it has a press response) and will not be useful if the assemblage has a pulse response to the disturbance.

The second method involves determining whether assemblages of the putatively impacted site recover following the removal of the impact (e.g. Rosenberg, 1972; Friberg *et al.*, 1998). This method will be useful as long as assemblages are not permanently altered by the disturbance.

In Chapter 4, it was found that assemblages of macrobenthic infauna differed between wash and no-wash zones of the upper Parramatta River. It was not possible, however, to determine whether this pattern was directly caused by wash from RiverCat ferries or was due to some other factor, because no data were available from prior to the commencement of services. During the Sydney Olympic Games, in September, 2000, RiverCat ferry services to the west of Homebush Bay were suspended for 5 weeks. If the patterns described in Chapter 4 were indeed

due to wash from RiverCat ferries, recovery of assemblages, impacted by wash, may occur over this period of time. Therefore, it was predicted that assemblages in wash zones, where the intensity of the disturbance is believed to be greatest, would change to become more similar to those in no-wash zones following the suspension of services and change back to their disturbed state following the return of ferries. It was also predicted that any change in response to the cessation of ferry services seen in the assemblages of the no-wash zone would be smaller than that seen in assemblages of the wash zone.

In Chapter 4, it was also found that the abundances of capitellids, nereids, spionids and amphipods were greater in the no-wash zone than the wash zone, in each of the habitats. If these patterns are due to wash, the abundances of these taxa in the wash zone should increase following the suspension of ferry services and decrease following the return of services. Any change to abundances in the no-wash zone should be less than in the no-wash zone.

5.2 Materials and Methods

RiverCat ferry services were temporarily suspended to the west of Homebush Bay from the 28th August - 2nd October, 2000. The area affected by the stoppage included both the upstream wash and no-wash zones previously sampled (Fig. 5.1). Services to the east of Homebush Bay continued to operate during this time.

In order to test the above hypotheses, macrobenthic infauna were sampled in unvegetated and vegetated habitat in two locations within the upstream no-wash zone (Silverwater Park, Silverwater [NW1] and 500 m east of Rydalmere Wharf, Rydalmere [NW2 – referred to as NW/NW3 in Chapter 4]), two locations within the wash zone (George Kendall Reserve, Ermington [W1] and Wilson Park, Silverwater [W2]) and two locations to the east of Homebush Bay (control locations; Settlers Park, Putney [C1] and Shepherd's Bay, Meadowbank [C2]; Fig. 5.1) at two times during the suspension of services (6th September 2000 [time 4] and 25th September [time 5], 2000) and two times after the re-introduction of services (26th October, 2000 [time 5] and 10th February, 2001 [time 6]).

At each time of sampling, 5 cores of sediment were collected from each of two sites in the unvegetated habitat and vegetated habitat using the method described in Section 4.2. The samples collected from wash and no-wash zones on 28th April, 2000 (time 1) and 30th May, 2000 (time 2; Chapter 4) were used as 'before-data'. Unfortunately, no data were collected from control locations at times 1 and 2 since the suspension of services was only publicized shortly before its commencement.

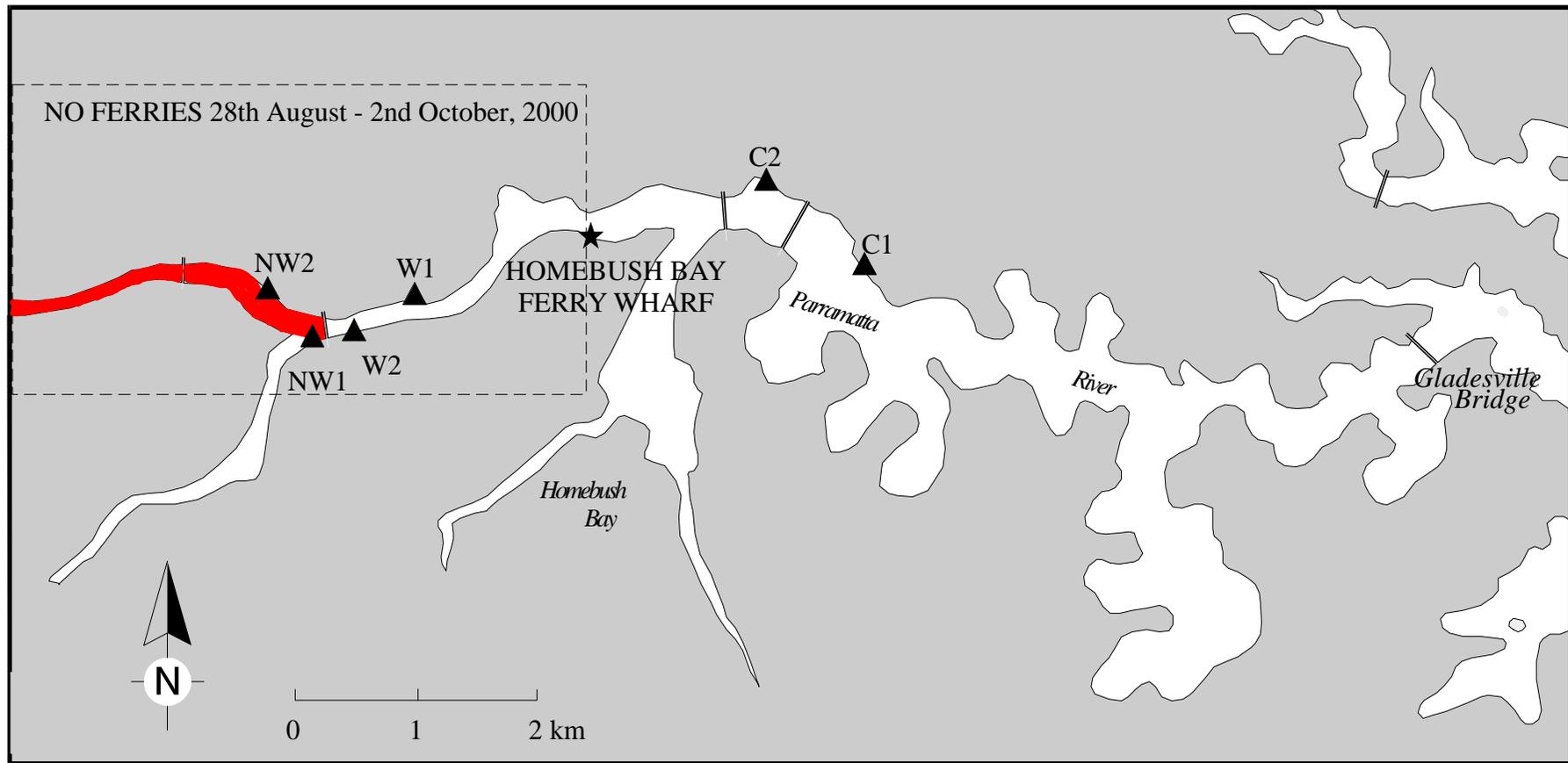


Figure 5.1 Map of the Parramatta River showing the no-wash zone of the upper Parramatta River █, the area to the west of Homebush Bay where services were suspended during the 2000 Olympic Games and the no-wash zone (NW), wash zone (W) and control locations (C) sampled.

Data collected from the unvegetated and vegetated habitats were analysed separately because the results presented in Chapter 4 suggested that the abundances of taxa differ between these. NP-MANOVAs were done on untransformed data to test the hypothesis of a significant site x time interaction, as would be expected if assemblages in the wash zone were more disturbed than were those in the no-wash zone (change following the removal of the disturbance should be greatest in the most impacted places). Because NP-MANOVAs can only handle two factors and sites within some locations contained very different assemblages, differences among locations were omitted from many of the analyses to leave the two factors, time and site. Presence-absence data were not analysed because the results in Chapter 4 suggested that any difference between wash and no-wash zones were primarily due to differences in the abundances of taxa and not due to differences in the taxa present or the number of cores occupied.

The results in Chapter 4 indicated that within-site variability in assemblages was less in the no-wash zone than in the wash zone. A model to explain this pattern is that disturbance by wash is the real cause of increases in the spatial variability of assemblages at this scale. Bray-Curtis measures of variability within sites of the wash and no-wash zone were compared to test the corresponding hypotheses that variability within sites of the wash zone would: (i) decrease following the removal of the disturbing force and (ii) increase again following its return. It was also hypothesized that less change would occur in the no-wash zone than the wash zone.

5.3 Results

5.3.1 Multivariate changes

Sorting of samples from control locations at times 3 and 4 indicated that their assemblages of macrobenthic fauna were very different from those from the wash or no-wash zone (Fig. 5.2). Differences were evident when assemblages of the control locations (at times 3 and 4) were compared to those in the wash or no-wash zone at times when the ferries were running (1 and 2; Fig. 5.2a). They were also evident in comparisons among assemblages of wash, no-wash and control sites, in the unvegetated and the vegetated habitat, during the suspension of services (Fig. 5.2b,c; Table 5.1). In both the unvegetated and the vegetated habitats, the abundances of oligochaetes and polychaetes of the family, Nephthyidae, were much greater in controls than at the other places. The abundances of sabellid polychaetes were also greater at control locations within the unvegetated habitat.

Given that the assemblages in control locations did not appear representative of the assemblages in wash or no-wash zones, at times before or during the cessation, it was decided

not to sort the samples collected from control locations at times 5 and 6, nor to include control locations in any of the subsequent analyses.

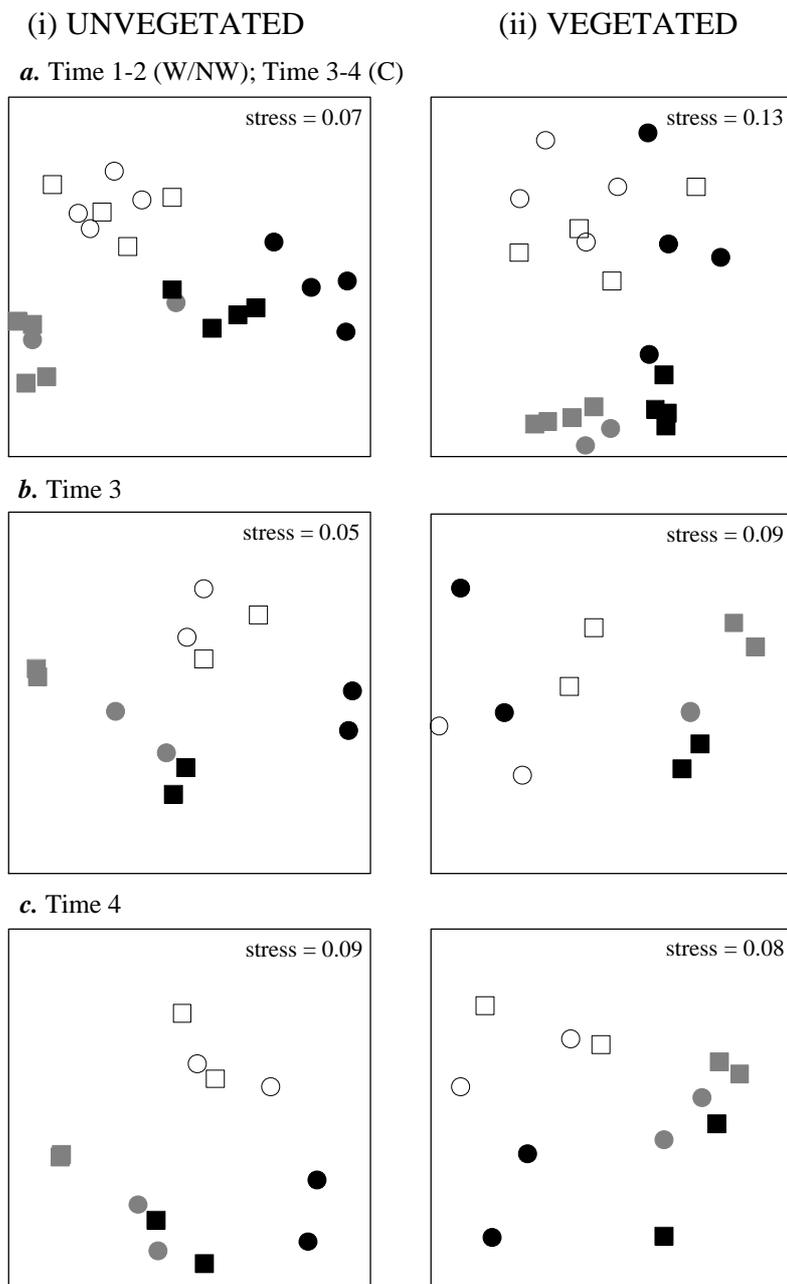


Figure 5.2 nMDS ordinations of assemblages of macrobenthic infauna found in (i) unvegetated and (ii) vegetated habitat of sites within the wash zone (black; circles: W1, squares: W2), the no-wash zone (grey; circles: NW1, squares: NW2) and control locations (unfilled; circles: C1, squares: C2), *a.* comparing assemblages in the wash or no-wash zone during the operation of ferries with assemblages in control locations at times 3 and 4 and *b, c* comparing assemblages between the wash and no-wash zones and control locations at individual times of sampling. Points represent centroids of untransformed data from each site. $n = 5$.

Table 5.1 Summaries of non-parametric MANOVAs comparing temporal change in assemblages of macrobenthic infauna among wash zones, no-wash zones and control locations of the upper Parramatta River. ti = time (2 levels: t3, t4), pl = place (3 levels: wash [W], no-wash [NW] and control [C]). $n = 4$ centroids of sites within each place.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | df | <i>p</i> | Sig. | <i>p</i> | Sig. |
|---------------------------|----|----------------|------|----------------|------|
| ti | 1 | 0.6708 | NS | 0.7656 | NS |
| pl | 2 | 0.0002 | *** | 0.0002 | *** |
| ti x pl | 2 | 0.9430 | NS | 0.7398 | NS |
| res | 18 | | | | |
| <i>a posteriori</i> tests | | pl: W ? NW ? C | | pl: W ? NW ? C | |

To determine whether any change occurred in the assemblages of wash or no-wash zones following the suspension of services, (i) nMDS ordinations of points representing the average assemblage at each site, at each time, were plotted for each of the two habitats (Fig. 5.3,4) and (ii) average measures of Bray-Curtis dissimilarity were calculated between the assemblages of the wash and no-wash zone at each time (Fig. 5.5). On the plot of data from the unvegetated habitat (Fig. 5.3a), points generally formed two groups corresponding to wash and no-wash zones. The groups were not, however, distinct from one another at all times. Convergence of the groups was evident following the suspension of services (squares; Fig. 5.3c) and was due to assemblages of the wash zone (filled symbols) becoming more similar to those of the no-wash zone (open symbols). By time 6 (large triangles; Fig. 5.3d), assemblages of the wash and no-wash were again distinct. The difference in assemblages between wash and no-wash zones was greatest at times prior to the temporary cessation of services (t1, t2) and smallest at time 4 (during the cessation) and time 5 (immediately after the re-introduction of services; Fig. 5.5a).

On the plot for the vegetated habitat (Fig 5.4), a similar distance was maintained between groups of points from the wash and no-wash zone across all times of sampling. This is more clearly seen by a comparison of average measures of Bray-Curtis dissimilarity between the wash and no-zone, between each of times 1-4 (Fig 5.5b). For this reason, samples collected from the vegetated habitat after the return of the ferries (times 5 and 6) were not sorted.

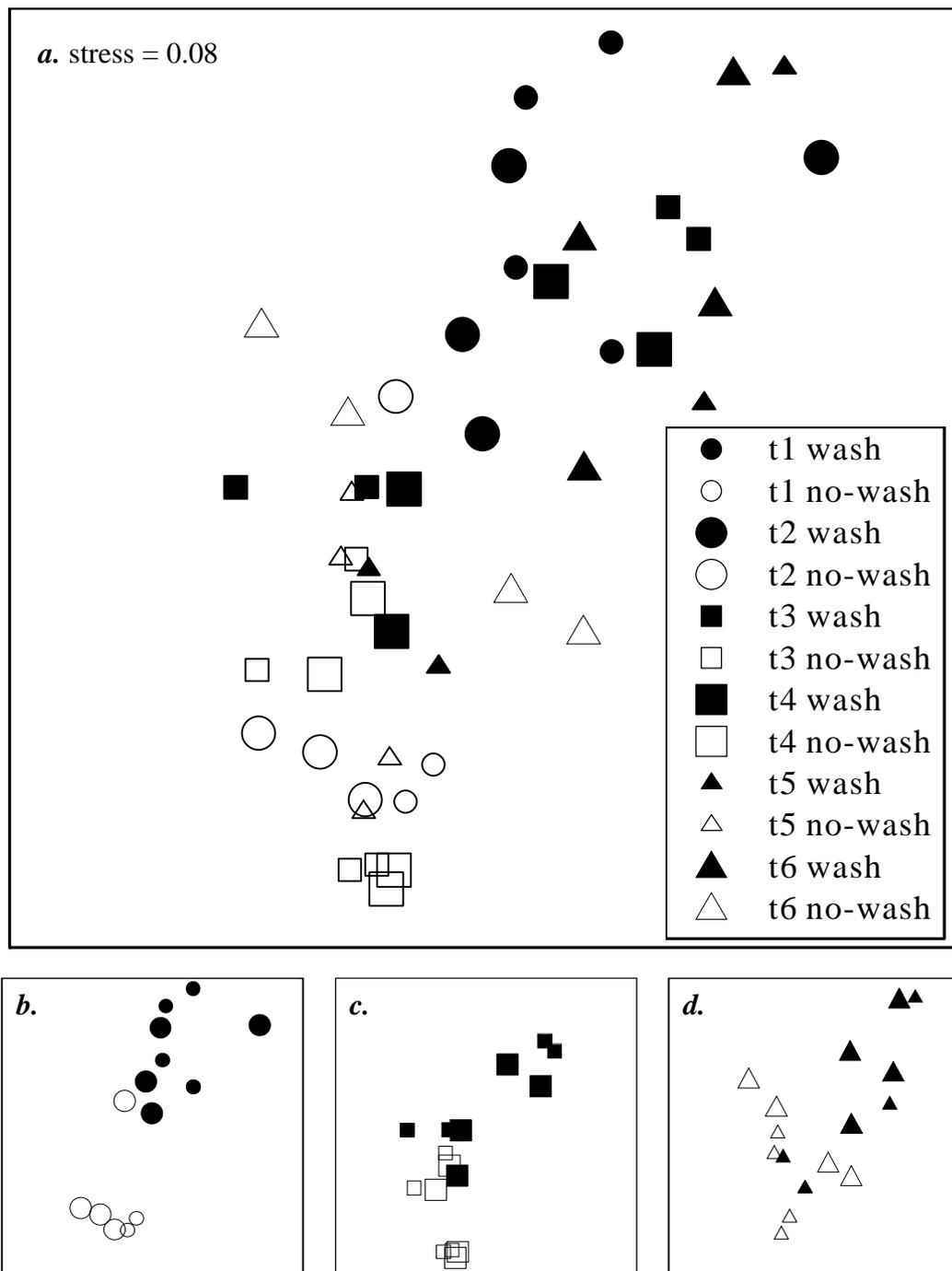


Figure 5.3 nMDS ordination of assemblages of macrobenthic infauna found within unvegetated habitat of the wash (black) and no-wash (unfilled) zone of the upper Parramatta River at **a.** all times and **b.** times before (t1, t2; circles), **c.** times during (t3, t4; squares) and **d.** times after (t5, t6; triangles) the temporary suspension of RiverCat ferry services to the west of Homebush Bay. Points represent centroids of untransformed data from each site. $n = 5$.

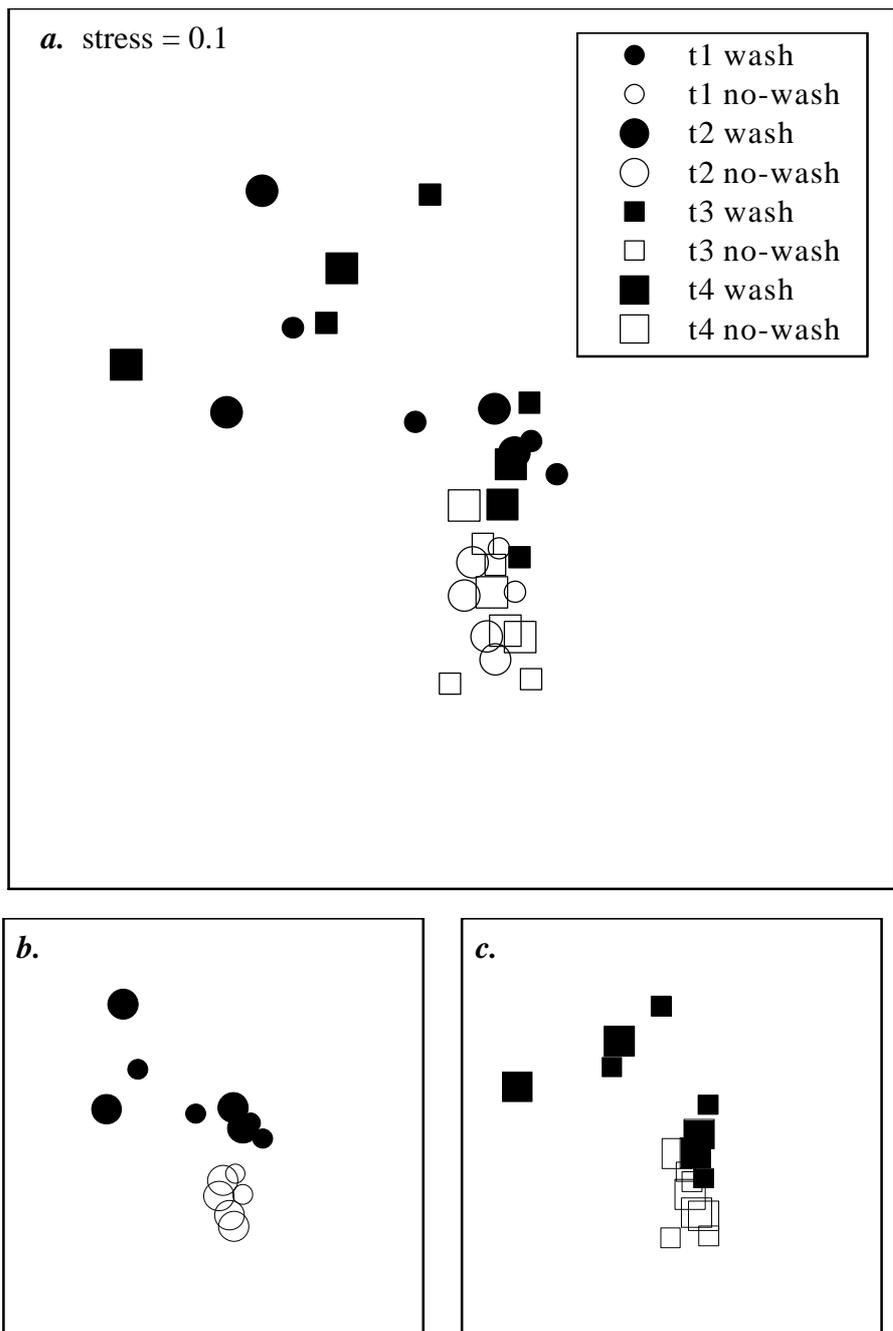


Figure 5.4 nMDS ordination of assemblages of macrobenthic infauna found within the vegetated habitat of the wash (black) and no-wash (unfilled) zone of the upper Parramatta River at **a.** all times and **b.** times before (t1, t2; circles) and **c.** times during (t3, t4; squares) the temporary suspension of RiverCat ferry services to the west of Homebush Bay. Points represent centroids of untransformed data from each site. $n = 5$.

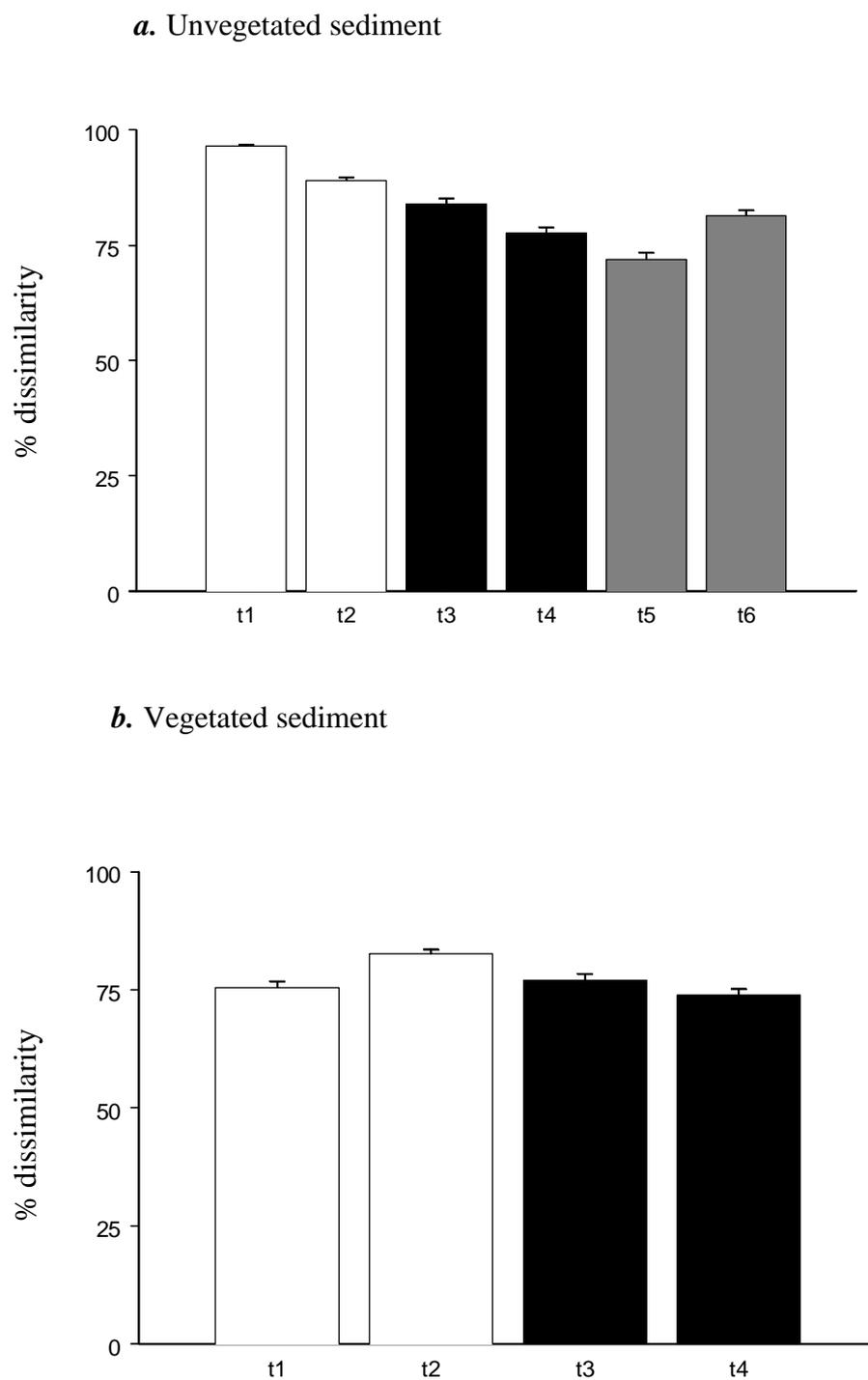


Figure 5.5 Mean (+ S.E.) Bray Curtis dissimilarity in assemblages of macrobenthic infauna between sites of the wash and no-wash zone, at times before (white), during (black) and after (grey) the temporary suspension of RiverCat ferry services to the west of Homebush Bay. $n = 200$ for time 1 and 400 for times 2-6.

Patterns of change in the assemblages of the unvegetated habitat were further examined through separate ordinations of the data from each site (Figure 5.6). These enabled the temporal change within each site to be seen without distortion of the plot by points from the other sites. These plots show that, within the wash zone, three of the four sites changed following the removal of ferries (shortly after time 2) and became more similar to their initial state following the return of services (times 5 and 6; Fig. 5.6b,c,d). The assemblage at the fourth site, W1(S1), changed randomly (Fig. 5.6a). Similar patterns were not generally found among plots of data from the no-wash zone. The assemblage at NW1(S1) became increasingly different from its original composition throughout the study (Fig. 5.6e). The assemblage at NW1(S2) displayed a similar pattern of change to sites in the wash zone (Fig. 5.6f). Sites at NW2 followed a cyclic pattern of change between times 1 and 5, consistent with the removal and return of ferry services (Fig. 5.6 g,h). Between times 5 and 6, however, assemblages changed to become very different in composition from every other time.

Spearman's rank correlations were done between the matrix of Bray-Curtis dissimilarities for each site, calculated using samples from all times, and a matrix of ranks corresponding to a pattern of cyclic change (RELATE, Clarke and Warwick, 2001; Table 5.2). These were to test the hypothesis that the pattern of change would be cyclic (i.e. change away from, and then back towards, the starting point) at sites of the wash zone but not at sites of the no-wash zone. The correlation at W2(S2) was significant.

In order to compare patterns of temporal change among sites, in the unvegetated habitat, second stage nMDS ordinations (Sommerfield and Clarke, 1995) were done (Fig. 5.7). The proximity of points (representing sites) on these ordinations indicates the extent to which different sites display the same temporal pattern of change. Two ordinations were done because the two sites at NW1 were not sampled at time 1. The first compared six sites (W1(S1), W1(S2), W2(S1), W2(S2), NW2(S1), NW2(S2)) across all (6) times of sampling (Fig. 5.7(a) and the other compared all sites (including NW1(S1) and NW1(S2)) across five times of sampling (times 2-6; Fig. 5.7b). The second-stage nMDS for temporal change in the six sites across all times showed the pattern within sites at NW2 to be very different from that in sites in the wash zone (Fig. 5.7a). W1(S1) did not, however, conform to the general pattern of change seen among the sites of the wash zone. When change at all sites was considered across five times of sampling, points did not separate into distinct groups. Sites within the no-wash zone did, however, generally display patterns of change that were more similar to one another than to the patterns in sites in the wash zone. The exception was NW1(S2), which appeared to have an identical pattern of change to W2(S1), according to the nMDS.

Two way NP-MANOVAs, with the factors time and site, were done on the data from the unvegetated habitat to test for a time x site interaction, which may be indicative of differing responses of the assemblages of wash and no-wash zones to the removal of the disturbance. Unfortunately the factors wash, location and period (before, after, during the cessation) could not be included in the analyses because NP-MANOVAs can only deal with two factors at a time. These analyses included all eight of the sites sampled (W1(S1), W1(S2), W2(S1), W2(S2), NW1(S1), NW1(S2), NW2(S1), NW2(S2)) and included five of the sampling times (2-6). Time 1 was omitted from analyses because there were no data available for the two sites at NW1, at this time. A significant time x site interaction was found (Table 5.3). *A posteriori* tests indicated that the pattern of temporal change was very variable among sites in the wash zone. In the no-wash zone, however, similar assemblages were generally found between times 3 and 4, with very different assemblages at times 2 and 6.

In the wash zone, variability was greatest at times prior to the cessation of services (Fig. 5.8; t1, t2: white bars) and at time 6, after the return of services. Variability was smallest at times 4 and 5. In the no-wash zone, the pattern of change was not consistent with the temporary cessation of services. Dissimilarity was greatest at time 6 and smallest at time 1.

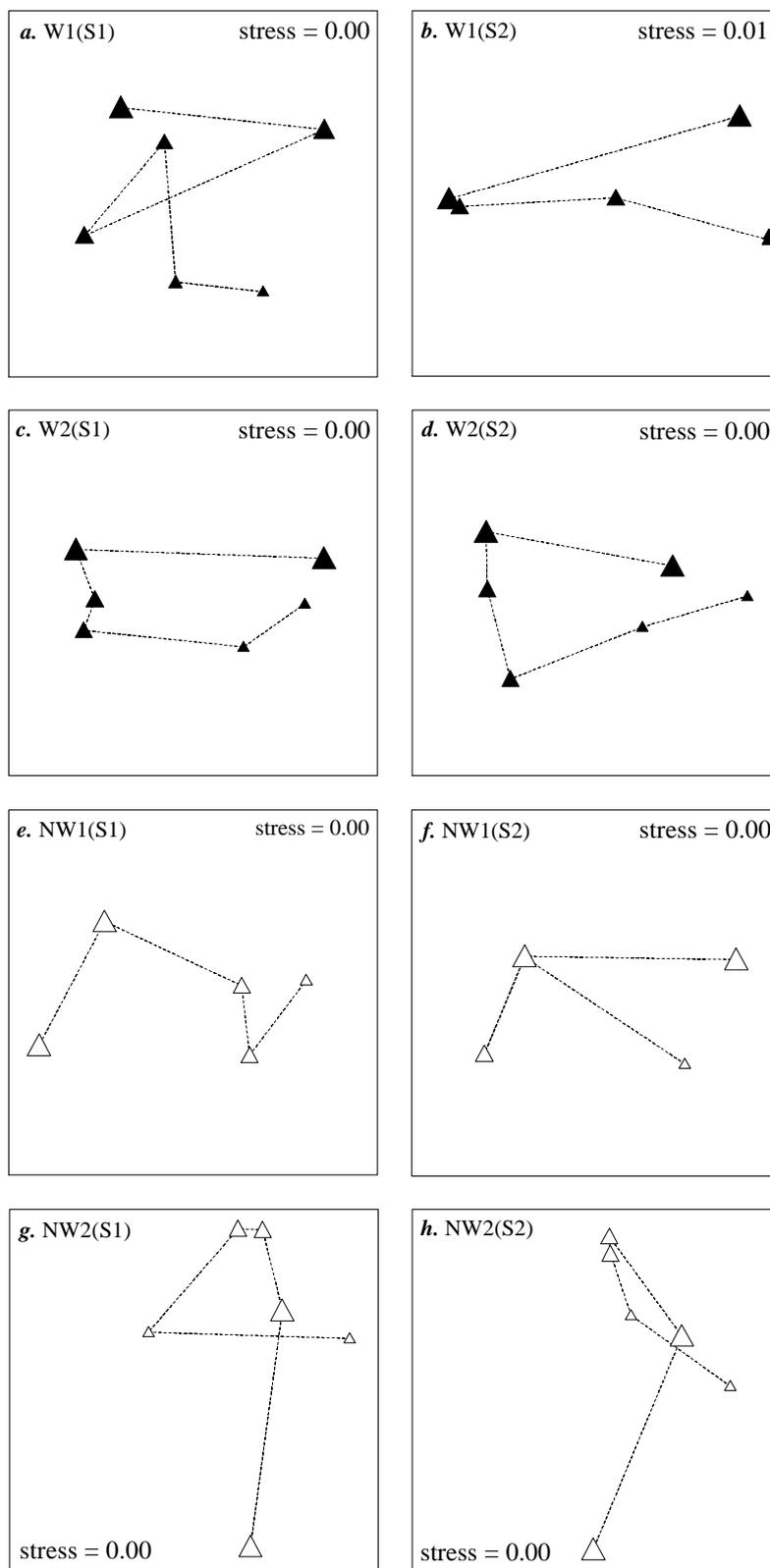


Figure 5.6 nMDS ordinations of temporal changes to assemblages in unvegetated habitat in *a-d* the wash zone (black) and *e-h* the no-wash zone (unfilled) of the upper Parramatta River at times prior to (small triangles), during (medium sized triangles) and after (large triangles) the temporary suspension of RiverCat ferries to the west of Homebush Bay. Points represent centroids of untransformed data. $n = 5$.

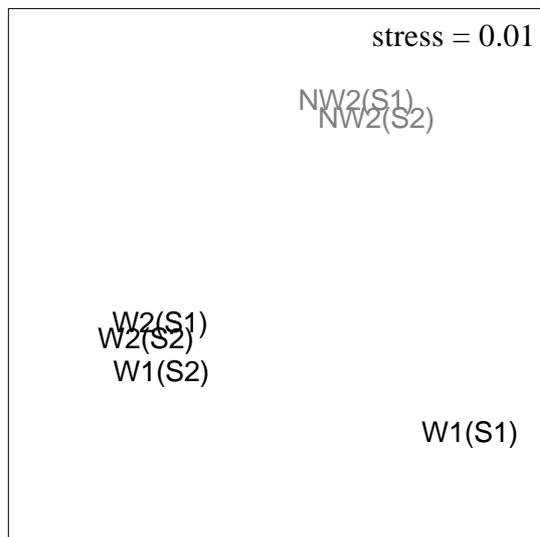
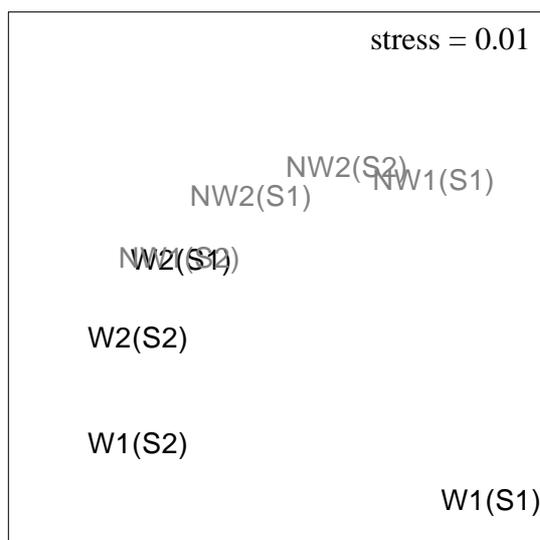
a. All times, NW1(S1) and NW1(S2) omitted**b.** All sites, t1 omitted

Figure 5.7 Second-stage nMDSs comparing temporal change in assemblages of macrobenthic fauna among sites of wash (black) and no-wash (grey) zones of the upper Parramatta River. The unvegetated habitat of all sites, except those at NW1, were sampled two times before (t1, t2), two times during (t3, t4) and two times following (t5, t6) the temporary cessation of RiverCat ferry services. NW1 was not sampled at time 1. The proximity of points indicates the extent to which the different sites displayed the same temporal pattern of change across the six times of sampling.

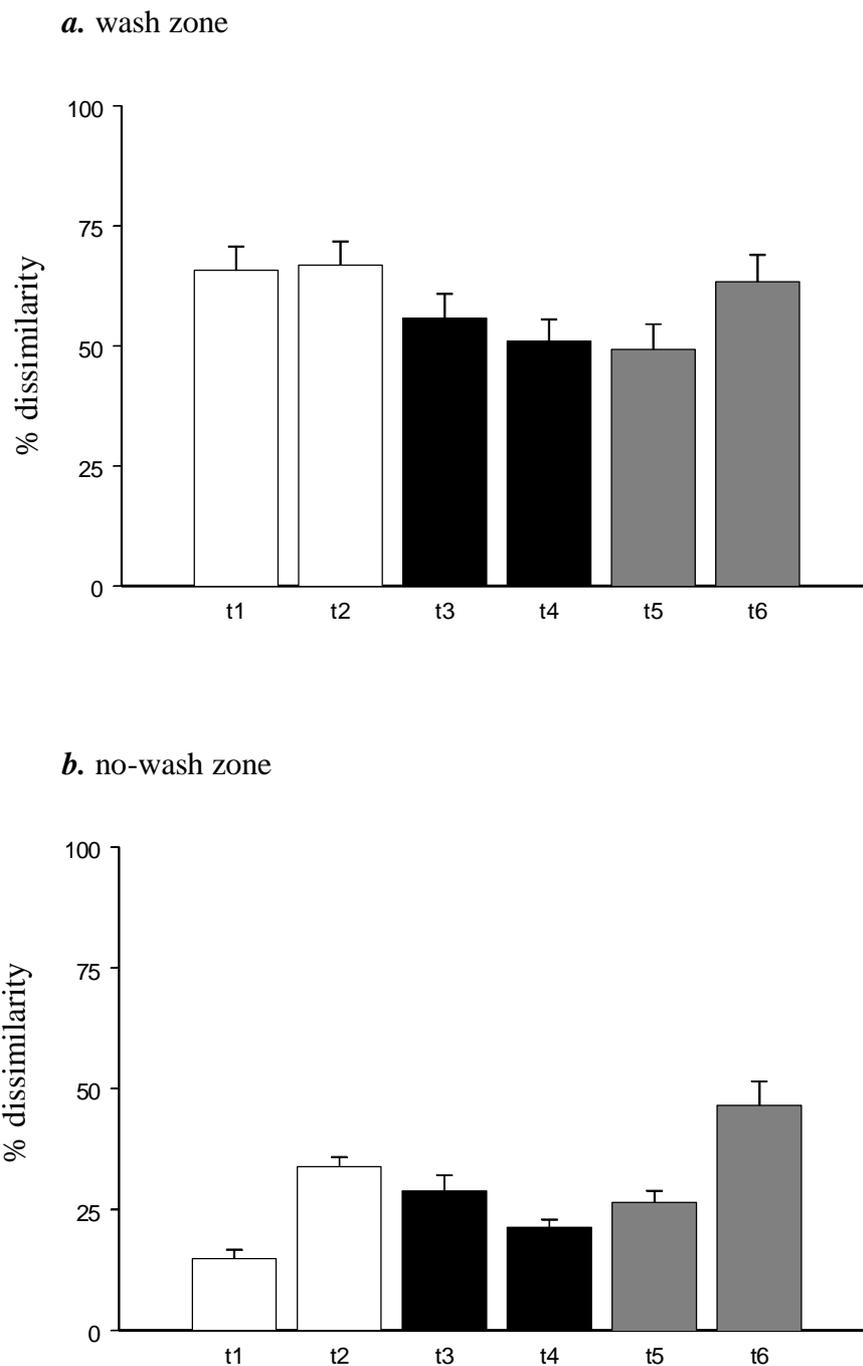


Figure 5.8 Mean (+ S.E.) Bray-Curtis measures of within-site dissimilarity in assemblages of macrobenthic infauna in unvegetated sediment of the **a.** wash zone and **b.** no-wash zone, at times before (white), during (black) and after (grey) the temporary suspension of RiverCat ferry services to the west of Homebush Bay. $n = 20$, with the exception of t1 within the no-wash zone, where $n = 10$.

Table 5.2 Summary of Spearman's rank correlations testing for a relationship between temporal change in the mean assemblage (centroids) of sites along the Parramatta River and cyclicity. Four of the sites were in the wash zone (W); the remainder were in the no-wash zone (NW). There were 5 times: 1 before, 2 during and 2 after the temporary cessation of ferry services. Centroids were calculated from 5 replicates at each site, at each time. The number of permutations in all tests was 999.

| | <i>rho</i> | probability |
|---------|------------|-------------|
| W1(S1) | -0.10 | 68% |
| W1(S2) | 0.41 | 14% |
| W2(S1) | 0.52 | 6% |
| W2(S2) | 0.62 | 2% |
| NW1(S1) | 0.24 | 52% |
| NW1(S2) | 0.31 | 50% |
| NW2(S1) | 0.11 | 32% |
| NW2(S2) | 0.15 | 21% |

Table 5.3 Summaries of non-parametric MANOVAs comparing spatial variation in assemblages of macrobenthic infauna among times of sampling in unvegetated habitat of wash (W) and no-wash (NW) zones. ti = time (5 levels: t2- t6), si = sites (8 levels). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | <i>df</i> | <i>p</i> | sig. |
|-----------------------------|-----------|----------------------------|------|
| ti | 4 | 0.0016 | *** |
| si | 7 | 0.0002 | *** |
| ti x si | 28 | 0.0002 | *** |
| res | 160 | | |
| <i>a posteriori</i> ti x si | | | |
| tests | W1(S1): | t2 = t3 = t4 = t5 = t6 | |
| | W1(S2): | uninterpretable | |
| | W2(S1): | (t2 = t6) ? (t3 = t4) ? t5 | |
| | W2(S2): | t2 ? t3 ? t4 ? t5 ? t6 | |
| | NW1(S1): | (t2 = t3 = t4) ? (t5 = t6) | |
| | NW1(S2): | t2 ? (t3 = t4 = t5) ? t6 | |
| | NW2(S1): | t2 ? (t3 = t4) ? t5 ? t6 | |
| | NW2(S2): | t2 ? (t3 = t4) ? t5 ? t6 | |

5.3.2 Univariate change

Temporal patterns of change in abundance are only presented for taxa within the unvegetated habitat because samples collected from the vegetated habitat at times 5 and 6 were not sorted (Section 5.3.1).

If, as predicted, the abundance of capitellids, nereids, spionids and amphipods increased in response to the temporary cessation of ferries and this increase was greater in the wash than the no-wash zone: (i) a significant time x zone interaction should be found in analyses for these taxa and (ii) SNK tests for temporal change within each of the zones should show no significant difference in the abundance of the taxon among times before and after the temporary cessation of the disturbing force, but should indicate a significant difference in the abundance of the taxon between these times and those during the cessation (i.e. $[t_2 = t_5 = t_6] \neq [t_3 = t_4]$ or $[t_2 = t_5 = t_6] \neq t_3 \neq t_4$). Such patterns do, however, assume that there is no temporal change in the abundance of taxa due to factors other than wash, nor a lag in response to the removal/return of ferries. They also assume that any response was within the time-frame of the experiment. SNK tests were also done on significant time x location and time x site interactions because exposure to wash may vary within each zone at these spatial scales.

At three out of four sites within the wash zone, the abundance of capitellids was greatest at times 4 and 5 (Fig. 5.9b,c,d). Of these sites, a statistically significant pattern was found only for W2(S2) (Table 5.4). At times 4 and 5 the abundances of capitellids at W1(S1), W1(S2) and W2(S2) were still, however, much smaller than abundances at NW(S1), NW2(S1) and NW2(S2). In the no-wash zone, there was no consistent pattern of temporal change among the four sites. Only the pattern of change at NW2(S1) was statistically significant (Table 5.4). Of the five times analysed (time 1 was omitted), capitellids were most abundant in NW2(S1) at times 3, 4 and 5, consistent with the hypothesis.

Temporal changes in the abundance of nereids varied among locations (Fig. 5.10). At W1, abundances were very small at all times (Fig. 5.10a,b). At W2, they were greatest at times 4 and 5 (Fig. 5.10c,d). Different patterns were evident at each of the sites at NW1 (Fig. 5.10e,f); at NW2, abundances were greater at times 3 and 4 (Fig. 5.10g,h). Abundances at W2 at times 4 and 5 were similar to those in the no-wash areas at times 1, 2 and 6. ANOVA indicated significant interaction between the factors time and site, and time and location (Table 5.4).

Increased abundances of spionids were observed at a number of sites, within each of the zones, at times 3 and 4 (Fig. 5.11). At other sites, however, decreases in the abundance of Spionids were observed following the suspension of services (e.g. NW1(S2), Fig. 5.11f). This

spatial variability in patterns of change was supported by a significant time by site interaction (Table 5.4).

Abundances of amphipods varied considerably among sites at each of the times (Fig. 5.12). No particular pattern of temporal change was evident (Table 5.4).

Table 5.4 Summaries of ANOVAs comparing spatial variation in the abundance of taxa of macrobenthic fauna in unvegetated habitat of wash (W) and no-wash zones (NW), among times of sampling. ti = time (5 levels: t2 - t6; random), zo = zones (2 levels; wash, no-wash; fixed), lo(z) = location (4 levels; random), si(lo(z)) = sites (8 levels; random). $n = 5$. NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | Capitellidae | | | | Nereididae | | | Spionidae | | | Amphipoda | | |
|----------------|--------------|--|---------|-----|----------------------------------|---------|-----|----------------------------|---------|-----|--|---------|-----|
| | df | MS | F | sig | MS | F | sig | MS | F | sig | MS | F | sig |
| ti | 4 | 7.51 | 5.63 | * | 25.2 | 6.95 | * | 9.5 | 2.99 | NS | 1.49 | 1.29 | NS |
| zo | 1 | 91.02 | NO TEST | | 334.2 | NO TEST | | 52.6 | NO TEST | | 20.63 | NO TEST | |
| lo(z) | 2 | 131.26 | NO TEST | | 87.1 | NO TEST | | 14.2 | NO TEST | | 3.87 | NO TEST | |
| si(lo(z)) | 4 | 5.60 | 4.25 | * | 3.1 | 3.07 | * | 1.4 | 1.44 | NS | 3.12 | 3.55 | * |
| ti x zo | 4 | 3.50 | 2.63 | NS | 6.1 | 1.69 | NS | 4.8 | 1.53 | NS | 0.65 | 0.56 | NS |
| ti x lo(z) | 8 | 1.33 | 1.01 | NS | 3.6 | 3.59 | * | 3.2 | 3.26 | * | 1.16 | 1.32 | NS |
| ti x si(lo(z)) | 16 | 1.32 | 2.72 | *** | 1.0 | 4.42 | *** | 1.0 | 4.66 | *** | 0.88 | 2.02 | * |
| res | 160 | 0.49 | | | 0.2 | | | 0.2 | | | 0.43 | | |
| Cochran's test | | C = 0.10 ** | | | C = 0.18 ** | | | C = 0.11 NS | | | C = 0.26 ** | | |
| transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| | | <i>ti x si(lo(z))</i> | | | <i>ti x lo(z)</i> | | | <i>ti x lo(z)</i> | | | <i>ti x si(lo(z))</i> | | |
| | | W1(S1), W1(S2), W2(S1), NW1(S1), NW1(S2), NW2(S2): | | | W1, W2, NW1: | | | W1, W2, NW1: | | | W1(S1), W1(S2), W2(S1), W2(S2), NW1(S2), NW2(S1), NW2(S2): | | |
| | | t2 = t3 = t4 = t5 = t6 | | | t2 = t3 = t4 = t5 = t6 | | | t2 = t3 = t4 = t5 = t6 | | | t2 = t3 = t4 = t5 = t6 | | |
| | | W2(S2): | | | (t3 = t4) > (t2 = t5) > t6 | | | uninterpretable | | | t2 = t3 = t4 = t5 = t6 | | |
| | | t5 > (t4 = t6) > (t2 = t3) | | | <i>ti x si(lo(z))</i> | | | <i>ti x si(lo(z))</i> | | | NW1(S1): | | |
| | | NW2(S1): | | | W1(S1), W1(S2), W2(S1), NW1(S2): | | | W1(S1), W1(S2), W2(S1): | | | (t2 = t3 = t4) > t5 = t6 | | |
| | | (t3 = t4 = t5) > t6 > t2 | | | t2 = t3 = t4 = t5 = t6 | | | W2(S2): | | | | | |
| | | | | | NW1(S1): | | | (t2 = t4 = t5) > (t3 = t6) | | | | | |
| | | | | | t2 > (t3 = t4) > (t5 = t6) | | | NW1(S1): | | | | | |
| | | | | | NW2(S1): | | | (t2 = t3 = t4) > (t5 = t6) | | | | | |
| | | | | | (t3 = t4) > (t2 = t5) > t6 | | | NW1(S2): | | | | | |
| | | | | | NW2(S2): | | | uninterpretable | | | | | |
| | | | | | (t3 = t4) > t2 > t5 > t6 | | | NW2(S1): | | | | | |
| | | | | | | | | (t3 = t4 = t5) > t2 > t6 | | | | | |
| | | | | | | | | NW2(S2): | | | | | |
| | | | | | | | | (t3 = t4) > (t2 = t5) > t6 | | | | | |

t2 (before) = 30/05/00, t3 (during) = 06/09/00, t4 (during) = 25/09/00, t5 (after) = 26/10/00, t6 (after) = 10/02/01

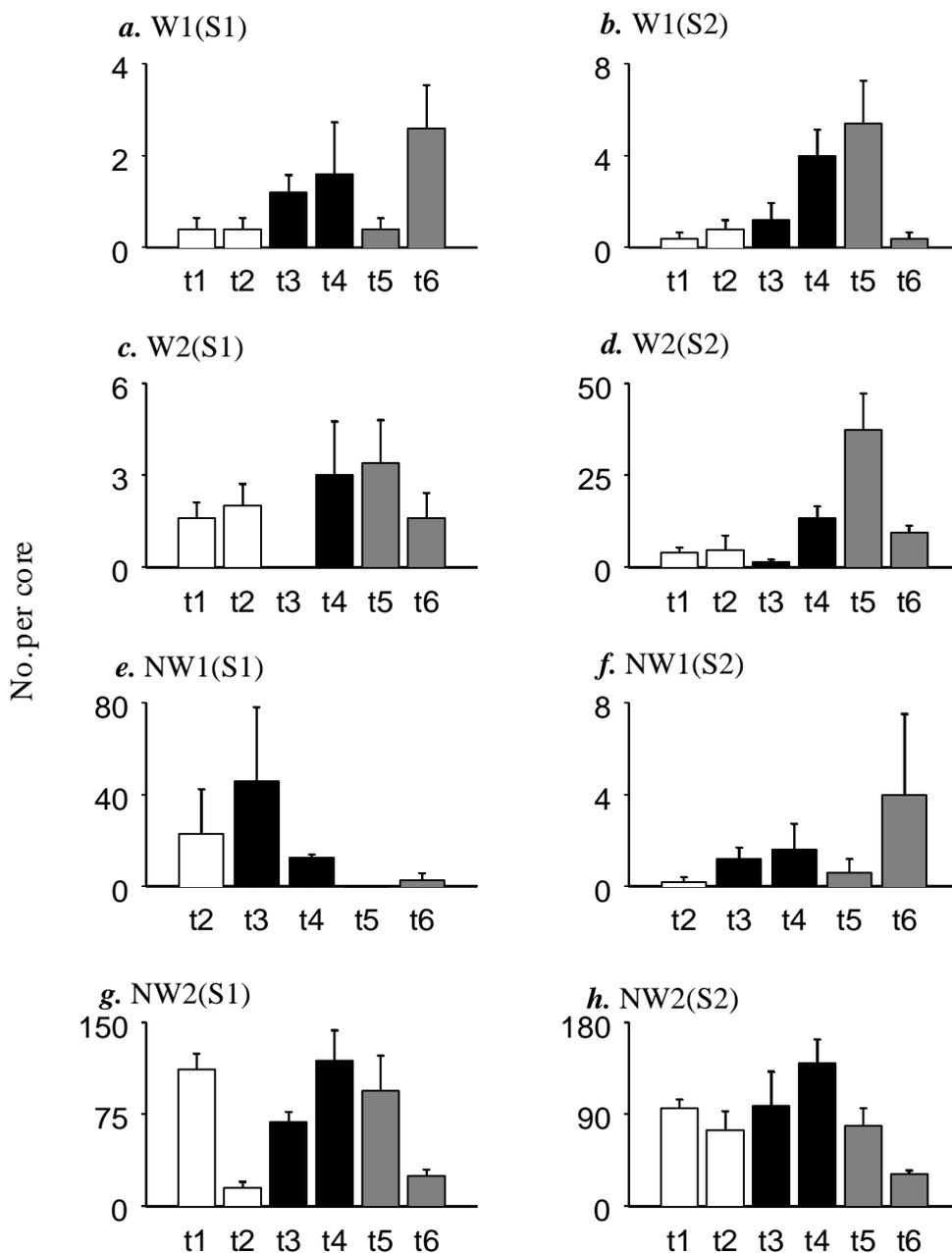


Figure 5.9 Mean (+ S.E.) abundance of Capitellidae in unvegetated habitat of sites in the wash (W) and the no-wash (NW) zone of the upper Parramatta River at times before (t1, t2; white), during (t3, t4; black) and after (t5, t6; grey) the temporary suspension of ferry services. Sites at NW1 were not sampled at t1. $n = 5$ for each site at each time.

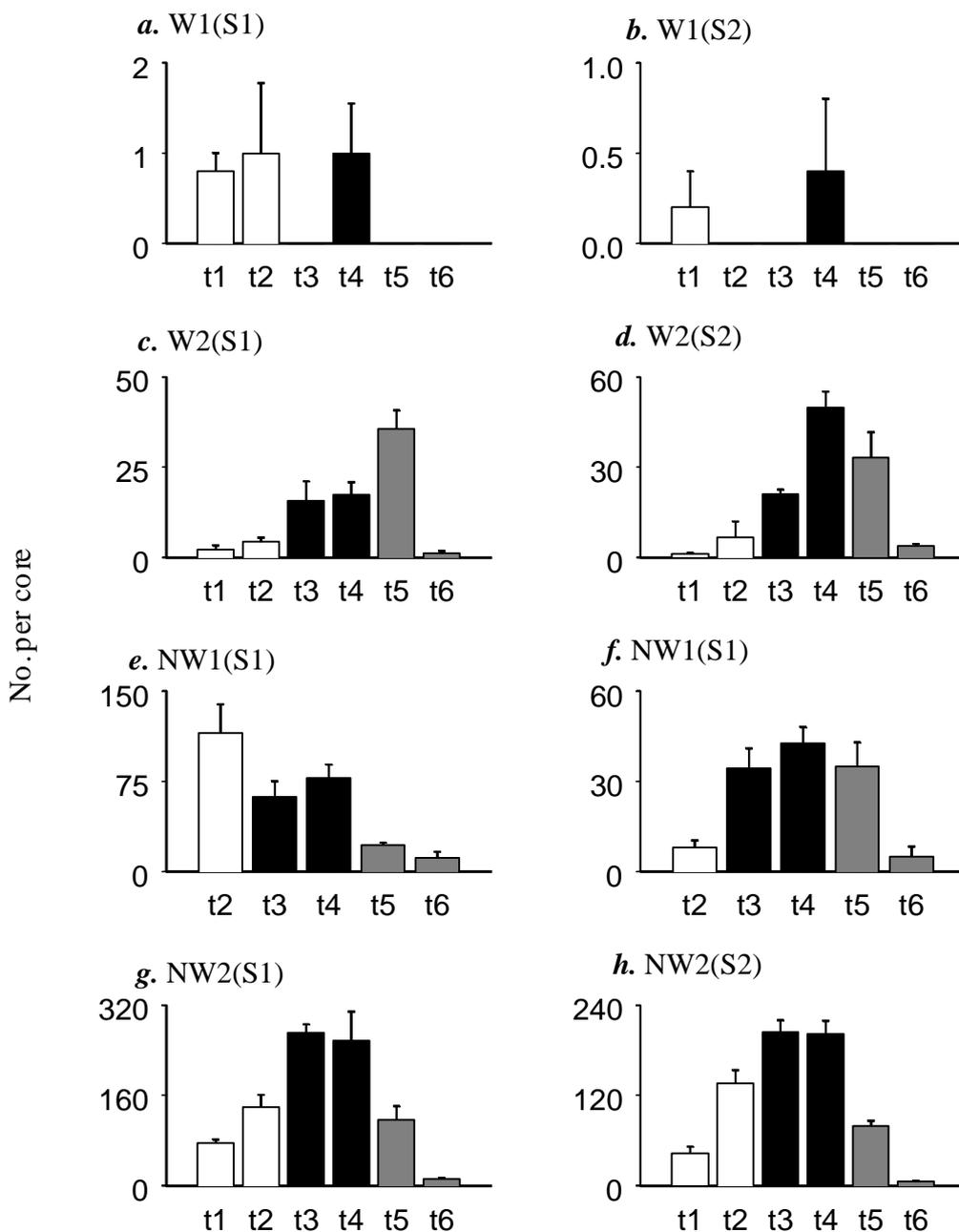


Figure 5.10 Mean (+ S.E.) abundance of Nereididae in unvegetated habitat of sites in the wash (W) and the no-wash (NW) zone of the upper Parramatta River at times before (t1, t2; white), during (t3, t4; black) and after (t5, t6; grey) the temporary suspension of ferry services. Sites at NW1 were not sampled at t1. $n = 5$ for each site at each time.

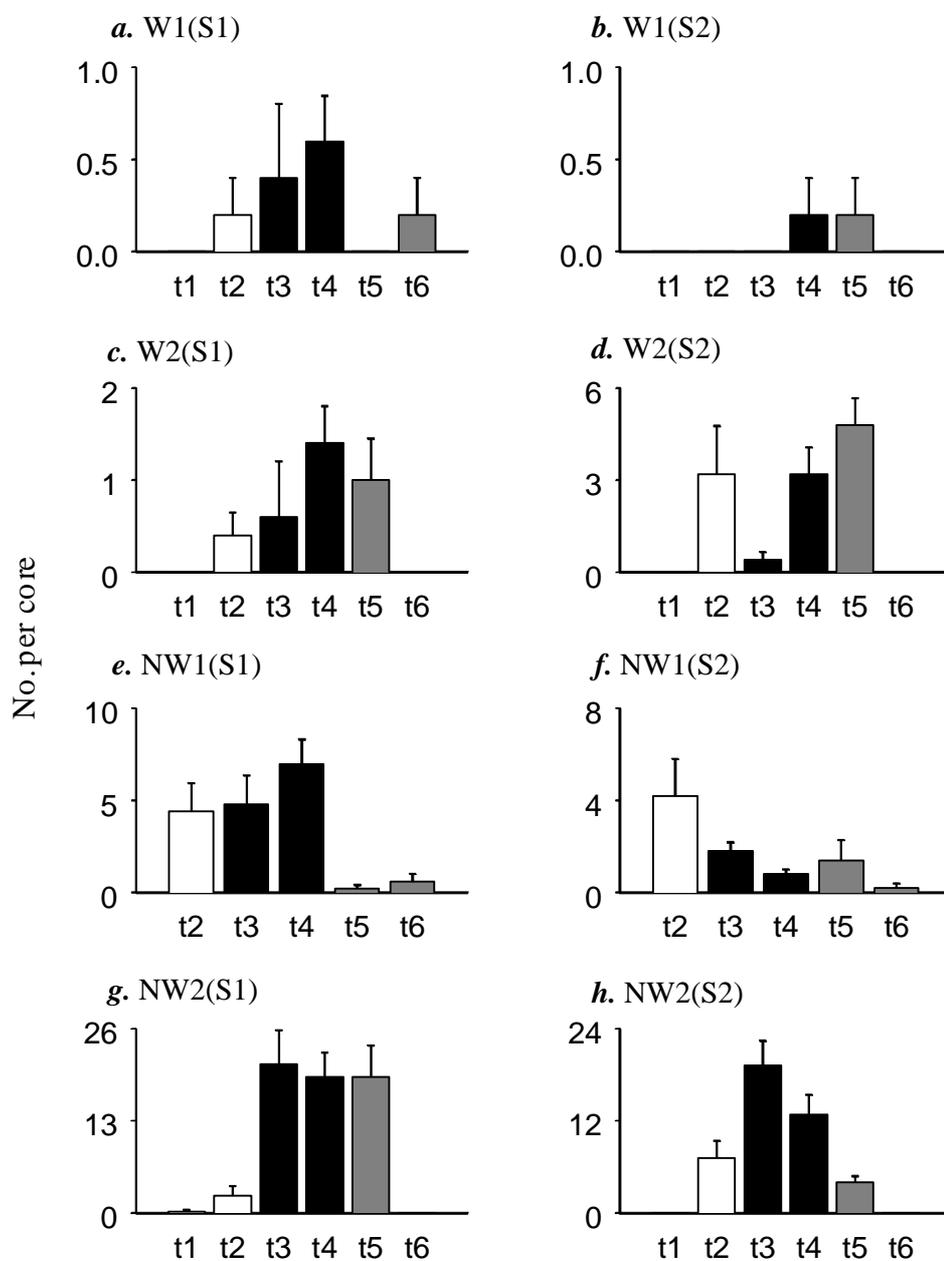


Figure 5.11 Mean (+ S.E.) abundance of Spionidae in unvegetated habitat of sites in the wash (W) and the no-wash (NW) zone of the upper Parramatta River at times before (t1, t2; white), during (t3, t4; black) and after (t5, t6; grey) the temporary suspension of ferry services. Sites at NW1 were not sampled at t1. $n = 5$ for each site at each time.

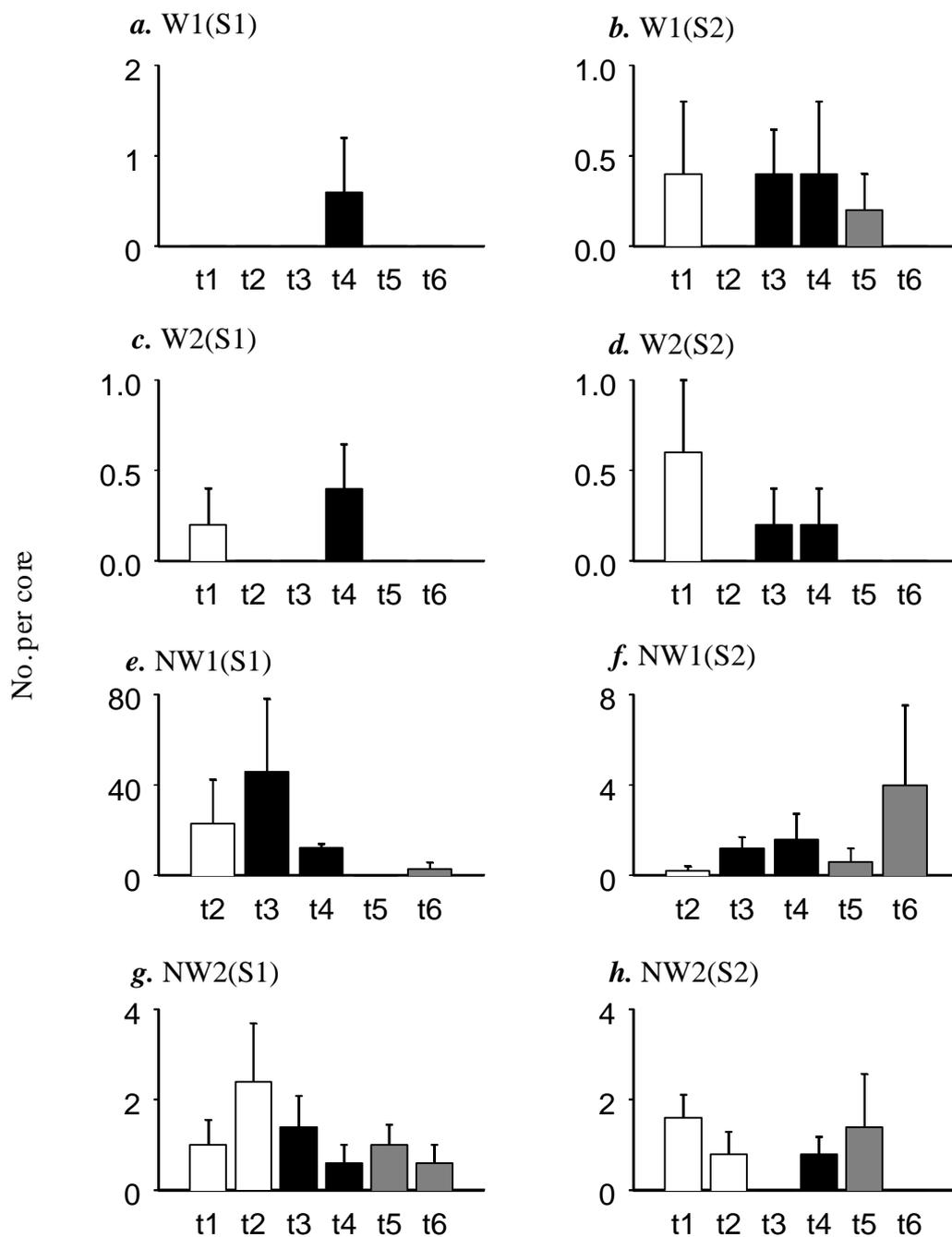


Figure 5.12 Mean (+ S.E.) abundance of Amphipoda in unvegetated habitat of sites in the wash (W) and the no-wash (NW) zone of the upper Parramatta River at times before (t1, t2; white), during (t3, t4; black) and after (t5, t6; grey) the temporary suspension of ferry services. Sites at NW1 were not sampled at t1. $n = 5$ for each site at each time.

5.4 Discussion

In the unvegetated habitat, assemblages at the majority of sites within the wash zone changed to become more similar to those of the no-wash zone following the temporary suspension of RiverCat ferry services. Several months after the return of services, these assemblages had returned to their previous, disturbed, state. Changes to the assemblages in some sites of the no-wash zone were also observed, coincident with the temporary cessation. Changes to the assemblages of the no-wash zone were, however, much smaller than changes to the assemblages of the wash zone. Following the return of services, the assemblages of these sites in the no-wash zone initially displayed change towards their previous state, before becoming very different from the assemblages found at any of the other times.

In contrast, assemblages in neither the wash nor the no-wash zone of the vegetated habitat appeared to respond to the temporary suspension of services. Assemblages changed little between times of sampling and any change that did occur appeared random.

The greater change in the assemblages of the unvegetated habitat of the wash zone than the no-wash zone following the suspension of ferry services is consistent with the removal of the disturbance of wash. Had change been due to some other disturbance associated with ferries (e.g. the emission of fuel or exhaust), a similar pattern of change should have been observed between the two zones following the cessation of services because the number of ferries traveling along these sections of river was identical. Thus, the pattern of change supports the model that wash is responsible for differences in the assemblages of wash and no-wash zones.

Change to assemblages of the unvegetated habitat appeared to be caused by changes in the abundances of capitellids and nereids. Abundances of these taxa increased following the suspension of services and decreased following their re-introduction. Changes in the abundances of capitellids and nereids and the structure of assemblages did, however, lag behind changes to ferry services. In most sites, no changes to assemblages or the abundances of capitellids and nereids were evident a week after the stoppage. It was generally not until a month after the stoppage that a change was seen. This is not surprising considering that colonization will only be observed if: (i) settlement occurs and (ii) organisms reach a size greater than 500 μm in diameter, such that they are retained on the sieve. Previous studies have suggested it may take over 6 months for abundances to peak (Pearson and Rosenberg, 1978; Lu and Wu, 2000).

A lag was also seen between the re-introduction of services and the return of assemblages/abundances to a disturbed state. This suggests that patterns in assemblages and abundances of taxa, between wash and no-wash zones, are not due to greater rates of erosion of organisms in the wash zone. Erosion of macrofauna is correlated with the velocity of wind and

the flux of sediment (Miller and Sternberg, 1988; Emerson and Grant, 1991; Armonies, 1992) and can have a significant influence on patterns of distribution and abundance (e.g. Thrush, 1986; Frid, 1989; Emerson and Grant, 1991; Günther, 1992; Snelgrove *et al.*, 1993). If erosion of organisms were greater in the wash than in the no-wash zone, assemblages and abundances of macrofauna in the wash zone should have reverted to a disturbed state immediately after the re-introduction of ferry services. This was not the case and suggests that patterns in macrofauna are an indirect effect of wash.

Sediment-related variables are widely believed to be important in structuring infaunal assemblages (reviewed by Gray, 1974, 1981; Rhoads, 1974; Probert, 1984, but see Zajac and Whitlatch, 1982a,b). The distributions of infaunal species are closely correlated with certain types of sediment (e.g. Rhoads, 1974; Scheltema, 1974; Butman, 1987; Snelgrove and Butman, 1994) and several studies have found a strong relationship between the distributions of animals and organic matter, a dominant source of food for deposit-feeders (Longbottom, 1970; Field, 1971; Ishikawa, 1989). Properties of the sediment, such as grain-size and organic content, are not only determined by the availability materials but also by the amount of energy imparted to the sediment from hydrodynamic processes (summarized in Royse, 1970). If: (i) properties of the sediment are important in determining the structure of assemblages and (ii) waves alter these properties in the wash zone, assemblages would differ between the wash zone and the no-wash zone due to an indirect effect of wash.

Changes in the abundance of capitellids and nereids were generally greater in the no-wash than in the wash zone. A possible model to explain this pattern is that the availability of larvae was greater in the no-wash than in the wash zone and may have limited colonization in the latter area. This is contrary to the model that exposure to boat-generated waves increases larval fluxes over intertidal mudflats (see Bertness *et al.*, 1991; Gaines and Bertness, 1993). If this were the case, settlement would be less in the no-wash zone.

In both the wash and no-wash zones, within-site variability in assemblages was smallest at times 4 and 5 (i.e. during the cessation and immediately after the return of ferries). This supports the model that the disturbance of wash increases spatial variability in assemblages. If this were the case, the pattern, described in Chapter 4 (of greater within-site variability in the wash than the no-wash zone) may be attributed to the different intensities of the disturbance between these places.

In any case, the results of this study must be treated with caution since neither undisturbed locations nor locations where ferries continued to run were used in analyses to control for background temporal and spatial variation in assemblages. The control locations sampled in this

study were situated more than four kilometres downstream from the wash and no wash zones, along a much wider section of river. They are likely to have been more exposed to wind-generated waves, subject to greater volumes of recreational boat-traffic and have had a greater salinity than were the case in sites further upstream. The assemblages in control locations were significantly different from those in wash or no-wash zones. They were consequently omitted from analyses because background temporal and spatial variability in these is unlikely to have been representative of change in the wash or no-wash zones.

This problem could not be avoided given that: (i) ferries only continued to operate to the west of Homebush Bay (Fig. 5.1) and (ii) there was a paucity of suitable habitat for sampling immediately downstream of the Homebush Bay ferry wharf. This problem of inappropriate control locations is a common one given the lack of randomization of unplanned impacts (Wiens and Parker, 1995). When inappropriate controls are included in analyses, they frequently lead to confounding of results.

In interpreting the results of this study, it was therefore assumed that background temporal variability in assemblages was negligible. Given that this study ran over a period of 10 months this assumption is probably not justified. Biological systems are not static and unchanging - many taxa display seasonal changes in abundance that reflect patterns of larval reproduction and transport (e.g. Lively *et al.*, 1993; Turner *et al.*, 1995). Therefore, the failure of assemblages in many sites to return to their previous state (i.e. composition prior to the temporary stoppage) by time 6 does not necessarily mean that no recovery occurred (see discussion of endpoints in Grayson *et al.*, 1999).

The impossibility of determining whether there was any temporal change to assemblages of the upper Parramatta River that was a result of factors other than the stoppage/return of ferries was particularly problematic in the case of assemblages in the unvegetated habitat of the no-wash zone. Following the return of services, these assemblages did not appear to return to their previous, presumably impacted, state. They appeared to be strongly influenced by some other factor between sampling times 5 and 6.

This is not the first study to observe a change in the ecology of benthic organisms following the cessation of ferry services. Davidson (1996, 1997) observed an increase in the abundance of molluscs on intertidal boulders in the Tory Channel and Queen Charlotte Sound, New Zealand, coincident with the off-seasons of the fast ferry, Condor 10. Although sampling was confounded with season, such change was not observed in control sites sheltered from wash, suggesting that the ferries were responsible for the pattern. These results suggest that the ecological impacts of wash are reversible.

In the present study, the abundances of capitellid and nereid polychaetes increased in the wash zone and in some sites of the no-wash zone during the temporary cessation of RiverCat ferry services. Abundances decreased following the return of services. Depressed abundances during the operation of services may be due to a greater rate of mortality of organisms, decreased rates of settlement or the erosion and passive transport of organisms down-stream. Davidson (1996, 1997) found increased numbers of recently dead and dying organisms in fixed quadrats during the operation of the Condor 10 than during the off-season. Thus, ferry services appeared to be responsible for increased mortality of subtidal organisms in the Tory Channel. Here, the return of assemblages to a similar state as found prior to the disturbance took several months. If changes were due to mortality, one would not expect such a long lag between the return of ferries and change in the assemblages.

In this study, the lack of response to the suspension of services by assemblages in the vegetated habitat may have been due to several factors. First, wash may not be important in determining the structure of assemblages in this habitat. This would be the case if pneumatophores dissipate wave-energy and/or the roots below-ground stabilize sediment such that invertebrates living in this habitat do not 'feel' the effects of wash. This model was, however, not supported by the results in Chapter 4. It could also be the case if the types of animal found in this habitat were resistant to the effects of wash. Given that the types of invertebrate present in this habitat were similar to those in the unvegetated sediment, where there appeared to be an impact of wash, this is also unlikely.

The second model is that wash is important in structuring the faunal assemblages of vegetated habitats, but change was not seen following the cessation of services because insufficient time was allowed for this to occur. Benthic 'recovery' following a disturbance is generally considered to be a slow process that may take up to several years (e.g. Boesch and Rosenberg, 1981; Stachowitsch, 1991; Lu and Wu, 2000). While change was observed in the unvegetated habitat over the period of this study, longer periods may be required in vegetated habitats. Empirical studies and modelling suggest that the interaction of tidal currents and vegetation generates zones of stagnant water in mangrove forests (Furukawa *et al.*, 1997; Wolanski and Ridd, 1986). This may increase the time required for recolonization of sediment because settlement is dependent on the availability of larvae in the water-column (e.g. Zajac and Whitlatch, 1982a; Kalejta and Hockey, 1991).

Finally, change in the assemblages of vegetated habitat may not have occurred following the removal of the disturbing force because the habitat was irreversibly modified by the

disturbance, such that it was no longer able to support the great densities of taxa found in the no-wash zone.

Thus, while the results presented here suggest that wash is important in structuring the assemblages of unvegetated but not vegetated habitat, further manipulative experiments would enable the results to be interpreted with greater confidence.

CHAPTER 6

MORE EXPERIMENTS TO DETERMINE THE ROLE OF RIVERCAT WASH IN STRUCTURING ASSEMBLAGES OF MACROBENTHIC INFAUNA

6.1 Introduction

A central issue in the assessment of environmental impacts is the distinction of change to assemblages induced by anthropogenic disturbance, from variation in those assemblages due to natural spatial and temporal variability (Levin, 1992; Peterson, 1993; Osenberg *et al.*, 1994). Where an environmental impact is large relative to background variation, this is relatively simple (Green, 1979). In soft-sediment habitats, benthic organisms are, however, often patchy in distribution and change markedly over short time-periods (Barry and Dayton, 1991; McIntosh, 1991; Morrissey *et al.*, 1992). This makes the detection of putative impacts very difficult. Statistical tests may not support an ecological impact despite differences in assemblages between control and impact locations.

Physical factors, such as depth and movement of water and sediment-type (e.g. Thorson, 1957; Gray, 1974; Barry and Dayton, 1991) are thought to be most important in determining large-scale patterns of distribution of benthic infauna. Disturbances, biotic and/or abiotic factors maintain heterogeneity at smaller scales (< 100s metres; Thrush *et al.*, 1989; Barry and Dayton, 1991). The role of sediment-related variables in structuring infaunal assemblages has received particular attention (reviewed by Rhoads, 1974; Gray, 1974, 1981; Probert, 1984). The distributions of infaunal species are closely correlated with certain types of sediment (e.g. Rhoads, 1974; Scheltema, 1974; Butman, 1987; Snelgrove and Butman, 1994). Contour, grain-size, porosity, organic content and adsorbed chemicals are believed to be important in determining recruitment of polychaetes and crustaceans (Jones, 1950; Thorson, 1957; Rhoads and Young, 1970; Gray, 1974).

Little experimental work has, however, been done to test the effects of sediment on the recolonization and succession of defaunated sediment (but see Zajac and Whitlatch, 1982a, 1982b; Stark, 1996; Wu and Shin, 1997). Zajac and Whitlatch (1982a, 1982b) showed that there were few differences in the initial colonization of defaunated plots of mud and sand. Wu and Shin (1997) showed that characteristics of the sediment were only significant for colonization of gastropods and bivalves, but not for polychaetes and amphipods.

In Chapter 4, assemblages of macrobenthic infauna differed between wash and no-wash zones of the upper Parramatta River, in vegetated and unvegetated habitat, at two times of sampling. These differences were, however, not statistically significant, possibly due to

considerable variability in assemblages at the scales of replicates (metres), sites (10s of metres) and locations (100s of metres) within zones. While sorting these samples, it was observed that characteristics of the sediment, such as grain-size and organic content also varied over similar spatial scales. This variability appeared particularly large from site to site. If characteristics of the sediment are important in determining the distribution and abundance of taxa along the Parramatta River, large spatial variability in characteristics of the sediment may be one important factor contributing to large natural variability in the distribution and abundance of infauna.

Artificial habitats, which offer the same microhabitat across different sites (e.g. Rosenberg and Resh, 1982; Edgar, 1991; Cairns and Pratt, 1993; Bologna and Heck, 1999), can be used to reduce natural variability in assemblages so that the effects of differing levels of a factor of interest might be more easily determined. While many studies, such as those employing acrylic plates (e.g. Deutsch, 1980) or artificial seagrass units (e.g. Barber *et al.*, 1979), have used this strategy to sample organisms associated with hard substrata, few have adopted this approach for soft sediments. If different sediments do determine the structure of infaunal assemblages, the use of artificial sampling units containing homogeneous sediment should reduce variability in assemblages among replicates and sites, allowing ecological impacts to be measured more easily.

It was hypothesised that if homogeneous sediment was transplanted to various sites along the Parramatta River, the assemblages that accumulate in this sediment over a period of 1 month would be less variable among replicates and sites than those that accumulate in natural sediment. The sediment was defaunated because the recruitment of macro-invertebrates may be affected by the fauna already living in the sediment (e.g. Highsmith, 1982; Pawlik, 1986) and similar conditions were required in all replicates. It was also hypothesised that, if spatial variability was smaller in the homogeneous sediment than in the site-specific sediment, a stronger pattern between wash and no-wash zones would be seen. This hypothesis does, however, assume a direct effect of wash on colonization. If the effect of wash on colonization is indirect, this pattern will not be seen.

Properties of the sediment, such as grain-size are not only a function of the sizes of available materials, but are also determined by the amount of energy imparted to the sediment from hydrodynamic processes (summarized in Royse, 1970). If: (i) properties of the sediment are important in determining colonization and (ii) waves alter these properties in the wash zone, colonization would differ between the wash zone and the no-wash zone due to an indirect effect of wash. In this case, colonization of homogeneous sediment would not differ between the wash and the no-wash zone. Differences in assemblages between the two zones would, instead, be greater in the site-specific than the homogeneous sediment.

Wash may, however, have no effect on colonization but, instead, affect adult invertebrates. In soft sediments, food-limitation (Zajac, 1986; Peterson, 1979, 1991; Wilson, 1980) and predation (e.g. Peterson, 1979) appear to be particularly important causes of mortality among adults. Wash could, potentially, affect the role of these processes in structuring assemblages. Alternatively, wash could affect adult-juvenile interactions, which are frequently cited as important in determining the abundance of invertebrates and the structure of assemblages (e.g. Hessle, 1924; Segerstråle, 1962, 1973; Elmgren *et al.*, 1986). The use of defaunated sediment will not enable any effect of wash on adult-juvenile interactions to be considered.

A second experiment was done in which both direct and indirect effects of wash on whole assemblages of macro-invertebrates were considered. Site-specific sediment and associated assemblages were transplanted within and across zones to evaluate the two models presented in Table 6.1. If wash directly determines the structure of assemblages, assemblages transplanted between zones should change so that they become more similar to natural assemblages at their destination than assemblages at their source. If wash indirectly determines the structure of assemblages by altering characteristics of the sediment: (i) these characteristics should differ between the wash and no-wash zone, (ii) assemblages transplanted across zones should remain more similar to assemblages at their source than destination and (iii) assemblages transplanted within zones should also remain more similar to assemblages at their source than their destination.

6.2 Materials and Methods

6.2.1 Colonization of defaunated sediment

The sediment for the homogenous treatment was collected from the top 4 cm of an intertidal mudflat on the western side of the entrance to Woollooware Bay (Georges River estuary, Sydney, Australia) in June, 2001. This site was chosen because it is located immediately adjacent to the Towra Point Aquatic Reserve and its sediment contained great densities of polychaetes, so presumably represents a favourable substratum. It was assumed that the top few centimetres of the sediment are fairly well mixed *in situ* by wind- and boat-generated waves (see Bell *et al.*, 1997) and that homogenization of this sediment would not significantly alter its characteristics. Cores of sediment, of depth 4 cm, were also collected from each site of the upper Parramatta River.

Table 6.1 Summary of the models tested by the experimental transplant and the hypotheses derived from these models. ‘Test’ indicates the type of transplant required to evaluate the model, ‘H_{support}’ is the hypothesis supporting the model, ‘H_{reject}’ is the hypothesis leading to rejection of the model. ‘Destination’ indicates change in assemblages to become more similar to assemblages at their destination than their source; ‘source’ indicates that change to assemblages following transplantation is no greater than change in assemblages at the source-site, over the study period.

| Model | Test | H_{support} | H_{reject} |
|---|-------------------------------|----------------------------|---------------------------|
| (i) The situation of an infaunal assemblage within the wash/no-wash zone directly determines its structure, at a large spatial scale (100s of metres). | Transplant: no-wash ↔ wash | destination | source |
| (ii) Within the wash/no-wash zone, characteristics of the sediment are important in determining the structure of infaunal assemblages, at smaller spatial scales (10s of metres, metres). | Transplant: within zone | source | destination |

All sediment was transported to the laboratory and frozen at -20°C for 2 weeks. Upon thawing, cores of sediment from Woollooware Bay were mixed together thoroughly and used to fill 48 containers, 15 x 15 x 3 cm deep (Fig. 6.1). Previous studies suggest that reductions in the flux of porewater may alter geochemistry of sediment and result in changes to productivity and composition of the benthos (e.g. Barko *et al.*, 1991; Pezeshki *et al.*, 1991). The containers were thus constructed to cause minimal blockage of flow – galvanized chicken-wire outers, lined with 250 μm nylon mesh (Allied Filter Fabrics Pty Ltd). Each core from the Parramatta River was mixed separately and placed in an individual container. The containers were then exposed to a continuous flow of filtered (250 μm) seawater for a week before being deployed in the field. This enabled the sediment to settle within containers, dead organisms to decompose further and the sediment to be colonized by micro-algae, which are widely acknowledged to play an important role in the stabilization of sediment (e.g. Sutherland *et al.*, 1998; Yallop *et al.*, 2000).

Five containers of defaunated, homogeneous sediment, collected from Woollooware Bay and 5 containers of defaunated sediment that was intrinsic to each particular site, were then deployed at the eight previously-sampled sites of the Parramatta River (two sites within each location, Fig. 6.2) on the 19th June, 2001. They were placed flush with the surface of the surrounding sediment (Fig. 6.1), with the two treatments interspersed.

A small sample of sediment (approximately 150 g, wet weight) was removed from each container at the times of deployment and retrieval. These samples were used to determine sediment grain-size and organic matter (described in Section 6.2.3). This was necessary considering that the hypotheses require that characteristics of the homogeneous sediment remain less spatially variable than those of the site-specific sediment.

Containers of sediment were left in the field for 1 month because previous studies on the re-colonization of sediment following small-scale disturbances have shown that most assemblages of macro-invertebrates recover to some extent within 1-40 days (Zajac and Whitlatch, 1982b; Bell and Devlin, 1983; Levin, 1984; but see Thrush *et al.*, 1996 for an example of a study in which recovery took longer).

After containers were retrieved, the infaunal assemblage of each was sampled by coring to a depth of 2 cm and diameter of 10 cm. A pilot study showed that, in the sites used for this study, there was no significant difference in the types or numbers of organisms found in cores of 2 cm or 10 cm depth (Appendix 1). Thus, the results of this experiment can be related directly to those described in previous chapters, despite the different sampling units. Cores of sediment were transported back to the lab and organisms greater than 500 μm were sorted to the taxonomic resolution described in Chapter 4.

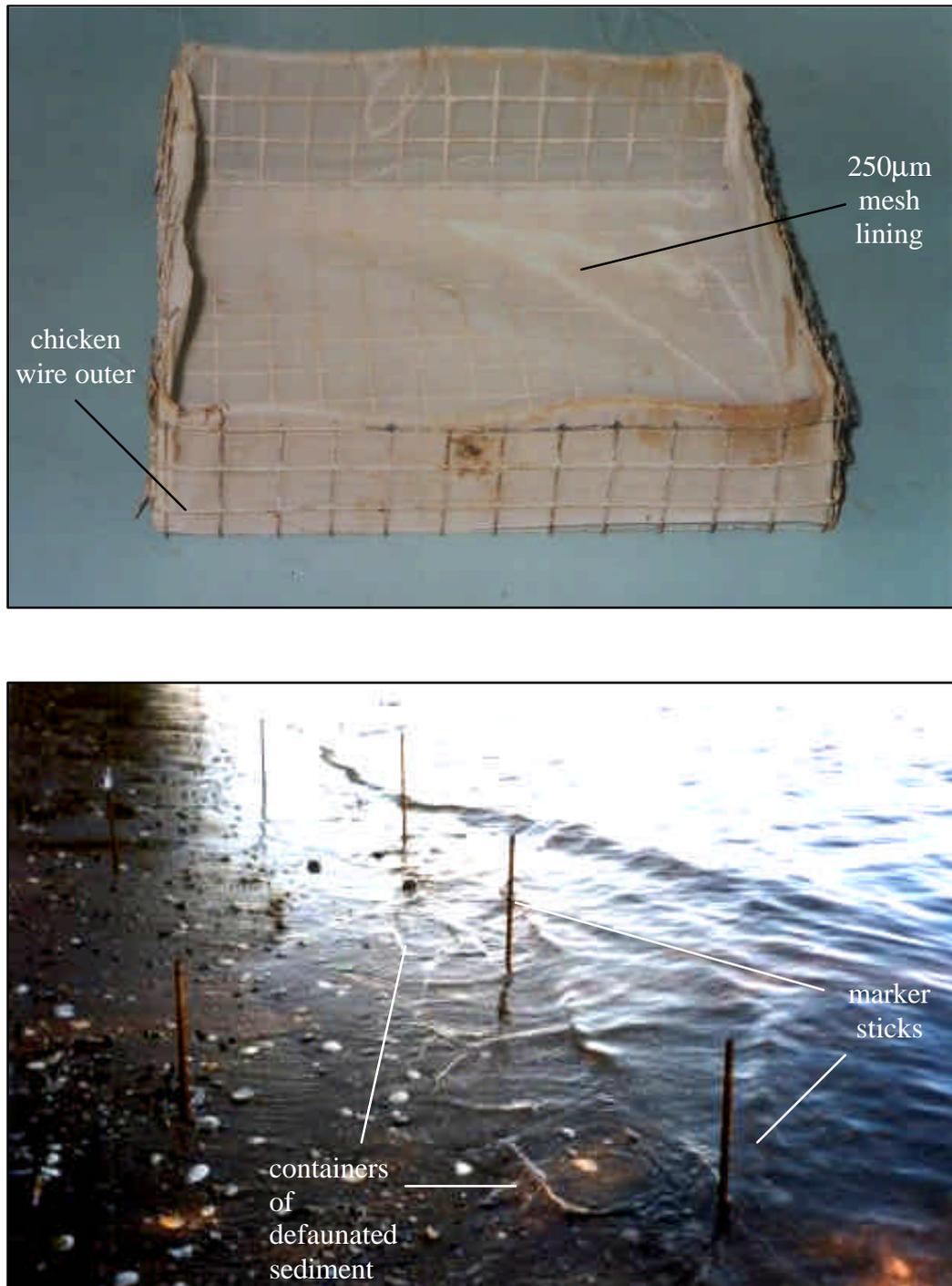


Figure 6.1 The containers used to deploy defaunated sediment. The location of each container in the sediment was marked with a dowel rod.

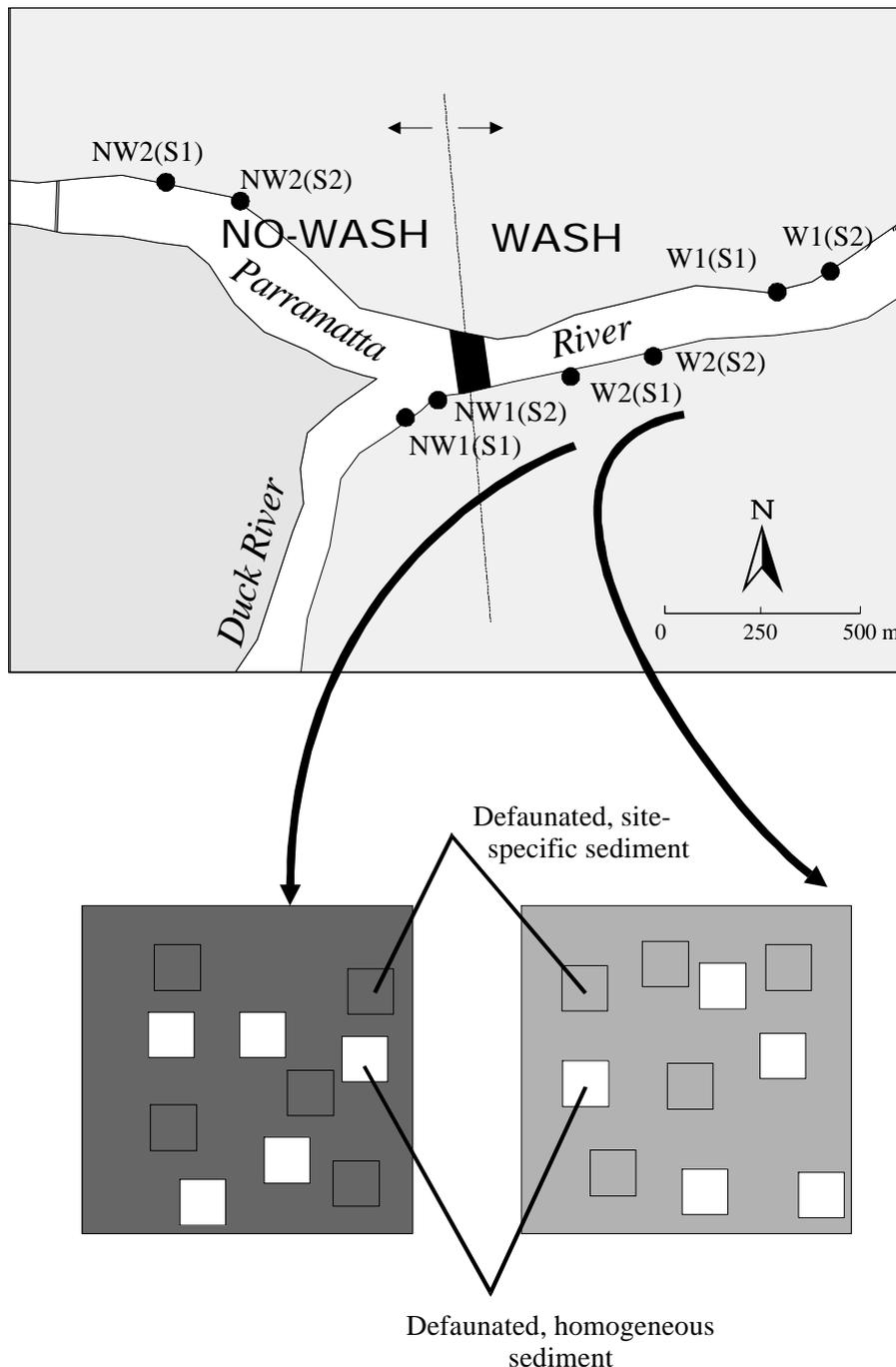


Figure 6.2 The experimental design for the defaunation experiment. Five containers of defaunated, homogeneous sediment and five containers of defaunated, site-specific sediment were deployed at two sites within each of four locations of the upper Parramatta River.

6.2.2 Transplant of infaunal assemblages

Sediment for the experimental transplant was taken from a site in each of the four locations, W1, W2, NW1 and NW2 on 21st June, 2002. The logistics of the experiment, which involved multiple transplants among sites and three control treatments, precluded the use of more than one site at each location. At each location, 25 cores, 10 cm deep and 10 cm wide, were collected. This size of core was used, despite the fact that the majority of organisms are found in the top 2 cm of the sediment (Appendix 1), because the integrity of the sediment is better maintained than if smaller cores were taken. The content of each core was carefully emptied into a circular plastic food container of depth 10 cm and maximal width 11 cm. The containers also assisted in maintaining the integrity of cores of sediment and were similar to those used by Stark (1996) and Small (1999). They had three 8 x 8 cm holes cut in the sides and an 8 cm diameter hole in the bottom that were covered with 250 μ m mesh. As with the containers used in the experimental defaunation, the mesh allowed water to flow through the containers but prevented movement of animals into or out of the core (excluding emigration or immigration over the surface of the sediment or recruitment into the sediment via the water column). In addition, 5 cores of sediment (undisturbed treatment, time 1) were collected from each location and taken back to the laboratory for processing and sorting.

Five containers of sediment from each location were haphazardly assigned to each of the following treatments (shown in Fig. 6.3):

- (i) Within-zone transplant – container of sediment deployed to the other location in the wash/no-wash zone where it was collected.
- (ii) Across-zone transplant – container of sediment deployed at one of the two locations in the other zone from where it was collected (5 cores to each).

It was hypothesized that if wash directly determines the structure of assemblages of infauna, assemblages would not change following transplant within their zone of origin but would change following transplant to the other zone.

Five containers of sediment were also assigned to each of the procedural controls (Fig 6.3):

- (i) Disturbance control – container of sediment returned to the hole from which the core was collected.
- (ii) Translocation control - container of sediment deployed at a different position in the location where it was collected.

These were required to test the hypothesis that any change in the assemblages of transplanted cores of sediment would be due to their new environment and not due to placing sediment in containers or moving the containers (Chapman, 1986).

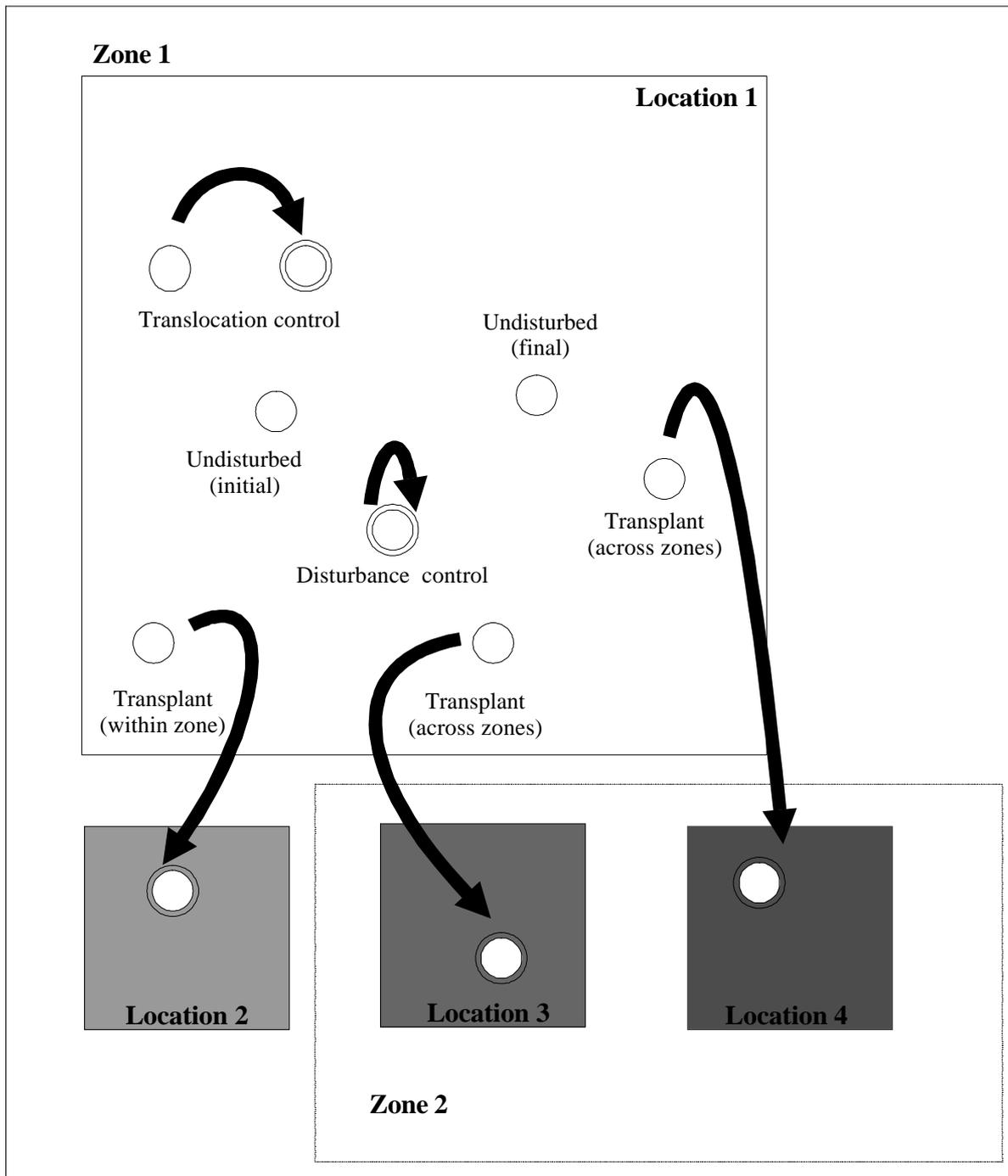


Figure 6.3 Schematic showing the various treatments of the experimental transplant. This design was replicated in each of the four locations. Single circles show where sediment was collected using a 10cm-diameter corer; double circles show where sediment was deployed in the pots. $n = 5$ for each treatment.

Containers were deployed by placing them in the holes left by the removal of cores of sediment. They were left in the field for 6 weeks, following which they were retrieved and their contents emptied into plastic bags. Samples were transported to the lab and organisms greater than 500 μm were sorted to the taxonomic resolution previously described. A further 5 cores of sediment were collected from each location to determine the structure of assemblages of undisturbed sediment at the end of the experiment (undisturbed treatment, time 2).

Assemblages in the disturbance controls were compared to those in undisturbed sediment, collected at time 2, to determine whether handling the sediment and deploying it in containers had an effect on organisms. To determine whether movement of cores and translocation to a new position in a location affected assemblages, assemblages of translocation controls were also compared to those in undisturbed sediment, collected at time 2.

6.2.3 Analysis of sediment-related variables

The organic matter in samples was determined using a similar method to Dean (1974). A teaspoon of sediment from each sample was placed in a pre-weighed crucible, dried to constant weight at 70°C and then reweighed to give the dry weight of the sediment. The sediment was then ashed at 480°C for 12 hours (see Byers *et al.*, 1978). The amount of organic matter in each sample was determined by weight-loss after combustion and is expressed as a percentage of total dry weight.

The remaining sediment was used for the analysis of grain-size. Particles of diameter less than 63 μm (4Φ) were removed from the samples by repeatedly mixing the sample in 1 litre of freshwater, leaving this to settle for a few minutes and then filtering the supernatant through pre-weighed, grade 595/2 folded filter paper (Schleicher and Schuell, Germany). This was repeated until the supernatant was clear. The filter papers and contents were dried to constant weight at 70°C and the weight of sediment determined. Excess water was decanted off the residual, unsuspended sediment and this fraction was also dried to constant weight at 70°C. Once dried, each sample of the coarser sediment was emptied into a column of dry sieves of mesh sizes 0, 1, 2, 2.5, 3, 3.5 and 4 Φ . The samples were sieved for 10 min using a Ro-Tap mechanical shaker and the fraction retained on each sieve weighed separately. The proportion (by weight) of each was calculated from the total weight.

6.3 Results

6.3.1 Colonization of defaunated sediment

As required by the hypothesis, the variability in grain-size among containers of homogeneous sediment was considerably less than among containers of site-specific sediment (Fig. 6.4a; results of np-DISP [Anderson, 2001]: $p < 0.001$). Large spatial variation in the grain-size of the site-specific sediment was also evident at the scale of locations (Fig. 6.4b; np-MANOVA: $p < 0.05$) and, at W2, assemblages differed considerably between sites.

Variability in the organic matter of site-specific sediment was greater than that of homogeneous sediment, at the spatial scales of sites and containers within sites (Fig. 6.5; Table 6.2). Within the site-specific treatment, sediment from the no-wash zone had more organic matter than did sediment from the wash zone (Fig. 6.5b). This difference was, however, not statistically significant (ANOVA: $p > 0.05$).

Changes to characteristics of sediment, in each of the homogeneous and site-specific treatments, were observed over the course of the study. A majority of the containers of sediment had a greater organic matter at the end of the experiment than at its start (Fig. 6.6). The increase in organic matter did not appear to be uniform among containers within the homogeneous nor in the site-specific sediment treatment, as shown by the scattering of points. In the homogeneous sediment, this resulted in increased variability in organic content among replicates, evident by the greater dispersion of points of this treatment along the y-axis than the x-axis. Spatial heterogeneity in organic matter did, however, remain smaller among containers of homogeneous sediment than among containers of site-specific sediment.

Few taxa colonized defaunated sediment (Table 6.3). Almost all containers had fewer than 10 individuals. The most common invertebrates found were the mussel, *Xenostrobus securis*, polychaetes of the family Nereididae and oligochaetes.

Nevertheless, patterns of colonization were tested to evaluate the hypotheses proposed in Section 6.1. In the case of the no-wash zone, data from only one site in each location (NW1[S1], NW2[S1]) are presented due to loss of containers during the experiment. As hypothesized, Bray-Curtis measures of dissimilarity for within-site comparisons in the colonization of containers were smaller for the homogeneous sediment than the site-specific sediment, in the wash and the no-wash zone (Fig. 6.7). This was also the case for between-site comparisons within the wash zone, but not in the no-wash zone. Contrary to the hypothesis, differences between assemblages of the wash and the no-wash zone were smaller in the homogeneous sediment than in the natural sediment (Fig. 6.7).

Figure 6.8 shows patterns in the abundance of Oligochaeta, Nereididae, Amphipoda and *Xenostrobus securis* between the homogeneous and site-specific sediment. Colonization of each of the treatments appeared very variable, at the scale of sites. At this scale, homogeneous sediment only decreased variability in colonization by *Xenostrobus securis*. Contrary to the hypothesis, Nereididae was more abundant in the no-wash zone than in the wash zone in the site-specific sediment, but not in the homogeneous sediment. Variability in the abundance of individual taxa was greater among replicates with site-specific sediment than among replicates with homogeneous sediment (Table 6.4).

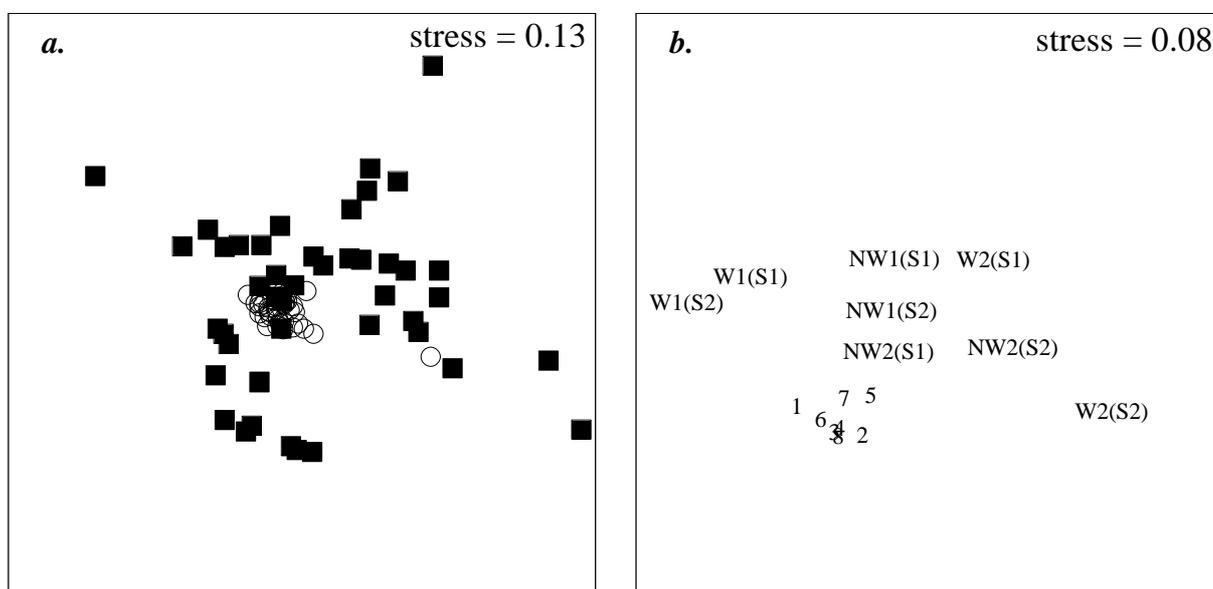


Figure 6.4 nMDS ordinations of sediment grain sizes in containers of homogeneous defaunated sediment (open circles; 1-8) and site-specific defaunated sediment (closed squares; W1(S1), W1(S2), W2(S1), W2(S2), NW1(S1), NW1(S2), NW2(S1), NW2(S2)) at time 1 (June, 2002). Points represent *a.* individual containers and *b.* centroids of untransformed data ($n = 5$). Ordinations were done using Euclidean distances.

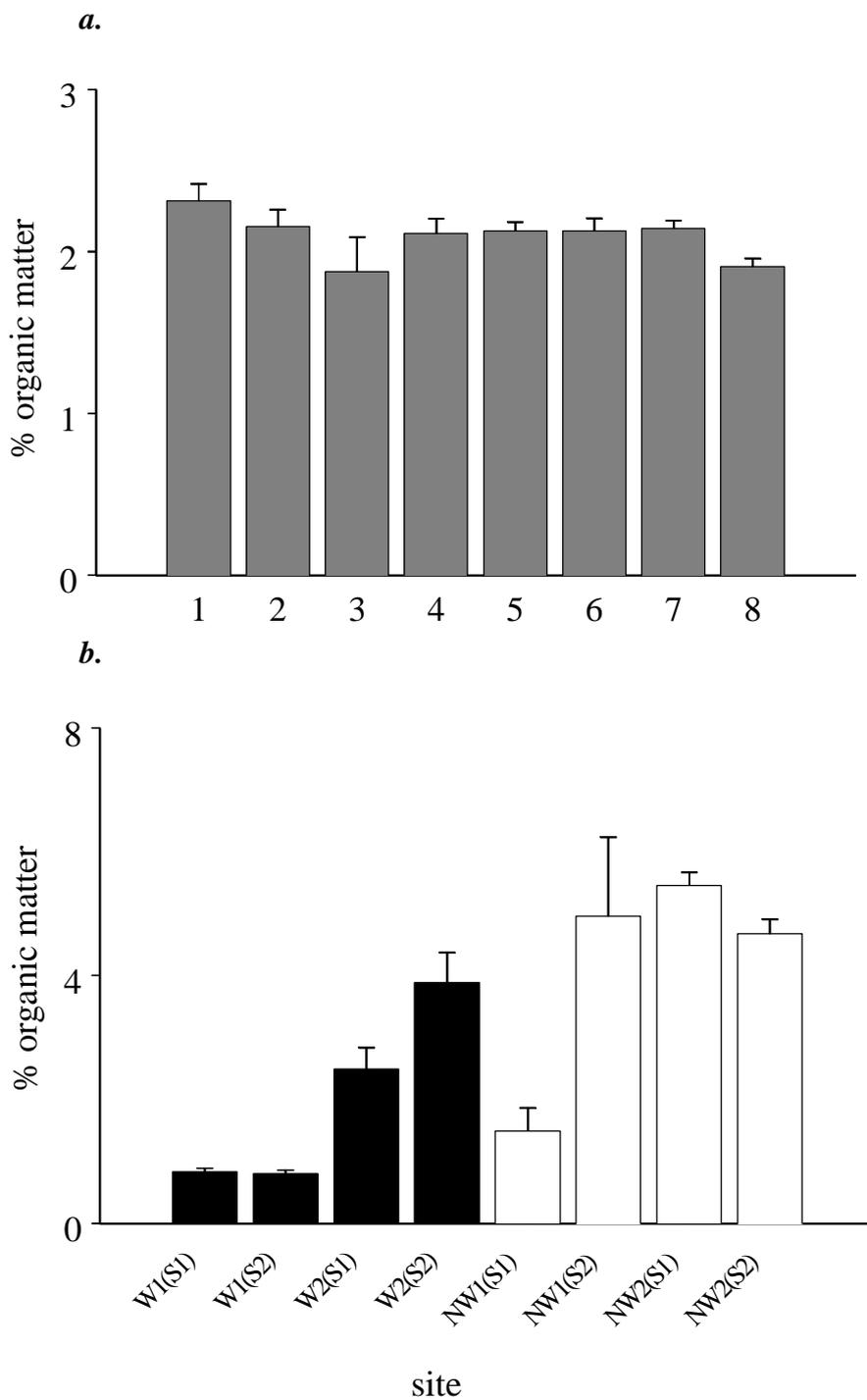


Figure 6.5 Mean (+S.E.) percentage organic matter of *a.* homogeneous sediment and *b.* site-specific sediment (black: wash zone; white: no-wash zone) at time 1. $n = 5$.

Table 6.2 Mean squares and estimates of the components of variance (σ^2) from one factor analysis of variance, examining variability in organic matter among sites within homogeneous (H) and site-specific (SS) sediment. Differences in the estimates of variance between the homogeneous and site-specific sediment, at each of the spatial scales, were tested for using 2-tailed *F*-tests.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | HOMOGENEOUS | | | SITE-SPECIFIC | | F -TEST | |
|-------|-------------|-------|-------|---------------|-------|-----------------|------------|
| | <i>df</i> | MS | s^2 | MS | s^2 | <i>F</i> -ratio | Sig. |
| sites | 7 | 0.110 | 0.007 | 16.08 | 3.12 | 425.2 | *** H < SS |
| res | 32 | 0.073 | 0.073 | 0.47 | 0.47 | 6.4 | *** H < SS |

Table 6.3 Taxa of macrobenthic infauna colonizing containers of site-specific (SS) and homogeneous (H) sediment deployed along the upper Parramatta River. * denotes the presence of the taxa in at least one of the containers.

| | | SS | H |
|-----------|---------------|---|---|
| Annelida | Oligochaeta | * | * |
| | Polychaeta | | |
| | Capitellidae | * | * |
| | Nephtyiidae | * | * |
| | Nereididae | * | * |
| | Ophelidae | | * |
| | Sabellidae | * | * |
| | Spionidae | * | * |
| Crustacea | Brachyura | * | |
| | Amphipoda | * | * |
| | Isopoda | * | * |
| | Tanaidacea | * | * |
| Mollusca | Bivalvia | <i>Arthritica helmsii</i> | * |
| | | <i>Spisula (Notospisula) trigonella</i> | |
| | | <i>Xenostrobus securis</i> | * |
| Nematoda | | | * |
| Nemertea | | * | * |
| Other | Insect larvae | | * |

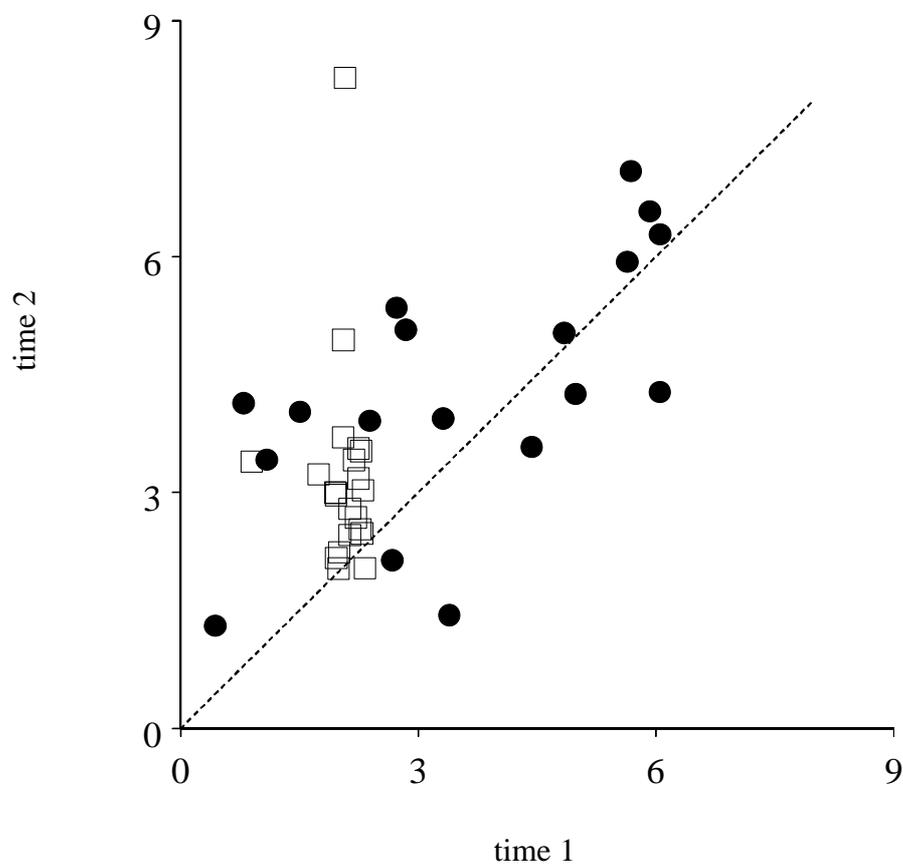


Figure 6.6 The relationship between the percentage organic matter in sediment in containers at the start (time 1) and end (time 2) of the colonization experiment. Filled circles represent containers of site-specific sediment; open squares represent containers of homogeneous sediment. The dotted line is time 2 = time 1.

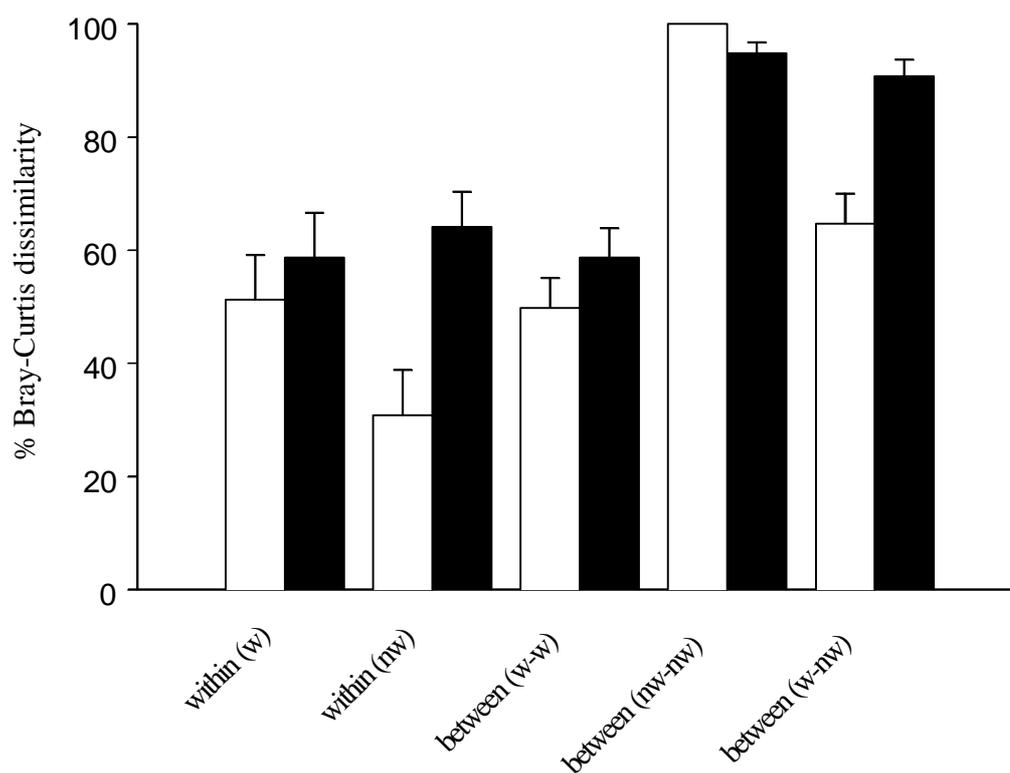


Figure 6.7 Mean (+ S.E) measure of Bray-Curtis dissimilarity for within-site and between-site comparisons in assemblages of homogeneous (white bars) and site-specific (black bars) sediment. w = wash zone; nw = no-wash zone. $n = 40$ or 20 for within (w) and within (nw), respectively; $n = 90$, 15 or 80 for among (w-w), among (nw-nw) and among (w-nw), respectively.

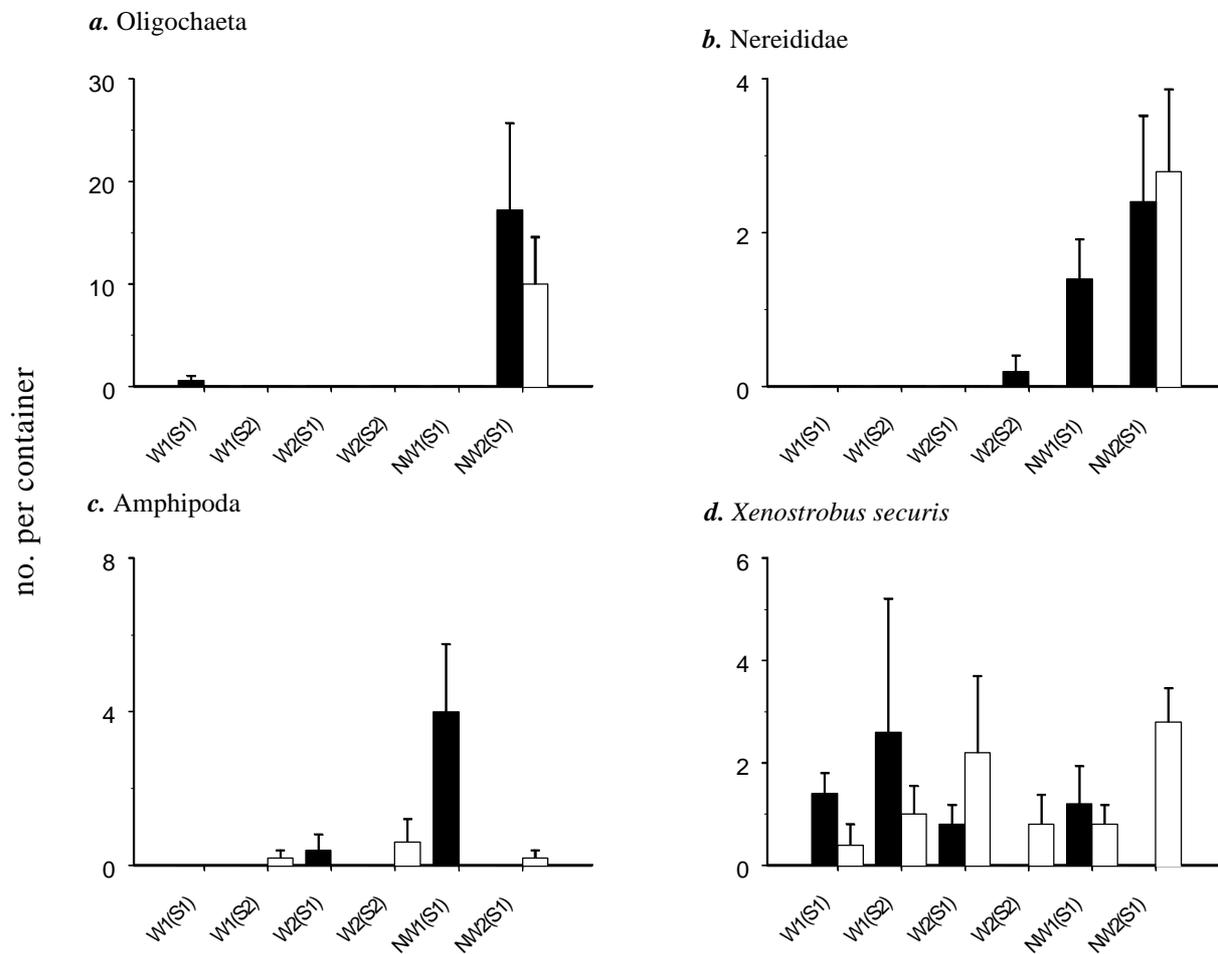


Figure 6.8 Mean (+ S.E.) abundance of macro-invertebrates recruiting to containers of site-specific defaunated sediment (black) and homogeneous defaunated sediment (white). $n = 5$. Data were not available for NW1(S2) and NW2(S2) due to loss of containers.

Table 6.4 Mean squares and estimates of the components of variance (σ^2) from one-factor analyses of variance, showing variability in the abundances of taxa among sites within homogeneous (H) and site-specific (SS) sediment. 2-tailed *F*-tests were done to test the hypotheses that (i) at the spatial scale of sites and (ii) at the scale of replicates, variability would be greater in the site-specific than the homogeneous sediment. $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | HOMOGENEOUS | | | SITE-SPECIFIC | | <i>F</i> -TEST | |
|--------------------------------------|-------------|------|-------|---------------|-------|-----------------|-----------|
| a. Oligochaeta | | | | | | | |
| | <i>df</i> | MS | s^2 | MS | s^2 | <i>F</i> -ratio | Sig. |
| sites | 5 | 83.3 | 13.2 | 234.4 | 34.9 | 2.64 | NS |
| res | 24 | 17.4 | 17.4 | 59.8 | 59.8 | 3.44 | ** H < SS |
| b. Nereididae | | | | | | | |
| | <i>df</i> | MS | s^2 | MS | s^2 | <i>F</i> -ratio | Sig. |
| sites | 5 | 6.53 | 1.12 | 5.09 | 0.76 | 1.47 | NS |
| res | 24 | 0.95 | 0.95 | 1.30 | 1.30 | 1.37 | * H < SS |
| c. Amphipoda | | | | | | | |
| | <i>df</i> | MS | s^2 | MS | s^2 | <i>F</i> -ratio | Sig. |
| sites | 5 | 0.27 | -0.02 | 12.9 | 2.0 | X | |
| res | 24 | 0.36 | 0.36 | 2.7 | 2.7 | 7.50 | ** H < SS |
| d. <i>Xenostrobus securis</i> | | | | | | | |
| | <i>df</i> | MS | s^2 | MS | s^2 | <i>F</i> -ratio | Sig. |
| sites | 5 | 4.45 | 0.29 | 4.80 | -0.31 | X | |
| res | 24 | 3.02 | 3.02 | 6.33 | 6.33 | 2.1 | * H < SS |

6.3.2 Transplant of infaunal assemblages

During the experiment, the following pots of sediment were lost: two transplanted from W2 to W1, two transplanted from NW1 to W1, two transplanted from NW2 to W1, three translocated at W2 and one transplanted from W1 to W2. All pots at NW1 and NW2 were retrieved.

At each location, assemblages in undisturbed sediment changed during the experiment (NP-MANOVA: time x location interaction, $p < 0.001$; *a posteriori* tests: time 1[U1] \neq time 2 [U2], at each of the locations). This change was greatest at W1 and NW2 (Fig. 6.9a). Consequently, assemblages in disturbance (DC) and translocation (TC) controls were compared to those of undisturbed sediment at the end of the experiment (U2) to determine whether any experimental artifacts were introduced by the handling of sediment and/or its deployment in containers. Differences among the three treatments were evident at all locations (Fig. 6.9b, NP-MANOVA: sig. treatment x location interaction, $p < 0.001$; *a posteriori* tests: U2 \neq DC \neq TC, for each location), but were greatest in the wash zone (W1, W2). So that the effects of transplantation were not confounded by the significant impact of handling the sediment, assemblages in transplants were compared to those in translocation controls to test hypotheses.

If wash directly determines the structure of assemblages, it was predicted that assemblages transplanted between wash and no-wash zones would become more similar to assemblages at their destination than their source and assemblages transplanted within a zone would not change markedly. If properties of the sediment contribute to within-zone variability, within-zone transplants would contain assemblages more similar to those of their source than their destination at the end of the experiment. In 6 of the 8 cross-zone transplants, assemblages were more similar to the translocation control at their source than the translocation control at their destination (Table 6.5). The exceptions were transplants from W1 to NW1 and to NW2, where assemblages were more similar to those at their destination. Within-zone transplants in the wash zone resulted in assemblages that were more similar to controls at their destination than at their source. In the no-wash zone, within-zone transplants yielded the opposite pattern – assemblages remained more similar to those at their source (Table 6.5).

Univariate patterns were also examined to test the hypothesis regarding the role of wash in determining abundances of taxa. If wash directly determines the abundances of taxa, densities should increase following transplantation of cores from the wash to the no-wash zone, decrease following transplantation from the no-wash zone to the wash zone and remain similar if cores are transplanted within a zone.

First, however, abundances of taxa were compared between undisturbed cores collected at the start of the experiment and at its end to determine whether any natural temporal change occurred. Only the abundance of Capitellidae at NW2 differed significantly between the two times of sampling (Table 6.6a), although there was a general, albeit patchy, pattern of smaller abundances at time 1 than time 2 (Figure 6.10). The abundances of taxa in disturbance and translocation controls were compared to abundances in undisturbed sediment at the end of the experiment to determine whether there were any experimental artifacts in abundances associated with the handling of sediment and its deployment in containers. The disturbance and translocation of sediment significantly increased the abundance of Nereididae in containers deployed at NW2 (Table 6.6b, Fig. 6.11b). At NW1, the abundance of Sabellidae was greater in disturbed sediment than in translocated or undisturbed cores (Table 6.6b, Fig. 6.11c). Although not statistically significant, the handling of sediment also increased the abundances of the other taxa at a majority of sites (Fig. 6.11). Due to the apparent artifacts involved in manipulating sediment, transplants were compared to translocation controls to enable tests of hypotheses.

Patterns in the abundances of common taxa of macro-invertebrates in cores (a) transplanted to a common destination from different sources and (b) transplanted to different destinations from a common source are shown in Figures 6.12-6.17 and are summarized in Table 6.7. At W2, NW1 and NW2, the abundances of many taxa were greater in sediment originating from the wash zone than the no-wash zone, despite the initially smaller abundances of taxa in the former. This pattern was, however, only significant for amphipods at W2 (ANOVA: $p < 0.01$; SNK: $TP[NW1] = TP[NW2] < TC[W2] = TP[W1]$). At W1, the opposite pattern was seen – taxa were generally more abundant, although not significantly so (ANOVA: $p > 0.05$), in cores from the no-wash zone. The abundances of Capitellidae, Nereididae, Amphipoda in sediment from a common source were smaller following transplant to a wash zone than transplant to a no-wash zone (Table 6.7). This pattern was statistically significant for capitellids at W1 (ANOVA: $p < 0.001$; SNK: $TC[W1] = TP[W2] < TP[NW1] = TP[NW2]$).

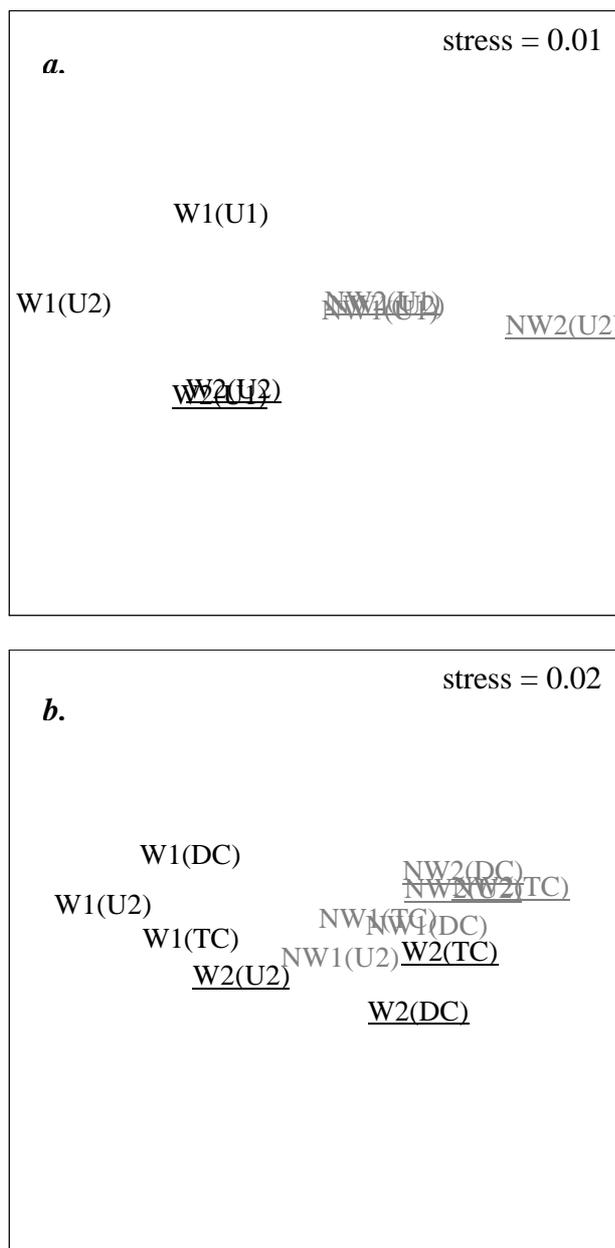


Figure 6.9 nMDS ordinations of assemblages of macroinvertebrates in **a.** undisturbed sediment, at the start (U1) and end (U2) of the experiment, and **b.** in undisturbed sediment (U2), disturbance controls (DC) and translocation controls (TC) at the end of the experiment. There were two locations in the wash zone (W1, W2; black) and two in the no-wash zone (NW1, NW2; grey). Symbols represent centroids of untransformed data. $n = 5$, except for W2(TC) where $n = 2$.

Table 6.5 Summary of average Bray-Curtis measures of dissimilarity between the assemblages of transplants and the translocation controls of their source and destination.

| Source | Destination | Transplant | Dissimilarity to source | Dissimilarity to destination | Most similar to |
|--------|-------------|-------------|-------------------------|------------------------------|-----------------|
| W1 | W2 | within zone | 78 ± 3 | 50 ± 5 | destination |
| | NW1 | W to NW | 90 ± 1 | 47 ± 2 | destination |
| | NW2 | W to NW | 87 ± 1 | 41 ± 3 | destination |
| W2 | W1 | within zone | 75 ± 3 | 52 ± 3 | destination |
| | NW1 | W to NW | 29 ± 4 | 44 ± 4 | source |
| | NW2 | W to NW | 44 ± 4 | 52 ± 3 | source |
| NW1 | W1 | NW to W | 53 ± 4 | 59 ± 2 | source |
| | W2 | NW to W | 35 ± 3 | 52 ± 3 | source |
| | NW2 | within zone | 32 ± 2 | 45 ± 4 | source |
| NW2 | W1 | NW to W | 35 ± 3 | 92 ± 2 | source |
| | W2 | NW to W | 30 ± 2 | 40 ± 2 | source |
| | NW1 | within zone | 22 ± 2 | 64 ± 4 | source |

Table 6.6 Summaries of ANOVAs comparing spatial variation in the abundance of taxa of macroinvertebrates **a.** between cores of undisturbed sediment collected at the start (U1) and the end (U2) of the transplant experiment and **b.** among undisturbed cores at the end of the experiment (U2), disturbance controls (DC) and translocation controls (TC). $n = 5$. NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a.

| | Capitellidae | | | | Nereididae | | | Sabellidae | | | Spionidae | | | Amphipoda | | | <i>Xenostrobus securis</i> | | | |
|----------------|--------------|----------------------|-------|------|------------|-------|------|-------------|------|------|-------------|------|------|-------------|------|------|----------------------------|------|------|--|
| | df | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | |
| ti | 1 | 3.12 | 0.81 | NS | 6.84 | 6.11 | NS | 0.81 | 3.15 | NS | 2.13 | 3.18 | NS | 0.59 | 1.77 | NS | 0.01 | 1.00 | NS | |
| zo | 1 | 11.79 | 1.50 | NS | 58.72 | 20.59 | * | 0.11 | 0.42 | NS | 0.13 | 0.07 | NS | 1.24 | 7.96 | NS | 0.01 | 1.00 | NS | |
| loc (zo) | 2 | 7.86 | 12.96 | *** | 2.85 | 7.99 | ** | 0.25 | 1.48 | NS | 1.81 | 5.91 | ** | 0.16 | 0.94 | NS | 0.01 | 0.33 | NS | |
| ti x zo | 1 | 2.78 | 0.72 | NS | 2.39 | 2.13 | NS | 0.01 | 0.05 | NS | 0.64 | 0.96 | NS | 0.30 | 0.90 | NS | 0.11 | 9.00 | NS | |
| ti x loc (zo) | 2 | 3.88 | 6.39 | ** | 1.12 | 3.14 | NS | 0.25 | 1.48 | NS | 0.67 | 2.19 | NS | 0.33 | 2.01 | NS | 0.01 | 0.33 | NS | |
| res | 32 | 0.61 | | | 0.36 | | | 0.17 | | | 0.31 | | | 0.17 | | | 0.04 | | | |
| Cochran's test | | C = 0.29 NS | | | C = 0.45 * | | | C = 0.57 ** | | | C = 0.29 NS | | | C = 0.36 NS | | | C = 0.33 NS | | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | |
| SNK | | ti x loc (zo) | | | | | | | | | | | | | | | | | | |
| | | W1, W2, NW1: U1 = U2 | | | | | | | | | | | | | | | | | | |
| | | NW2: U1 < U2 | | | | | | | | | | | | | | | | | | |

ti = time (2 levels: U1, U2), zo = zone (2 levels: wash, no-wash), loc (zo) = location (2 levels, random)

b.

| | Capitellidae | | | | Nereididae | | | Sabellidae | | | Spionidae | | | Amphipoda | | | <i>Xenostrobus securis</i> | | | | | | | | |
|----------------|--------------|------------------|-------|------|-------------|--------|------|-----------------------|------|------|-------------|-------|------|------------------------|------|------|----------------------------|------|------|-------------------|--|--|--|--|--|
| | df | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | | | | | | |
| tr | 2 | 1.34 | 2.65 | NS | 1.97 | 3.65 | NS | 0.99 | 0.69 | NS | 0.55 | 0.86 | NS | 0.96 | 2.44 | NS | 0.96 | 6.03 | NS | | | | | | |
| loc | 2 | 44.91 | 58.67 | *** | 52.94 | 418.46 | *** | 3.93 | 2.73 | NS | 5.74 | 16.38 | *** | 2.34 | 4.06 | * | 0.56 | 3.49 | NS | | | | | | |
| tr x loc | 4 | 0.51 | 0.66 | NS | 0.54 | 4.26 | ** | 1.44 | 3.45 | * | 0.64 | 1.84 | NS | 0.39 | 0.68 | NS | 0.16 | 0.64 | NS | | | | | | |
| res | 36 | 0.77 | | | 0.13 | | | 0.42 | | | 0.35 | | | 0.58 | | | 0.25 | | | | | | | | |
| Cochran's test | | C = 0.40 * | | | C = 0.35 NS | | | C = 0.70 ** | | | C = 0.23 NS | | | C = 0.33 NS | | | C = 0.46 ** | | | | | | | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | | | | | | |
| SNK | | tr x loc | | | | | | | | | | | | | | | | | | | | | | | |
| | | W1: U2 < DC < TC | | | | | | W1, NW2: U2 = DC = TC | | | | | | NW1, NW2: U2 = DC = TC | | | | | | NW1: U2 = TC < DC | | | | | |

tr = treatment (3 levels: U2, DC, TC); loc = location (3 levels: W1, NW1, NW2. NW1 was omitted due to the loss of replicates of the TC treatment at this site).

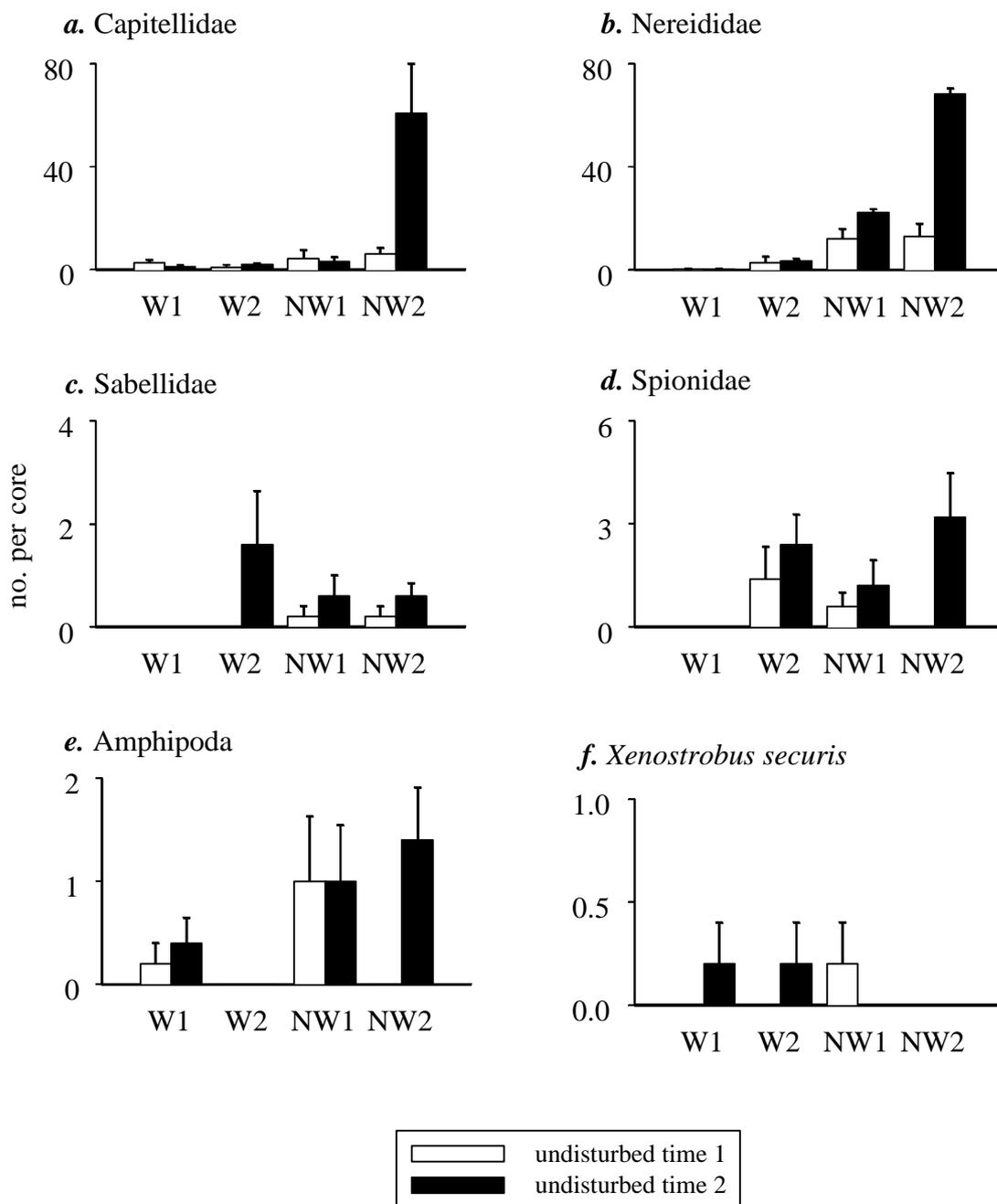


Figure 6.10 Mean (+S.E.) abundance of taxa of macro-invertebrates in cores of sediment collected from the wash zone (W) and no-wash zone (NW) of the upper Parramatta River, at the start (time 1, white) and end (time 2, black) of the manipulative experiment. $n = 5$.

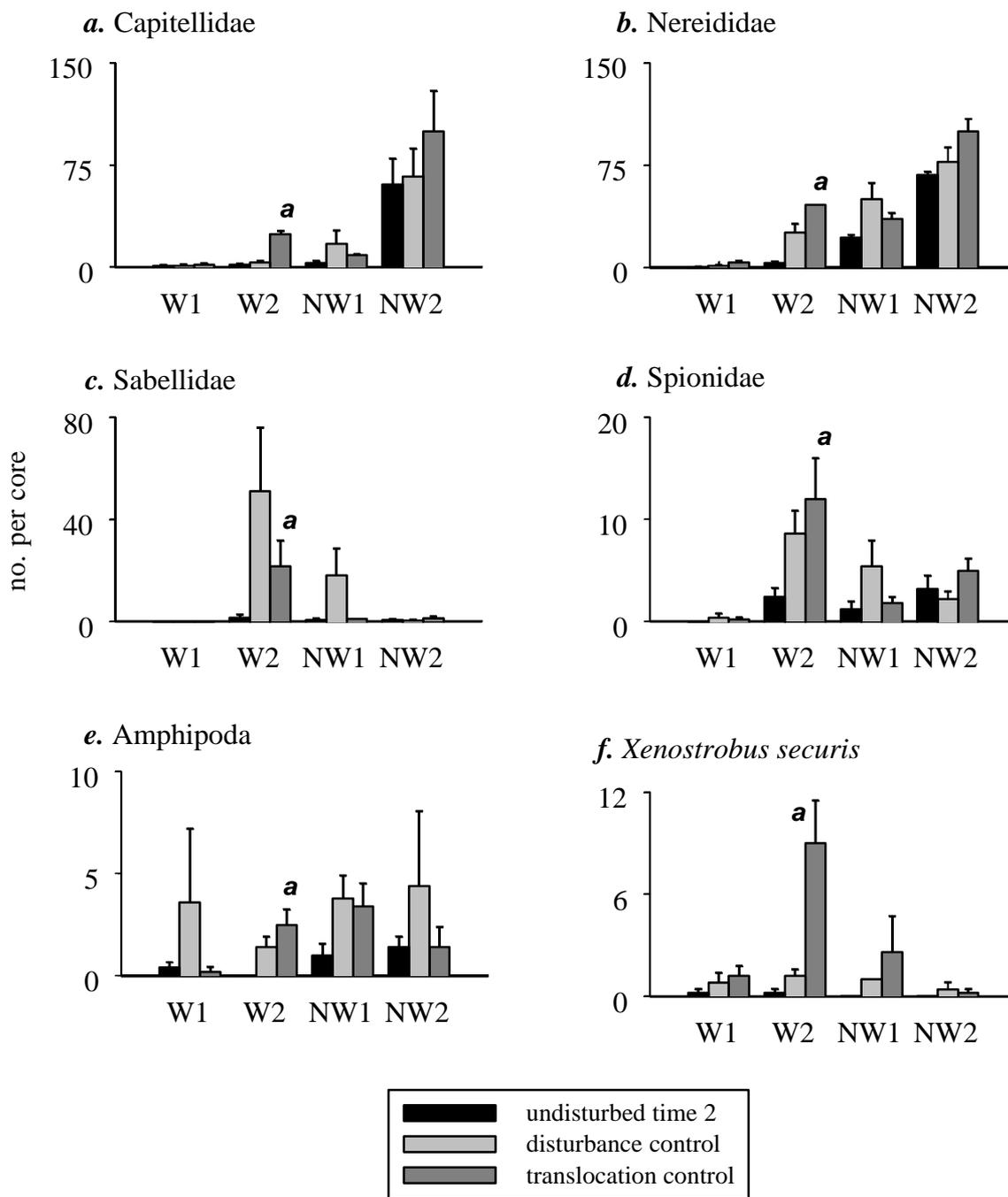


Figure 6.11 Mean (+S.E.) abundance of taxa of macro-invertebrates in cores of sediment collected from the wash zone (W) and no-wash zone (NW) of the upper Parramatta River, at the end (time 2, black) of the manipulative experiment and in disturbance (light grey) and translocation (dark grey) controls. $n = 5$ except where otherwise indicated ($a: n = 2$).

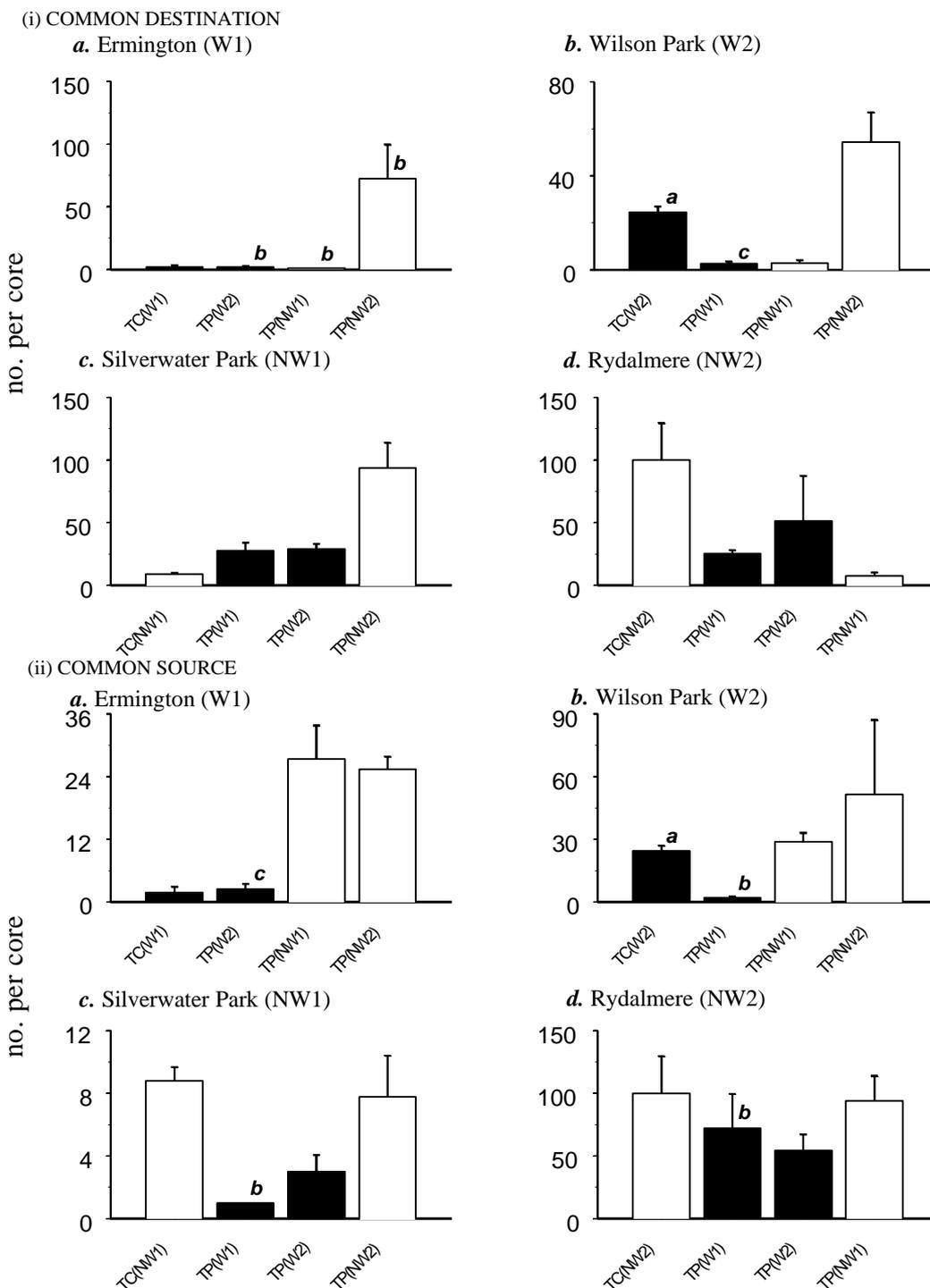


Figure 6.12 Mean (+S.E.) abundance of Capitellidae in containers of sediment (i) transplanted from sites in the wash zone (black) and no-wash zone (white) to a common destination (x-axis) and (ii) transplanted from a common source to each of the sites (x-axis). TC = translocation control; TP = transplant. $n = 5$ except where otherwise indicated (**a**: $n = 2$, **b**: $n = 3$, **c**: $n = 4$).

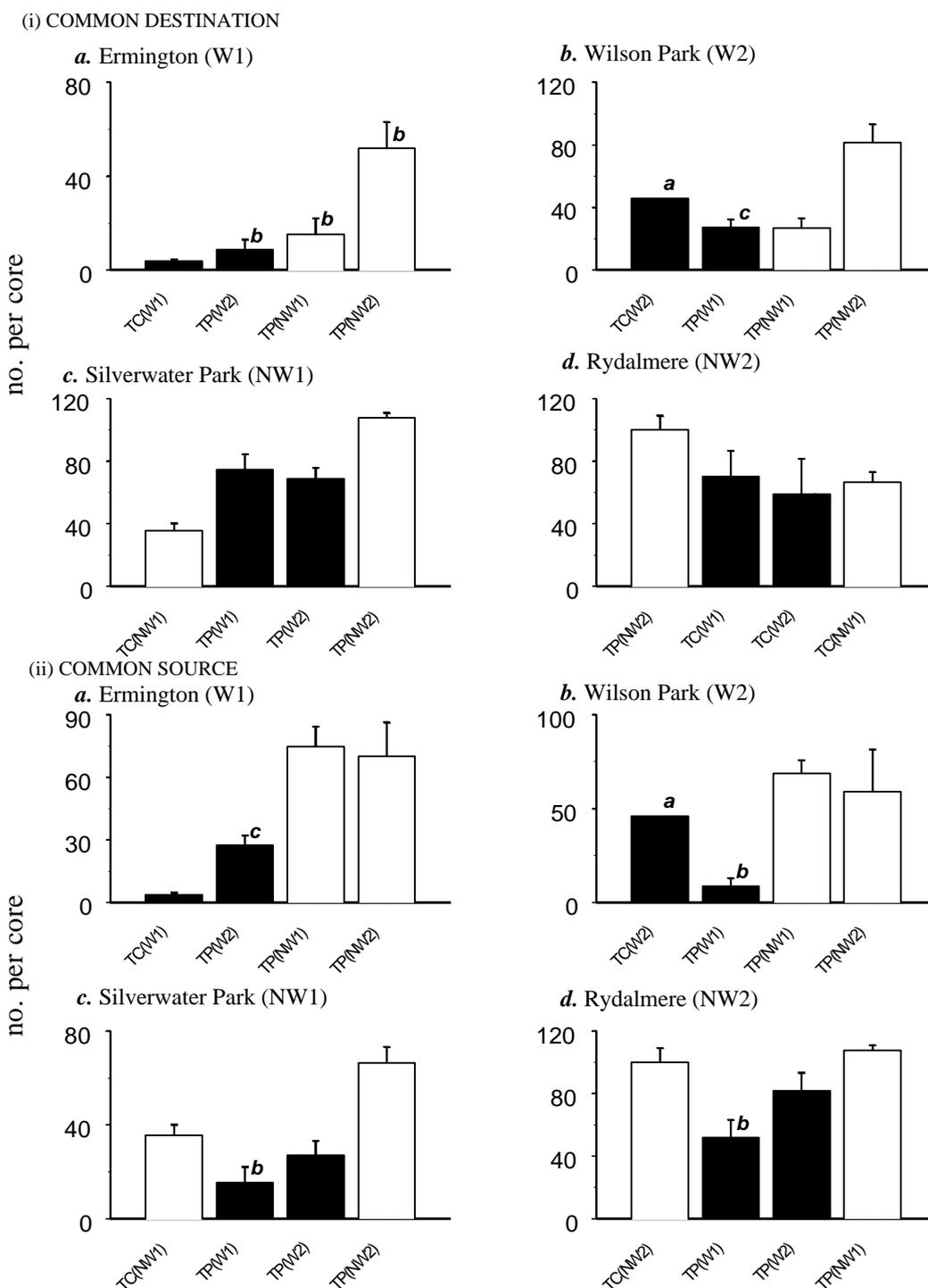
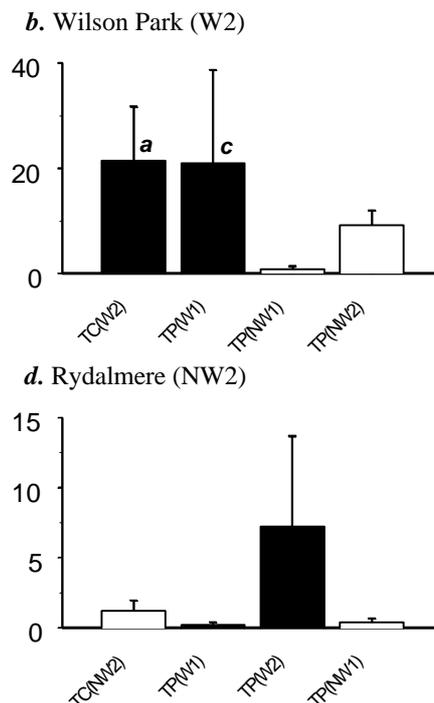
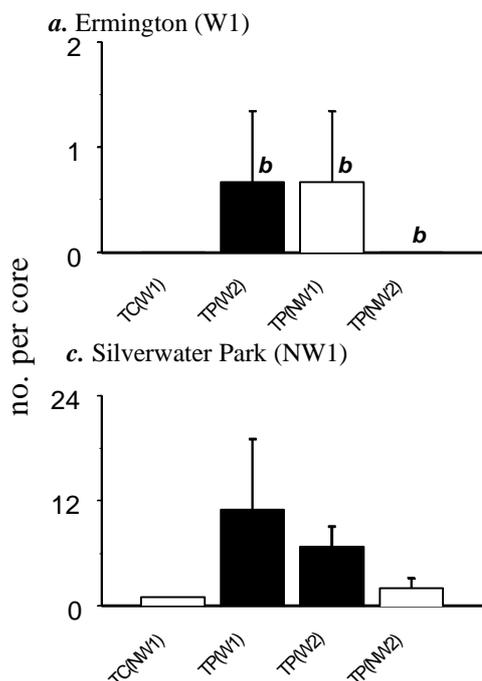


Figure 6.13 Mean (+S.E.) abundance of Nereididae in containers of sediment (i) transplanted from sites in the wash zone (black) and no-wash zone (white) to a common destination (x-axis) and (ii) transplanted from a common source to each of the sites (x-axis). TC = translocation control; TP = transplant. $n = 5$ except where otherwise indicated (**a**: $n = 2$, **b**: $n = 3$, **c**: $n = 4$).

(i) COMMON DESTINATION



(ii) COMMON SOURCE

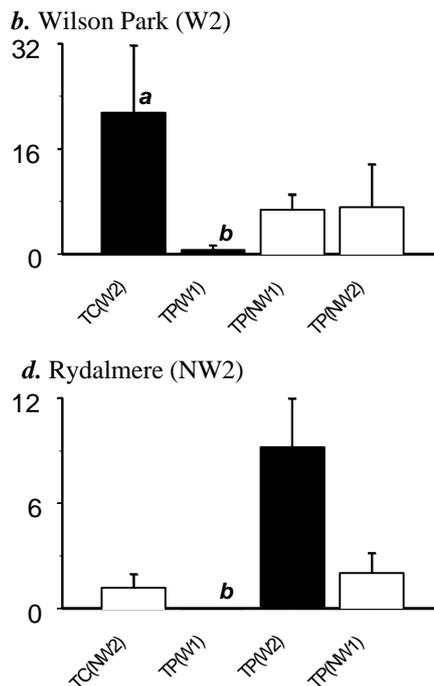
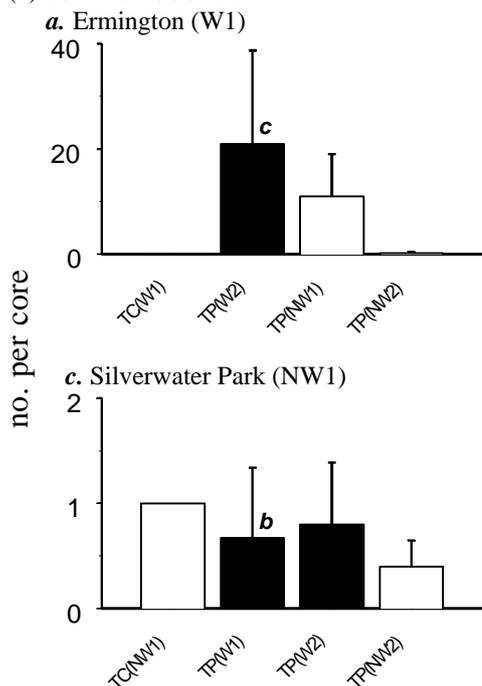


Figure 6.14 Mean (+S.E.) abundance of Sabellidae in containers of sediment (i) transplanted from sites in the wash zone (black) and no-wash zone (white) to a common destination (x-axis) and (ii) transplanted from a common source to each of the sites (x-axis). TC = translocation control; TP = transplant. *n* = 5 except where otherwise indicated (*a*: *n* = 2, *b*: *n* = 3, *c*: *n* = 4).

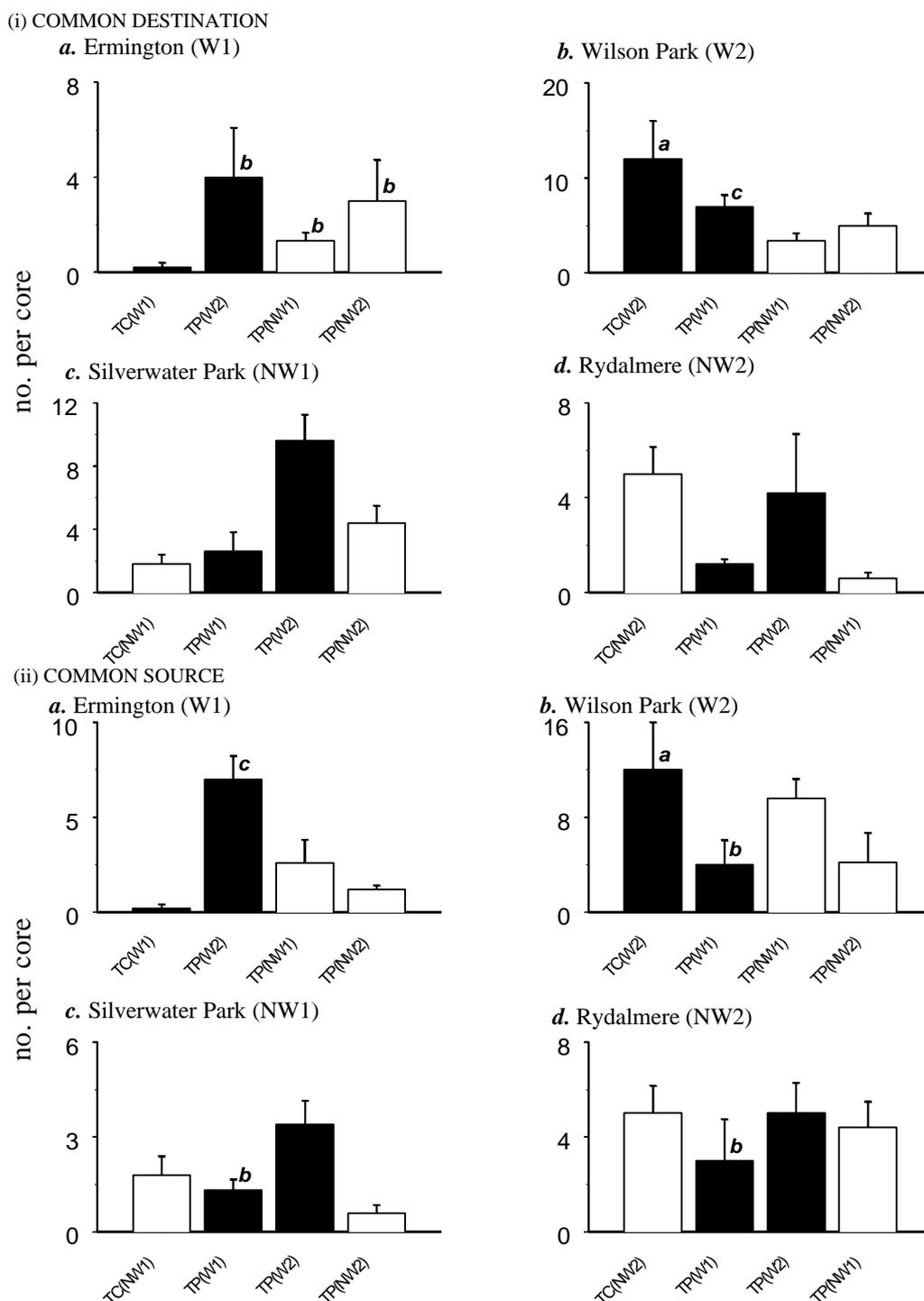


Figure 6.15 Mean (+S.E.) abundance of Spionidae in containers of sediment (i) transplanted from sites in the wash zone (black) and no-wash zone (white) to a common destination (x-axis) and (ii) transplanted from a common source to each of the sites (x-axis). TC = translocation control; TP = transplant. $n = 5$ except where otherwise indicated (*a*: $n = 2$, *b*: $n = 3$, *c*: $n = 4$).

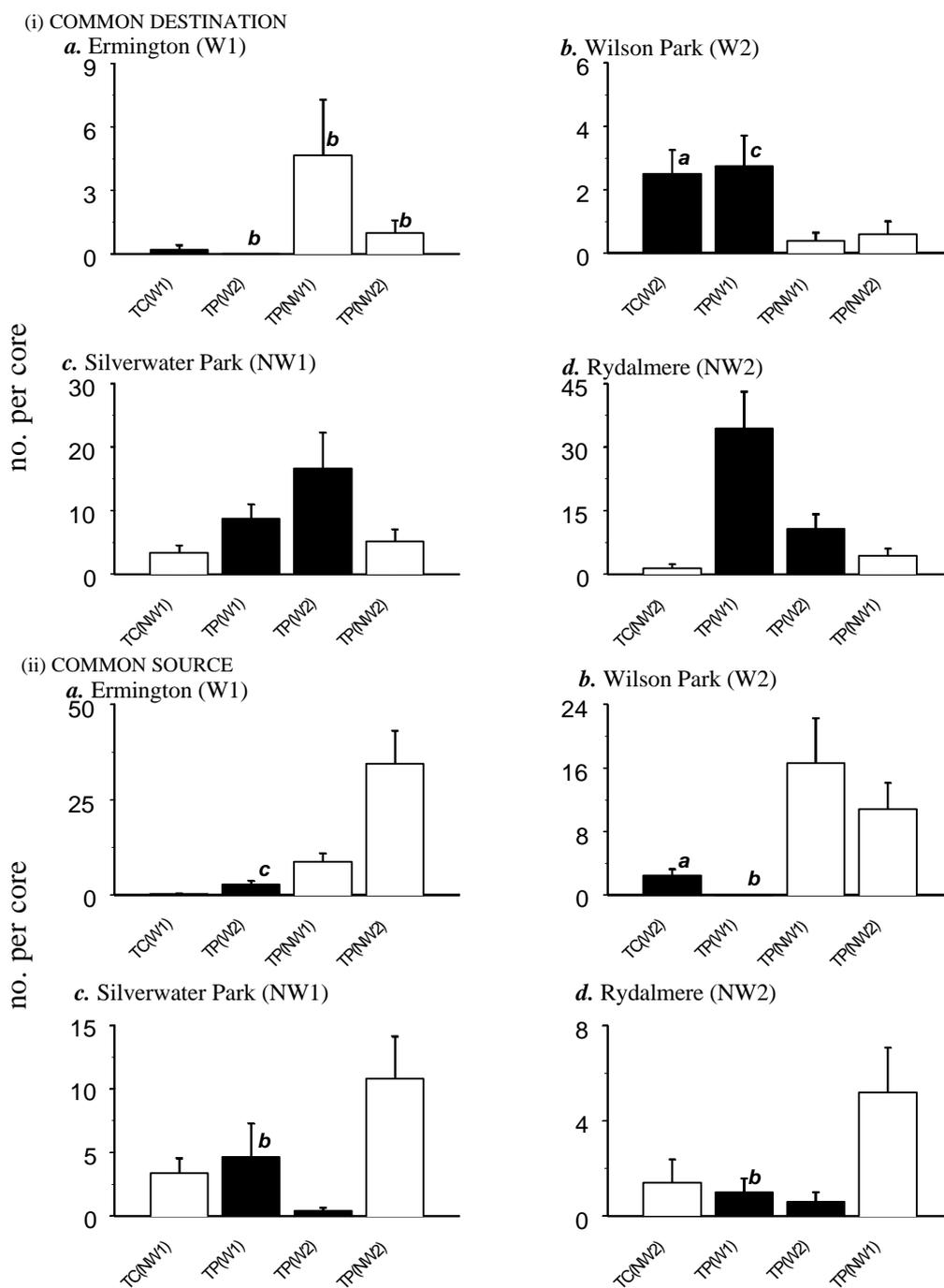


Figure 6.16 Mean (+S.E.) abundance of Amphipoda in containers of sediment (i) transplanted from sites in the wash zone (black) and no-wash zone (white) to a common destination (x-axis) and (ii) transplanted from a common source to each of the sites (x-axis). TC = translocation control; TP = transplant. $n = 5$ except where otherwise indicated (**a**: $n = 2$, **b**: $n = 3$, **c**: $n = 4$).

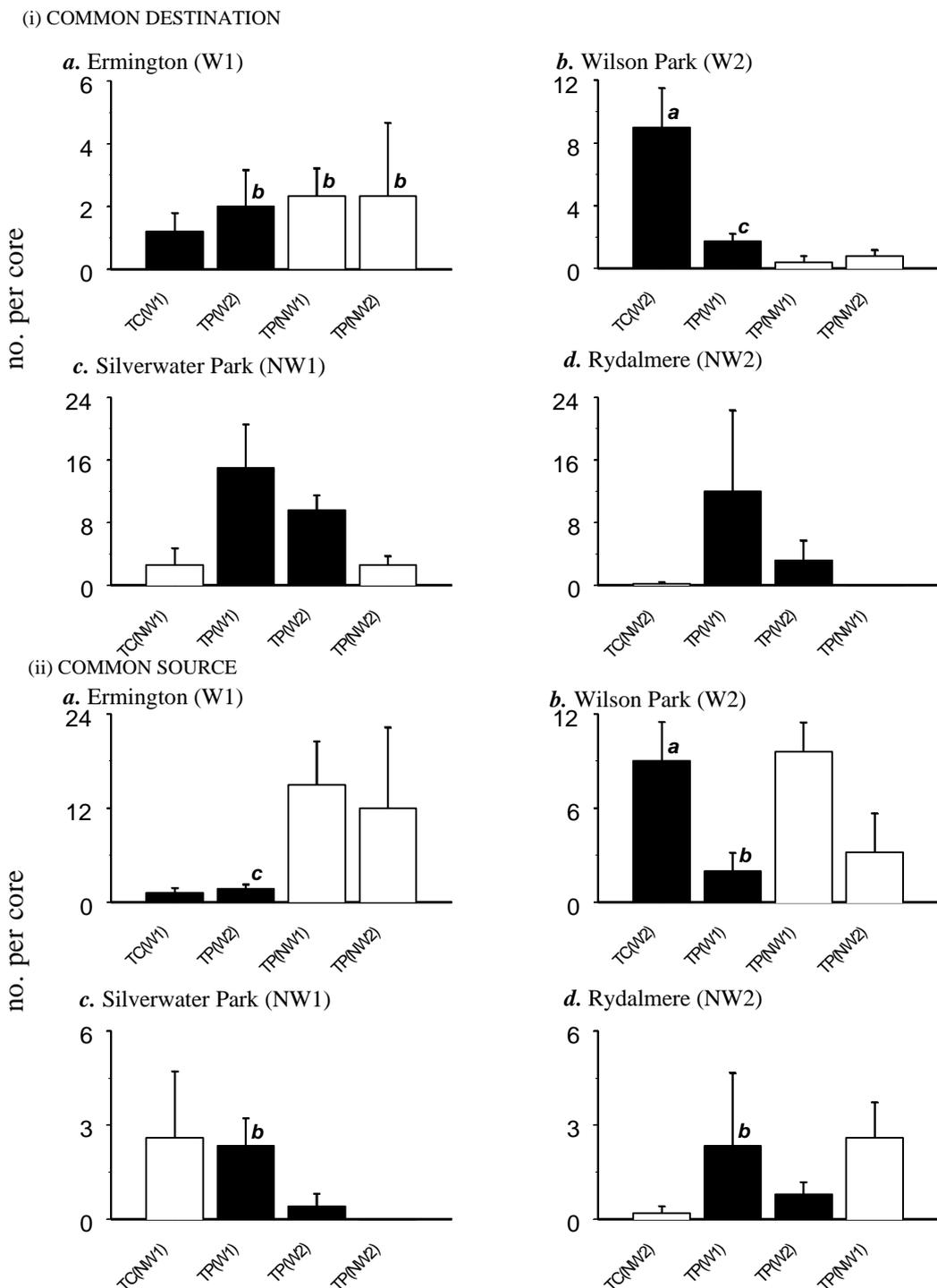


Figure 6.17 Mean (+S.E.) abundance of *Xenostrobus securis* in containers of sediment (i) transplanted from sites in the wash zone (black) and no-wash zone (white) to a common destination (x-axis) and (ii) transplanted from a common source to each of the sites (x-axis). TC = translocation control; TP = transplant. $n = 5$ except where otherwise indicated (**a**: $n = 2$, **b**: $n = 3$, **c**: $n = 4$).

Table 6.7 Summary of patterns in the abundances of macroinvertebrates, shown in Figures 6.11-6.17, **a.** at a common destination (indicated on table) following transplantation from other locations within the wash (W) or no-wash (NW) zone and **b.** in sediment from a common source (indicated on table) when it is transplanted to locations within the wash or no-wash zone. Translocation controls were included in these comparisons; no pattern indicates that there was either no-difference among treatments or the pattern does not relate to wash/no-wash zones.

a. COMMON DESTINATION

| | Ermington (W1) | Wilson Park (W2) | Silverwater Park (NW1) | Rydalmere (NW2) |
|----------------------------|-----------------------|-------------------------|-------------------------------|------------------------|
| Capitellidae | no pattern | no pattern | no pattern | no pattern |
| Nereididae | W < NW | no pattern | no pattern | no pattern |
| Sabellidae | no pattern | W > NW | W > NW | no pattern |
| Spionidae | no pattern | W > NW | no pattern | no pattern |
| Amphipoda | W < NW | W > NW | W > NW | W > NW |
| <i>Xenostrobis securis</i> | W < NW | W > NW | W > NW | W > NW |

b. COMMON SOURCE

| | Ermington (W1) | Wilson Park (W2) | Silverwater Park (NW1) | Rydalmere (NW2) |
|----------------------------|-----------------------|-------------------------|-------------------------------|------------------------|
| Capitellidae | W < NW | W < NW | W < NW | W < NW |
| Nereididae | W < NW | W < NW | W < NW | W < NW |
| Sabellidae | no pattern | no pattern | no pattern | no pattern |
| Spionidae | no pattern | no pattern | no pattern | no pattern |
| Amphipoda | W < NW | W < NW | no pattern | W < NW |
| <i>Xenostrobis securis</i> | W < NW | no pattern | no pattern | no pattern |

6.4 Discussion

6.4.1 Colonization experiment

In natural habitats, assemblages frequently vary among replicates because of differences in micro-habitat (e.g. Underwood and Chapman, 1996; Evans and Norris, 1997). This variability makes it difficult to compare the effects of different levels of a factor of interest. Artificial substrata are appealing to ecologists because, through the provision of identical replicates, they minimize background variability in assemblages (e.g. Myers and Southgate, 1980). The usefulness of artificial substrata is, however, dependent on the degree to which processes structuring their assemblages match those structuring assemblages in natural habitats (Smith, 2000). The results presented here suggest that, as with variability in assemblages of hard substrata (e.g. Myers and Southgate, 1980), variability in assemblages of sedimentary habitats can be reduced through the use of artificial sampling units.

Sampling of the sediment-related variables, organic content and grain-size, showed that, like the fauna, these varied along the Parramatta River at the spatial scales of metres, tens of metres and hundreds of metres. If sediment-related variables are as important in structuring infaunal assemblages as suggested by the literature (e.g. Gray, 1974; Ishikawa, 1989), variability in sediment grain-size and organic content along the Parramatta River may be contributing to variability in assemblages.

Assemblages colonizing containers of homogeneous defaunated sediment, deployed in the wash or the no-wash zone of the Parramatta River, were less spatially variable among replicates than were those colonizing defaunated site-specific sediment. They were also less variable among sites in the wash zone. Moreover, the abundances of the four taxa that were analysed separately were less variable among replicates in the homogeneous than in the site-specific sediment. This suggests that characteristics of the sediment are indeed important in determining patterns of recruitment of these macro-invertebrates, as has been reported by studies such as Gray (1974), Ishikawa (1989) and Etter and Grassle (1992) and that spatial variability in these characteristics does contribute to spatial variability in assemblages.

Despite the reduced spatial variability of assemblages colonizing the homogeneous sediment, a difference between assemblages colonizing these containers was not seen between the wash and no-wash zone. Contrary to the hypothesis, the dissimilarity between assemblages in the wash and in the no-wash zone was greater in the site-specific sediment. Thus, wash does not appear to be as important in determining recruitment of infauna over the temporal scale of the study as are intrinsic characteristics of sediments in different locations. The number of organisms colonizing containers was, however, very small. After one month, many containers contained no organisms

and almost all contained fewer than 10 individuals. Thus, the similarity of assemblages colonizing defaunated sediment in the wash or no-wash zone may have been because recruitment was not sufficient for the test to be fairly assessed. It is recommended that future studies employing this methodology should deploy containers for a longer period of time.

Previous studies have suggested that artificial substrata sampled during cold weather are colonized by fewer individuals, of fewer species, than during warm-weather (e.g. Shaw and Minshall, 1980; Williams, 1980). These were, however, done at higher latitudes than the present study, in places where winters are much colder than in Sydney. Thus, although the present study was done during winter, this is unlikely to be the main reason for small rates of colonization given: (i) the comparatively small seasonal change in temperature in Sydney and (ii) the majority of taxa identified in sediments of the Parramatta River were opportunistic (Chapters 4, 5) and should, therefore, have larvae present in the water throughout the year.

The absence of any effect of wash on the colonization of sediments is in contrast to studies on rocky shores that suggest a role of waves in determining patterns of larval settlement and recruitment (e.g. Denny and Shibata, 1989; Bertness et al., 1991; Gaines and Bertness, 1993). Flows associated with waves can result in greater larval fluxes over exposed shores than sheltered shores (Bertness et al., 1991; Gaines and Bertness, 1993) and turbulence associated with breaking waves may result in increased rates of larval settlement (reviewed by Meadows and Campbell, 1972). While larval fluxes and turbulence should also be greater on exposed than on sheltered intertidal mudflats, this study found no difference in colonization between the wash zone and no-wash zone of the upper Parramatta River. This may be because the magnitude of waves produced by RiverCats is much smaller than the majority of waves that break on exposed rocky shores and differences in larval flux and turbulence between wash and no-wash zones of the Parramatta River are insufficient to cause detectable differences in colonization between these places.

Alternatively, the differing results of this study and previous work on rocky shores may be because characteristics of flow differ markedly between soft- and hard-bottomed habitats, due to differing topographic complexity between these and/or the rigidity of hard surfaces versus the plasticity of sediments (e.g. Smith and McLean, 1977; Grant and Madsen, 1982).

Few studies have previously considered the role of colonization in determining the structure of assemblages in sedimentary habitats (but see Summerson and Peterson, 1990; Peterson, 1991; Peterson and Summerson, 1992). Most of the research on recruitment-limitation has come from hard-bottomed and pelagic habitats (see Gaines and Roughgarden, 1985; Menge and Sutherland, 1987; Underwood and Fairweather, 1989). This study supports the conclusion of Ólaffson *et al.*

(1994) that colonization is not the main processes influencing populations of macroinvertebrates in soft sediments. Patterns in assemblages between the wash and no-wash zone of the upper Parramatta River could not be explained by differences the recruitment of invertebrates to homogeneous or site-specific sediment.

Wash may, instead, influence the structure of assemblages by affecting processes that occur subsequent to colonization. The effect of wash on whole assemblages of macro-invertebrates was considered by the experimental transplant.

6.4.2 Transplantation experiment

In general, the results of the experimental transplant did not support a direct role of wash in determining the structure of assemblages. It was expected that, when transplanted across zones, assemblages would change to become more similar to those in locations to which they were transplanted. Instead, all transplants from locations within the no-wash zone retained assemblages more similar to those at their source than those at their destination, regardless of whether they were transplanted within the no-wash zone or to the wash zone. This was also the case for assemblages transplanted from W2 to the no-wash zone. The persistence of assemblages, regardless of the location to which they are transplanted, supports the model that characteristics of the sediment are of primary importance in structuring assemblages of the upper Parramatta River.

Such persistence was, however, not seen in assemblages transplanted from W1. These assemblages changed to become more similar to those at their destination, whether it was a location of the wash or the no-wash zone. Moreover, assemblages transplanted from W2 to W1 changed to become more similar to assemblages at W1. This suggests that there is some property of the location W1 - perhaps exposure or availability of larvae - that is important in determining the assemblages found there. The influence of this intrinsic factor appears, however, to be less important than characteristics of the sediment from the no-wash zone in determining the structure of assemblages - transplants from the no-wash zone to this location retained assemblages that were similar to those of their source.

In contrast, the model that abundances of individual taxa are directly determined by wash appears to be supported by univariate data. Abundances of Capitellidae, Nereididae and Amphipoda increased when sediment was transplanted from the wash to the no-wash zone and decreased when sediment was transplanted from the no-wash zone to the wash zone. Little change occurred when sediment was transplanted within a zone. Following the transplant of assemblages from different sources to a common destination, abundances of organisms increased

in sediment from the wash zone such that abundances were, in many cases, greater in this sediment than in that from the no-wash zone. These results suggest that it is not the sediment of the wash zone that is limiting the size of these populations. Characteristics of the sediment from wash zones may, in fact, be more favorable for larval settlement than are those of the no-wash zone. Small abundances of taxa in the wash zone may instead be due to greater rates of post-settlement mortality than in the no-wash zone.

Unfortunately the interpretation of this experiment is limited due to experimental artifacts associated with the manipulation of sediment in plastic containers. At some of the sites, assemblages in disturbance controls, where cores of sediment were removed, placed in containers and returned to their source, or translocation controls, where cores of sediment were placed in containers and transplanted to a different position within the site, contained different assemblages to natural sediment. This was most evident at W1. The abundance of polychaetes of the families Capitellidae, Nereididae and Spionidae, Amphipods and the mussel *Xenostrobus securis* were greater in disturbance and translocation controls than in undisturbed sediment at a majority of the sites sampled. Consequently, assemblages and abundances of taxa in transplants could not be directly compared to those of undisturbed sediment but were instead compared to those of translocation controls.

It was intended that by comparing transplants to translocation controls, any effect on assemblages due to a change in environment would be separated from the effects of handling the sediment and placing it in containers (see Connell, 1974). This will not, however, be the case if handling the sediment and placing it in containers does not have a uniform effect among treatments (see Kennelly, 1983). In addition, if the handling of the sediment dominates the experimental conditions, the results will only be applicable to disturbed sediments and not to natural sediments, for which the models were proposed (Peterson and Black, 1994).

Previous studies, using these containers, have not reported any artifacts associated with the structure of the containers or the handling of sediment. Small (1999) used the containers in an experiment examining the effect of polyaromatic hydrocarbons (PAHs) on macrofaunal assemblages. The experiment was done in the muddy sediment of Glades Bay, situated on the lower Parramatta River. She found no difference between the assemblages of natural (undisturbed) cores and control cores, where sediment was placed in containers and injected with seawater (to control for the injection of PAHs), after two weeks. Stark (1996) used similar containers in an experiment where sediment and associated assemblages were transplanted between places polluted with heavy metals and clean places. While the assemblages of undisturbed sediment and disturbance and translocation controls were determined, these were,

however, not directly compared. Thus, it was assumed that there was no experimental artifact associated with their use.

Both the Stark (1996) and Small (1999) studies were done in bays that were relatively sheltered from boat-generated waves. Thus, one of the main differences between the experimental conditions of these studies and the present one is exposure to wash from RiverCats. As RiverCats pass, water accelerates across the adjacent seabed (Patterson Britton 2000c). Thus, the observation of experimental artifacts in the present study, in which sites were exposed to wash from RiverCat ferries, but not in studies by Stark (1996) and Small (1999), where sites were sheltered, suggests that the artifact may be due to a reduction in flow by the structure of the containers. The cages used in predator exclusion/inclusion experiments are widely acknowledged to cause reductions in water flow and shading (e.g. Virnstein, 1977, 1978; Peterson, 1979; Hurlberg and Oliver, 1980; Schmidt and Warner, 1984; Hayworth and Quinn, 1990; Peckarsky and Penton, 1990). The dispersal of larvae, microbial population growth, local recruitment of fauna and particle-feeding are all flow-dependent processes (Jumars and Nowell, 1984).

6.4.3 Conclusions

The experiments on colonization and transplantation suggested that characteristics of the sediment are important in determining the structure of infaunal assemblages. Thus, although wash does not appear to be directly responsible for differences in assemblages between wash and no-wash zones, it could be indirectly responsible for this pattern. An indirect effect of wash would occur if a difference, between wash and no-wash zones, in the intensity of the disturbance were responsible for differences in sediment-related variables between these places and the sediment-related variable(s) were, in turn, important in structuring assemblages. Although the distribution of grain-sizes did not appear to differ between wash and no-wash zones, organic matter did. Organic matter in sediments is a dominant source of food for deposit-feeders and several studies have suggested that there is a strong relationship between the distributions of animals and organic-carbon (e.g. Longbottom, 1970; Field, 1971; Ishikawa, 1989). Further manipulative experiments would clearly be required to establish causation between: (i) wash and a sediment-related variable such as organic matter and (ii) the sediment-related variable and fauna.

In contrast, the experimental transplant indicated that wash may directly influence the abundances of opportunistic polychaetes, amphipods and the bivalve, *Xenostrobus securis*. Differences in the colonization of these taxa were, however, not seen between the wash and no-

wash zones. Thus, the model that there is a greater mortality of macro-invertebrates in the wash than in the no-wash zone may better explain patterns.

Perhaps the best experiment to evaluate the model of mortality would employ a combination of the approaches described in this chapter. Change in the abundances of taxa of known density, in homogeneous sediment, following deployment to wash and no-wash zones, will occur due to a combination of the processes of recruitment and mortality. Recruitment could be estimated by examining colonization of defaunated sediment and then subtracted from net change in the seeded sediment to give mortality within the wash and the no-wash zone. In order for the model to be supported, greater mortality should be seen in the wash than in the no-wash zone. This experiment was not done because it is very labour-intensive and resources were not available.

Section II.

Seagrasses: baffles or beaters?

CHAPTER 7

BAFFLES OR BEATERS: THE ROLE OF SEAGRASSES IN PROTECTING MACRO-INVERTEBRATES FROM WASH

7.1 Introduction

Seagrass is often the dominant subtidal vegetation of nearshore coastal marine environments and estuaries and it supports dense and diverse assemblages of fauna (e.g. Petersen, 1918; Lewis and Stoner, 1983; Sogard and Able, 1991; Orth, 1992). Infauna are found amongst the rhizomes, motile epifauna are associated with stems and leaves and the surface of the sediment, sessile invertebrates attach to the blades and larger mobile animals are loosely associated with larger-scale features of the seagrass-beds. The abundances and diversities of many faunal groups, including fish, clams, amphipods and polychaetes are often much greater in seagrass beds than in adjacent unvegetated areas (Stoner, 1980; Lewis, 1984; Orth *et al.*, 1984; Summerson and Peterson, 1984; Turner and Kendall, 1999). Seagrass is frequently cited as a nursery ground for marine invertebrates (e.g. Boesch and Turner, 1984; NRC, 1995; Butler and Jernakoff, 1999) because it is perceived to contribute disproportionately to the production of juveniles that will recruit to adult populations.

Many studies have attempted to explain why seagrasses have such large diversities and abundances of organisms associated with them. Amongst the various models that have been proposed are: (i) the reduced efficiency of predators in this habitat due to the shelter provided by its structural complexity (Orth *et al.*, 1984; Castel *et al.*, 1989; Irlandi *et al.*, 1995; but see Lewis, 1984 for an example of a study where this was not the case); (ii) the abundance of food provided by the many epiphytes attached to seagrass blades (see Virnstein *et al.*, 1984; Sánchez-Jerez *et al.*, 1999) and (iii) the enhanced deposition of fine sediment, detritus, plankton and invertebrate larvae due to reduced flow velocities under the canopy (Fonseca *et al.*, 1982).

In addition, seagrasses may have large densities and diversities of associated organisms because they offer protection against hydrodynamic disturbances (see Orth 1975, 1977). The root-mass of seagrasses may offer protection to infaunal organisms from wave-action through stabilization of the substratum. In unvegetated sediments, small wind-driven waves can mix sediment to a depth of 2 cm and larger disturbances such as storms, have been observed to mix sediments to depths greater than 8 cm (see Bell *et al.*, 1997). Previous studies (Orth, 1975, 1977) suggest that the protection offered by the roots of seagrass facilitates greater rates of larval settlement than in unvegetated habitats and reduces the number of adults that are resuspended and transported away by waves. Sedentary species that require stable conditions for maintenance

of their permanent tubes and burrows may also have greater abundances in vegetated areas (Posey, 1988).

Beds of seagrass may also offer protection to epifaunal organisms from wave-action. Seagrass and macroalgae, like terrestrial plants (Oliver, 1971; Shaw *et al.*, 1983; Cionco, 1985), modify flow (Fonseca *et al.*, 1983; Jackson and Winant, 1983). Plants bend when a wave or current passes, deflecting the flow over or around the patch (Madsen and Warnke, 1983), greatly reducing the velocity of the current under the canopy (e.g. Fonseca *et al.*, 1982; Eckman, 1983; Fonseca *et al.*, 1983; Eckman, 1987; Irlandi and Peterson, 1991). Flow through beds is reduced by the drag of seagrass blades (Fonseca *et al.*, 1982; Eckman, 1983). Water-motion can generate large hydrodynamic forces that challenge the attachment of sessile organisms (e.g. Denny *et al.*, 1985; Denny 1987, 1995; Carrington, 1990; Gaylord *et al.*, 1994). Any deflection or dissipation of flow may allow epifaunal taxa that would be displaced by hydrodynamic forces in higher-flow environments to maintain their positions.

Alternatively, the effects of wave-action on epifaunal assemblages may be greater in seagrass beds. Oscillating flows generated by waves cause blades to flap back and forth at the frequency of the waves (Koch and Gust, 1999). This may displace epifaunal organisms living on the blades. Further, beds of seagrass may be fragmented by waves and currents into mosaics of discrete patches surrounded by a matrix of unvegetated sediment (Fonseca *et al.*, 1982; Robbins and Bell, 1994; Fonseca and Bell, 1998). This may indirectly affect assemblages of macro-invertebrates since the abundances of fauna within seagrass beds appear to be correlated with the structure of the bed, particularly density (Heck and Wetstone, 1977; Webster *et al.*, 1998; Attrill *et al.*, 2000) and biomass (Attrill *et al.*, 2000) of shoots.

In this chapter, the impacts of boat-generated waves from the Atlantic Intracoastal Waterway on the invertebrate assemblages in seagrass and unvegetated habitats are compared to determine whether seagrass plays any role in reducing the impact of this disturbance. Initially, cores of sediment were collected from seagrass beds and unvegetated habitats to test the hypotheses that, in unvegetated habitats, assemblages of invertebrates will differ between sites that are exposed to or sheltered from boat-wash, but in seagrass habitat, no such difference will be seen. Subsequent sampling, where blades of seagrass were collected with and without the associated core of sediment was done to test the hypotheses that: (i) differences between the invertebrate assemblages of sheltered and exposed beds of seagrass would be greater when only the epifauna associated with seagrass blades are sampled than when the infauna are also included and (ii) any differences in assemblages between exposures would be primarily due to smaller abundances of epifauna in the exposed places.

7.2 Materials and Methods

7.2.1 Study sites

The Atlantic Intracoastal Waterway (AIW) is a series of federally maintained navigation channels that extend along the southeastern coast of the USA from Norfolk, Virginia to Miami, Florida. For most of its length, the system consists of naturally deep estuaries, rivers and sounds. These have been connected by a series of man-made channels.

In North Carolina, one of the natural waterways through which the AIW passes is the east-west running Bogue Sound (34°40' N, 77°2' W; Fig 7.1). At the western end of the Sound, sediment has been dredged from the AIW and deposited in the center of the Sound, forming spoil islands that have been colonized by salt-marsh. These islands effectively divide this part of the sound into two sections, one that is exposed to the wash of vessels traveling along the AIW and one that is sheltered from wash (Fig. 7.1).

Two places within the sound, approximately 2 km apart, were selected for study. At each, dredge-spoil islands divide the body of water into two sections, each about 1 km wide. It was assumed that their exposure to wind-generated waves would be similar because of their comparable fetches. At each place, samples were collected from four sites (Fig. 7.1): on the exposed side, adjacent to the bank (EB) and dredge-spoil island (ES) and on the sheltered side, also adjacent to the bank (SB) and the dredge-spoil island (SS). ES1 and ES2 were located closer to the main channel of the Atlantic Intracoastal Waterway than to EB1 and EB2. Sites were 25 m long (i.e. in the direction parallel to the shore) and 5 m wide.

The bottom of the sound is composed of sand-flats and grass-flats, with tidal channels running in between. The grass-flats are a mixture of the eelgrass *Zostera marina* (L.) and the shoal grass *Halodule wrightii* (Ascherson). Sites were located in areas where the distribution of seagrass was patchy, so that assemblages of invertebrates within the seagrass habitat could be directly compared with those of the unvegetated sediment in each site.

The water at the sites was approximately 30 cm deep at low tide. Shallow areas were chosen because seagrasses lose their effectiveness in reducing wave-energy as the depth of water increases over the canopy. When the canopy of the seagrass is greater than 25 cm from the water's surface, waves may pass over the canopy without any interaction with the grass (Fonseca and Cahalan, 1992).

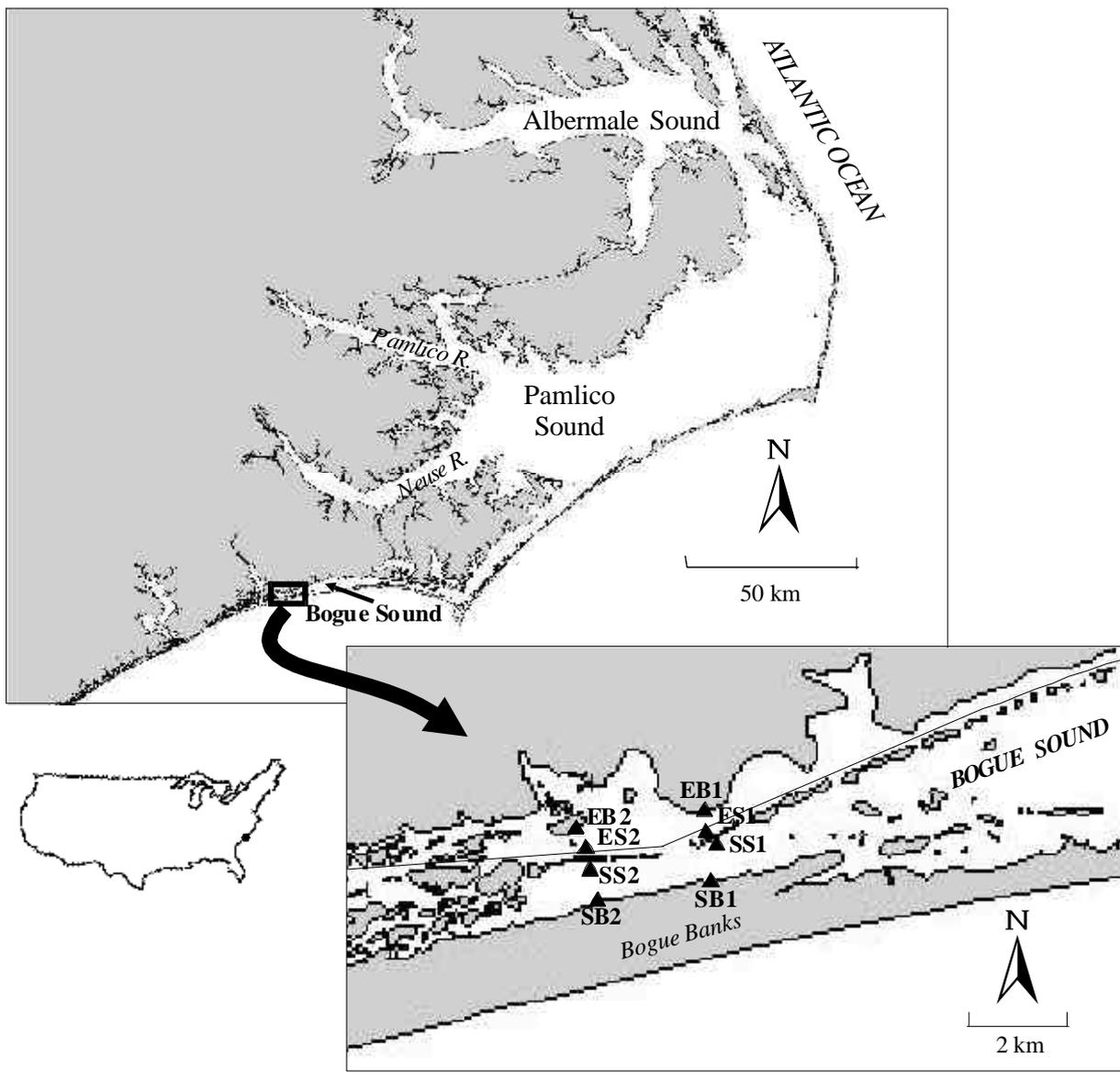


Figure 7.1 Map of the western section of the Bogue Sound, North Carolina, U.S.A., showing the location of sites sampled on the 18th September and 22nd October, 2001 (▲) and the dredged channel of the Atlantic Intracoastal Waterway (—).

EB = exposed side, adjacent to the bank; ES = exposed side, adjacent to the dredge-spoil island; SB = sheltered side, adjacent to the bank; SS = sheltered side, adjacent to the dredge spoil island.

It was hypothesized that within seagrass, there would be no significant difference in the assemblage of invertebrates among sites. Within the unvegetated habitat, assemblages at sites on the sheltered side (i.e. SB and SS) were predicted to be more similar to one another than to sites on the exposed side (EB and ES), within each place. Sites on the exposed side that are adjacent to the dredge spoil island (ES) were predicted to contain assemblages most different from those on the sheltered side because, in the section of the sound studied, the main channel of the AIW is closer to the spoil islands than to the bank and, in shallow water, waves lose energy with distance travelled.

7.2.2 Sampling methods

Invertebrate assemblages in the unvegetated and seagrass habitats were sampled on 18th September 2001 at each of the 8 sites described above. At each site, 5 cylindrical cores of sediment, 10 cm in diameter and 10 cm deep, were haphazardly collected from each of the habitats (unvegetated, seagrass). In the case of the seagrass habitat, these cores included the above-ground biomass of the seagrass (i.e. the blades) and any below-ground component (i.e. roots) in the core.

Samples were placed on ice and transported to the laboratory where they were washed over a 500 μm mesh. The portion of the sample retained by the sieve was preserved in 7% formalin and stained with Rose Bengal. A pair of forceps was run along the length of each blade of seagrass to remove all epifauna. Infauna were also removed from the sediment. No attempt was made to enumerate epifauna and infauna separately because epifauna were probably knocked off seagrass blades and into the sediment during transportation. All animals were identified to the taxonomic groups shown in Table 7.1.

Three additional cores of sediment, 10 cm in length and 2 cm in diameter, were collected from each site using a plastic syringe to determine sediment grain-size (Section 7.2.3). Flow is widely recognized to influence sedimentology (e.g. Gallivan and Davis, 1981; Christie *et al.*, 1999; Li and Amos, 1999) and any difference found between the assemblages of exposed and sheltered places may be due to an indirect effect of changes to the grain-size of the sediment by boat-generated waves. Sediment grain-size analyses were also used to test whether natural differences in characteristics of the sediment among sites caused by Aeolian transport of sand from the Atlantic Ocean, across the 1 km-wide Bogue Bank, to sites along the sheltered bank (SB1, SB2) could affect the fauna.

Table 7.1 Taxa of macro-invertebrates found in cores of unvegetated sediment (U), cores of sediment vegetated with seagrass (S) and on the blades of seagrass (B) collected from the Bogue Sound, North Carolina, U.S.A on 18th September and 22nd October, 2001.

* Amphipods and isopods were present in unvegetated sediment but were not identified to family.

| | | | | |
|----------------|--------------|------------------|------------------------------|-------|
| Annelida | Polychaeta | Ampharetidae | | S |
| | | Arabellidae | | U S |
| | | Capitellidae | | U S |
| | | Chaetopteridae | | U S |
| | | Cirratulidae | | U S |
| | | Dorvilleidae | | U S |
| | | Eunicidae | | U S B |
| | | Glyceridae | | U S |
| | | Goniadidae | | U S |
| | | Lumbrineridae | | U S |
| | | Magelonidae | | U |
| | | Maldanidae | | U S |
| | | Nephtyidae | | U |
| | | Nereididae | | U S B |
| | | Onuphidae | | U S |
| | | Ophelidae | | U S |
| | | Orbinidae | | U S |
| | | Paraonidae | | U S |
| | | Polynoidae | | S |
| | | Sabellidae | | U S B |
| Spionidae | | U S B | | |
| Syllidae | | U S B | | |
| Terebellidae | | S | | |
| Chelicerata | Pycnogonida | Phoxichilidiidae | <i>Anoplodactylus lentus</i> | S B |
| | | | <i>Tanystylum orbiculare</i> | B |
| Chordata | Osteichthyes | Syngnathidae | <i>Syngnathus</i> sp. | S |
| Cnidaria | Anthazoa | Edwardsiidae | <i>Edwardsia elegans</i> | U S |
| | | Haloclavidae | <i>Haloclava producta</i> | U S |
| Crustacea | Eucarida | Alpheidae | <i>Alpheus heterochaelis</i> | S |
| | | Palaemonidae | <i>Palaemonetes pugio</i> | B |
| | | Penaeidae | <i>Penaeus duorarum</i> | S |
| | Decapoda | Portunidae | <i>Callinectes sapidus</i> | U S |
| | | Crab megalops | | U S B |
| | Amphipoda | Caprellidae | | * S B |
| | | Ampeliscidae | | * S B |
| | | Ampithoidae | | * S B |
| | | Aoridae | | * S |
| | | Corophidae | | * S B |
| Gammaridae | | | * S B | |
| Leucothoidae | | | * S B | |
| Liljeborgiidae | | | * S B | |
| Lyssianasidae | | * S B | | |
| Melitidae | | * S B | | |
| Stenothoidae | | * B | | |

Table 7.1 cont.

| | | | | |
|---------------|---------------|------------------|--|-------|
| | Cumacea | | | S |
| | Isopoda | Anthuridae | <i>Cyathura burbanki</i> | * S B |
| | | Idoteidae | <i>Erichsonella attenuata</i> | * S B |
| | | Sphaeromatidae | <i>Paracereis caudata</i> | * S B |
| | Tanaidacea | | | S B |
| | Copepoda | | | U |
| | Ostracoda | | | S B |
| Echinodermata | Ophiuroidea | Amphiuridae | <i>Axiognathus squamatus</i> | S |
| | | Ophiodermatidae | <i>Ophioderma brevisipina</i> | B |
| | | Ophiothricidae | <i>Ophiothrix angulata</i> | S |
| | Echinoidea | Arabaciidae | <i>Arbacia punctulata</i> | S |
| | Holothuroidea | Cucumariidae | <i>Thyonella gemmata</i> | S |
| | | | <i>Thyone briareus</i> | S |
| | | Synaptidae | <i>Leptosynapta tenuis</i> | S |
| Mollusca | Bivalvia | Arcidae | <i>Anadara ovalis</i> | S B |
| | | | <i>Anadara transversa</i> | S |
| | | Nuculidae | <i>Nucula proxima</i> | S |
| | | Cardiidae | <i>Lavaecardium</i> sp. | S |
| | | | <i>Trachycardium muricatum</i> | S |
| | | Pectinidae | <i>Agropecten irradians concentricus</i> | S B |
| | | Mytilidae | <i>Brachiodontes exustus</i> | S B |
| | | Veneridae | <i>Mercenaria</i> spp. | S |
| | | | <i>Gemma gemma</i> | U S B |
| | | | <i>Chione</i> spp. | S |
| | | Mactridae | <i>Mulinia lateralis</i> | U S |
| | | Lucinidae | <i>Divaricalla quadrisulcata</i> | U |
| | | Tellinidae | <i>Tellina</i> spp. | U S |
| | | Lyonsiidae | <i>Lyonsia hyalina</i> | S B |
| | | Solecurtridae | <i>Tagelus divisus</i> | S |
| | | | <i>Tagelus plebeius</i> | S |
| | | Solenidae | <i>Ensis minor</i> | S |
| | | Solemyidae | <i>Solemya velum</i> | U S |
| | | juvenile bivalve | | U S |
| | Gastropoda | Epitoniidae | <i>Epitonium rupicola</i> | S |
| | | | <i>Epitonium multistriatum</i> | S |
| | | Cerithiidae | <i>Bittium varium</i> | U S B |
| | | Nassariidae | <i>Nassarius vibex</i> | S |
| | | Pyramidellidae | <i>Pyramidella crenulata</i> | S |
| | | Turridae | <i>Pyrgocythara plicosa</i> | U S B |
| | | Collumbellidae | <i>Costoanachis avara</i> | S B |
| | | | <i>Astyris lunata</i> | S B |
| | | Scaphandridae | <i>Acteocina canaliculata</i> | U S |
| | | Crepidulidae | <i>Crepidula fornicata</i> | S B |
| Nematoda | | | | U S B |
| Nemertea | | | | U S B |

To test hypotheses regarding the impact of wash on phytal assemblages of epifauna, blades of seagrass were sampled with and without the associated core of sediment on 22nd October, 2001. At each of the 8 sites, five cores of sediment and five samples of blades were collected from patches of seagrass. Cores were collected using the method described above. Blades were sampled using a similar method to Jernokoff and Nielsen (1998). Circular quadrats, 10 cm in diameter were haphazardly placed in the patches of seagrass and all material within each quadrat was collected by carefully cutting the seagrass just above the substratum and placing the seagrass and attached epiphytes slowly and carefully into plastic bags so that mobile epifauna stayed with the cut clumps.

Blades of seagrass from each of the 'blade-only' samples were retained for measurement of dry weight to test the hypothesis that the biomass per unit area would be less in the exposed than in the sheltered sites. Dry weight was determined by drying the seagrass at 80°C for 48 hours (constant weight) as per Lee *et al.* (2001).

7.2.3 Analyses of sediment grain-size

Cores were frozen for two weeks at -40°C. When defrosted, samples were homogenized and placed in a 4 ϕ (63 μ m) size sieve so that the fine fraction (< 63 μ m - to be used for pipette analysis) could be separated from the coarse fraction (= 63 μ m - to be passed through dry sieves). A tightly-fitting funnel with a 1000 ml graduated cylinder attached to it was placed under the sieve. The sample was washed until the stream leaving the funnel contained no fine sediment and was clear in colour. The total volume of sediment and water in the graduated cylinder was made up to 1000 ml.

The fine fraction in the graduated cylinder was carefully mixed by moving a plastic rod up and down, from bottom to top, for exactly one minute. The sample was left to settle for 1 min 56 sec, at which time a 20 ml sample was taken from a depth of 10 cm using a pipette (see Folk, 1974 for a full description of pipette analysis). The contents of the pipette were transferred to a small, pre-weighed aluminum pan. All water was removed from the sample by drying it at 85°C for 48 hours (or constant weight). The dry-weight of the sample was multiplied by 50 to determine the total quantity of sediment of grain-size less than 63 μ m in the core. A full pipette analysis, where the weights of finer fractions are also determined, was not done because: (i) the sediment was fairly coarse and these fractions contributed little to the overall weight and (ii) small fractions are unlikely to be of ecological significance to macrobenthic invertebrates.

Sediment retained on the 4 ϕ sieve was transferred to pre-weighed aluminum pans and dried to constant weight at 85°C. This sediment was then placed in a 0 ϕ (1 mm) sieve, at the top of a stack also containing 1 ϕ (500 μm), 2 ϕ (250 μm), 2.5 ϕ (177 μm), 3 ϕ (125 μm), 3.5 ϕ (88 μm) and 4 ϕ (63 μm) sieves and a pan for the collection of fine sediment at its base. The column of sieves was mechanically shaken for 10 min using a Ro-Tap (Tyler) sieve-shaker. The dry weight of each fraction was determined and the proportion each contributed to total mass was calculated.

7.3 Results

7.3.1 Analyses of sediment grain-size

nMDS ordinations of grain-sizes of sediment collected from unvegetated areas and patches of seagrass at eight sites along the Bogue Sound are shown in Figure 7.2. In each habitat, there were distinct differences in sediment grain-size among sites. Sites adjacent to the natural banks of the sound (i.e. EB1, SB1, EB2, SB2) generally had more similar sediment than did sites located adjacent to the dredge spoil islands (ES1, SS1, ES2, SS2), evident by the separation of points into two groups. The exception was the sediment at EB2, which appeared more similar to sediment at the dredge spoil islands than to sites along the other banks of the sound. The similarity of sediment from EB1, on the northern bank of the sound, to that from SB1 and SB2, on the southern side, indicates that wind-driven transport of sediment from the Atlantic coastline is not a major factor influencing characteristics of the sediment along the southern bank of the sound. Differences between assemblages representing cores from ES1 and ES2 (the most exposed sites sampled) and assemblages in less-exposed sites were no greater than differences among assemblages in less-exposed sites.

7.3.2 Assemblages of unvegetated sediment and sediment vegetated with seagrass (September)

Eighty-nine taxa were collected from cores of sediment and blades of seagrass (Table 7.1). Assemblages of unvegetated sediment and sediment with seagrass were analysed separately because (i) they appeared very different and (ii) hypotheses regarding the effects of wash did not require direct comparisons.

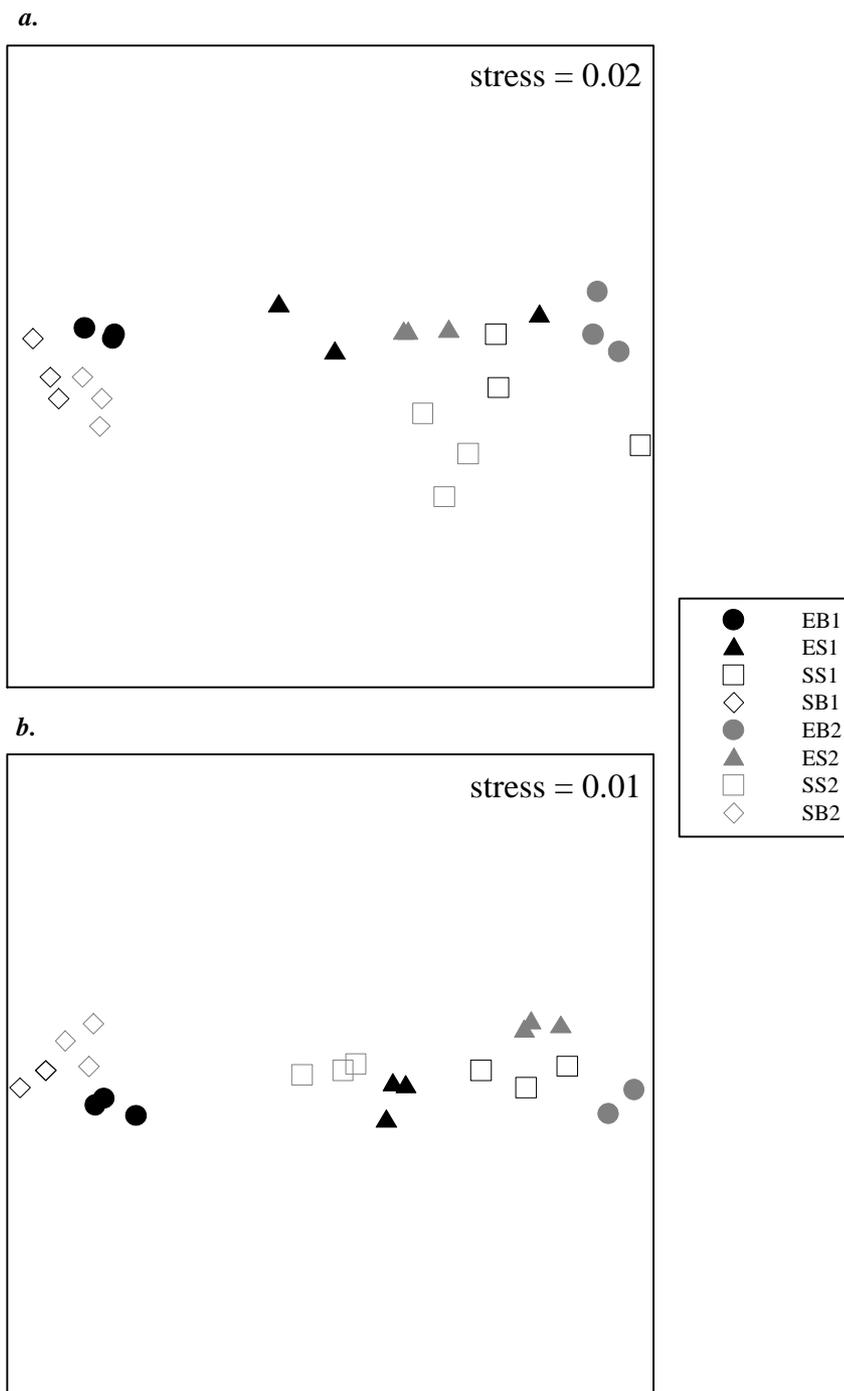


Figure 7.2 nMDS ordination of grain-sizes of samples of **a.** unvegetated sediment and **b.** sediment vegetated with seagrass, collected from the four sites within each of the two places along the Bogue Sound where macro-invertebrates were sampled; $n = 3$. Normalized Euclidean distances were used.

EB = exposed bank, ES = exposed spoil, SS = sheltered spoil, SB = sheltered bank.

Ordination of centroids representing average assemblages at sites shows that in the unvegetated habitat (Fig. 7.3 (i) a), there was no apparent difference in assemblages between sites that were exposed to and sheltered from boat-traffic along the Atlantic Intracoastal Waterway (AIW). Points separated out into four groups that bore no relationship to exposure or grain-size of the sediment. Assemblages of the vegetated sediment, in contrast, separated into two groups that corresponded, to some extent, to exposure (Fig. 7.3 (ii) a). The first group included sites along the sheltered bank and sheltered side of spoil islands and the site on the exposed bank of place 1 (EB1). The other group contained the other sites (i.e. sites sampled along exposed spoil islands and the exposed bank of place 2).

Separate ordinations of individual replicates within sites were done for each of the two habitats and two places sampled (Fig. 7.3 b, c). A gradient in environmental variables along the sound could result in differences between the assemblages in the two places that, on ordinations including all replicates, may preclude the observation of patterns relating to exposure. No clear separation of points into exposure-groups was evident in an ordination of replicates from unvegetated sediment at place 1 (Fig. 7.3 (i) b). At place 2, however, replicates from the unvegetated sediment of EB2 and ES2 (the two exposed sites) appeared to differ from those of other places (Fig. 7.3 (i) c). These patterns were confirmed by NP-MANOVA (Table 7.2).

Table 7.2 Summaries of non-parametric MANOVAs comparing spatial variation in assemblages of macro-invertebrates associated with *a.* unvegetated sediment and *b.* sediment vegetated with seagrass among sites differing in exposure to boat-wash from the Atlantic Intracoastal Waterway, Bogue Sound. Samples were collected on 18th September, 2001. pl = place (2 levels; random), ex = exposure of site (4 levels: exposed spoil [ES], exposed bank [EB], sheltered spoil [SS], sheltered bank [SB]; fixed). $n = 5$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| source of variation | df | <i>a.</i> unvegetated | | <i>b.</i> vegetated | |
|---------------------------|----|---------------------------|-----|---------------------------|-----|
| | | <i>p</i> | sig | <i>p</i> | sig |
| pl | 1 | 0.0866 | NS | 0.0048 | ** |
| ex | 3 | 0.2938 | NS | 0.1944 | NS |
| pl x ex | 3 | 0.0002 | *** | 0.0002 | *** |
| res | 32 | | | | |
| <i>a posteriori</i> tests | | pl 1: EB ? (ES = SS) ? SB | | pl 1: (EB = SB) ? ES ? SS | |
| | | pl 2: (EB = ES) ? SS ? SB | | pl 2: (EB = SS) ? ES ? SB | |

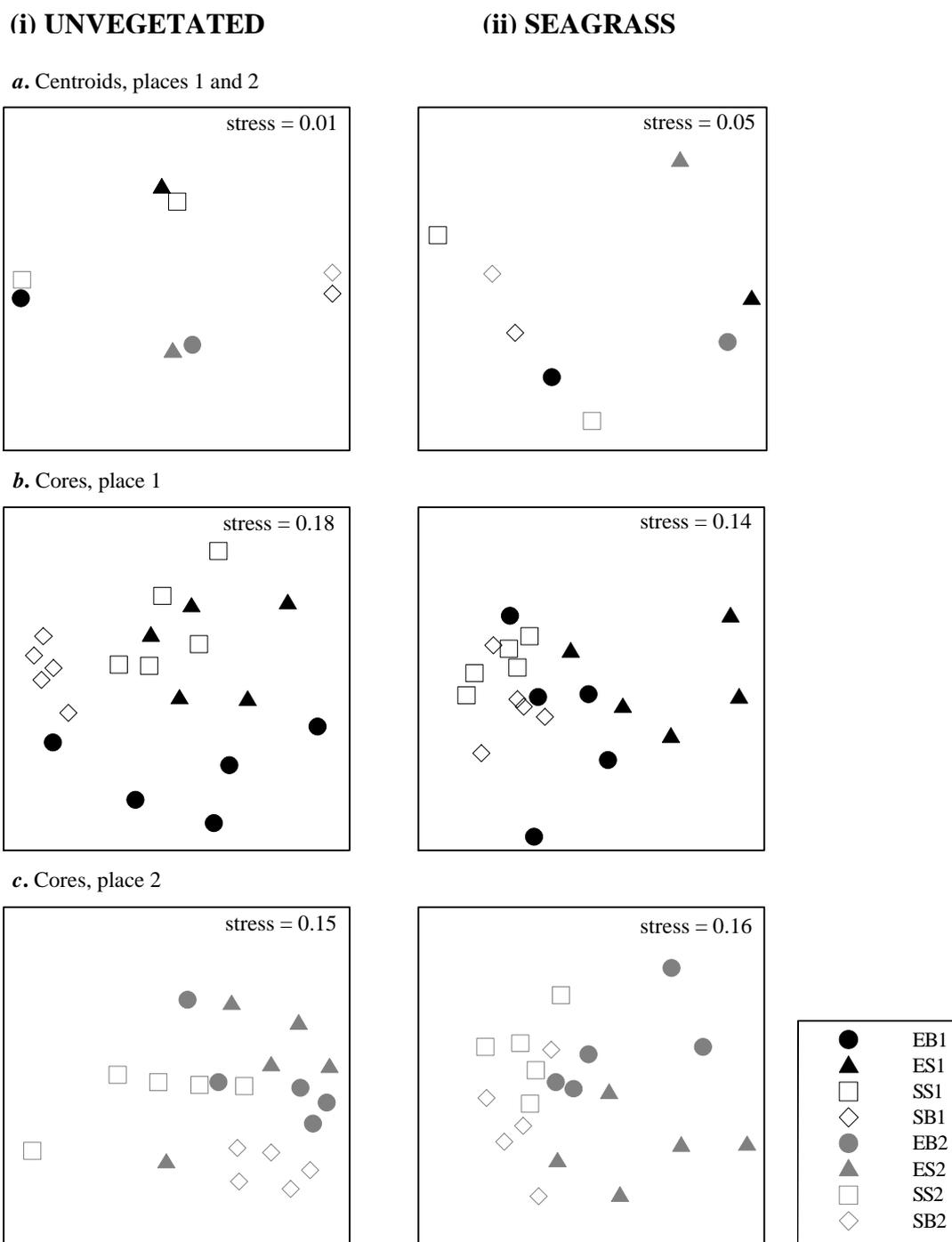


Figure 7.3 nMDS ordinations of assemblages of macro-invertebrates in: (i) unvegetated sediment and (ii) sediment vegetated with seagrass on 18th September, 2001 at sites exposed to (closed symbols; circles = exposed bank [EB], triangles = exposed spoil [ES]) and sheltered from (open symbols; squares = sheltered spoil [SS]; diamonds = exposed bank [EB]) boat wash from the Atlantic Intracoastal Waterway, Bogue Sound, North Carolina. Sampling was done at two places within the sound (place 1 = black, place 2 = gray). Ordinations of **a.** centroids of untransformed data from all sites, **b.** individual replicates from place 1 and **c.** individual replicates from place 2 are shown; $n = 5$ for each site.

In the case of the vegetated sediment, the ordination of points from each of the two places was consistent with an effect of boat-wash (Fig. 7.3 (ii) b, c). At place 1, distances between replicates from the most exposed site, ES1, and replicates from the other 3 sites were greater than distances among replicates within the group of sheltered sites, as predicted (Fig. 7.3 (ii) b). On the ordination for place 2, points fell into two groups, corresponding to exposed sites (EB2, ES2), north of the dredge spoil island and sheltered sites (SS2, SB2), south of the island (Fig. 7.3 (ii) c). Although a statistically significant place x exposure interaction was found using NP-MANOVA (Table 7.2; $p < 0.001$), *a posteriori* tests examining this interaction did not support these observations. The dispersion of replicates appeared greater in the exposed sites (EB2, ES2) than in the sheltered sites (SS2, SB2).

For each habitat, species contributing most to differences among sites were identified through pair-wise comparisons (Table 7.3). In the unvegetated habitat, polychaetes appeared to be driving differences among sites at both places 1 and 2. The family Paraonidae consistently contributed most to the dissimilarity between pairs of sites. The taxa Cirratulidae, Glyceridae, Lumbrineridae, Nereididae, Orbinidae, Syllidae, Amphipoda and the bivalve *Gemma gemma* also appeared important in contributing to dissimilarity (Table 7.3a). In the vegetated habitat, Amphipoda appeared the most important taxon. Lumbrineridae, Maldanidae, Nereididae, Orbinidae, Paraonidae, Sabellidae, Spionidae, *Crepidula fornicata* and Nematoda were important contributors (Table 7.3b). The mean abundances of these taxa at each of the sites sampled are shown in Figure 7.4 (unvegetated habitat) and Figure 7.5 (vegetated habitat).

In the unvegetated habitat, none of the species examined appeared to display a pattern of abundance that, across both places, consistently corresponded to exposure (Figure 7.4). The absence of the hypothesized pattern in these taxa was confirmed by two-way analyses of variance (Table 7.4).

Patterns consistent with exposure to boat-wash were, however, evident in the cores collected from patches of seagrass (Fig. 7.5). The clearest of these was seen in the taxon Amphipoda (Fig. 7.5h). At place 1, the abundance of amphipods was smallest at ES1, the most exposed site, but was similar among the other three sites. At place 2, abundances were similarly smaller at exposed sites (EB2, ES2). This pattern was not, however, statistically significant (ANOVA, Table 7.5). Graphical representations of abundances of other taxa may be found in Figure 7.5. While the abundances of the families Lumbrineridae, Orbinidae and *Crepidula fornicata* followed patterns closely related to exposure, except in the case of Orbinidae, these were not supported by statistical analyses (ANOVA, Table 7.5).

Table 7.3 Taxa contributing most to Bray-Curtis measures of dissimilarity in assemblages for pair-wise comparisons between sites in *a.* unvegetated sediment and *b.* sediment vegetated with seagrass, sampled at two places along the Bogue Sound on 18th September, 2001.

EB = exposed bank, ES = exposed spoil, SS = sheltered spoil, SB = sheltered bank, % cont. = % contribution of taxon to the average dissimilarity between two sites

| <i>a.</i> | | EB-ES | | EB-SS | | EB-SB | | ES-SS | | ES-SB | | |
|----------------|--------------------|------------|--------------------|------------|--------------------|------------|--------------------|------------|--------------------|------------|--------------------|------------|
| | Taxon | % contrib. |
| Place 1 | Cirratulidae | 16 | Paraonidae | 17 | Paraonidae | 35 | Paraonidae | 16 | Paraonidae | 34 | Paraonidae | 34 |
| | Paraonidae | 13 | Cirratulidae | 11 | Syllidae | 17 | Cirratulidae | 12 | Syllidae | 16 | Syllidae | 16 |
| | Nereididae | 10 | Amphipoda | 9 | <i>Gemma gemma</i> | 9 | Amphipoda | 8 | <i>Gemma gemma</i> | 8 | <i>Gemma gemma</i> | 8 |
| | Juvenile bivalves | 9 | Nereididae | 8 | Nereididae | 6 | Glyceridae | 6 | Cirratulidae | 8 | Cirratulidae | 8 |
| | Lumbrineridae | 8 | Lumbrineridae | 6 | Nematoda | 5 | Juvenile bivalves | 6 | Nematoda | 5 | Nematoda | 5 |
| | Av. Dissim. | 77 | Av. Dissim. | 77 | Av. Dissim. | 78 | Av. Dissim. | 58 | Av. Dissim. | 77 | Av. Dissim. | 77 |
| Place 2 | Paraonidae | 30 | Paraonidae | 36 | Syllidae | 23 | Paraonidae | 27 | Syllidae | 23 | Syllidae | 23 |
| | Orbinidae | 14 | Cirratulidae | 12 | Paraonidae | 21 | Orbinidae | 13 | Paraonidae | 18 | Paraonidae | 18 |
| | Nematoda | 9 | Orbinidae | 11 | Orbinidae | 10 | Cirratulidae | 11 | Orbinidae | 11 | Orbinidae | 11 |
| | Cirratulidae | 8 | Lumbrineridae | 9 | Cirratulidae | 8 | Lumbrineridae | 10 | Cirratulidae | 8 | Cirratulidae | 8 |
| | Glyceridae | 7 | Nematoda | 7 | Nematoda | 6 | Nematoda | 7 | Nematoda | 6 | Nematoda | 6 |
| | Av. Dissim. | 60 | Av. Dissim. | 71 | Av. Dissim. | 66 | Av. Dissim. | 72 | Av. Dissim. | 72 | Av. Dissim. | 72 |

| <i>b.</i> | | EB-ES | | EB-SS | | EB-SB | | ES-SS | | ES-SB | | |
|----------------|--------------------|------------|----------------------------|------------|----------------------------|------------|----------------------------|------------|----------------------------|------------|----------------------------|------------|
| | Taxon | % contrib. | Taxon | % contrib. | Taxon | % contrib. | Taxon | % contrib. | Taxon | % contrib. | Taxon | % contrib. |
| Place 1 | Amphipoda | 28 | Amphipoda | 17 | Amphipoda | 26 | Amphipoda | 21 | Amphipoda | 29 | Amphipoda | 29 |
| | Lumbrineridae | 10 | Nereididae | 11 | Paraonidae | 12 | Nereididae | 8 | Paraonidae | 13 | Paraonidae | 13 |
| | Nereididae | 7 | Sabellidae | 8 | Lumbrineridae | 11 | Orbinidae | 7 | Spionidae | 7 | Spionidae | 7 |
| | Paraonidae | 7 | Nematoda | 7 | Spionidae | 9 | Paraonidae | 7 | Nereididae | 6 | Nereididae | 6 |
| | Maldanidae | 4 | Paraonidae | 7 | Nereididae | 8 | Nematoda | 7 | Isopoda | 5 | Isopoda | 5 |
| | Av. Dissim. | 70 | Av. Dissim. | 62 | Av. Dissim. | 55 | Av. Dissim. | 72 | Av. Dissim. | 70 | Av. Dissim. | 70 |
| Place 2 | Nereididae | 21 | Amphipoda | 31 | Amphipoda | 26 | Amphipoda | 27 | Amphipoda | 26 | Amphipoda | 26 |
| | Amphipoda | 21 | Lumbrineridae | 9 | Nereididae | 12 | Nereididae | 21 | Nereididae | 12 | Nereididae | 12 |
| | Sabellidae | 7 | Nereididae | 6 | <i>Crepidula fornicata</i> | 9 | Lumbrineridae | 8 | <i>Crepidula fornicata</i> | 8 | <i>Crepidula fornicata</i> | 8 |
| | Orbinidae | 6 | <i>Crepidula fornicata</i> | 5 | Nematoda | 8 | Sabellidae | 7 | Nematoda | 7 | Nematoda | 7 |
| | Lumbrineridae | 5 | Orbinidae | 5 | Lumbrineridae | 6 | <i>Crepidula fornicata</i> | 4 | Lumbrineridae | 7 | Lumbrineridae | 7 |
| | Av. Dissim. | 72 | Av. Dissim. | 63 | Av. Dissim. | 69 | Av. Dissim. | 76 | Av. Dissim. | 76 | Av. Dissim. | 71 |

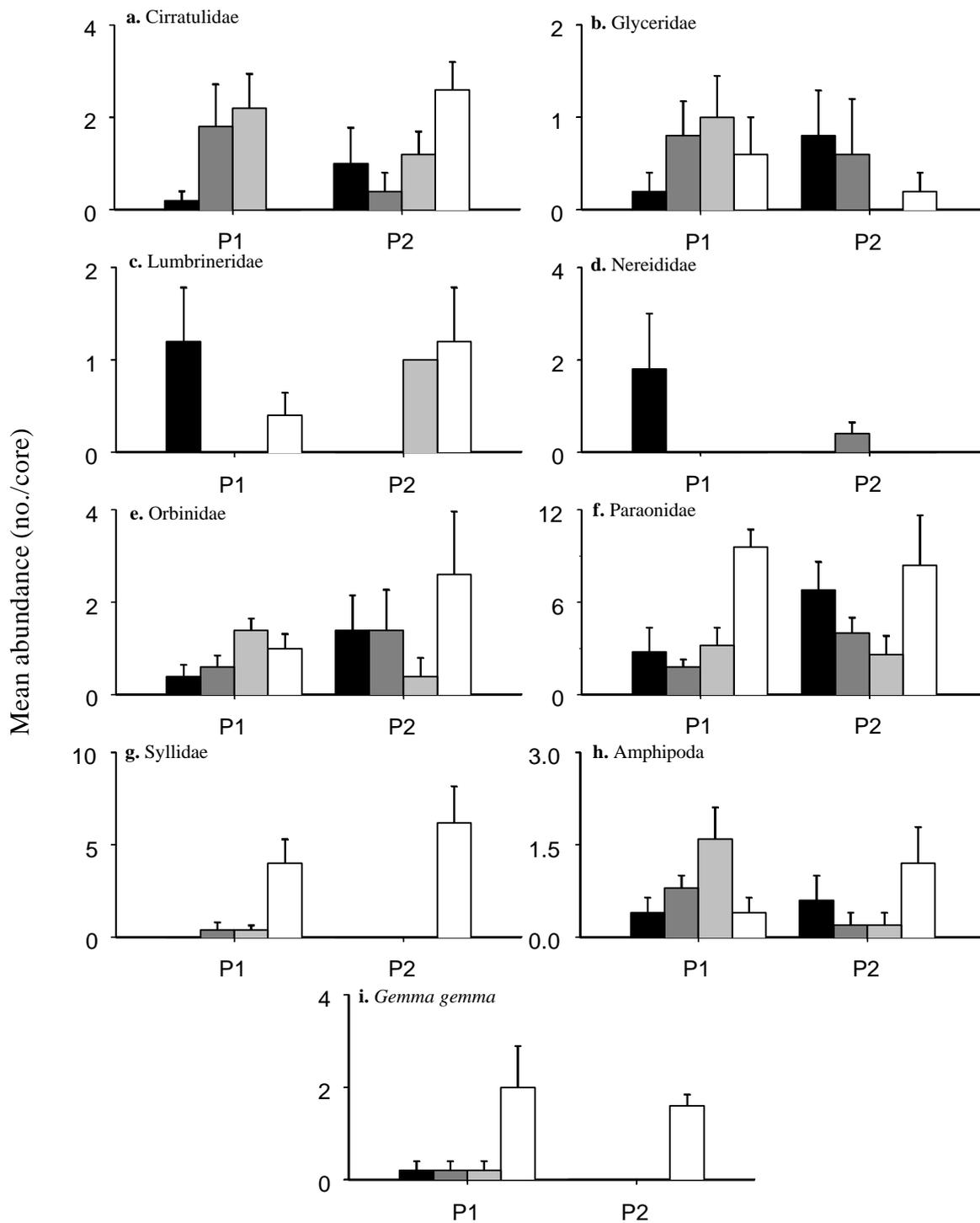


Figure 7.4 Mean (+ S.E.) abundance of taxa of macro-invertebrates in cores of unvegetated sediment collected from sites at two places (P1, P2) along the Bogue Sound, North Carolina on 18th September, 2001. $n = 5$ for each site.

Exposed bank
 Exposed spoil
 Sheltered spoil
 Sheltered bank

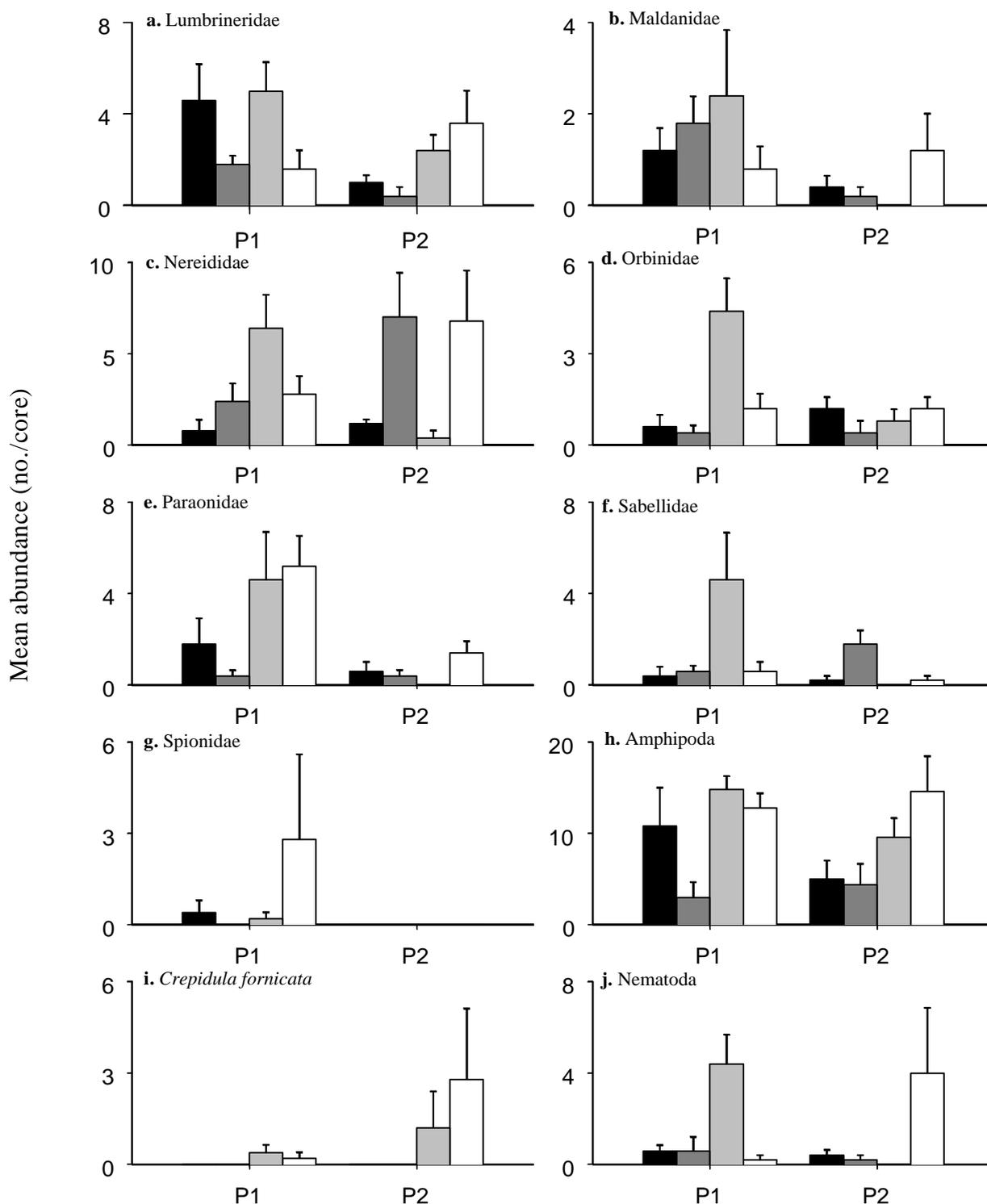


Figure 7.5 Mean (+ S.E.) abundance of taxa of macro-invertebrates in cores of seagrass collected from sites at two places (P1, P2) along the Bogue Sound, North Carolina on 18th September, 2001. *n* = 5 for each site.

Exposed bank
 Exposed spoil
 Sheltered spoil
 Sheltered bank

Table 7.4 Summaries of analyses comparing spatial variation in the abundances of macro-invertebrates in unvegetated sediment among sites differing in their exposure to boat-wash from the Atlantic Intracoastal Waterway on 18th September, 2001. Sites were sampled at two places along the Bogue Sound. pl = place (2 levels; random), ex = exposure (4 levels: exposed bank [EB], exposed spoil [ES], sheltered spoil [SS], sheltered bank [SB]; fixed). $n = 5$. **NS** $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | Cirratulidae | | | | Glyceridae | | | Lumbrenneridae | | | Nereididae | | | Orbinidae | | |
|---------------------|--------------|-----------------------------|------|------|-------------|------|-----------------------------|----------------|------|------|-------------|-------------------------|------|-------------|------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 2.13 | 0.83 | NS | 0.32 | 1.48 | NS | 0.11 | 0.92 | NS | 0.09 | 0.75 | NS | 0.10 | 0.33 | NS |
| ex | 3 | 0.59 | 0.36 | NS | 0.03 | 0.11 | NS | 0.39 | 0.48 | NS | 0.25 | 0.62 | NS | 0.31 | 0.49 | NS |
| pl x ex | 3 | 1.66 | 6.49 | ** | 0.33 | 1.51 | NS | 0.81 | 6.89 | *** | 0.40 | 3.17 | * | 0.63 | 2.16 | NS |
| res | 32 | 0.26 | | | 0.22 | | | 0.12 | | | 0.13 | | | 0.29 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.30 NS | | | C = 0.22 NS | | | C = 0.42 * | | | C = 0.86 ** | | | C = 0.29 NS | | |
| SNK | | pl 1: (EB = SB) < (ES = SS) | | | | | pl 1: EB = ES = SS = SB | | | | | pl 1: EB > ES = SS = SB | | | | |
| | | pl 2: EB = ES = SS = SB | | | | | pl 2: (EB = ES) < (SS = SB) | | | | | pl 2: EB = ES = SS = SB | | | | |

| | Paraonidae | | | | Syllidae | | | Amphipoda | | | <i>Gemma gemma</i> | | | Nematoda | | |
|---------------------|------------|---------------------|------|------|-------------|-------|-------------------------|-------------|------|------|--------------------|---------------------|------|-------------|------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 0.53 | 1.34 | NS | 0.00 | 0.02 | NS | 0.30 | 1.58 | NS | 0.10 | 0.94 | NS | 0.50 | 1.95 | NS |
| ex | 3 | 2.27 | 3.01 | NS | 5.73 | 23.00 | * | 0.07 | 0.13 | NS | 1.83 | 111.25 | ** | 0.58 | 1.13 | NS |
| pl x ex | 3 | 0.75 | 1.91 | NS | 0.25 | 1.26 | NS | 0.58 | 3.07 | * | 0.02 | 0.16 | NS | 0.51 | 2.00 | NS |
| res | 32 | 0.39 | | | 0.20 | | | 0.19 | | | 0.10 | | | 0.25 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.19 NS | | | C = 0.47 ** | | | C = 0.26 NS | | | C = 0.59 ** | | | C = 0.29 NS | | |
| SNK | | (EB = ES = SS) < SB | | | | | pl 1: EB = ES = SS = SB | | | | | (EB = ES = SS) < SB | | | | |
| | | | | | | | pl 2: EB = ES = SS = SB | | | | | | | | | |

Table 7.5 Summaries of analyses comparing spatial variation in the abundances of macro-invertebrates in seagrass beds among sites differing in their exposure to boat-wash from the Atlantic Intracoastal Waterway on 18th September, 2001. Sites were sampled at two places along the Bogue Sound. pl = place (2 levels; random), ex = exposure (4 levels: exposed bank [EB], exposed spoil [ES], sheltered spoil [SS], sheltered bank [SB]; fixed). $n = 5$. **NS** $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | Lumbrenereidae | | | | Maldanidae | | | Nereididae | | | Orbinidae | | | Paraonidae | | |
|---------------------|----------------|-------------|------|------|-------------|------|------|-----------------------------|------|------|---------------------------|------|------|-------------|-------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 2.35 | 6.78 | * | 2.59 | 8.76 | ** | 0.03 | 0.07 | NS | 0.38 | 1.79 | NS | 4.73 | 14.37 | *** |
| ex | 3 | 1.12 | 1.29 | NS | 0.01 | 0.03 | NS | 1.86 | 0.59 | NS | 1.12 | 1.12 | NS | 1.70 | 1.78 | NS |
| pl x ex | 3 | 0.87 | 2.51 | NS | 0.56 | 1.89 | NS | 3.17 | 8.42 | *** | 1.01 | 4.67 | ** | 0.95 | 2.89 | NS |
| res | 32 | 0.35 | | | 0.30 | | | 0.38 | | | 0.22 | | | 0.33 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.26 NS | | | C = 0.28 NS | | | C = 0.19 NS | | | C = 0.15 NS | | | C = 0.35 NS | | |
| SNK | | | | | | | | pl 1: EB = ES = SS = SB | | | pl 1: (EB = ES = SB) < SS | | | | | |
| | | | | | | | | pl 2: (EB = SS) < (ES = SB) | | | pl 2: EB = ES = SS = SB | | | | | |

| | Sabellidae | | | | Spionidae | | | Amphipoda | | | <i>Crepidula fornicata</i> | | | Nematoda | | |
|---------------------|------------|---------------------------|------|------|-------------|------|------|---------------------------|------|------|----------------------------|------|------|-------------|------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 0.92 | 4.45 | NS | 0.51 | 2.24 | NS | 0.52 | 0.98 | NS | 0.36 | 1.39 | NS | 0.48 | 1.28 | NS |
| ex | 3 | 0.82 | 0.47 | NS | 0.13 | 1.00 | NS | 4.30 | 7.98 | NS | 0.56 | 2.30 | NS | 0.56 | 0.24 | NS |
| pl x ex | 3 | 1.75 | 8.42 | *** | 0.13 | 0.59 | NS | 0.54 | 1.01 | NS | 0.24 | 0.92 | NS | 2.33 | 6.20 | ** |
| res | 32 | 0.21 | | | 0.23 | | | 0.53 | | | 0.26 | | | 0.38 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.40 ** | | | C = 0.81 ** | | | C = 0.26 NS | | | C = 0.52 ** | | | C = 0.47 ** | | |
| SNK | | pl 1: (EB = ES = SB) < SS | | | | | | pl 1: (EB = ES = SB) < SS | | | | | | | | |
| | | pl 2: EB = SS = SB < ES | | | | | | pl 2: EB = ES = SS = SB | | | | | | | | |

7.3.3 Assemblages in sediment vegetated with seagrass and on seagrass blades (October)

There was no apparent relationship between the assemblages of macro-invertebrates and the dry weight of above-ground plant material (Fig. 7.6). This was confirmed by a non-significant Spearman's rank correlation between normalized Euclidean distances for pair-wise comparisons of dry weights of seagrass and Bray-Curtis dissimilarities for comparisons of invertebrate assemblages ($r = 0.044$, $p > 0.05$, 38 df). There was no consistent pattern in dry weight of seagrass blades among sites of different exposure across the two places sampled (Fig. 7.7; ANOVA, Table 7.6). Thus, abundances of macro-invertebrates did not need to be standardized according to biomass of seagrass.

As with the invertebrate data collected in September, ordinations were done on centroids representing average assemblages at places 1 and 2 to determine broad-scale patterns and on replicates from individual places to investigate patterns of variability at a smaller scale. For the assemblages in cores with seagrass, there was no consistent difference between exposed and sheltered sites across the two places sampled (Fig. 7.8(i)a; NP-MANOVA: significant place x exposure interaction, Table 7.7a). At place 1, assemblages at EB1, a sheltered site, appeared to differ most from the other assemblages (Fig. 7.8(i)b). At place 2, no obvious pattern among sites was seen (Fig. 7.8(i)c).

Ordination of data from the samples of seagrass blades showed that, as predicted, assemblages differed most between sites on the exposed side of the dredge spoil islands and sites on the sheltered side, at each of the places. This pattern was evident in the nMDS of centroids (Fig. 7.8(ii)a) and nMDSs of replicates within places (Fig. 7.8(ii)b,c). Points representing assemblages at the exposed bank did not clearly separate from points representing assemblages at sheltered locations (along the sheltered spoil and the sheltered bank) at place 1 (Fig. 7.8(ii)b), nor at place 2 (Fig. 7.8(ii)c). Statistical analysis indicated that assemblages differed among all sites in each of the two places and that the way in which these varied was different between the two places (NP-MANOVA, Table 7.7b).

The families of amphipod, Ampithoidae and Ampeliscidae, the polychaete family, Nereididae and the isopod, *Erichsonella attenuata*, contributed most to Bray-Curtis measures of dissimilarity between the assemblages of cores of seagrass collected from sites at place 1 (Table 7.8a). At place 2, Ampithoidae and Ampeliscidae contributed most to between-site variability in the assemblages in the cores (Table 7.8a). Between-site dissimilarity in the assemblages of seagrass blades was largely due to differences in the abundance of the gastropod *Bittium varium*, which explained up to 71.3% of the variation among sites (Table 7.8b).

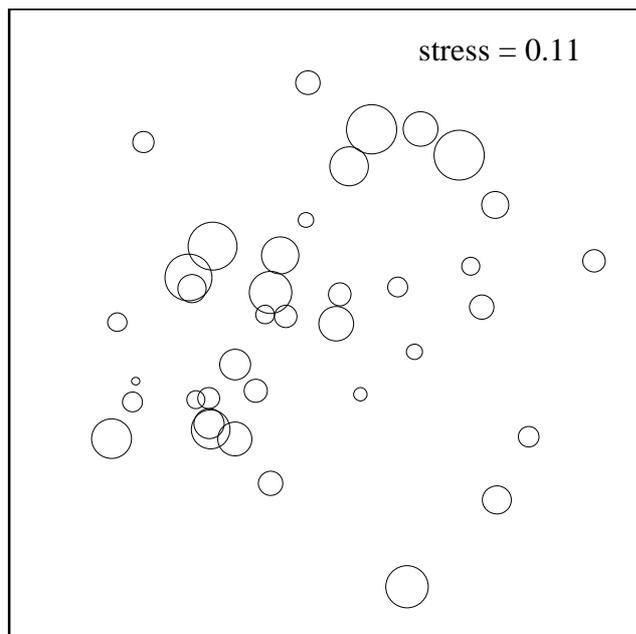


Figure 7.6 nMDS ordination of the assemblages of macro-invertebrates on seagrass-blades collected from the Bogue Sound on 22nd October, 2001. The superimposed circles represent the dry weight of seagrass in each sample. The size of the circle is directly proportional to mass.

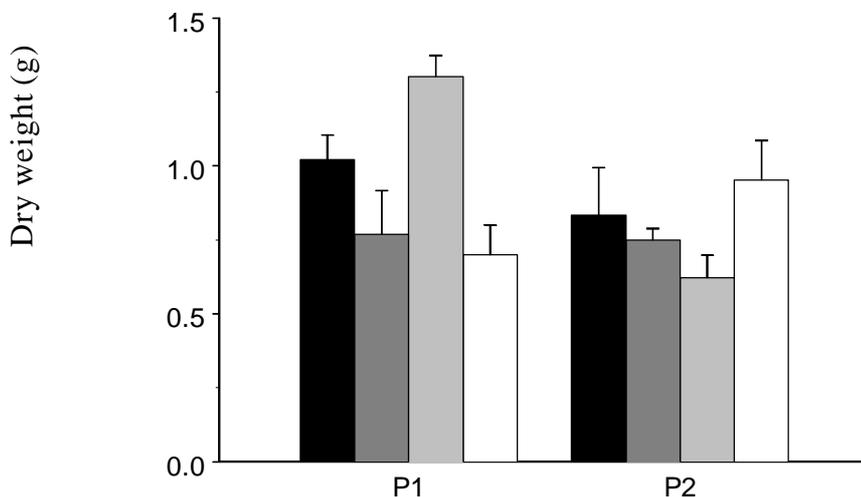


Figure 7.7 Mean (+ S.E.) dry weight of seagrass blades in samples collected from sites at two places along the Bogue Sound, North Carolina on 22nd October, 2001. Sites varied in their exposure to boat-wash from the Atlantic Intracoastal Waterway. $n = 5$ for each site.

Exposed bank
 Exposed spoil
 Sheltered spoil
 Sheltered bank

Table 7.6 Analysis of variance comparing spatial variation in the dry weight of seagrass blades collected at sites differing in their exposure to boat-wash from the Atlantic Intracoastal Waterway on 22nd October, 2001. pl = place (2 levels; random), ex = exposure (4 levels: exposed bank [EB], exposed spoil [ES], sheltered spoil [SS], sheltered bank [SB]; fixed). $n = 5$. NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| source of variation | df | MS | F | sig. |
|---------------------|----|--|------|------|
| pl | 1 | 0.25 | 4.30 | * |
| ex | 3 | 0.09 | 0.22 | NS |
| pl x ex | 3 | 0.38 | 6.52 | ** |
| res | 32 | 0.06 | | |
| transformation | | | | |
| Cochran's test | | C = 0.27 NS | | |
| SNK | | place 1: uninterpretable place 2: EB = ES = SS = SB | | |

Table 7.7 Summaries of non-parametric MANOVAs comparing spatial variation in assemblages of macro-invertebrates among sites differing in exposure to boat-wash from the Atlantic Intracoastal Waterway. Seagrass was sampled on 22nd October, 2001 using *a.* corers and *b.* scissors to cut the blades just above the surface of the sediment. pl = place (2 levels; random), ex = exposure (4 levels: exposed bank [EB], exposed spoil [ES], sheltered spoil [SS], sheltered bank [SB]; fixed).

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a.

| source of variation | df | <i>p</i> | sig. |
|---------------------------|----|--|------|
| pl | 1 | 0.5212 | NS |
| ex | 3 | 0.1228 | NS |
| pl x ex | 3 | 0.0026 | ** |
| res | 32 | | |
| <i>a posteriori</i> tests | | place 1: EB ? ES ? (SS = SB) place 2: uninterpretable | |

b.

| source of variation | df | <i>p</i> | sig. |
|---------------------------|----|--|------|
| pl | 1 | 0.0002 | *** |
| ex | 3 | 0.3484 | NS |
| pl x ex | 3 | 0.0002 | *** |
| res | 32 | | |
| <i>a posteriori</i> tests | | place 1: EB ? ES ? SS ? SB place 2: EB ? ES ? SS ? SB | |

(i) SEAGRASS CORES

(ii) SEAGRASS BLADES

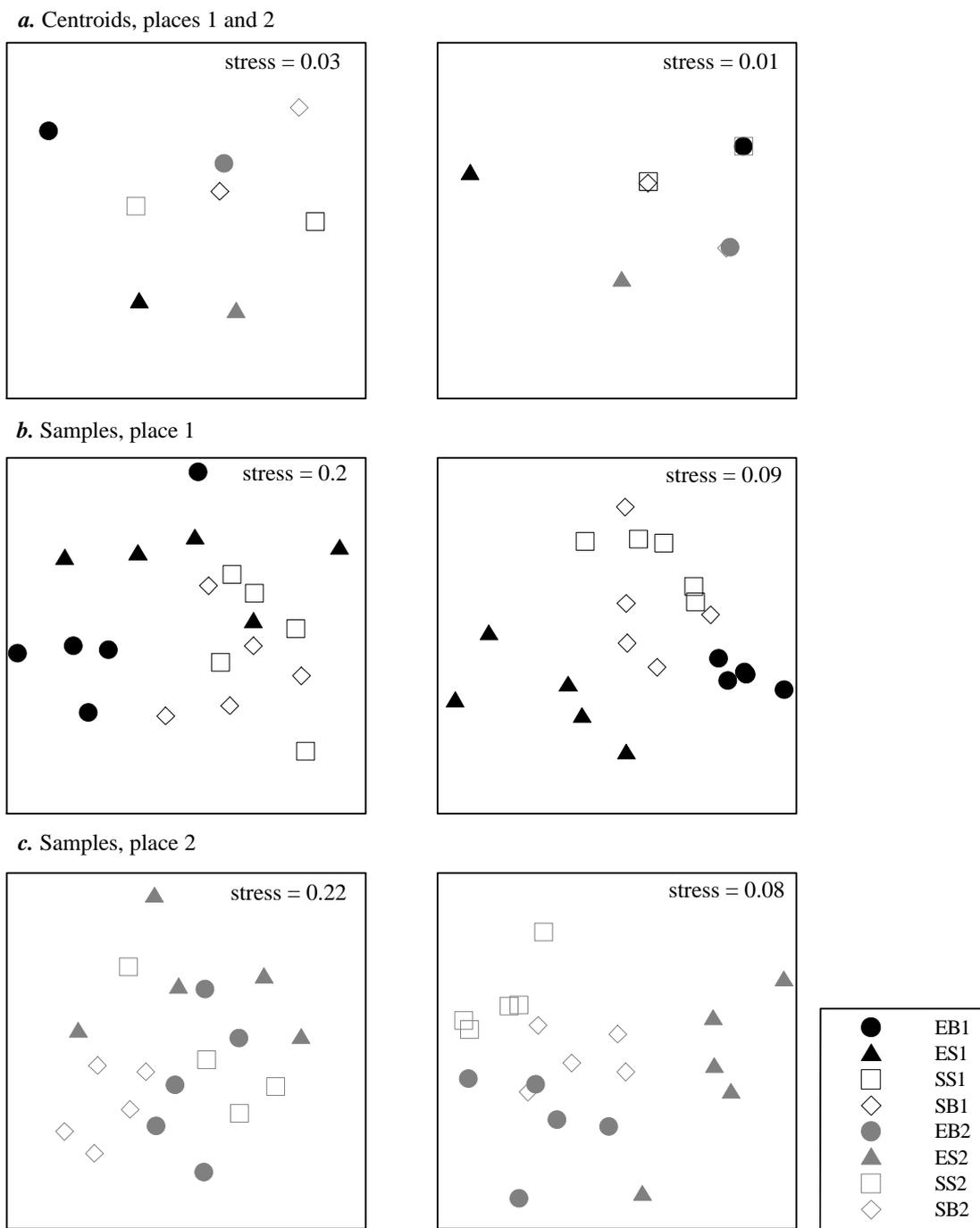


Figure 7.8 nMDS ordinations of assemblages of macro-invertebrates in: (i) cores of seagrass and (ii) samples of seagrass-blades collected on 22nd October, 2001 from sites exposed to (closed symbols; circles = exposed bank [EB], triangles = exposed spoil [ES]) and sheltered from (open symbols; squares = sheltered spoil [SS]; diamonds = exposed bank [EB]) boat wash from the Atlantic Intracoastal Waterway, Bogue Sound, North Carolina. Sampling was done at two places within the sound (place 1 = black, place 2 = gray). Ordinations of **a.** centroids of untransformed data from all sites, **b.** individual replicates from place 1 and **c.** individual replicates from place 2 are shown; $n = 5$ for each site.

Table 7.8 Taxa contributing most to Bray-Curtis measures of dissimilarity in assemblages for pair-wise comparisons between sites *a.* in sediment vegetated with seagrass and *b.* on seagrass blades, sampled at two places along the Bogue Sound on 22nd October, 2001.

EB = exposed bank, ES = exposed spoil, SS = sheltered spoil, SB = sheltered bank; % cont. = % contribution of taxon to the average dissimilarity between two sites

| <i>a.</i> | EB-ES | | EB-SS | | EB-SB | | ES-SS | | ES-SB | |
|----------------|-------------------------------|-----------|-------------------------------|-----------|--------------------|-----------|-------------------------------|-----------|-------------------------------|-----------|
| | Taxon | % cont. | Taxon | % cont. | Taxon | % cont. | Taxon | % cont. | Taxon | % cont. |
| Place 1 | Ampithoidae | 11 | Ampeliscidae | 11 | Ampithoidae | 10 | Ampeliscidae | 12 | Ampeliscidae | 10 |
| | Nereididae | 10 | Nereididae | 9 | Nereididae | 10 | Nereididae | 7 | Nereididae | 8 |
| | <i>Erichsonella attenuata</i> | 7 | <i>Erichsonella attenuata</i> | 8 | Ampeliscidae | 10 | <i>Erichsonella attenuata</i> | 7 | Nematoda | 7 |
| | Maldanidae | 6 | Ampithoidae | 7 | Nematoda | 7 | Capitellidae | 5 | Ampithoidae | 5 |
| | Lumbrineridae | 6 | Tellinid | 5 | Lumbrineridae | 5 | Tellinid | 5 | <i>Erichsonella attenuata</i> | 4 |
| | Av. Dissim. | 78 | Av. Dissim. | 81 | Av. Dissim. | 76 | Av. Dissim. | 73 | Av. Dissim. | 73 |
| Place 2 | Ampeliscidae | 11 | Ampeliscidae | 10 | Syllidae | 12 | Nereididae | 11 | Nereididae | 14 |
| | Nereididae | 10 | Nereididae | 8 | Paraonidae | 10 | Ampeliscidae | 7 | Nematoda | 10 |
| | Maldanidae | 6 | Ampithoidae | 8 | Orbinidae | 9 | Ampithoidae | 7 | Syllidae | 10 |
| | Ampithoidae | 5 | Maldanidae | 6 | Cirratulidae | 8 | Glyceridae | 6 | Ampeliscidae | 7 |
| | <i>Crepidula fornicata</i> | 5 | <i>Crepidula fornicata</i> | 5 | Nematoda | 5 | Capitellidae | 4 | Maldanidae | 5 |
| | Av. Dissim. | 70 | Av. Dissim. | 68 | Av. Dissim. | 63 | Av. Dissim. | 72 | Av. Dissim. | 74 |

| <i>b.</i> | EB-ES | | EB-SS | | EB-SB | | ES-SS | | ES-SB | |
|--------------------|-----------------------|--------------------|-------------------------------|--------------------|----------------------------|--------------------|-------------------------------|--------------------|----------------------------|-----------|
| | Taxon | % cont. | Taxon | % cont. | Taxon | % cont. | Taxon | % cont. | Taxon | % cont. |
| Place 1 | <i>Bittium varium</i> | 84 | <i>Bittium varium</i> | 45 | <i>Bittium varium</i> | 64 | Caprellidae | 19 | <i>Bittium varium</i> | 27 |
| | Ampithoidae | 8 | Caprellidae | 14 | Nereididae | 9 | <i>Bittium varium</i> | 18 | Ampithoidae | 23 |
| | | | Nereididae | 11 | Ampithoidae | 7 | Nereididae | 16 | Nereididae | 15 |
| | | | <i>Erichsonella attenuata</i> | 9 | <i>Crepidula fornicata</i> | 3 | <i>Erichsonella attenuata</i> | 12 | <i>Crepidula fornicata</i> | 8 |
| | | | Ampithoidae | 3 | Caprellidae | 3 | Ampithoidae | 7 | Corophiidae | 5 |
| Av. Dissim. | 85 | Av. Dissim. | 62 | Av. Dissim. | 63 | Av. Dissim. | 84 | Av. Dissim. | 75 | |
| Place 2 | <i>Bittium varium</i> | 37 | <i>Bittium varium</i> | 34 | <i>Bittium varium</i> | 31 | <i>Bittium varium</i> | 71 | <i>Bittium varium</i> | 49 |
| | Ampithoidae | 15 | Ampithoidae | 18 | Ampithoidae | 14 | Ampithoidae | 9 | Ampithoidae | 13 |
| | Leucothoidae | 10 | Leucothoidae | 10 | Leucothoidae | 10 | Nereididae | 4 | Nereididae | 5 |
| | Stenothoidae | 8 | Stenothoidae | 7 | Stenothoidae | 9 | Stenothoidae | 2 | Leucothoidae | 5 |
| | Gammaridae | 7 | Gammaridae | 7 | Gammaridae | 9 | <i>Crepidula fornicata</i> | 2 | <i>Crepidula fornicata</i> | 5 |
| | Av. Dissim. | 74 | Av. Dissim. | 59 | Av. Dissim. | 47 | Av. Dissim. | 84 | Av. Dissim. | 65 |

The abundances of Lumbrineridae, Ampeliscidae and Ampithoidae in cores of seagrass were smallest at sites adjacent to the exposed spoil, where exposure to wash from the AIW is greatest (Fig. 7.9a,d,e). No statistically significant difference was, however, found in the abundance of Lumbrineridae in cores among the four levels of exposure (Table 7.9). A significant place x exposure interaction was found in the abundance of Ampeliscidae (ANOVA: $p < 0.05$, Table 7.9) due to smaller abundances at the exposed bank and the exposed spoil of place 1 and at the exposed spoil of place 2. The abundance of Ampithoidae varied significantly among levels of exposure (ANOVA: $p < 0.01$, Table 7.9), but SNK tests did not detect any pair-wise differences.

On the seagrass blades, the abundances of *Bittium varium* and *Crepidula fornicata* were much smaller in samples from the exposed spoil than from other locations (Fig. 7.10h,i). This pattern in the abundance of *Crepidula fornicata* was significant statistically (ANOVA: $p < 0.05$, Table 7.10). A significant place x exposure interaction was found for *Bittium varium* (ANOVA: $p < 0.01$, Table 7.10) due to greater abundances at the exposed bank in place 1 and smaller abundances at the exposed spoil of place 2.

7.4 Discussion

Invertebrate assemblages sampled on the 18th September showed no significant difference between unvegetated sediment from exposed or sheltered sites. Contrary to the hypothesis, differences were, however, found in cores of sediment from the seagrass habitat, with the greatest dissimilarity between sites differing most in exposure. Subsequent sampling indicated that this pattern was strongest when only epifaunal taxa were considered. Dissimilarities among assemblages at the most exposed sites (ES1, ES2) and the more sheltered areas (SS1, SS2, SB1, SB2) were greater for samples of seagrass blades, which include only epifauna, than for cores of seagrass, containing infauna and epifauna.

The abundances of epifaunal taxa were much greater in samples of seagrass blades collected in plastic bags than in cores of seagrass. For example, up to 226 *Bittium varium* were found in samples of seagrass blades, whereas a maximum of 5 were found in cores. Thus, it appears that, while coring is an appropriate method of collecting infauna, the abundances of epifauna are underestimated using this method. Mobile taxa such as amphipods and isopods may disperse into adjacent habitat in response to the disturbance of coring; gastropods may be knocked off.

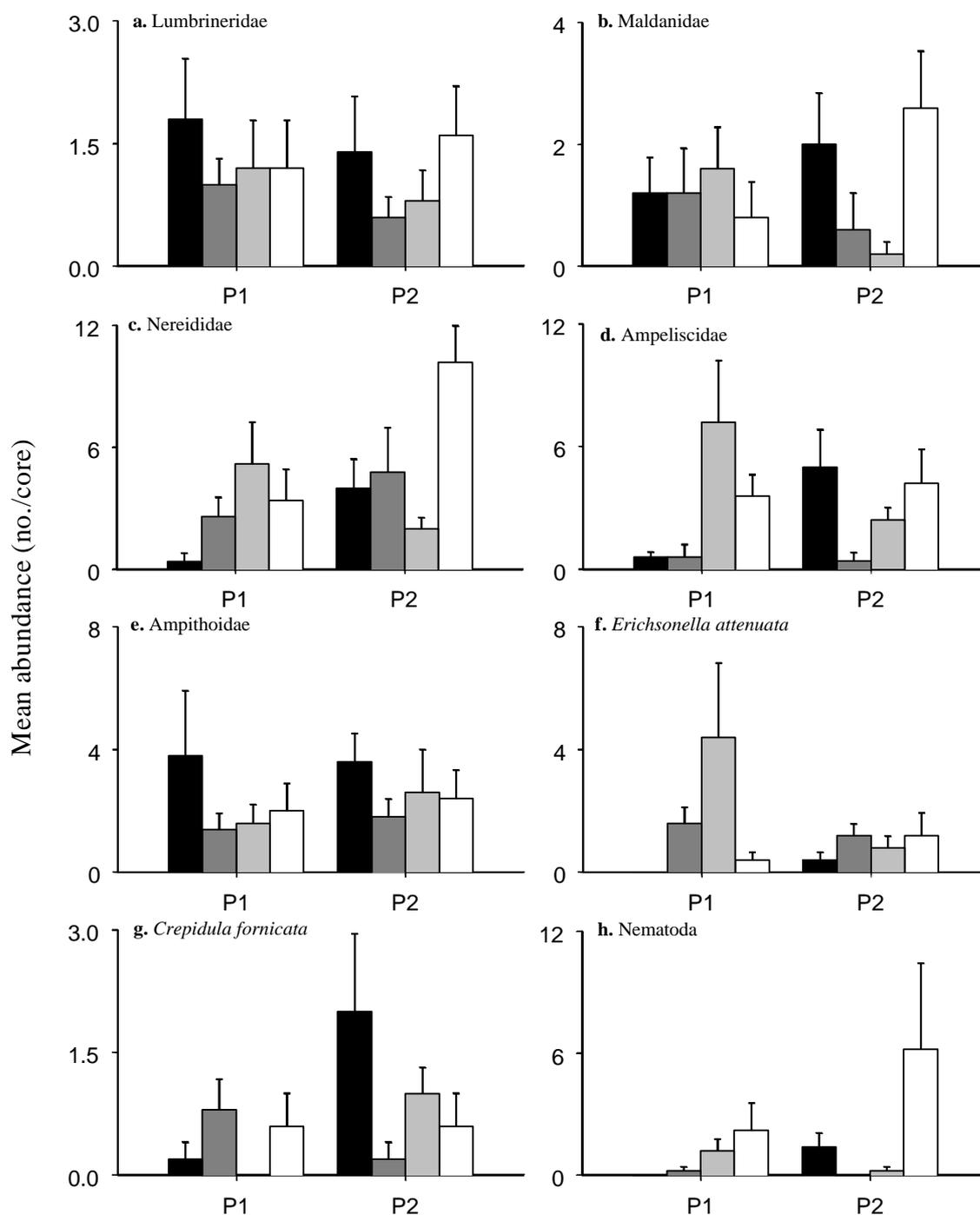


Figure 7.9 Mean (+ S.E.) abundance of taxa of macro-invertebrates in cores of sediment vegetated with seagrass, collected from sites at two places (P1, P2) along the Bogue Sound, North Carolina on 22nd October, 2001. $n = 5$ for each site.

Exposed bank
 Exposed spoil
 Sheltered spoil
 Sheltered bank

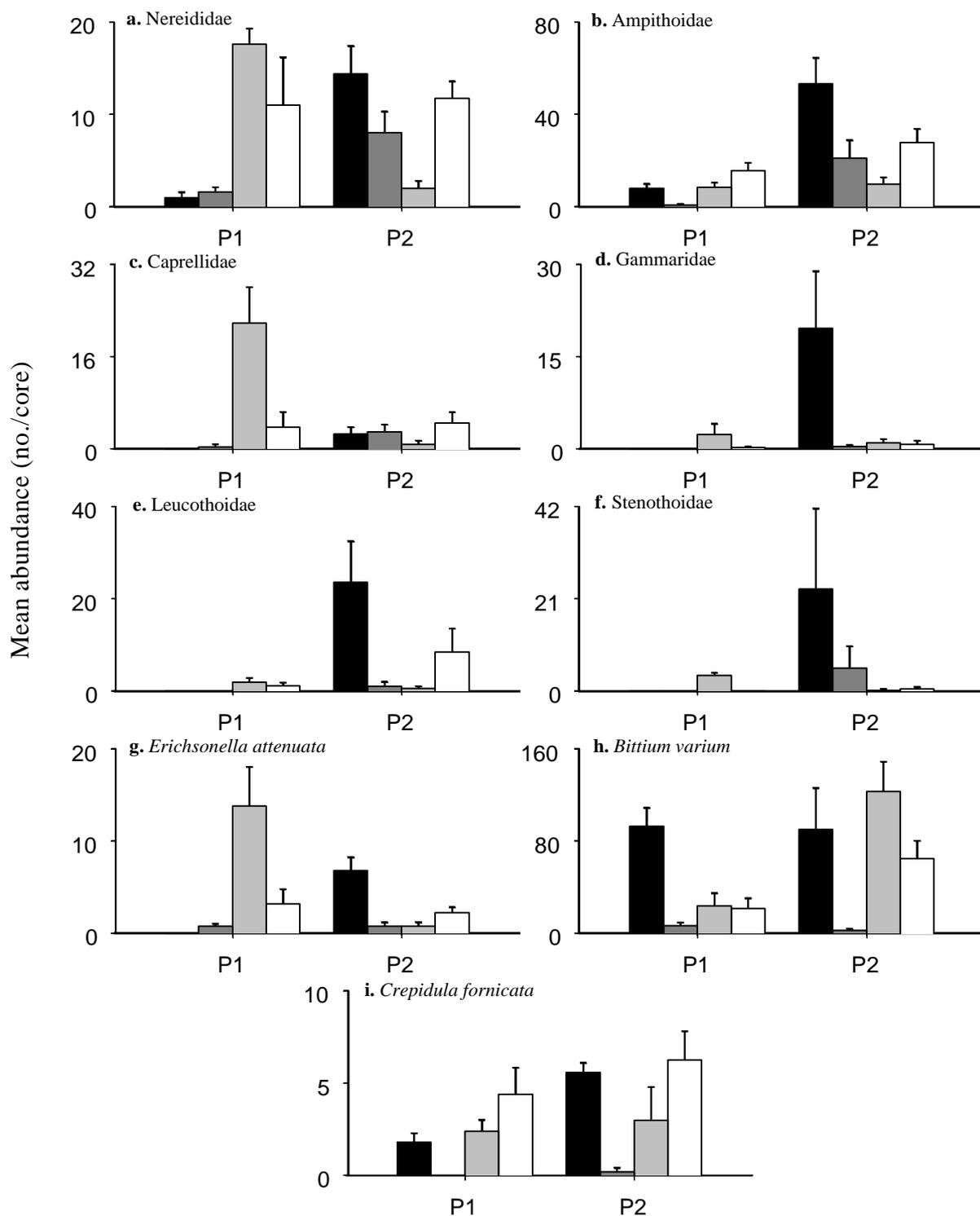


Figure 7.10 Mean (+ S.E.) abundance of taxa of macro-invertebrates associated with seagrass-blades, collected from sites at two places (P1, P2) along the Bogue Sound, North Carolina on 22nd October, 2001. *n* = 5 for each site.

Exposed bank
 Exposed spoil
 Sheltered spoil
 Sheltered bank

Table 7.9 Summaries of analyses comparing spatial variation in the abundances of macro-invertebrates associated with seagrass among sites differing in their exposure to boat-wash from the Atlantic Intracoastal Waterway on 22nd October, 2001. Sites were sampled at two places (pl) along the Bogue Sound using corers. pl = place (2 levels; random), ex = exposure (4 levels: exposed bank [EB], exposed spoil [ES], sheltered spoil [SS], sheltered bank [SB]; fixed). $n = 5$.

NS $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | Lumbrenereidae | | | | Maldanidae | | | Nereididae | | | Ampeliscidae | | |
|---------------------|----------------|-------------|------|------|-------------|------|------|-------------------------|------|-----------------------------|--------------|-------------------------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 0.07 | 0.23 | NS | 0.00 | 0.00 | NS | 2.66 | 5.89 | * | 0.03 | 0.06 | NS |
| ex | 3 | 0.16 | 1.73 | NS | 0.32 | 0.35 | NS | 1.70 | 0.94 | NS | 3.23 | 2.01 | NS |
| pl x ex | 3 | 0.09 | 0.29 | NS | 0.93 | 2.41 | NS | 1.81 | 4.00 | * | 1.60 | 3.77 | * |
| res | 32 | 0.32 | | | 0.38 | | | 0.45 | | | 0.43 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.19 NS | | | C = 0.18 NS | | | C = 0.21 NS | | | C = 0.27 NS | | |
| SNK | | | | | | | | pl 1: EB = ES = SS = SB | | pl 1: (EB = ES) < (SS = SB) | | pl 2: EB = SS = SB > ES | |

| | Ampithoidae | | | | <i>Erichsonella attenuata</i> | | | <i>Crepidula fornicata</i> | | | Nematoda | | |
|---------------------|-------------|-------------------------|-------|------|-------------------------------|------|------|----------------------------|------|------|-------------------------|------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 0.25 | 0.58 | NS | 0.12 | 0.47 | NS | 0.62 | 2.78 | NS | 0.41 | 1.08 | NS |
| ex | 3 | 0.47 | 92.16 | ** | 1.31 | 1.63 | NS | 0.07 | 0.11 | NS | 1.92 | 2.01 | NS |
| pl x ex | 3 | 0.01 | 0.01 | NS | 0.80 | 3.13 | * | 0.67 | 3.00 | * | 0.96 | 2.52 | NS |
| res | 32 | 0.43 | | | 0.26 | | | 0.22 | | | 0.38 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.24 NS | | | C = 0.29 NS | | | C = 0.38 NS | | | C = 0.35 NS | | |
| SNK | | pl 1: EB = ES = SS = SB | | | pl 1: EB = ES = SS = SB | | | pl 1: EB = ES = SS = SB | | | pl 2: EB = ES = SS = SB | | |
| | | pl 2: EB = ES = SS = SB | | | pl 2: EB = ES = SS = SB | | | pl 2: EB = ES = SS = SB | | | pl 2: EB = ES = SS = SB | | |

Table 7.10 Summaries of analyses comparing spatial variation in the abundances of macro-invertebrates associated with seagrass among sites differing in their exposure to boat-wash from the Atlantic Intracoastal Waterway on 22nd October, 2001. Sites were sampled at two places (pl) along the Bogue Sound by cutting blades just above the surface of the sediment. pl = place (2 levels; random), ex = exposure (4 levels: exposed bank [EB], exposed spoil [ES], sheltered spoil [SS], sheltered bank [SB]; fixed). $n = 5$.

NS $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | Nereididae | | | | Ampithoidae | | | Caprellidae | | | Gammaridae | | | Leucothoidae | | |
|---------------------|------------|---------------------------|-------|------|---------------------------|-------|------|-------------------------|-------|------|-------------------------|-------|------|---------------------------|-------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 1.94 | 6.33 | * | 14.37 | 52.14 | *** | 0.05 | 0.09 | NS | 5.39 | 15.99 | *** | 8.32 | 14.32 | *** |
| ex | 3 | 1.43 | 0.19 | NS | 4.27 | 1.43 | NS | 2.90 | 0.40 | NS | 2.92 | 0.67 | NS | 2.96 | 0.60 | NS |
| pl x ex | 3 | 7.41 | 24.18 | *** | 3.00 | 10.87 | *** | 7.27 | 14.47 | *** | 4.33 | 12.85 | *** | 4.96 | 8.53 | *** |
| res | 32 | 0.31 | | | 0.28 | | | 0.50 | | | 0.34 | | | 0.58 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.36 NS | | | C = 0.24 NS | | | C = 0.25 NS | | | C = 0.34 NS | | | C = 0.34 NS | | |
| SNK | | pl 1: SS > SB > (EB = ES) | | | pl 1: ES < (EB = SS = SB) | | | pl 1: uninterpretable | | | pl 1: EB = ES = SS = SB | | | pl 2: EB > SB > (ES = SS) | | |
| | | pl 2: (EB = ES = SB) > SS | | | pl 2: uninterpretable | | | pl 2: EB = ES = SS = SB | | | | | | | | |

| | Stenothoidae | | | | <i>Erichsonella attenuata</i> | | | <i>Bittium varium</i> | | | <i>Crepidula fornicata</i> | | |
|---------------------|--------------|---------------------------|------|------|-------------------------------|-------|------|---------------------------|------|------|----------------------------|------|------|
| source of variation | df | MS | F | sig. | MS | F | sig. | MS | F | sig. | MS | F | sig. |
| pl | 1 | 2.18 | 3.68 | NS | 0.02 | 0.07 | NS | 4.38 | 4.91 | NS | 1.21 | 4.03 | NS |
| ex | 3 | 1.70 | 0.33 | NS | 1.67 | 0.25 | NS | 16.20 | 3.72 | NS | 4.91 | 9.93 | * |
| pl x ex | 3 | 5.21 | 8.81 | *** | 6.66 | 24.88 | *** | 4.36 | 4.89 | ** | 0.49 | 1.64 | NS |
| res | 32 | 0.59 | | | 0.27 | | | 0.89 | | | 0.30 | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| Cochran's test | | C = 0.50 ** | | | C = 0.35 NS | | | C = 0.32 NS | | | C = 0.32 NS | | |
| SNK | | pl 1: EB = ES = SB < SS | | | pl 1: uninterpretable | | | pl 1: EB > (ES = SS = SB) | | | (EB = SS = SB) > ES | | |
| | | pl 2: EB > (ES = SS = SB) | | | pl 2: EB > (ES = SS = SB) | | | pl 2: ES < (EB = SS = SB) | | | | | |

At place 1, assemblages of macro-invertebrates on the exposed bank were generally indistinguishable from those at sheltered places, on the southern side of the dredge-spoil islands. If exposure to boat-wash were important in structuring assemblages of macroinvertebrates, this observation could be explained by the attenuation of wave-energy with distance from the point of generation because the AIW is situated closer to the dredge-spoil islands than to the northern bank of the sound. At place 2, however, assemblages at the exposed bank were more similar to those at the exposed spoil, than to assemblages on the sheltered side of the sound. The different patterns observed at the two places may be due to local differences in the profile of the waterway, which influences the behaviour of waves.

The different assemblages of macro-invertebrates at the exposed spoil and exposed bank of place 1 suggest that patterns are more likely to be due to wash than to any of the many other disturbances associated with boating. If the discharge of contaminants from vessels were causing patterns, assemblages at the exposed spoil and exposed bank would be similar because hydrodynamic processes should disperse these throughout the northern section of the sound.

This is the first study to consider the effect of wave-exposure on the faunal assemblages of seagrass beds. Several studies have, however, described the distribution and abundance of phytal amphipods as following gradients of wave-exposure on rocky intertidal shores (Fenwick, 1976; Fenchel and Kolding, 1979; Tararam and Wakabara, 1981; Lancellotti and Trucco, 1993). The relationship between these variables appears to differ among species. Fenwick (1976) found a strong positive correlation between wave-exposure and the density of amphipods on the rocky shores of Kaikoura, NZ; Lancellotti and Trucco (1993) found that some species of the genus *Hyale* were more abundant in exposed places, whereas others occurred in protected environments along the Chilean coastline.

In the present study, differences in assemblages between sheltered and exposed areas were primarily due to smaller abundances of taxa in the latter. Taxa displaying the strongest patterns were the gastropod *Bittium varium*, the slipper limpet *Crepidula fornicata* and several families of amphipod (Ampithoidae and Ampeliscidae). These taxa are all mobile and are usually found loosely attached to seagrass blades via a foot or modified appendage. Thus, a possible model to explain their small abundances in exposed locations is that they are displaced from seagrass blades during flapping, induced by the orbital motion of waves (Koch and Gust, 1999; van Katwijk and Hermus, 2000).

Molluscs that are knocked off seagrass blades will fall to the sediment below. On the surface of the sediment, they are more susceptible to epibenthic predators, such as the blue crab, *Callinectes sapidus*, which consumes a variety of infaunal and epifaunal taxa (Tagatz, 1968;

Orth, 1977; Virnstein, 1977, 1979; Nelson, 1981; Laughlin, 1982; Stanhope *et al.*, 1982; Warren, 1985). Several of these taxa of mollusc display reduced mobility with size (e.g. *Crepidula*, Hoagland, 1978) and consequently adults may be unable to recolonize seagrass blades, particularly if the frequency of disturbance is great.

Amphipods, by comparison, are highly mobile. They may move among patches of seagrass by active swimming or by passive tidal transport (Virnstein and Curran, 1986). Phytal amphipods that are knocked into the water-column by flapping of seagrass will, presumably, rapidly recolonise blades. Abundances of amphipods on seagrass blades will only be depressed following their displacement if: (i) the frequency of wave-events is greater than the time required for recolonization or (ii) they are more susceptible to predation in the water-column than when attached to blades.

In addition, the flapping of blades results in alternate 'opening' (leaves in the upright position) and 'closing' (leaves bent over) of the meadow. This may increase the accessibility of epifaunal assemblages to predatory fish associated with seagrass. Epifaunal invertebrates form the major part of the diet of these fish (Adams, 1976; Klumpp *et al.*, 1989).

Alternatively, wash may indirectly affect the faunal assemblages of seagrass via changes in the morphology of the seagrass beds themselves. Water-motion is important in determining the spatial configuration of seagrass beds (Keddy, 1982; Fonseca *et al.*, 1983; Fonseca and Kenworthy, 1987; Chambers *et al.*, 1991; Coops *et al.*, 1991). Fragmentation of beds by waves and currents (Fonseca *et al.*, 1982; Robbins and Bell, 1994; Fonseca and Bell, 1998) may result in increased fractal dimensions of exposed beds (Turner *et al.*, 1999). Composition of beds can also be affected by exposure - *Halodule wrightii* is more abundant in exposed areas; *Zostera marina* is more abundant in sheltered areas (Keddy, 1982; Coops *et al.*, 1991).

Fauna in seagrass beds are frequently correlated with the structure, shoot-density and biomass of seagrass beds (Heck and Wetstone, 1977; Webster *et al.*, 1998; Attrill *et al.*, 2000). While most studies have investigated the relationship between density of seagrass and faunal assemblages (Leber, 1985; Bell and Westoby, 1986b; Lee *et al.*, 2001), the size and shape of patches also appear to be important in determining faunal assemblages. Eggleston *et al.* (1998) observed that densities of grass shrimp did not scale up directly with area – small patches with greater perimeter to area ratios, contained significantly greater densities of grass shrimp than did larger patches. Bowden *et al.* (2001) found that samples from larger patches of seagrass contained more taxa than did those from smaller patches.

In contrast to the above references, the present study did not find a pattern in the dry weight (per unit area) of seagrass that was consistent with the composition of assemblages. Similarly,

there was no relationship between the dry weight of seagrass and exposure. The effect of exposure on the larger-scale morphology of seagrass beds was not, however, considered. Consequently, it is possible that boat-wash from the AIW indirectly affects assemblages of macro-invertebrates on seagrass blades via fragmentation of seagrass beds.

Finally, wash may indirectly influence epifaunal assemblages if it changes the biomass of epiphytes attached to seagrass blades. Epiphytes attract epifauna (Hall and Bell, 1988) and are consumed by invertebrates in preference to seagrass tissue (Kikuchi and Pérés, 1977; Zimmerman *et al.*, 1979; Orth and van Montfrans, 1984).

This study has, however, not demonstrated a causal relationship between wash and the structure of assemblages of macro-invertebrates. Patterns may be due to natural spatial variability within the sound, with their apparent relationship to exposure purely coincidental. In the next chapter, a manipulative experiment that attempts to establish a causal relationship between boat-wash and decreased abundances of taxa of epifauna is described.

CHAPTER 8

DISPLACEMENT OF MOBILE EPIFAUNA FROM SEAGRASS BLADES BY WASH

8.1 Introduction

Crustaceans are highly mobile organisms. Copepods, ostracods and peracarids (amphipods, isopods, mysids, cumaceans and tanaids) exhibit localized horizontal and vertical migration (e.g. Hobson and Chess, 1976; Alldredge and King, 1977; Hammer and Zimmerman, 1979). At night, many of these organisms move upwards, migrating from sediment into the canopy of seagrasses, or from the canopy to the water-column. Such behavior may result in the redistribution of individuals across plants (Virnstein and Curran, 1986; Edgar, 1992). Preliminary work suggests that turnover of crustaceans in seagrass beds is less than one day and, in the case of many amphipods, appears to be less than 6 h (Howard, 1985; Taylor, 1998). Amphipods may move among seagrass patches within a habitat by active swimming or by passive tidal transport (Virnstein and Curran, 1986).

The mobility of organisms is likely to be an important factor in determining the temporal scale of ecological impacts on populations. For most sessile invertebrates on hard substrata, only the pre-settlement larvae are able to reject substrata and relocate (Woodin, 1991 but see Bayne, 1964 for a notable exception). The dislodgement of adults of these species will almost surely result in death and, consequently, press (long-term) responses can result from pulse (short-duration) disturbances. Highly mobile organisms, such as small crustaceans are, however, capable of redistribution in response to a disturbance and may rapidly re-colonize habitat following the end of a disturbance. Any response of mobile organisms to pulse disturbances is likely to be short-lived.

In Chapter 7, it was found that the epifaunal assemblages of seagrass meadows differed between places exposed to and sheltered from the wash of boats travelling along the Atlantic Intracoastal Waterway. This pattern appeared to be primarily due to smaller abundances of the gastropod *Bittium varium*, the slipper limpet *Crepidula fornicata* and several families of amphipod (Ampithoidae and Ampeliscidae) in exposed than in sheltered places. Wave-action results in a flapping movement of seagrass blades at the frequency of the waves (Koch and Gust, 1999; van Katwijk and Hermus, 2000). Thus, a model to explain the smaller abundances of *B. varium* and *C. fornicata* in exposed places is that boat-generated waves cause seagrass blades to flap with sufficient force to dislodge gastropods. If this model were correct, any impact of boat-wash on these organisms should be evident immediately after the disturbance.

This model alone cannot, however, explain patterns in the abundance of these mobile taxa. In order for their abundances to be permanently depressed by the flapping of seagrass blades, the frequency of the disturbance must be greater than the time taken for recolonization and/or mortality must be significantly greater during the period during which the animals are displaced.

In New South Wales, the epifaunal assemblages of seagrass blades appear to be dominated by small crustaceans, in particular copepods and amphipods (pers. obs.). These assemblages appear to contain few gastropods. In this chapter, the hypotheses that (i) change in assemblages of mobile invertebrates will result from exposure to boat-generated waves and (ii) change will be due to decreases in the abundances of individual taxa are tested in controlled experiments.

8.2 Materials and Methods

8.2.1 Study sites

Narrabeen Lake is located on the northern beaches of Sydney, New South Wales, Australia (151°19'E, 34°43' S), approximately 15 km north of the city (Fig. 8.1). The lake has a total area of 2.2 km² and a catchment of 55 km². Remnants of rainforest and dry sclerophyll forest are found on the western side of the lake; the eastern side is predominately urbanized. The lake is supplied by four creeks - Middle, Deep and South Creeks from the west and Mullet Creek from the north-east. These have deposited mud on the underlying Hawkesbury sandstone. The lake has a spring tidal range of 0.3 m.

Narrabeen Lake is an important recreational area and sail-boarding, fishing and picnicking are particularly popular. Eight-knot speed limits on the lake have ensured that the impact of power-boating on the shores of the lake has been minimal. Much of its shore is vegetated with reeds, casuarinas and other wetland species. The lake supports about 0.5 km² of seagrass, primarily *Zostera capricorni* (Ascherson) and *Halophila ovalis* (R. Br.) Hook f. (NSW DLWC, 2000c).

The Georges River lies 30 km south of Sydney (151°10'E, 34°00'S; Fig. 8.1). It rises 3 km south-east of Appin, flows northwards to Liverpool, south-east at Chipping Norton and finally eastwards to Botany Bay. The main channel is about 100 km long with a mean depth of 4 m and drains an area of 960 km². The main tributaries of the Georges River are the Woronora River and Prospect, Salt Pan, Little Salt Pan, Bunbury Curran, Cabramatta, Williams, Mill, Deadmans and O'Hare's Creeks. The tidal limit of the river is the Liverpool Weir, approximately 50 km upstream.

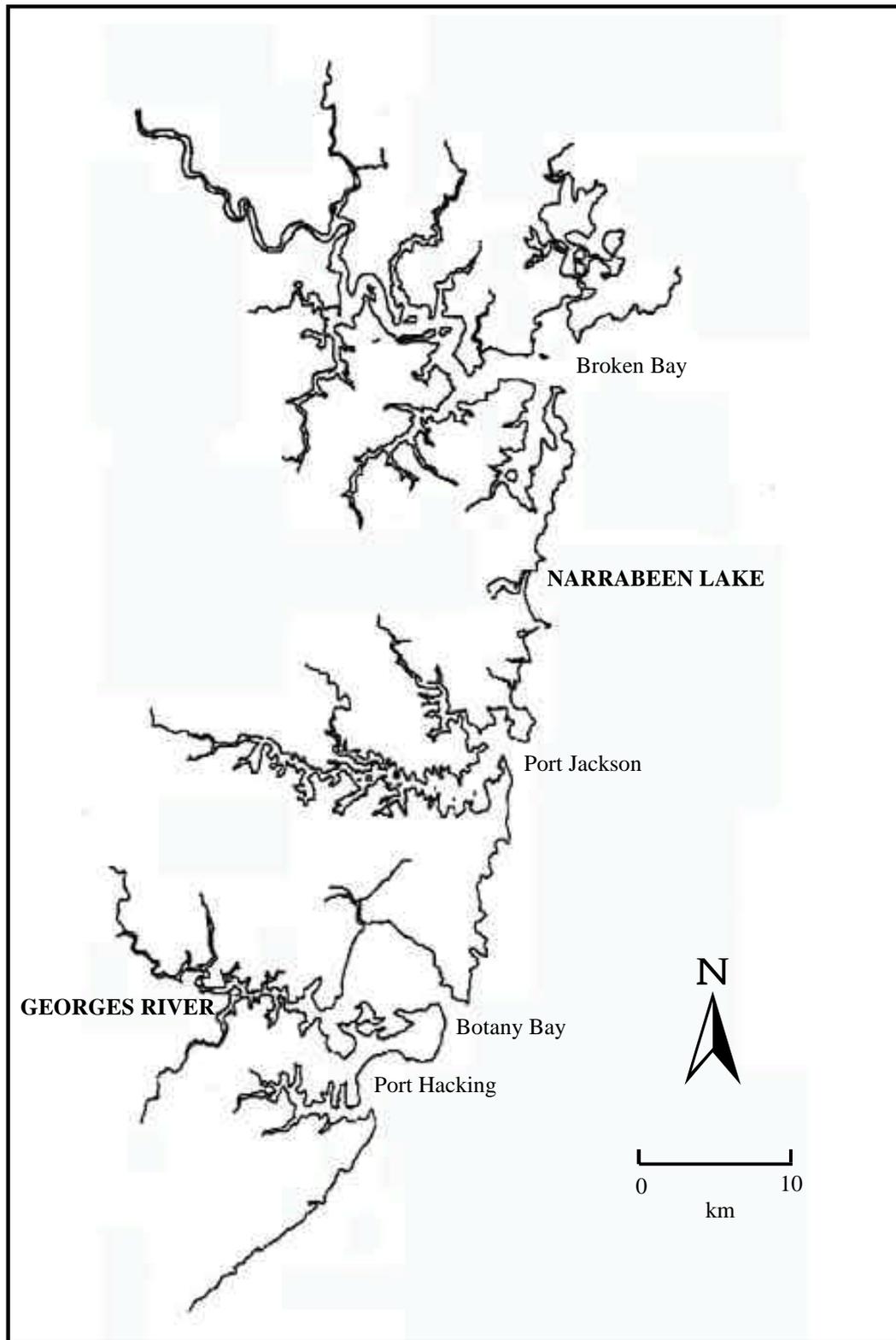


Figure 8.1 Map of the Sydney coastline showing the location of Narrabeen Lake and the Georges River.

In addition to being used intensively for recreation (boating, swimming, angling), a wide range of commercial activities occur within the catchment and include land-development, fishing, waste-disposal, soil-extraction, poultry and pig farming, market gardening and some industrial processing, mainly along Prospect Creek at Smithfield and in Bankstown on tributaries of the Georges River (Department of Urban Affairs and Planning, 1998). The estuary contains over 2 km² of mangroves, 0.27 km² of seagrass and 0.25 km² of saltmarsh (NSW DLWC, 2000d).

8.2.2 Sampling methods

Any impact of waves on assemblages of epifauna is likely to be greatest at depths of less than one half the wave-length, where the wave-form interacts with the bottom. Shallow patches of *Zostera capricorni*, growing at depths of less than 1.0 m below MLWS, were selected for study at Narrabeen Lake and the Georges River, NSW. These locations were chosen due to their low background levels of power-boating and their minimal exposure to wind-generated waves. Patches were typically narrow (less than 3 m wide) and were situated on a steeply grading bottom, so that a small vessel (5.25 m in length) could be driven immediately adjacent to the patches.

Sampling at Narrabeen was done on 13th March, 2002 during daylight hours. Four sites, 50 m in length, were selected for study (Fig. 8.2). Two were located on the northern bank of the lake and two on the southern bank. On each bank there was one disturbed (I) and one undisturbed (C) site (Fig. 8.2). The experimental disturbance was created by driving a 5.25 m long vessel with a 50-horse power, 4-stroke engine back and forth in a direction parallel to the shore and approximately 5 m away from the patches of seagrass for a period of 5 minutes. The bow of the boat was weighed down to maximize the production of wash.

Samples were collected at two times prior to the disturbance and immediately afterwards. There was approximately one hour separating each 'before' time. At each time of sampling, three samples of seagrass were taken from three patches in each site. Patches of seagrass were typically small (1-2 m in diameter) and different patches were therefore sampled on each occasion. Sampling was as described in Section 7.2.2.

Sampling in the Georges River was on 11th June, 2002. Along the central section of the river, from Como to Picnic Point, there are shallow sand bars. Patches of *Z. capricorni* are found fringing these bars. Three sand bars that appeared, from preliminary sampling, to have similar densities of crustaceans were selected for study (Fig. 8.3). At each of the eastern and western bars, one large patch of seagrass was randomly assigned to remain undisturbed (C) and another

to be exposed (I) to wash. At the middle sand-bar, there were two undisturbed sites only. This arrangement at the central bar enabled tests to be done to ensure that the undisturbed sites at the western and eastern bars were independent of the disturbed sites, following exposure to boat-wash.

Ten samples were collected from each site at two times before the disturbance and a single time immediately after. Sampling was done within 2 hours of low tide because the disturbance due to wash is greatest in shallow water. Time-intervals between sampling and the method of generation of wash were as at Narrabeen.



Figure 8.2 Photograph of Narrabeen Lake showing the location of study sites.

C1 = control site 1, C2 = control site 2, I1 = disturbed site 1, I2 = disturbed site 2

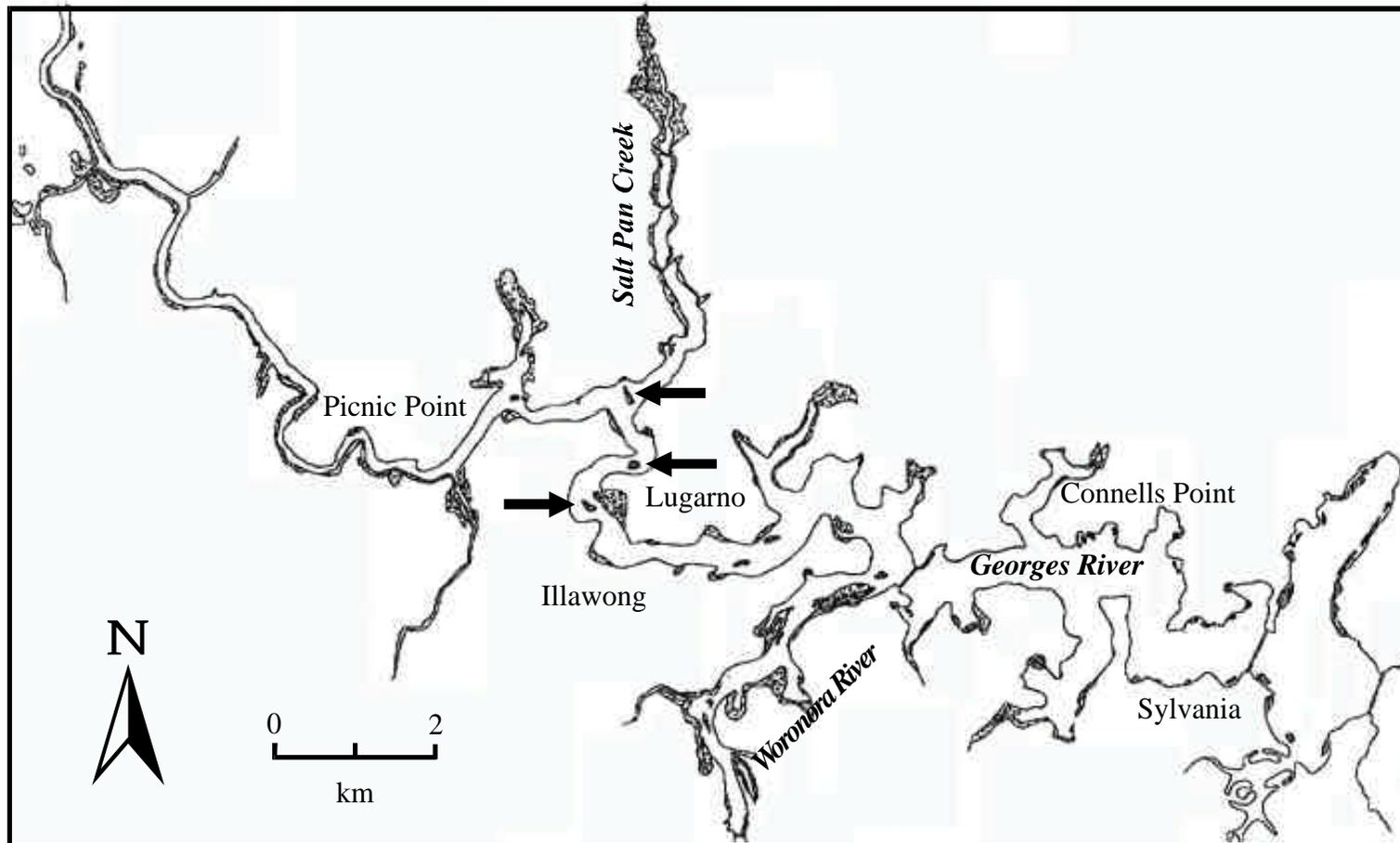


Figure 8.3 Map of the Georges River, Sydney, Australia showing the location of the three sand-bars sampled (arrows). Shading indicates the presence of aquatic vegetation (Zosteraceae, Mangroves, Saltmarsh).

At Narrabeen and the Georges River, the current velocity associated with incoming boat-generated waves was measured in the patches of seagrass using an electromagnetic flow meter (EM; Valeport, Model 801). The probe was mounted on a tripod and held 5 cm below the surface of the water, with the flat sensor uppermost and the paddle pointing perpendicularly outward from the shore (Fig. 8.4). The EM system measures the flow twice every second and calculates the real-time flow every second as the average of the half-second readings. At each disturbed site, readings were taken for 2 minutes before the disturbance and then for the duration of the disturbance-event. The maximal velocity (in either a positive or negative direction) was determined for disturbed and undisturbed conditions.

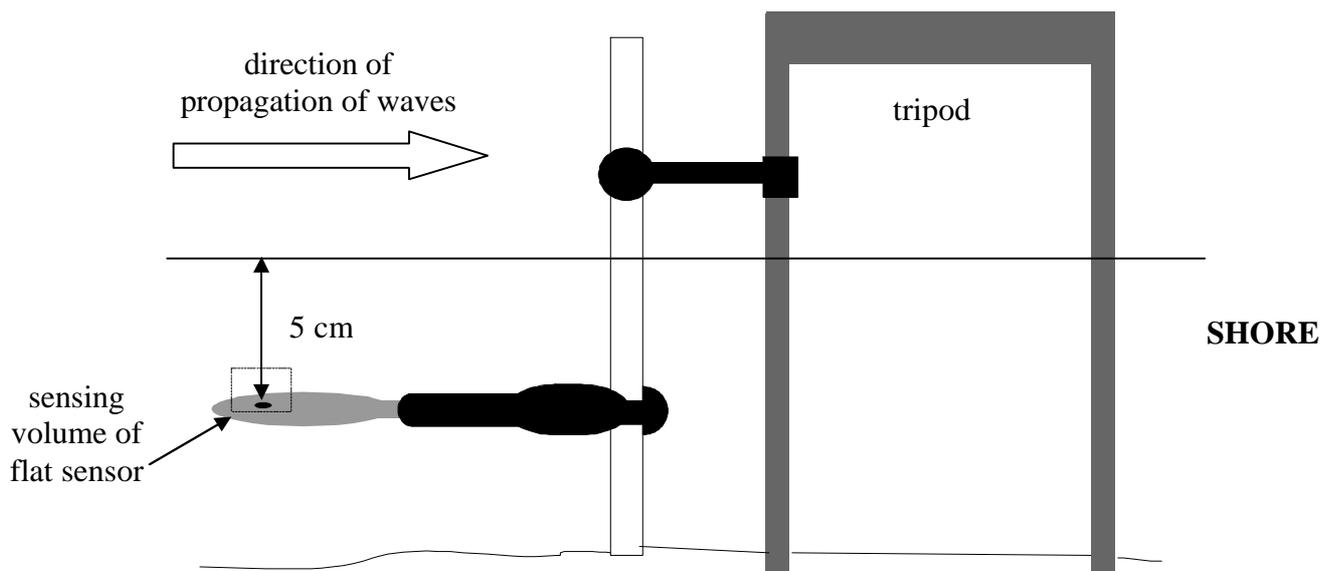


Figure 8.4 Diagram showing the set-up of the electromagnetic flow-meter in the field.

All samples were taken to the laboratory and excess water was removed from each by draining them on a 250 μm sieve. Samples were preserved using 7% formalin in seawater and stained using Biebrich scarlet. Epifaunal organisms were removed from the blades of seagrass by running a pair of forceps along the length of each. All mobile organisms were identified and counted. Gastropods and bivalves were identified to species, amphipods and polychaetes to family and all other organisms to order.

Blades of seagrass were retained to determine biomass. These were dried at 80°C to constant weight. For each site, the dry weight of the samples was correlated with the abundance of amphipods to determine whether samples needed to be standardized for biomass, as has been done in previous studies (e.g. Jernakoff and Nielsen, 1998).

8.2.3 Analyses

As a maximum of two factors may be included in any one NP-MANOVA, testing for a significant interaction between times before and after the disturbance and control and disturbed sites could not be done. Instead, analyses were done with the two factors, time and site (both fixed). In the case of a significant time x site interaction, *a posteriori* tests were done to determine whether temporal changes were consistent between disturbed or undisturbed sites.

Asymmetrical analyses of variance were used to compare the abundances of individual taxa before and after the disturbance, between disturbed and undisturbed sites (see Underwood 1992, 1993, 1994). In the case of an effect of wash, a significant before vs after x control vs impact interaction should be found. Separate analyses were done for each of the four sites at Narrabeen because their abundances were very different, which may preclude any patterns of temporal change being found across sites. Variance at the scales of patch and sample (i.e. residual) were partitioned into before and after times to test the hypothesis that there would be greater spatial variability in assemblages following the disturbance.

At Narrabeen, analyses were also done comparing the proportional change in abundances of the taxa, Ampithoidae, Corophiidae and total amphipods between the periods, B1 and B2, and B2 and A, in an attempt to standardize for the large discrepancy in abundances among sites. The mean abundance of the taxon in each patch at time (t + 1) was divided by the mean number across all patches at time (t). All proportions were $\ln(x + 1)$ transformed. There were three replicate patches within each site, at each period. Two of the sites were disturbed and two undisturbed by boat wash. In the case of an impact, a significant period x disturbance interaction should be found, with the ratio smaller at period 2 than at period 1, if abundances are decreasing.

8.3 Results

Similar taxa were found at Narrabeen Lake and the Georges River (Table 8.1). At Narrabeen, the maximal current-speed associated with incoming boat-waves was 0.167 ms^{-1} at I1 and 0.227 ms^{-1} at I2, in a direction perpendicular to the shore. At I2, depth drops away much closer to shore than at I1 and the boat was driven closer to shore (approximately 5 m away) than at I1 (10 m away). At both sites, the maximal current speed recorded in the 2 minutes prior to the disturbance was 0.030 ms^{-1} .

Along the Georges River, the maximal current-speed associated with incoming boat-waves was 0.400 ms^{-1} at I1 and 0.181 ms^{-1} at I2, in a direction perpendicular to the shore. The maximal current-speed recorded in the 2 minutes prior to the disturbance was 0.024 ms^{-1} at I1 and 0.028 ms^{-1} at I2. Sites were disturbed shortly after low tide, at a time of minimal tidal flow. These values for 'background' flow are not representative of flow at 'before' times, when the tide was still dropping and currents were noticeably greater.

8.3.1 Narrabeen

Before the disturbance, there was no relationship between the dry weight of seagrass and the assemblage of macro-invertebrates associated with it (Fig. 8.5). A Spearman's rank correlation of the Euclidean distances between the dry weights of samples of seagrass and the Bray-Curtis dissimilarities between their assemblages of invertebrates was, however, significant ($r_s = 0.09$, number of permutations = 999, $p < 0.05$). The significance of this test was probably due to the large number of degrees of freedom because the r_s value was very close to zero. No relationship was found between the dry weight of seagrass and the total abundance of amphipods (Fig. 8.6; Pearson's $r = -0.004$, 70 df, $p > 0.05$). It was therefore decided not to standardize abundances of macro-invertebrates to the biomass of seagrass. Thus, all analyses presented for Narrabeen are done on the raw data.

Assemblages of macro-invertebrates were very different at 'disturbed' sites and 'undisturbed' sites, before the disturbance (Fig. 8.7); there were significant differences (NP-MANOVA) among all four of the sites sampled and these were independent of time (Table 8.2). Change in the assemblages of all sites was not significant and there was no consistent direction of change between the two disturbed sites following the disturbance (Fig. 8.7, Table 8.2).

The disturbance did not appear to have any effect on the spatial variability of the assemblages that was consistent between the two disturbed sites (Table 8.3). At none of the four sites, was there an obvious increase in the scatter of points representing the average assemblages of patches about their centroids from before to after the disturbance (Fig. 8.8).

Table 8.1 Macro-invertebrates found in samples of seagrass from Narrabeen Lake (N) on 13th March, 2002 and the Georges River (G) on the 11th June, 2002.

* Isopods and copepods were present at Narrabeen but were not identified to smaller taxonomic groups

| | | | | | |
|-------------|--------------|---------------------------------|------------------------------|---|---|
| Oligochaeta | | | | N | G |
| Annelida | Polychaeta | Capitellidae | | N | G |
| | | Dorvilleidae | | N | |
| | | Hesionidae | | | G |
| | | Nephtyidae | | | G |
| | | Nereididae | | N | G |
| | | Opheliidae | | N | G |
| | | Orbiniidae | | N | G |
| | | Paraonidae | | N | G |
| | | Phyllodoceidae | | N | |
| | | Polynoidae | | | G |
| | | Sabellidae | | N | G |
| | | Spionidae | | N | G |
| | | Syllidae | | N | G |
| Chelicerata | Arachnida | | mite | | G |
| Chordata | Osteichthyes | Gobiidae | <i>Arenigobius frenatus</i> | | G |
| | | | <i>Redigobius macrostoma</i> | | G |
| | | Syngnathidae | <i>Hippocampus whitei</i> | N | G |
| Cnidaria | | brown anemone | | N | |
| Crustacea | Caridea | | | N | G |
| | Decapoda | Grapsidae | <i>Paragrapsus laevis</i> | | G |
| | | Hymenosomatidae | <i>Amarinus lacustris</i> | N | |
| | | unidentifiable crab | | N | |
| | | crab megalops | | N | G |
| | Amphipoda | Caprellidea | | | G |
| | | Ampithoidae | | N | G |
| | | Corophiidae | | N | G |
| | | Dexaminidae | | N | G |
| | | Gammaridae | | N | G |
| | | Hyalidae | | N | G |
| | | Phoxocephalidae | | | G |
| | Isopoda | Sphaeromatidae | | * | G |
| | | Oniscoidea | | * | G |
| | Tanaidacea | | | | G |
| | Copepoda | Calanoida | | * | G |
| | | Cyclopoda | | * | G |
| | | Harpacticoida | | * | G |
| | | Ostracoda | | | G |
| Mollusca | Bivalvia | Erycinidae | <i>Arthritica helmsii</i> | N | |
| | | Mytilidae | <i>Mytilus</i> sp. | N | |
| | | | <i>Xenostrobus securis</i> | N | |
| | | Tellinidae | <i>Tellina</i> sp. | | G |
| | | Veneridae | <i>Irus crebrelamellatus</i> | N | |
| | | unidentifiable juvenile bivalve | | N | |
| | Gastropoda | Hydrobiidae | <i>Ascorhis victoriae</i> | | G |
| | | Littorinidae | <i>Bembicium auratum</i> | | G |
| | | Neritidae | <i>Neritina oualaniensis</i> | | G |
| | Pulmonata | Onchidiidae | <i>Onchidium</i> sp. | | G |
| Nematoda | | | | N | G |
| Nemertea | | | | N | G |
| Sipuncula | | | | N | |
| Uniramia | Insecta | Chironomidae | | N | |
| | | Diptera | | | G |

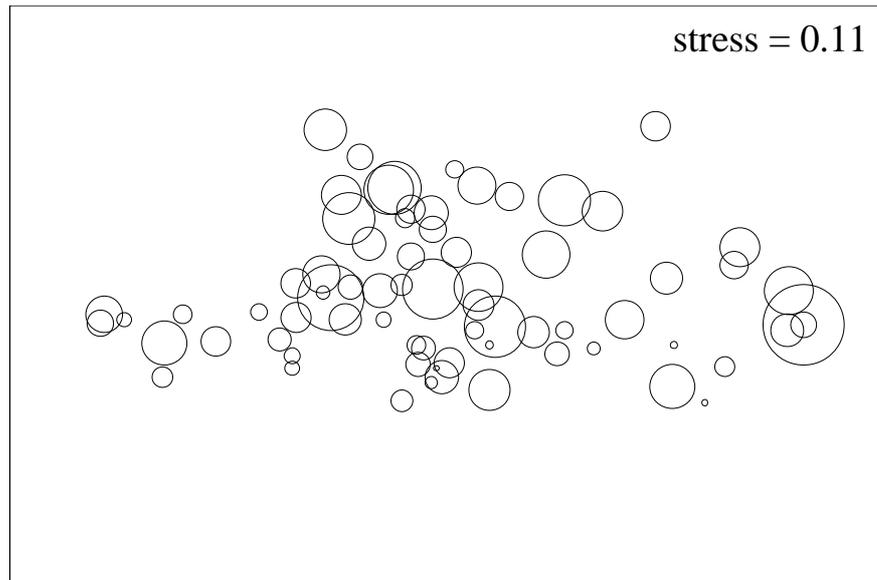


Figure 8.5 nMDS ordination of the assemblages of macro-invertebrates on seagrass blades collected from Narrabeen Lake on 13th March, 2002, prior to disturbance. The superimposed circles represent the dry weight of seagrass in each sample. The size of the circle is directly proportional to mass.

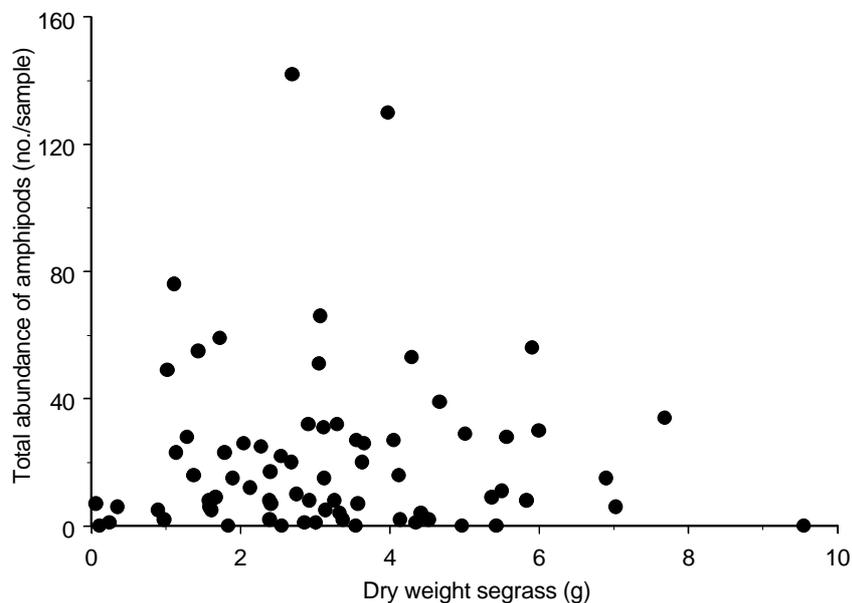


Figure 8.6 The relationship between the dry weight of seagrass and the total abundance of amphipods in samples collected from from Narrabeen Lake on 13th March, 2002, prior to disturbance.

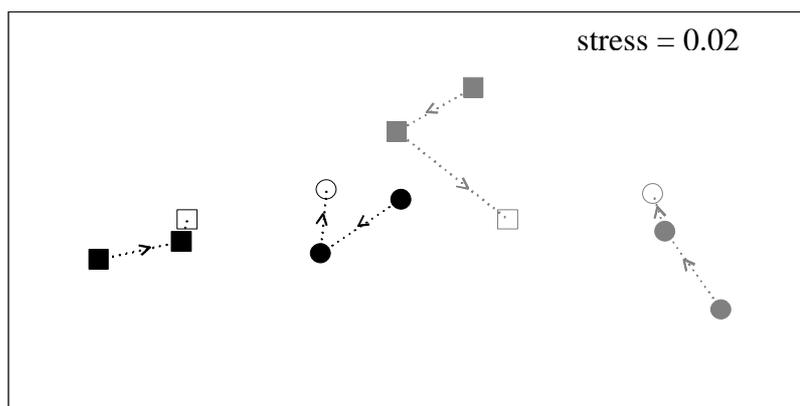


Figure 8.7 nMDS of average assemblages of macro-invertebrates at Narrabeen Lake prior to (closed symbols) and following (open symbols) the disturbance of the sites, I1 (grey circles) and I2 (grey squares), with boat-wash. The sites C1 (black circles) and C2 (black squares) were not disturbed. $n = 3$ within 3 patches at each site, at each time.

Table 8.2 Summary of a non-parametric MANOVA comparing spatial variation in assemblages of epifaunal macro-invertebrates among sites of Narrabeen Lake, disturbed and undisturbed by boat-wash. Samples were collected on 13th March, 2002. ti = time (3 levels; before 1 [B1], before 2 [B2], after [A]; fixed), si = Site (4 levels: control 1 [C1], control 2 [C2], disturbed 1 [I1], disturbed 2 [C2]; fixed). $n = 3$ within 3 patches at each site.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| source of variation | df | p | Sig. |
|---------------------------|-----------------------|--------|------|
| ti | 2 | 0.4064 | NS |
| si | 3 | 0.0002 | *** |
| ti x si | 9 | 0.0642 | NS |
| res | 32 | | |
| <i>a posteriori</i> tests | si: C1 ? C2 ? I1 ? I2 | | |

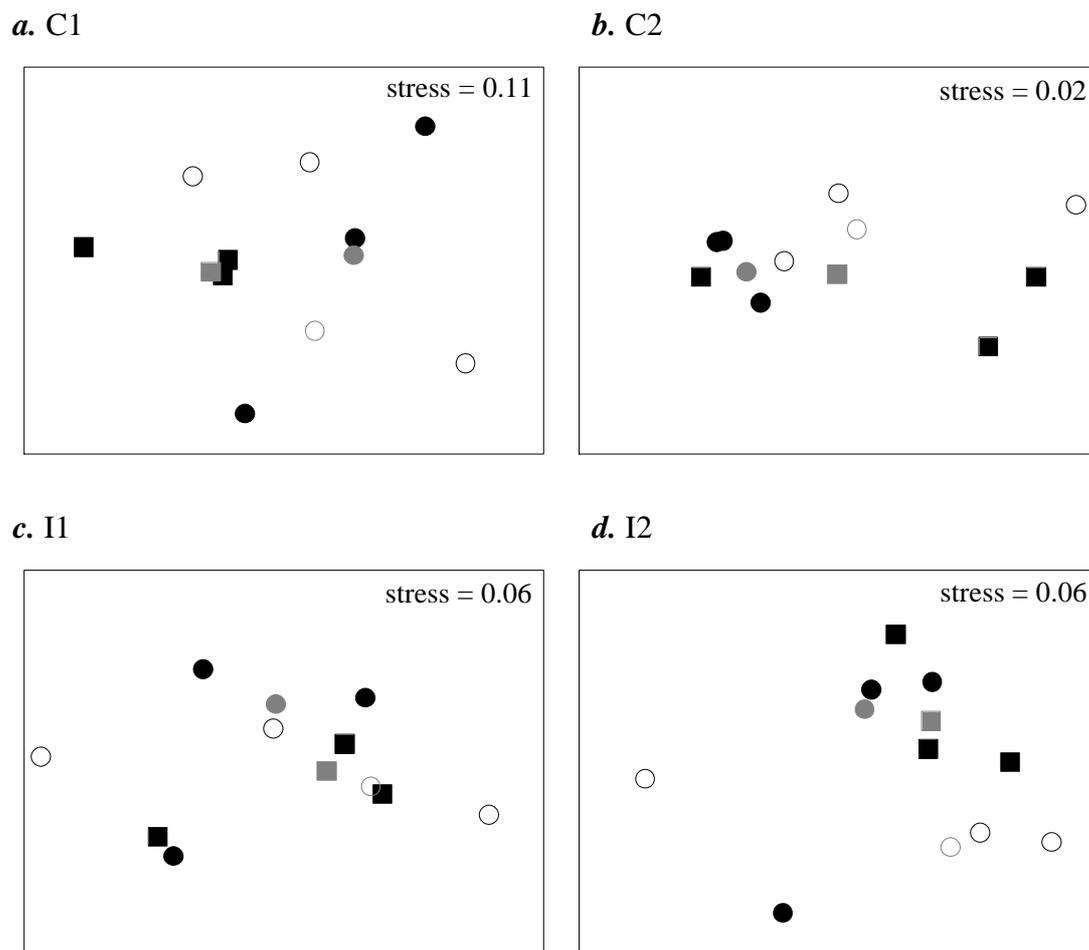


Figure 8.8 nMDS ordinations of assemblages of macro-invertebrates in patches of seagrass at Narrabeen. Average assemblages within each patch are shown in black; centroids for the three patches sampled at each time within each site, are shown in grey. Different patches were sampled at two times before (B1: filled circles, B2: filled squares) and a single time after (A: open circles) the disturbance of the sites I1 and I2 with boat-wash. C1 and C2 are control sites and were not disturbed. $n = 3$ for each patch.

The abundances of amphipods, Ampithoidae and Corophiidae and the total numbers of amphipods decreased in disturbed sites following exposure to boat-wash (Fig. 8.9, a,b,e). Contrary to the hypothesis, the abundance of copepods increased in disturbed sites after exposure to boat-wash (Fig. 8.9f). None of these patterns was, however, supported by asymmetrical analyses of variance (before vs after, Table 8.3).

In the case of Ampithoidae and Total Amphipods, a significant interaction between period and site was found in the proportional changes through time (Table 8.4, $p < 0.05$ and $p < 0.01$, respectively). In both cases, SNK tests showed no difference in the ratio of abundance ($[t + 1]/\text{mean}[t]$) between the two periods for sites C1, C2 and I1 and a smaller ratio for period 2 than period 1 at I2. A significant period x disturbance interaction was found for Corophiidae (Table 8.4), with the ratio smaller for period 1 than period 2 in control sites and greater for period 1 in disturbed sites. Neither a period x site nor a period x disturbance interaction was found for Copepoda.

The abundances of other common taxa of mobile invertebrate did not display any pattern of change consistent with an effect of wash (Dexaminidae, Gammaridae; Figure 8.9c,d).

Table 8.3 Summaries of asymmetrical analyses comparing spatial variation in the abundances of epifaunal macro-invertebrates between times before and after the disturbance of the sites, I1 and I2, by boat-wash. Seagrass was sampled at Narrabeen Lake on 13th March, 2002. $n = 3$, within 3 patches at each site. C1 = control site 1, C2 = control site 2, I1 = disturbed site 1, I2 = disturbed site 2.

NS $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

a. Ampithoidae

| | df | C1 | | | C2 | | | I1 | | | I2 | | |
|-------------------|----|-------------|------|------|-------------|------|------|-------------|------|------|-------------|-------|------|
| | | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. |
| times | 2 | 182.26 | | | 354.70 | | | 0.26 | | | 277.48 | | |
| before vs after | 1 | 52.02 | 1.17 | NS | 444.91 | 1.68 | NS | 0.30 | 1.35 | NS | 312.96 | 1.29 | NS |
| among before | 1 | 312.50 | | | 264.50 | | | 0.22 | | | 242.00 | | |
| patches (times) | 6 | 70.44 | | | 208.26 | | | 1.89 | | | 32.41 | | |
| patches (before) | 4 | 39.94 | 3.29 | NS | 161.50 | 1.87 | NS | 1.11 | 3.10 | NS | 43.94 | 4.71 | NS |
| patches (after) | 2 | 131.44 | | | 301.78 | | | 3.44 | | | 9.33 | | |
| residual | 18 | 152.63 | | | 266.89 | | | 2.22 | | | 45.15 | | |
| residual (before) | 12 | 146.33 | 1.13 | NS | 380.83 | 9.76 | ** | 1.28 | 4.15 | * | 65.44 | 14.37 | ** |
| residual (after) | 6 | 165.22 | | | 39.00 | | | 5.31 | | | 4.56 | | |
| Cochran's test | | C = 0.39 NS | | | C = 0.42 NS | | | C = 0.60 ** | | | C = 0.42 NS | | |
| Transformation | | | | | | | | | | | | | |

Table 8.3 cont.**b. Corophiidae**

| | df | C1 | | | C2 | | | I1 | | | I2 | | |
|-------------------|----|-------------|------|------|-------------|------|------|-------------|------|------|-------------|--------|------|
| | | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. |
| times | 2 | 1.70 | | | 0.53 | | | 0.10 | | | 2.90 | | |
| before vs after | 1 | 1.37 | 0.68 | NS | 0.75 | 2.43 | NS | 0.08 | 0.64 | NS | 5.76 | 162.75 | * |
| among before | 1 | 2.03 | | | 0.31 | | | 0.13 | | | 0.04 | | |
| patches (times) | 6 | 2.38 | | | 1.60 | | | 0.83 | | | 1.02 | | |
| patches (before) | 4 | 0.79 | 6.98 | NS | 1.20 | 2.00 | NS | 0.89 | 1.25 | NS | 1.45 | 9.06 | NS |
| patches (after) | 2 | 5.54 | | | 2.40 | | | 0.71 | | | 0.16 | | |
| residual | 18 | 1.16 | | | 1.39 | | | 0.37 | | | 0.59 | | |
| residual (before) | 12 | 1.08 | 1.25 | NS | 1.40 | 1.02 | NS | 0.48 | 3.18 | NS | 0.75 | 2.80 | NS |
| residual (after) | 6 | 1.34 | | | 1.37 | | | 0.15 | | | 0.27 | | |
| Cochran's test | | C = 0.28 NS | | | C = 0.25 NS | | | C = 0.36 NS | | | C = 0.29 NS | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |

c. Total amphipods

| | df | C1 | | | C2 | | | I1 | | | I2 | | |
|-------------------|----|-------------|-------|------|-------------|------|------|-------------|-------|------|-------------|-------|------|
| | | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. |
| times | 2 | 946.78 | | | 564.59 | | | 2.70 | | | 526.26 | | |
| before vs after | 1 | 1700.17 | 8.79 | NS | 8.96 | 0.01 | NS | 5.35 | 96.26 | NS | 696.96 | 1.96 | NS |
| among before | 1 | 193.39 | | | 1120.22 | | | 0.06 | | | 355.56 | | |
| patches (times) | 6 | 176.74 | | | 1224.41 | | | 11.11 | | | 64.74 | | |
| patches (before) | 4 | 40.06 | 11.24 | NS | 1136.22 | 1.23 | NS | 14.61 | 3.55 | NS | 85.06 | 3.53 | NS |
| patches (after) | 2 | 450.11 | | | 1400.78 | | | 4.11 | | | 24.11 | | |
| residual | 18 | 482.15 | | | 1258.89 | | | 8.44 | | | 89.59 | | |
| residual (before) | 12 | 351.94 | 2.11 | NS | 1580.06 | 2.56 | NS | 9.00 | 1.23 | NS | 128.33 | 10.60 | ** |
| residual (after) | 6 | 742.56 | | | 616.56 | | | 7.33 | | | 12.11 | | |
| Cochran's test | | C = 0.27 NS | | | C = 0.34 NS | | | C = 0.28 NS | | | C = 0.47 NS | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |

d. Copepoda

| | df | C1 | | | C2 | | | I1 | | | I2 | | |
|-------------------|----|-------------|------|------|-------------|------|------|-------------|------|------|-------------|------|------|
| | | MS | F | Sig. |
| times | 2 | 2.42 | | | 18.35 | | | 0.64 | | | 0.91 | | |
| before vs after | 1 | 1.87 | 0.63 | NS | 2.43 | 0.23 | NS | 0.09 | 0.07 | NS | 0.13 | 0.07 | NS |
| among before | 1 | 2.97 | | | 10.39 | | | 1.19 | | | 1.69 | | |
| patches (times) | 6 | 0.83 | | | 7.55 | | | 1.38 | | | 3.31 | | |
| patches (before) | 4 | 0.74 | 1.36 | NS | 7.33 | 1.07 | NS | 0.81 | 3.12 | NS | 2.19 | 2.54 | NS |
| patches (after) | 2 | 1.01 | | | 6.88 | | | 2.53 | | | 5.56 | | |
| residual | 18 | 1.70 | | | 1.97 | | | 0.96 | | | 1.31 | | |
| residual (before) | 12 | 1.54 | 7.89 | ** | 2.05 | 1.08 | NS | 0.76 | 1.78 | NS | 1.25 | 1.14 | NS |
| residual (after) | 6 | 12.17 | | | 2.21 | | | 1.36 | | | 1.43 | | |
| Cochran's test | | C = 0.25 NS | | | C = 0.22 NS | | | C = 0.38 NS | | | C = 0.26 NS | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |

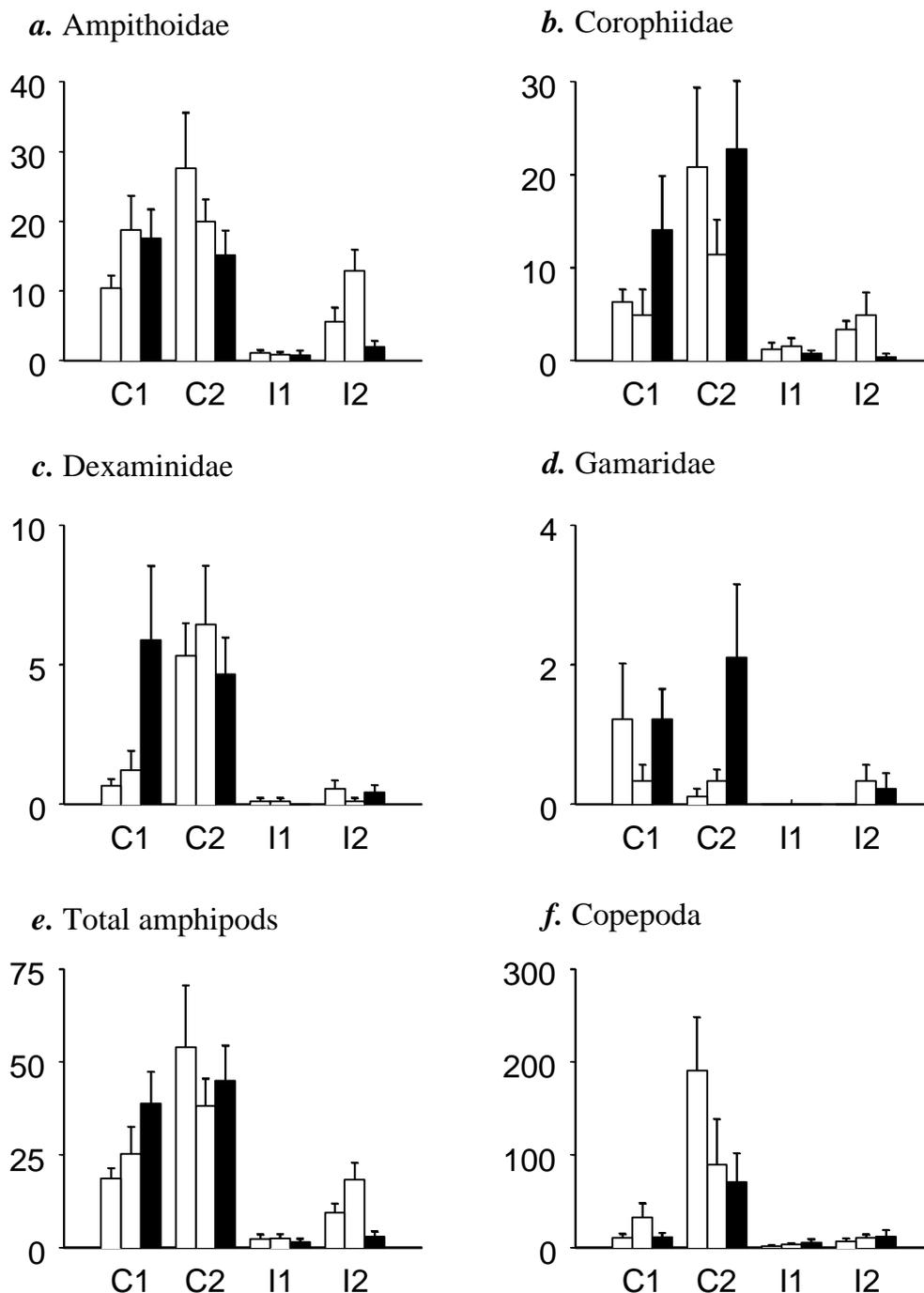


Figure 8.9 Mean (+ S.E.) abundance of mobile crustaceans in samples of seagrass from Narrabeen Lake, two times before (white) and a single time after (black) the exposure of disturbed sites to boat-wash. $n = 3$ within 3 patches at each site.

C1 = control site 1, C2 = control site 2, I1 = disturbed site 1, I2 = disturbed site 2.

Table 8.4 Summaries of analyses comparing proportional change in the abundances of epifaunal macro-invertebrates among sites, disturbed (disturbed site 1 [I1], disturbed site 2 [I2]) and undisturbed (control site 1 [C1], control site 2 [C2]) by boat-wash. Seagrass was sampled at Narrabeen Lake on 13th March, 2002. pe = period (2 levels: pe 1 [B2-B1], pe 2 [A-B2]; fixed), im = impact (2 levels: control, disturbed; fixed), si (im) = site (2 levels, random).

NS $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | Ampithoidae | | | | Corophiidae | | | Total Amphipods | | | Copepoda | | |
|----------------|--------------|---------------|------|------|-------------|--------------|------|-----------------|---------------|------|-------------|------|------|
| | df | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. |
| pe | 1 | 0.85 | 2.00 | NS | 0.01 | 0.23 | NS | 0.28 | 1.43 | NS | 0.75 | 1.29 | NS |
| im | 1 | 0.05 | 0.28 | NS | 0.54 | 18.77 | * | 0.19 | 2.08 | NS | 0.27 | 1.07 | NS |
| si (im) | 2 | 0.16 | 2.13 | NS | 0.03 | 0.13 | NS | 0.09 | 1.78 | NS | 0.25 | 0.88 | NS |
| pe x im | 1 | 0.21 | 0.50 | NS | 1.92 | 44.97 | * | 0.76 | 3.94 | NS | 0.02 | 0.03 | NS |
| pe x si (im) | 2 | 0.42 | 5.62 | ** | 0.04 | 0.19 | NS | 0.19 | 3.71 | * | 0.59 | 2.04 | NS |
| res | 16 | 0.08 | | | 0.22 | | | 0.05 | | | 0.29 | | |
| Cochran's test | | C = 0.62 ** | | | C = 0.37 NS | | | C = 0.3600 NS | | | C = 0.28 NS | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |
| SNK | pe x si (im) | C1: pe1 = pe2 | | | pe x im | C: pe1 < pe2 | | pe x si (im) | C1: pe1 = pe2 | | | | |
| | | C2: pe1 = pe2 | | | | I: pe1 > pe2 | | | C2: pe1 = pe2 | | | | |
| | | I1: pe1 = pe2 | | | | | | | I1: pe1 = pe2 | | | | |
| | | I2: pe1 > pe2 | | | | | | | I2: pe1 > pe2 | | | | |

8.3.2 Georges River

In contrast to Narrabeen, a strong relationship was evident between assemblages of mobile invertebrates and the dry weight of seagrass (Fig. 8.10; Spearman's $r_s = 0.15$, number of permutations = 999, $p = 0.001$). There was also a significant positive relationship between the dry weight of seagrass and the total number of amphipods in samples (Fig. 8.11; Pearson's correlation: $r = 0.72$, 118 df, $p < 0.001$). Consequently, samples were standardized for dry weight of seagrass.

Prior to the analysis of disturbed sites (I1, I2), temporal change in the assemblages of control sites, on the same sand-bars as the disturbed sites (C1, C2), was compared to temporal change in the assemblages of control sites on a different sand-bar (C3, C4). This was to ensure that any temporal change at C1 and C2, following the disturbance of I1 and I2, was independent of any change at the disturbed sites. Non-independence would be indicated by similar patterns of change between C1 and C2 following the disturbance, differing from patterns of change at C3 and C4. This was not the case. All four sites displayed very different patterns of temporal change (Figure 8.12a; Table 8.5a, NP-MANOVA: *a posteriori* tests for the significant time x site interaction).

Univariate analyses indicated that temporal change in the abundances of individual taxa between before and after times did not differ between control sites situated on (i) the same sand bank as another control site or (ii) the same sand bar as a disturbed site. (Before vs after) x treatment and (before vs after) x site (treatment) interactions were non-significant for all taxa (Table 8.6). This meant that temporal change at C1 and C2 was not confounded by change at I1 and I2.

The direction of change following the disturbance was comparable across the two disturbed sites, I1 and I2 (Figure 8.12b). The difference in the structure of the assemblage between before and after times was, however, no greater than the difference between the two before times. A *posteriori* tests examining a significant time x site interaction (NP-MANOVA, $p < 0.001$; Table 8.5b) did not indicate any consistent difference in temporal pattern between control and disturbed sites, nor a similarity in pattern, relating to the disturbance, between the disturbed sites.

The abundances of individual taxa were very variable in time and space (Fig. 8.13). No taxon displayed a change in abundance between before and after times at the disturbed sites, I1 and I2, that was evident above the background 'noise' and that was consistent with an effect of wash (Fig. 8.13, Table 8.7). The (before vs after) x impact interaction for Gammaridae was less significant than Cochran's test (Table 8.7). No change in the abundance of this taxon, consistent with an effect of wash, was evident when this data was graphed (Fig. 8.13f).

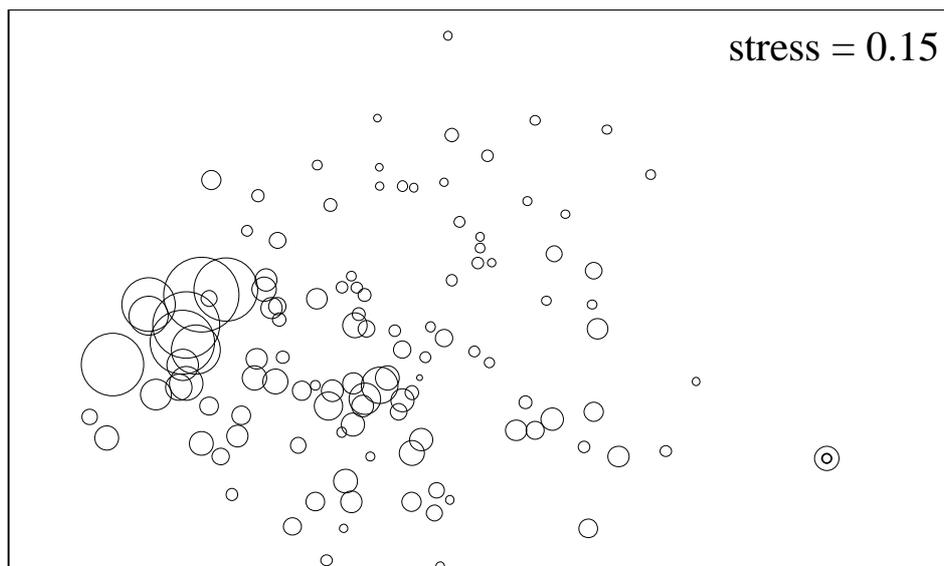


Figure 8.10 nMDS ordination of the assemblages of macro-invertebrates on seagrass blades from the Georges River on 11th June, 2002, prior to disturbance. The superimposed circles represent the dry weight of seagrass in each sample. The size of the circle is directly proportional to mass.

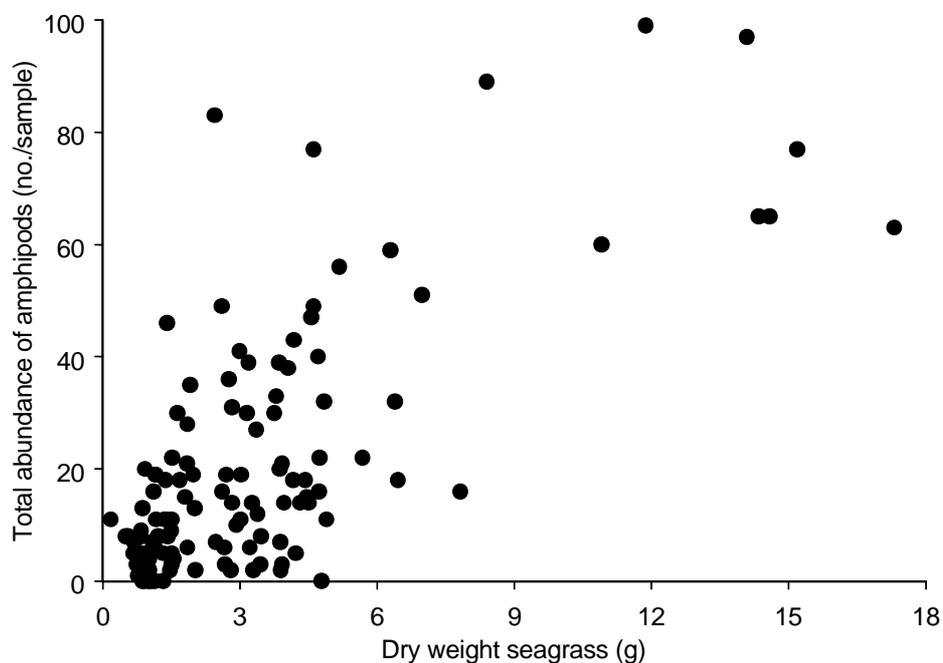


Figure 8.11 The relationship between the dry weight of seagrass and the total abundance of amphipods in samples collected from from the Georges River on 11th June, 2002, prior to disturbance.

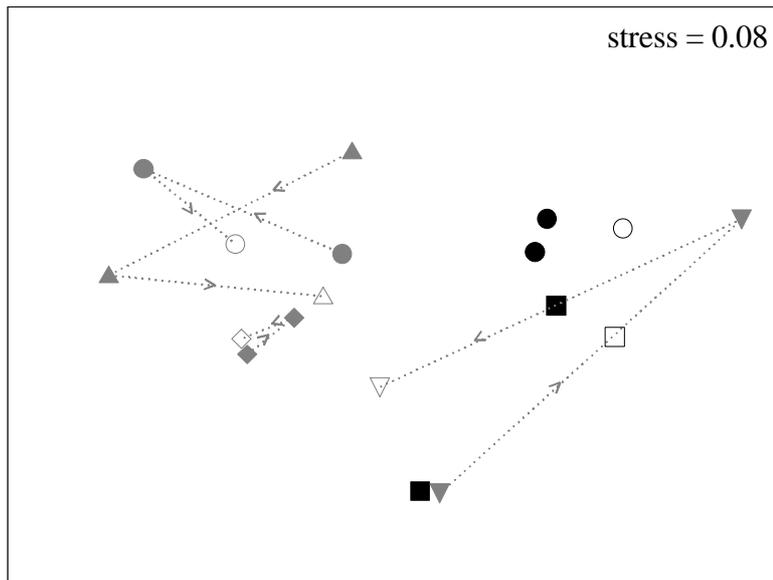
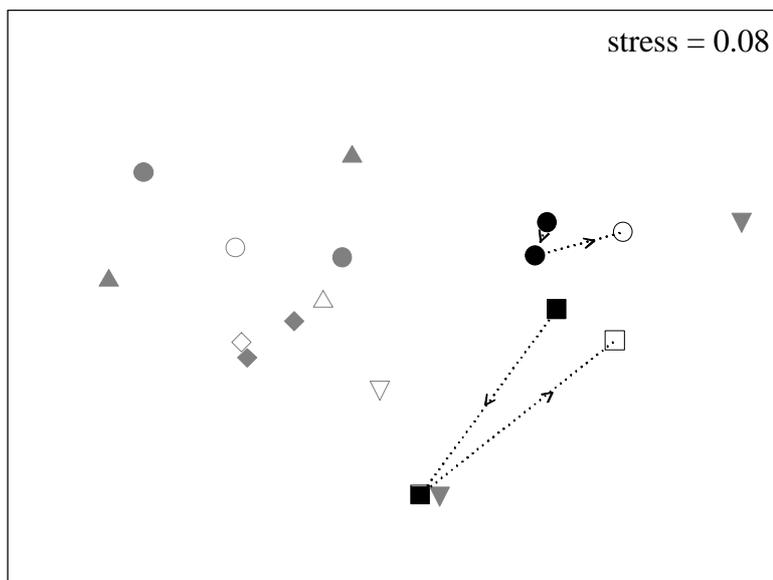
a.**b.**

Figure 8.12 nMDS ordinations of assemblages of macro-invertebrates at control sites (grey symbols; triangle = C1, inverted triangle = C2, diamond = C3, circle = C4) and sites disturbed by boat wash (black symbols; circle = I1, square = I2) along the Georges River on 11th June, 2002. Points represent the average assemblage of mobile taxa per gram of seagrass before (closed symbols) and after (open symbols) the disturbance. Temporal change in assemblages at **a.** control sites and **b.** disturbed sites is shown. $n=10$.

Table 8.5 Summary of non-parametric MANOVAs comparing spatial variation in assemblages of epifaunal macro-invertebrates among **a.** control sites of the Georges River on the same sandbar (C1, C2) and on a separate sandbar (C3, C4) to disturbed sites **b.** sites undisturbed (C1, C2) and disturbed by boat-wash (I1, I2). Samples were collected on 11th June, 2002. ti = time (3 levels; before 1 [B1], before 2 [B2], after [A]; fixed). $n = 10$.

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

a.

| source of variation | df | p | Sig. |
|---------------------------|---------|--|------|
| ti | 2 | 0.0002 | *** |
| si | 3 | 0.0002 | *** |
| ti x si | 6 | 0.0002 | *** |
| res | 108 | | |
| <i>a posteriori</i> tests | ti x si | C1: (B1 = A) ? B2 C2: B1 ? B2 ? A C3: B1 = B2 = A C4: uninterpretable | |

b.

| source of variation | df | p | Sig. |
|---------------------------|---------|--|------|
| ti | 2 | 0.0570 | NS |
| si | 3 | 0.0002 | *** |
| ti x si | 6 | 0.0002 | *** |
| res | 108 | | |
| <i>a posteriori</i> tests | ti x si | C1: B1 = B2 = A C2: B1 ? B2 ? A I1: (B1 = A) ? B2 I2: B1 ? B2 ? A | |

Table 8.6 Summaries of asymmetrical analyses comparing spatial variation in the abundances of epifaunal macro-invertebrates between undisturbed sites on the same (S) and different (D) sand banks as disturbed sites, before and after disturbance with boat-wash. Seagrass was sampled along the Georges River on 11th June, 2002. Treatment has two levels, S and D , with two sites in each. $n = 10$.
NS $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | df | Ampithopidae | | | Corophiidae | | | Dexaminidae | | | Gammaridae | | | Total Amphipods | | |
|--------------------------------------|-----|--------------|------|------|-------------|------|------|-------------|------|------|-------------|------|------|-----------------|------|------|
| | | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. |
| time | 2 | 0.12 | | | 1.59 | | | 0.29 | | | 0.03 | | | 1.05 | | |
| treatment | 1 | 0.27 | | | 0.46 | | | 0.24 | | | 0.08 | | | 1.00 | | |
| site (treatment) | 2 | 3.29 | | | 1.56 | | | 0.09 | | | 0.18 | | | 4.73 | | |
| time x treatment | 2 | 1.21 | | | 0.38 | | | 0.14 | | | 0.05 | | | 0.12 | | |
| (before vs after) x treatment | 1 | 0.00 | 0.00 | NS | 0.14 | 0.22 | NS | 0.00 | 0.01 | NS | 0.04 | 0.64 | NS | 0.01 | 0.02 | NS |
| (among before) x treatment | 1 | 2.41 | | | 0.62 | | | 0.28 | | | 0.06 | | | 0.24 | | |
| time x site (treatment) | 4 | 2.08 | | | 0.50 | | | 0.02 | | | 0.03 | | | 1.45 | | |
| (before vs after) x site (treatment) | 2 | 0.75 | 0.22 | NS | 0.42 | 0.71 | NS | 0.01 | 0.40 | NS | 0.02 | 0.48 | NS | 1.58 | 1.20 | NS |
| (among before) x site (treatment) | 2 | 3.41 | | | 0.59 | | | 0.03 | | | 0.04 | | | 1.31 | | |
| residual | 108 | 0.36 | | | 0.39 | | | 0.05 | | | 0.03 | | | 0.44 | | |
| Cochran's test | | C = 0.24 * | | | C = 0.16 NS | | | C = 0.36 ** | | | C = 0.60 ** | | | C = 0.26 ** | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |

| | df | Calanoida | | | Harpacticoida | | |
|--------------------------------------|-----|-------------|------|------|---------------|------|------|
| | | MS | F | Sig. | MS | F | Sig. |
| time | 2 | 5.63 | | | 0.09 | | |
| treatment | 1 | 7.14 | | | 0.43 | | |
| site (treatment) | 2 | 4.90 | | | 0.49 | | |
| time x treatment | 2 | 2.97 | | | 0.27 | | |
| (before vs after) x treatment | 1 | 0.64 | 0.12 | NS | 0.01 | 0.02 | NS |
| (among before) x treatment | 1 | 5.29 | | | 0.52 | | |
| time x site (treatment) | 4 | 10.26 | | | 0.58 | | |
| (before vs after) x site (treatment) | 2 | 6.34 | 0.45 | NS | 0.43 | 0.59 | NS |
| (among before) x site (treatment) | 2 | 14.17 | | | 0.73 | | |
| residual | 108 | 0.27 | | | 0.15 | | |
| Cochran's test | | C = 0.16 NS | | | C = 0.31 ** | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | |

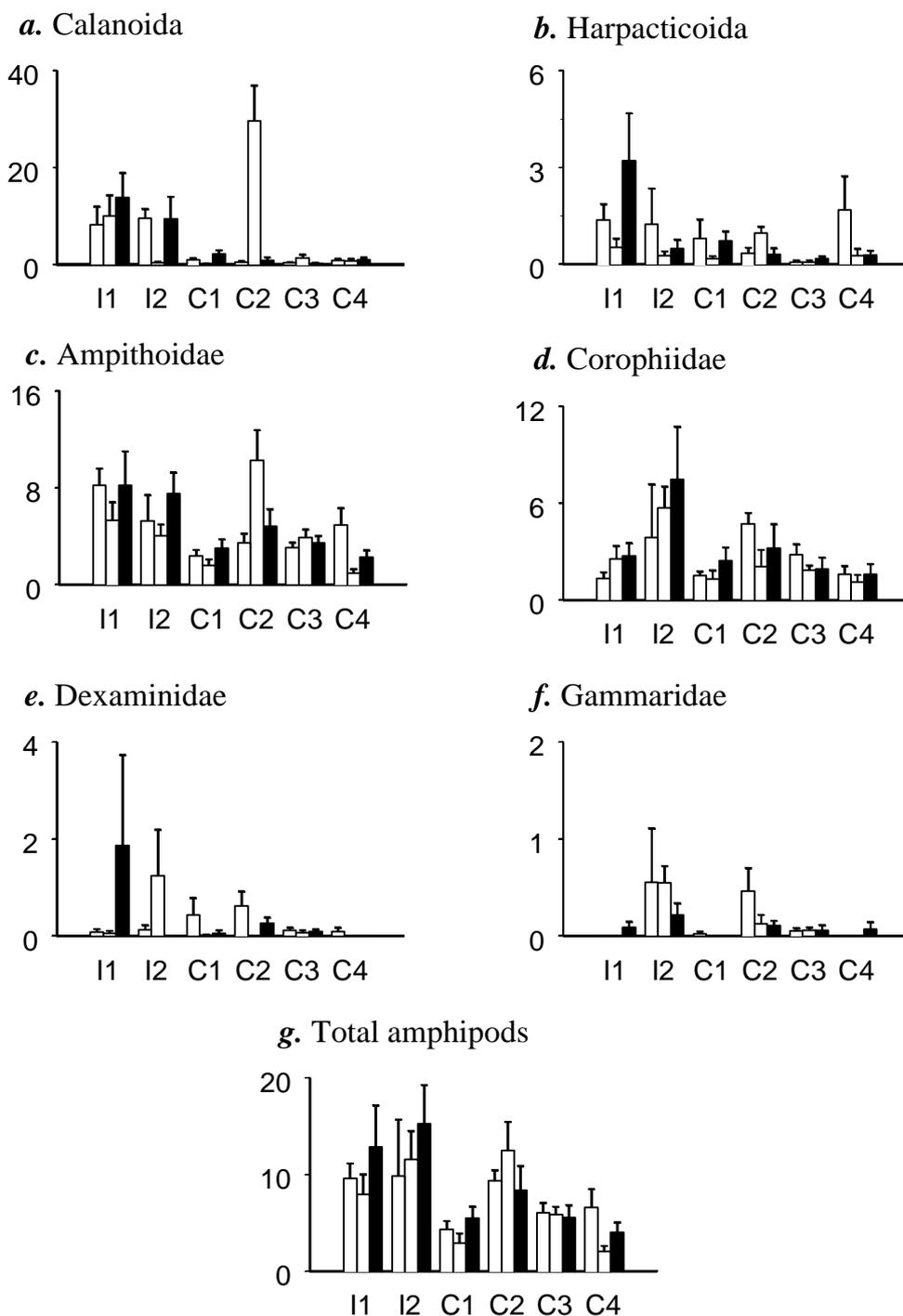


Figure 8.13 Mean (+ S.E.) abundance of mobile crustaceans in samples of seagrass collected from the Georges River, two times before (white) and a single time after (black) the exposure of disturbed sites to boat-wash. $n = 3$ within 3 patches at each site.

C1 = control site 1, C2 = control site 2, C3, control site 3, control site 4, I1 = disturbed site 1, I2 = disturbed site 2.

Table 8.7 Summaries of asymmetrical analyses comparing spatial variation in the abundances of epifaunal macro-invertebrates between undisturbed and disturbed sites, before and after disturbance with boat-wash. Seagrass was sampled along the Georges River on 11th June, 2002. $n = 10$. NS $p > 0.05$ * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| | df | Ampithopidae | | | Corophiidae | | | Dexaminidae | | | Gammaridae | | | Total Amphipods | | |
|---------------------------------------|-----|---------------|-------|------|---------------|------|------|---------------|------|------|---------------|--------|------|-----------------|------|------|
| | | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. | MS | F | Sig. |
| time | 2 | 0.20 | | | 0.59 | | | 0.04 | | | 0.02 | | | 0.32 | | |
| location | 1 | 3.76 | | | 0.81 | | | 0.01 | | | 0.08 | | | 2.98 | | |
| impact | 1 | 0.80 | | | 3.90 | | | 0.17 | | | 1.01 | | | 3.63 | | |
| time x location | 2 | 0.90 | | | 4.18 | | | 0.51 | | | 0.10 | | | 1.01 | | |
| time x impact | 2 | 2.17 | | | 0.03 | | | 0.19 | | | 0.07 | | | 2.03 | | |
| (before vs after) x impact | 1 | 0.01 | 0.00 | NS | 0.03 | 1.41 | NS | 0.32 | 6.75 | NS | 0.13 | 649.50 | * | 0.38 | 0.10 | NS |
| (among before) x impact | 1 | 4.32 | | | 0.02 | | | 0.05 | | | 0.00 | | | 3.68 | | |
| location x impact | 1 | 4.60 | | | 0.05 | | | 0.02 | | | 0.03 | | | 3.17 | | |
| time x location x impact | 2 | 1.40 | | | 1.79 | | | 0.47 | | | 0.09 | | | 1.99 | | |
| (before vs after) x location x impact | 1 | 2.61 | 13.38 | NS | 0.76 | 0.27 | NS | 0.60 | 1.83 | NS | 0.02 | 0.11 | NS | 3.41 | 6.12 | NS |
| (among before) x location x impact | 1 | 0.19 | | | 2.83 | | | 0.33 | | | 0.16 | | | 0.56 | | |
| residual | 108 | 0.59 | | | 0.56 | | | 0.17 | | | 0.07 | | | 0.71 | | |
| Cochran's test | | $C = 0.17$ NS | | | $C = 0.19$ NS | | | $C = 0.44$ ** | | | $C = 0.43$ ** | | | $C = 0.21$ NS | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | | ln (x + 1) | | |

| | df | Calanoida | | | Harpacticoida | | |
|---------------------------------------|-----|--------------|------|------|---------------|------|------|
| | | MS | F | Sig. | MS | F | Sig. |
| time | 2 | 0.31 | | | 0.22 | | |
| location | 1 | 14.79 | | | 0.51 | | |
| impact | 1 | 0.36 | | | 0.90 | | |
| time x location | 2 | 12.58 | | | 0.44 | | |
| time x impact | 2 | 3.10 | | | 1.00 | | |
| (before vs after) x impact | 1 | 4.29 | 2.25 | NS | 1.23 | 0.61 | NS |
| (among before) x impact | 1 | 1.91 | | | 2.00 | | |
| location x impact | 1 | 14.24 | | | 1.25 | | |
| time x location x impact | 2 | 22.71 | | | 0.10 | | |
| (before vs after) x location x impact | 1 | 8.08 | 0.22 | NS | 0.00 | 0.00 | NS |
| (among before) x location x impact | 1 | 37.02 | | | 0.20 | | |
| residual | 108 | 0.67 | | | 0.29 | | |
| Cochran's test | | $C = 0.23$ * | | | $C = 0.29$ ** | | |
| Transformation | | ln (x + 1) | | | ln (x + 1) | | |

8.4 Discussion

At Narrabeen, no change in the assemblage of macro-invertebrates was found in disturbed sites following exposure to wash. The abundances of Ampithoidae and Corophiidae and the total abundance of amphipods did, however, decrease in these sites following exposure, but not significantly. In the case of Corophiidae and the total number of amphipods, this change did not appear to be due to natural spatial or temporal variability. In the control sites, the abundances of each of these taxa increased between sampling times before (B2) and after (A) the disturbance. Abundances of Ampithoidae, however, decreased in control sites between B2 and A and, therefore, the decrease in the disturbed sites may be explained by natural change over time. Copepods, in contrast, increased in numbers in response to the disturbance, despite a decrease in the abundance of this taxon in control sites.

The apparent decrease in the abundance of amphipods in response to the disturbance of wash is consistent with smaller abundances of the families Ampithoidae and Ampeliscidae in places exposed to wash from the Atlantic Intracoastal Waterway (Chapter 7). This pattern also supports the model that boat-wash reduces the abundance of certain taxa of mobile invertebrates. Abundances of all taxa were, however, naturally much greater in control than disturbed sites at Narrabeen, before and after the disturbance. Thus, temporal and spatial variability within the 'control' sites may not reflect variability within the disturbed sites, making the comparison of changes in these inappropriate for the detection of an impact. The small abundances at disturbed sites also meant that decreases at this site were constrained, relative to control sites. These results should therefore be treated cautiously. It was decided not to repeat the experiment at Narrabeen, using different sites, because, if assemblages display large spatial variability at the scale of hundreds of metres across the lake, the same problem would be encountered again.

Instead, a similar experiment was done along the Georges River. Preliminary sampling was done prior to the experiment to ensure that all sites had fairly similar abundances. Wash was found to have no effect on assemblages or the abundance of any of the taxa of mobile macroinvertebrates sampled.

Many differences between Narrabeen Lake and the Georges River may have contributed to the contrasting results obtained at these places, but the greatest is probably tidal regime. At Narrabeen, the tidal range is typically 30 cm due to the attenuation of currents at the bridge. Along the Georges River, the range is much greater – around 1.5 m. Even at the river's tidal limit, 50 km upstream, the range is approximately equal to that at the mouth, resulting in very strong currents along its entire length. During this study, strong tidal currents were observed at sites along the Georges River up to half an hour before low water. These currents flattened

seagrass against the sandy substratum and varied in intensity from site to site, according to the local geomorphology of the river. Strong currents were not evident at Narrabeen.

Current-speed appears to be important in determining the level and type of activity of a number of species of amphipod. Activity of the intertidal amphipod *Marinogammarus marinus* increased with flow at all states of the tide (Fincham, 1972); the direction of movement of *Gammarus pseudolimnaeus* (i.e. upstream, downstream) was dependent on the speed of the current (Williams and Moore, 1989). Moreover, during times of great flow, amphipods may migrate to sheltered microhabitats (Williams and Moore, 1986). Thus, flow is likely to affect patterns in the distribution and abundance of crustaceans and may increase spatial heterogeneity of populations, through interactions with topography and microhabitat.

Flow may increase within-patch variability in assemblages of epifaunal invertebrates on seagrass blades, in addition to variability at the scale of sites. Work by Turner *et al.* (1999) indicated that there are a greater number of individuals and species at the leeward edge of patches than at the leading edges. This may be due to the dynamic nature of the leading edge of the patch relative to the less disturbed, leeward edges (e.g. Orth *et al.*, 1984; Peterson, 1986; Eckman, 1987; Irlandi and Peterson, 1991; Irlandi, 1994, 1996). Thus, a model to explain the apparent impact of wash on mobile invertebrates at Narrabeen Lake, but not along the Georges River, is that, at Narrabeen, tidal currents are minimal and wash is consequently relatively important in structuring assemblages. Along the Georges River, where tidal currents are greater, the effects of wash are insignificant compared to the great spatial and temporal variability in assemblages caused by currents.

Alternatively, the differing results obtained at the two locations may be due to a greater susceptibility of organisms to disturbance at Narrabeen than at the Georges River since organisms at the former location are not naturally exposed to large hydrodynamic forces. Amphipods with strong grasping appendages often dominate algal fauna at exposed sites (Dommasnes, 1968; Nagle, 1968; Moore, 1973), presumably because they can attach firmly to substrata and are less susceptible to hydrodynamic disturbances. In this study, however, similar taxa were observed at Narrabeen Lake and the Georges River, so a difference in susceptibility is unlikely. The less than ideal experimental design at Narrabeen Lake means that the change in numbers of amphipods at the disturbed sites of this location could not necessarily be attributed to wash.

It is unlikely that results were confounded by temporal change in the activity of crustaceans, related to the endogenous rhythm of the tide. Light is a powerful inhibitor of swimming activity (Jansson and Källender, 1968) and tide-related patterns of vertical and horizontal migration

among seagrass fauna are primarily a nocturnal phenomena (Hobson and Chess, 1976; Alldredge and King, 1977; Hammer and Zimmerman, 1979).

Possibly the method of sampling used here was not appropriate for testing hypotheses regarding crustaceans. Sampling involved placing a plastic bag of fixed dimensions over blades of seagrass, resulting in the collection of epifauna attached to the seagrass and any organisms in the water immediately surrounding the plant-material. If the flapping of seagrass does, as postulated, knock crustaceans off blades, they may still have been caught, unless the current was sufficient to displace them to areas outside the patch of seagrass. It is not possible to sample blades without sampling the associated water unless a significant proportion of the epifaunal assemblage is lost. It may be more appropriate to sample free-swimming crustaceans in the water-column before and after the disturbance, in control and disturbed sites, within patches of seagrass and above adjacent areas of unvegetated sediment. If crustaceans are knocked off seagrass-blades, but are *not* displaced beyond the boundaries of the patch, abundances in the water-column within seagrass beds should increase following exposure to wash. If they *are* displaced outside the patch, abundances in the water-column above adjacent areas of unvegetated sediment should increase. No change should be seen in control sites that are undisturbed.

It is advisable that future tests of hypotheses about the impact of wash on epifauna over short-temporal scales consider this methodology.

CHAPTER 9

GENERAL DISCUSSION

Previous studies suggest that waves are important in determining the structure of intertidal assemblages in soft and in hard-bottomed habitats (e.g. Dayton, 1975; Menge, 1978a; Underwood, 1981; Tamaki, 1987; Turner *et al.*, 1999). This finding is often based on comparisons between the ecology of exposed and sheltered locations at a single time of sampling (e.g. McQuaid and Branch, 1985; Bustamante and Branch, 1996), or of a single location at times before and after storm activity (e.g. Dobbs and Vozarik, 1983; Posey *et al.*, 1996). Such studies do not unambiguously demonstrate a causal relationship between wave-action and ecological variables. Where possible, manipulative experiments are required to demonstrate a cause-effect relationship (Underwood, 1990).

Unpredictability in the timing and scale of storms makes the design of large-scale manipulative experiments investigating the ecological effects of such disturbances very difficult or even impossible. A number of studies have, however, successfully examined processes causing changes in assemblages following storms by coupling long-term observational studies with smaller-scale controlled manipulations (Underwood, 1998, 1999). For example, Underwood (1998) used small-scale manipulative experiments, in which fronds of the alga, *Hormosira banksii*, were cut or holdfasts were scraped away, to show that variability in the rate of recovery of patches of this alga, following a large storm, was due to variability in the amount of damage sustained.

The production of boat-generated waves is, in contrast to natural waves, predictable (see Stumbo *et al.*, 1999) and can be easily manipulated over large and small spatial scales. At a small scale, the disturbance of wash may be modified by when and where a boat is driven, its distance off-shore and speed (e.g. Das and Johnson, 1970; Bhowmik, 1975; Dand, 1982). At a large spatial scale, the production of waves is manipulated by managers through the enforcement of no-wash zones, where vessels must minimize the production of waves, or by imposing regulations on where and when boating may occur (see Asplund and Cook, 1999). These decisions are manipulations that can be treated as testable hypotheses (Hilborn and Walters, 1981; Underwood, 1989). Although rarely analysed, the outcomes of these decisions may be utilized by scientists as experiments to test for causal relationships.

In this thesis, managerial decisions were used as experiments to test hypotheses regarding the role of boat-wash in structuring assemblages of invertebrates. Some of these experiments, such as the use of no-wash zones to test hypotheses regarding the effect of differing intensities of

wash, were mensurative and drew upon strategies of management that were already in place. Others, such as the experiment that used the temporary cessation of ferry services to test whether there was any change in assemblages following the removal of the disturbance, were manipulative and enabled the evaluation of models postulating causal relationships. In addition, a number of smaller-scale manipulative experiments were done to evaluate models developed from observations made during larger-scale monitoring. These included experiments where assemblages of infauna were transplanted between wash and no-wash zones to determine whether assemblages changed in response to exposure. These three approaches were used collectively to examine the role of boat-generated waves in structuring assemblages and the effectiveness of large-scale environmental decisions in minimizing any impact resulting from wash.

9.1 The role of boat-generated waves in structuring estuarine assemblages

In general, this thesis provided little evidence of a deleterious effect of regulated boat wash on the benthic organisms of estuaries. While previous studies cite wind-generated waves as important in determining the composition of assemblages in sedimentary habitats (e.g. Tamaki, 1987; Committo *et al.*, 1995a,b; Turner *et al.*, 1999), there was no difference in the types of species associated with the sediment between sections of the Parramatta River that were purportedly subject to lesser (no-wash zone) and greater (wash zone) intensities of wash from RiverCats (Chapter 4). Nor was there any difference between the types of species found on the intertidal section of seawalls located close to and further from the ferry route (Chapter 3), contrary to the multitude of studies suggesting wave-exposure is an important force in structuring assemblages of rocky shores (e.g. McQuaid and Branch, 1985; Phillips *et al.*, 1997; Kautsky and Kautsky, 1989).

Differences in assemblages of macrobenthic infauna were, however, found between a wash and a no-wash zone of the upper Parramatta River due to greater abundances of amphipods the bivalve, *Xenostrobus securis* and opportunistic polychaetes in the latter (Chapter 4). This pattern was seen regardless of whether samples were collected from unvegetated habitat or from amongst the pneumatophores of mangroves. Thus, despite the alleged role of mangroves in stabilizing shorelines (e.g. Bennett and Reynolds, 1993) and dissipating the energy of surface waves in shallow water (e.g. Kobayashi *et al.*, 1992; Massel *et al.*, 1999), pneumatophores did not appear to be effective in reducing the impact of wash on infauna.

Subsequent manipulative experiments supported the model that, in the unvegetated habitat, differences between the two zones were due to wash and not some other factor. Following the

temporary suspension of services during the 2000 Sydney Olympic Games, assemblages in the wash zone changed to become more similar to those in the no-wash zone (Chapter 5).

Abundances of taxa in each of the zones increased. When services returned, the assemblages of these two places diverged and abundances of taxa decreased in each. The results of an experimental transplant (Chapter 6) also supported the model that exposure to wash reduces abundances of infaunal taxa. The transplant of sediment from the wash to the no-wash zone resulted in increased abundances of Capitellids, Nereids and Amphipods, while the reciprocal transplant from the no-wash zone to the wash zone resulted in decreased abundances.

Transplants within zones had little effect on abundances.

In contrast, the no-wash zone of the lower Parramatta River did not appear effective in reducing the impact of wash on infauna (Chapter 4). This may be due to poorer compliance with the regulations in the no-wash zone on this section of river than further upstream, where ferry-captains may be fined for speeding (Patterson Britton, 2000a). Alternatively, no pattern may have been seen because, in the lower Parramatta River, the magnitude of the disturbance is not sufficient to cause an impact. The energy and height of boat-generated waves decreases with distance from their source (Das and Johnson, 1970; Bhowmik, 1975). The Parramatta River widens close to its mouth and boat-traffic is at a greater distance from the shore (pers. obs.), so that the magnitude of the disturbance of wash may be less on this section of river than further upstream. The similarity of infaunal assemblages between exposed and sheltered sides of the Bogue Sound, which is wider still, is consistent with this model of no impact of wash.

Differences in the taxa present at each of the study sites may also have contributed to the differing effects of wash seen between the upper Parramatta River, the lower Parramatta River and the Bogue Sound. Assemblages along the upper Parramatta River were dominated by polychaetes of the families Capitellidae, Nereididae and Spionidae, the lower Parramatta by Hesionidae, Syllidae and oligochaetes and the Bogue Sound by Cirratulidae, Paraonidae, Orbinidae and Glyceridae. Susceptibility to passive transport by waves and currents, which is important in determining the distributions of several species of molluscs (Matthiessen, 1960; Gilbert, 1968; Edwards, 1969; Thompson, 1982; Donn *et al.*, 1986), polychaetes (Dales, 1952; Brown, 1982; McDermott, 1983), peracarid crustaceans (Fincham, 1970; Grant, 1980, 1981) and an echinoderm (Mukai *et al.*, 1986), varies among taxa (Tamaki, 1987). Species that can burrow to deeper layers in the sediment appear to be less affected by wave-action (Tamaki, 1987).

This study adopted a relatively coarse taxonomic resolution to: (i) reduce the time needed to process the samples, so that a greater number of replicates could be collected and (ii) minimize variation at the level of species that may preclude an impact from being detected

(Clarke and Warwick, 2001). This was necessary due to the great spatial and temporal variability of assemblages (e.g. Chapter 4) and should not have resulted in a significant loss of ecological information (e.g. James *et al.*, 1995; Chapman, 1998). It does, however, mean that conclusions could not be drawn about how wave-action affects the biology of individual species. Strategies of feeding and the life-histories of species of polychaete vary considerably within families (see Beesley *et al.*, 2000) so that generalizations, regarding features of their biology, cannot be reliably made.

Where an impact of wash on infauna was observed, it did not appear to be particularly detrimental. Assemblages recovered rapidly following the removal of the disturbing force, indicating that the impact is reversible. This may be attributable to the larger number of opportunistic taxa (Capitellidae, Nereididae, Spionidae) comprising these assemblages. Although this study did not attempt to identify polychaetes to a finer taxonomic resolution, dominant species are likely to be as previously determined at nearby Homebush Bay (i.e. *Prionospio yuriei* [Spionidae], *Ceratonereis aequisetis* [Nereididae] and *Capitella capitata* [Capitellidae]; Johnstone Environmental Technology, 1987; Jones and Frances, 1988). Opportunistic taxa, such as polychaetes of the *Capitella* 'capitata' complex are capable of invading areas where significant defaunation has occurred (Grassle and Grassle, 1974). They spawn frequently (around every 30 days; Qian and Chia, 1992) and produce great numbers of juveniles (a single female may produce 1650; Qian and Chia, 1992).

Studies have suggested that the infaunal assemblages of other estuaries are also dominated by opportunistic taxa (e.g. Pearson and Rosenberg, 1978; Schaffner *et al.*, 1987). Most of the populations of infauna found in estuaries should, therefore, be fairly resilient to any disturbance caused by wash. Reduced abundances of opportunistic infauna may, however, be of concern if they affect abundances of higher-level consumers, to which they transfer energy and nutrients (Krebs, 1978). For example, benthic taxa such as polychaetes, bivalves, gastropods and crustaceans are the primary source of food for many species of estuarine fish (e.g. Burke, 1995; Edgar and Shaw, 1995). Although most studies examining trophic links between fish and benthos have focused on the role of fishes in regulating benthic populations through predation (e.g. Robertson, 1984; Möller *et al.*, 1985; Bennett and Branch, 1990), populations of fish may be dependent on the biomass of the benthos if food is a limiting factor. For example, calculations by Edgar and Shaw (1995) showed that virtually all benthic production in Western Port, southern Australia is consumed by small fish. If wash significantly decreases the abundance of invertebrates so that the availability of food becomes limiting to consumers, such as larger crustaceans and fish, higher-order taxa that are less resilient may be lost from disturbed areas.

The greatest impact of wash on estuarine organisms detected in this study was on epifaunal gastropods, associated with seagrass blades. Abundances of the taxa *Crepidula fornicata* and *Bittium varium* were much smaller in exposed than sheltered sections of the Bogue Sound (Chapter 7). In contrast, abundances of more mobile taxa, such as amphipods and isopods, did not consistently differ between seagrass beds in sheltered and exposed places, in Sydney or North Carolina (Chapters 7 and 8). These results support the model that the mobility of an organism is important in determining its susceptibility to disturbance (Denny *et al.*, 1985; Menge and Sutherland, 1987).

Differences in assemblages of epifauna between beds of seagrass exposed to or sheltered from wash were despite similar assemblages of infauna among places of differing exposure. This clearly illustrates that impacts can differ markedly between soft and hard substrata. This is not surprising considering the many differences between these substrata and the organisms that colonize them. For example, infauna are able to avoid disturbances by burrowing into the third dimension of their substratum, while epifauna, attached to hard substrata, are limited to a two dimensional substratum where they are subject to forces such as lift and drag (see Lake, 1990).

9.2 The suitability of the estuarine environment for this study

In Section 1.7 (General Introduction) the reasons for choosing to study the effects of boat-wash in estuarine environments were outlined. Estuarine environments were selected because: (i) boat-traffic is particularly concentrated in estuaries because they are close to many people and (ii) the narrow width of estuaries means that the fetch over which wind-driven waves are generated is generally short and the size of naturally-produced waves is small. In addition, estuaries contain a range of assemblages of macro-invertebrates, of diverse forms and habits. These may respond in different ways to environmental stresses (Rosenberg and Resh, 1993). Despite these advantages of examining the effects of wash in an estuarine environment there are, as seen in this thesis, a number of disadvantages of basing the study in this environment.

Estuarine assemblages are naturally variable over many spatial and temporal scales. Repeated sampling of sites showed that abundances of many invertebrates changed by orders of magnitude over periods as short as a month. The taxa present also varied considerable among sampling times. This great background of natural variability would make it very difficult to detect impacts resulting from anthropogenic disturbances unless they are extremely severe.

Great spatial variability among sites, at each time of sampling, was also evident, further contributing to the difficulty in assessing whether wash has an ecological impact. Characteristics of the sediment, widely documented as important in structuring infaunal assemblages (e.g. Gray,

1974; Ishikawa, 1989), varied over similar spatial scales as assemblages, suggesting that these may be important in determining the structure of assemblages and their variability. Artificial sampling units (Chapter 6), containing homogeneous, defaunated sediment, were used in an attempt to reduce spatial variability in assemblages among locations, sites and replicates within each level of the disturbance. This method was effective in eliminating some of the background variability so that hypotheses could be evaluated with greater confidence.

The large number of opportunistic taxa comprising assemblages is also likely to have contributed to the background variability. Opportunists have life-histories and dispersal that facilitate rapid colonization of new or disturbed substrata (Boesch and Rosenberg, 1981). Consequently, they may display significant changes in abundance over relatively short periods of time. For this reason, they are often cited as good indicators of environmental change (e.g. Rosenberg, 1973; Grassle and Grassle, 1974).

In addition to responding to wash – the disturbance of interest – opportunists may, however, also respond to other anthropogenic disturbances or natural disturbances co-occurring within the area of study. In estuaries, there are often many anthropogenic disturbances co-occurring within a small area because of the great pressures society places on this environment. Thus, the separation of an impact of wash from impacts of other disturbances is difficult. It requires the collection of a large numbers of replicates from control and putatively impacted locations, at times before and after the disturbance so that changes due to disturbances other than the one of interest can be factored out. In this study, large numbers of replicates could not be collected due to limited time and the small number of suitable sites for sampling. Thus, the emphasis has been on patterns in assemblages and abundances of taxa rather than the statistical significance of tests, which was rarely seen due, presumably, to the great background of temporal and spatial variability in the abundances of taxa.

The other potential problem in estuaries is that the constant exposure to a multitude of disturbances may result in assemblages being dominated by organisms that are resistant to the variable environmental conditions. Assemblages which are characteristic of small or variable salinities have shown greater resistance to organic pollution (Rosenberg, 1972, 1973), toxic contaminants (Boesch, 1973) and drastic salinity reductions (Larsen, 1974; Boesch *et al.*, 1976). If this is the case, only the most severe disturbances will have any impact on assemblages. A large number of contaminants are found in the Georges River (Florence *et al.*, 1999) as compared to the relatively pristine Narrabeen Lake. Thus, the apparent impact of wash on epifaunal invertebrates in seagrass of Narrabeen Lake, but not on those in seagrass in the

Georges River (Chapter 8) may be explained by the model that wash only has an impact where the impacts of co-occurring disturbances are small.

9.3 Cumulative effects

In contrast to the above model, which proposes that, in highly disturbed environments, additional disturbances will have no effect on the already perturbed ecology of organisms, the effects of disturbances may add to give a cumulative effect. For example, while clearing individual patches, 10 - 2000 hectares in size, from a forest of several million hectares does not cause any significant impact to the forest, the clearing of multiple patches can be detrimental (Gosselink *et al.* 1990).

Cumulative effects may result from: (i) multiple disturbances of a single kind overlapping in time, (ii) multiple disturbance of one or more types overlapping in space, (iii) indirect effects or (iv) accumulation of small, apparently insignificant disturbances that result in a significant impact in total (Beanlands *et al.*, 1986). They may be additive, where their collective effects is equal to their sum, antagonistic, where one effect subtracts from another, or synergistic, where their collective effect is greater than the sum of the individual impacts (Gosselink *et al.*, 1990; Spaling and Smit, 1993).

This study only considered any impact of wash over and above the combined impact of other disturbances co-occurring within the area of study. It did not attempt to determine how pre-existing disturbances at each of the study sites might affect the way in which wash affected macro-invertebrates. In addition, this study did not attempt to determine whether a single disturbance of wash has a different effect from that caused by multiple disturbances of wash, nor how the frequency of disturbance affects the magnitude of effect. Cumulative effects were not considered because it had not previously been demonstrated unambiguously that wash has an impact on the ecology of estuaries. A basic understanding of the ways in which this disturbance affects assemblages is required before more complex models regarding cumulative effects can be usefully proposed.

Given the increasing pressure that society is placing on estuaries, it is advisable that future studies consider the way in which other disturbances, co-occurring with wash, affect its impact. The scenario of repeated exposure to wash as opposed to single events of disturbance will also be of interest.

9.4 The role of science in management

This study estimated the way in which the estuarine environment responds to an additional stress. An estimation of environmental responses to perturbations should be an integral part of management, if managers are indeed going to take environmental protection seriously (Underwood and Peterson, 1988; Underwood, 1989, 1990, 1991; Keough and Quinn, 1991). Such estimation should be used to make managerial decisions (i.e. feedback management; Holling, 1978; de la Mare, 1986; Walters, 1986).

Science can aid in environmental decision-making by determining the types of impact that may be expected from a particular disturbance, the size of the effects that can be measured (the power of the assessment techniques) and the likely consequences of effects at different intensities of the activity. The public could then use this information to make choices as to the types and sizes of effects that are unacceptable (Constable, 1991).

Despite the obvious importance of science in decision-making, it is, however, often given a low value by managers. This may, in part, be attributed to the great uncertainty associated with ecological data (probabilistic uncertainty) and theories (uncertainty due to complexity and diversity; Ludwig *et al.*, 1993) that is in stark contrast to the certainties society claims to need for deciding between alternatives.

The low value science has been given by managers may also be attributed to the frequently poor quality of ecological assessments (discussed in Green, 1979; Underwood, 1989, 1991). For example, many assessments have sampled only a single site before and after a disturbance (e.g. Bachelet, 1986; Lopez-Jamar *et al.*, 1986; discussed in Underwood, 1991) and others have failed to collect data from before an obvious incident (e.g. Borowitzka, 1972; López Gappa, 1990). These experimental designs cannot attribute changes in ecology in time or space to the putative disturbance (Underwood and Peterson, 1988, Underwood, 1989); changes may be due to any number of causes. A concerted effort to improve sampling designs for ecological impact assessment (e.g. Underwood, 1991, 1992, 1993, 1994) coupled with the recognition that human impacts, as disturbances to the ecological system, are linked to ecological theory (Underwood, 1989) has resulted in a recent improvement in applied ecological research (e.g. Chapman *et al.*, 1995; Glasby and Underwood, 1996).

Ecological assessments also suffer from rarely addressing the consequences of different intensities of the proposed activity. For example, the majority of studies on the ecological impacts of sewage outfalls have focused on their effects relative to non-impacted, control locations (e.g. Borowitzka, 1972; May, 1985; Fairweather, 1990; López Gappa *et al.*, 1990) and have not considered the impacts of primary-treated effluent versus effluent that has received

secondary, tertiary or quaternary treatment. Consequently, a decision on whether to develop an activity is often an all-or-nothing debate.

This thesis attempted to address the question of whether differing intensities of the disturbance, wash, affect assemblages of macro-invertebrates in different ways. This was done by comparing assemblages of infauna in wash zones, where the production of wash is unrestricted and, presumably, great, and no-wash zones, where wash is of typically of a smaller magnitude. While this study suggests that the impact of wash on infauna does increase with the intensity of the disturbance, the minimum intensity of the disturbance required for an impact to be detected over and above other factors could not be determined because of the absence of suitable undisturbed locations that could be used as controls.

While controlled experiments, involving the collection of data before and after disturbances of interest, will be most informative in ascertaining how organisms respond to anthropogenic activities (see Underwood, 1992, 1993, 1994), these are not always possible. For example, data from prior to the introduction of RiverCat ferries were not available for this study. In such instances, planned field experiments with clearly-defined hypotheses can still be of use in improving predictions of impacts. This type of approach (discussed in Lincoln-Smith, 1991) was used for a proposed marina development at Brooklyn on the Hawkesbury River, NSW (Anon, 1988). It was reasoned that if differences were consistently found between existing marinas and nearby natural areas, a logical prediction would be that construction of a marina in a natural area would cause a change in benthic assemblages there.

Here, the problem of no 'before' data was overcome by using a multi-faceted approach. Mensurative experiments, based on pre-existing strategies of management that manipulated the disturbance over a large scale, enabled observations to be made regarding differences in the distribution and abundance of organisms in exposed or sheltered places. These observations were then used to design smaller-scale manipulative experiments, which examined processes causing these patterns. For example, abundances of several mobile taxa, associated with seagrass-blades differed between sections of the Bogue Sound that were sheltered from or exposed to wash from the Atlantic Intracoastal Waterway. While it was proposed that this large-scale pattern was due to wash, an appropriate experiment to determine causation could not be done at this scale. Small-scale experiments, in which changes in the abundances of taxa were examined at control and putatively impacted sites, before and immediately after the generation of wash by a small boat enabled evaluation of the model that exposure to wash reduces the abundance of a number of epifaunal taxa.

On their own, neither the large-scale mensurative experiments nor the small-scale manipulative experiments provided much information on the role of wash in structuring assemblages. Together, however, they showed that, under certain conditions, wash can reduce the abundance of epifaunal taxa. Where this effect occurs, it is immediate. This study, with previous work by McCook and Chapman (1991, 1993, 1997) and Underwood (1998, 1999), clearly shows that, although it is often difficult or even impossible to manipulate large-scale disturbances directly, observations of these disturbances may be coupled with smaller-scale controlled manipulative experiments to identify processes that are important in determining the distribution and abundance of organisms. Thus, the large scale of a disturbance should not be seen as a barrier to experimental tests of processes, but rather unique ecological opportunities to be exploited.

LITERATURE CITED

- Adams, S. M. 1976. The ecology of eelgrass (*Zostera marina* L.) fish communities. I. Structural analysis. *Journal of Experimental Marine Biology and Ecology* 22: 269-91.
- Albright, C. J. 2000. Wake-up call: using the Washington shoreline management act to protect the shorelines of Puget Sound from high-speed-vessel wake wash. *Washington Law Review* 75: 519-47.
- Alexander, W. B., B. A. Southgate, and R. Bassindale. 1935. *Survey of the River Tees. II. The estuary: chemical and biological*. D.S.I.R. Water Pollution Research, Technical Paper No. 5
- Allredge, A. L., and J. M. King. 1977. Distribution, abundance and substrate preferences of demersal reef zooplankton at lizard Island Lagoon, Great Barrier Reef. *Marine Biology* 41: 317-33.
- Allen, K. O. and J. W. Hardy. 1980. *Impacts of navigational dredging on fish and wildlife: A literature review*, Biological Services Program, U.S. Fish and Wildlife Service. FWS/OBS-80/07.
- Alzieu, C., M. Heral, Y. Thiebaud, M. J. Dardignac, and M. Feuillet. 1981. Influence des peintures antisalissures a base d'organostanniques sur la calcification de la coquille de l'huitre *Crassostrea gigas*. *Revue des Travaux de l'Institut des Peches Maritimes* 45: 101-16.
- Alzieu, C., Y. Thibaud, M. Heral, and B. Boutier. 1980. Evaluation des risques dus à l'emploi des peintures anti-salissures dans les zones conchylicoles. *Revue des Travaux de l'Institut des Peches Maritimes* 44: 301-48.
- Anderson, F.E. 1976. Rapid settling rates observed in sediments resuspended by boat waves over a tidal flat. *Netherlands Journal of Sea Research* 10: 44-58.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.
- Anderson, M. J., and P. Legendre. 1999. An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *Journal of Statistical Computation and Simulation* 62: 271-303.
- Andrews, G. 1975. *The ferries of Sydney*. Terry Hills, NSW: Reed.
- Anger, K. 1975. On the influence of sewage pollution on inshore benthic communities in the South Kiel Bay. Part 2. Quantative studies on community structure. *Helgolaender Meeresuntersuchungen* 32: 73-148.
- Anon. 1988. *Brooklyn resort environmental impact statement*. Planning workshop, for Brooklyn Resorts Pty Ltd, Sydney.
- Anon. 2000. Early problems for latest Dutch service. *Fast Ferry International* 39: 47.
- Armonies, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Marine Ecology Progress Series* 83: 197-206.

- Asplund, T., and C. Cook. 1999. Can no-wake zones effectively protect littoral zone habitat from boating disturbance? *Lakeline*: 6-18, 48-52.
- Attrill, M. J., J. A. Strong, and A. A. Rowden. 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23: 114-21.
- AuClair, A. N., and G. Goff. 1971. Diversity relations of upland forests in the western great lakes area. *American Nature* 105: 499-528.
- Austin, I. 1999. *High-speed vessels and their impacts on wetlands and habitat: A case study from San Fransisco*. High Speed Conference. 17-19 May 1999, Victoria, BC, Canada
- Bachelet, G. 1986. Recruitment and year-to-year variability in a population of *Macoma balthica* (L.). *Long-term changes in coastal benthic communities*. Eds. C. Heip, B. F. Keegan, and J. R. Lewis, 233-58. Dordrecht: Junk.
- Banwell, K. 1996. *Structure of intertidal rocky shore assemblages following the removal of sewage*. MSc Thesis. University of Sydney.
- Barber, W. E., J. G. Greenwood, and P. Crocos. 1979. Artificial seagrass - a new technique for sampling the community. *Hydrobiologia* 65: 135-40.
- Barko, J. W., D. Gunnison, and S. R. Carpenter. 1991. Sediment interactions with submerged macrophyte growth and community dynamics. *Aquatic Botany* 41: 41-65.
- Barry, J. P. 1989. Reproductive response of a marine annelid to winter storms: an analog to fire adaptation in plants? *Marine Ecology Progress Series* 54: 99-107.
- Barry, J. P., and P. K. Dayton. 1991. Physical heterogeneity and the organization of marine communities. *Ecological Heterogeneity*. Eds. J. Kolasa, and S. T. A. Pickett, 270-320. Springer-Verlag.
- Bassindale, R. 1943. Studies on the biology of the Bristol Channel. XI. The physical environment and intertidal fauna of the southern shores of the Bristol Channel and Severn Estuary. *Journal of Ecology* 31: 1-29.
- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33: 513-23.
- Beanlands, G. E., W. J. Erckmann, G. H. Orians, D. O'Riordan, D. Policansky, M. H. Sadlar, and B. Sadler. 1986. *Cumulative environmental effects: A binational perspective*. 175pp Canadian Environmental Assessment Research Council, Ottawa, Ontario and US National Research Council, Washington, DC.
- Beesley, P. L., G. J. B. Ross, and C. J. Glasby, Ed. 2000. *Polychaetes and allies: the southern synthesis.*, Fauna of Australia. Volume 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. Collingwood, Vic: CSIRO Publishing Australia.
- Bell, E. C., and M. W. Denny. 1994. Quantifying 'wave exposure': a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181: 9-29.

- Bell, J. D., and M. Westoby. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia* 68: 205-9.
- Bell, R. G., T. M. Hume, T. J. Dolphin, M. O. Green, and R. A. Walters. 1997. Characterization of physical environmental factors on an intertidal sandflat, Manukau Harbour, New Zealand. *Journal of Experimental Marine Biology and Ecology* 216(1-2): 11-31.
- Bell, S. S., and D. J. Devlin. 1983. Short-term macrofaunal recolonization of sediment and epibenthic habitats in Tampa Bay, Florida. *Bulletin of Marine Science* 33: 102-8.
- Bellan, G., and D. Bellan-Santini. 1972. Influence of pollution on marine populations in the Marseilles region. *Marine pollution and sea life*. Ed. M. Ruivo, 396-401. FAO, Fishing News (Books), London.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65, no. 1: 1-13.
- Bennett, E. L., and C. J. Reynolds. 1993. The value of a mangrove area in Sarawak. *Biodiversity and Conservation* 2: 359-75.
- Bertness, M. D., S. D. Gaines, E. G. Stephens, and P. O. Yund. 1991. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 156: 199-215.
- Bhowmik, N. G. 1975. Boat-generated waves in lakes. *Journal of the Hydraulics Division, Proceedings American Society of Civil Engineers* 101, no. HY11: 1465-68.
- Bhowmik, N. G., M. Demissie, and C. Y. Guo 1982. *Waves generated by river traffic and wind on the Illinois and Mississippi Rivers*. WRC Research Report No. 167. University of Illinois Water Resources Center.
- Bhowmik, N. G., T. W. Soong, W. F. Reichelt, and N. M. L. Seddik. 1991. *Waves generated by recreational traffic on the Upper Mississippi River system*, Research Report 117. Department of Energy and Natural Resources, Illinois State Water Survey, Champaign, IL.
- Bishop, M. J., A. J. Underwood, and P. Archambault. 2002. Sewage and environmental impacts on rocky shores: necessity of identifying relevant spatial scales. *Marine Ecology Progress Series* 236: 121-28.
- Blanchette, C. A. 1997. Size and survival of intertidal plants in response to wave action: A case study with *Fucus gardneri*. *Ecology* 78: 1563-78.
- Blockley, D. J. 1999. *Sandstone seawalls as intertidal habitats in Sydney Harbour*. BSc (Hons) Thesis, University of Sydney.
- Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Marine Biology* 21: 226-44.
- Boesch, D. F. 1977. A new look at the zonation of benthos along the estuarine gradient. *Ecology of Marine Benthos*. B. C. Coull, 245-66. Columbia: University of South Carolina Press.
- Boesch, D. F., R. J. Diaz, and R. W. Virnstein. 1976. Effects of Tropical Storm Agnes on soft-

- bottom macrobenthic communities of the James and York River estuaries and the bay mouth. *Chesapeake Science* 17: 246-59.
- Boesch, D. F., and R. Rosenberg. 1981. Response to stress in marine benthic communities. *Stress Effects on Natural Ecosystems*. G. M. Barrett, and R. Rosenberg, 179-200. New York: John Wiley.
- Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7: 460-468.
- Bologna, P. A. X., and K. L. Heck Jr. 1999. Macrofaunal associations with seagrass epiphytes. Relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology* 242: 21-39.
- Borowitzka, M. A. 1972. Intertidal algal species diversity and the effect of pollution. *Australian Journal of Marine and Freshwater Research* 23: 73-84.
- Bowden, D. A., A. A. Rowden, and M. J. Attrill. 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblage of *Zostera marina* seagrass Eds. *Journal of Experimental Marine Biology and Ecology* 259: 133-54.
- Box, G. E. P. 1953. Non-normality and tests on variances. *Biometrika* 40: 318-35.
- Braddock, J. F., J. E. Lindstrom, and E. J. Brown. 1995. Distribution of hydrocarbon-degrading microorganisms in sediments from Prince William Sound, Alaska Following the Exxon Valdez oil spill. *Marine Pollution Bulletin* 30: 125-32.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27: 325-49.
- British Columbia Ferry Corporation. 2000. *Fast ferry program - Wake and wash report*. Unpublished report.
- Broadhurst, M. K., S. J. Kennelly, and B. Isaksen. 1996. Assessment of modified codends that reduce the by-catch of fisheries in New South Wales, Australia. *Fisheries Research* 27: 89-111.
- Brown, A. C., and A. McLachlan. 1990. *Ecology of sandy shores*. Amsterdam: Elsevier.
- Brown, B. 1982. Spatial and temporal distribution of a deposit-feeding polychaete on a heterogeneous tidal flat. *Journal of Experimental Biology and Ecology* 65: 213-27.
- Brown, K. M., and J. F. Quinn. 1988. The effect of wave action on growth in three species of intertidal gastropods. *Oecologia* 75: 420-425.
- Bryan, G. W., P. E. Gibbs, L. G. Hummerstone, and G. R. Burt. 1986. The decline of the gastropod *Nucella lapillus* around south-west England: Evidence for the effect of tributyltin from antifouling paints. *Journal of the Marine Biological Association of the United Kingdom* 66: 611-40.
- Buchanan, J. B. 1963. The bottom fauna communities and their sediment relationships off the coast of Northumberland. *Oikos* 14: 154-75.

- Bunch, J. N. 1987. Effects of petroleum releases on bacterial numbers and microheterotrophic activity in the water and sediment of an arctic marine ecosystem. *Arctic* 40, Supp. 1: 172-83.
- Burke, J. S. 1995. Role of feeding and prey distribution of summer and southern flounder in selection of estuarine nursery habitats. *Journal of Fish Biology* 47: 355-66.
- Bustamante, R. H., and G. M. Branch. 1996. Large-scale patterns and trophic structure of Southern African rocky shores: The roles of geographic variation and wave action. *Journal of Biogeography* 23: 339-51.
- Butler, A. J., and P. Jernokoff. 1999. *Seagrass in Australia: Strategic review and development of an R & D plan*, CSIRO Publishing, Collingwood, Australia.
- Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamic processes. *Oceanography and Marine Biology: an Annual review* 25: 113-65.
- Byers, S. C., E. L. Mills, and P. L. Stewart. 1978. A comparison of methods of determining organic carbon in marine sediments, with suggestions for a standard method. *Hydrobiologia* 58, no. 1: 43-47.
- Cairns, J. Jr., and J. R. Pratt. 1993. A history of biological monitoring using benthic macroinvertebrates. *Freshwater biomonitoring and benthic macroinvertebrates*. Eds. D. M. Rosenberg, and V. H. Resh, 10-27. New York: Routledge, Chapman and Hall, Inc.
- Cameron, W. M., and D. W. Pritchard. 1963. Estuaries. *The Sea*. Ed. M. N. Hill, 306-24. Vol. Vol. 2. New York: Wiley.
- Carrington, E. 1990. Drag and dislodgment of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützing. *Journal of Experimental Marine Biology and Ecology* 139: 185-200.
- Castel, J, P-J Labourg, V Escaravage, I Auby, and M. E. Garcia. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass pattern of meio- and macrobenthos in tidal flats. *Estuarine, Coastal and Shelf Science* 28: 71-85.
- Chambers, P. A. 1987. Nearshore occurrence of submerged aquatic macrophytes in relation to wave action. *Canadian Journal of Fisheries & Aquatic Sciences* 44: 1666-69.
- Chambers, P. A., E. E. Prepas, H. R. Hamilton, and M. L. Bothwell. 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. *Ecological Applications* 1: 249-57.
- Chapman, M. G. 1986. Assessment of some controls in experimental transplants of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* 103: 181-201.
- Chapman, M. G. 1998. Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. *Marine Ecology Progress Series* 162: 71-78.
- Chapman, M. G., and F. Bulleri. 2003. Intertidal seawalls: new features of landscape in intertidal environments. *Landscape and Urban Planning* 62: 159-172.

- Chapman, M. G., A. J. Underwood, and G. A. Skilleter. 1995. Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *Journal of Experimental Marine Biology and Ecology* 189: 103-22.
- Christie, M. C., K. R. Dyer, and P. Turner. 1999. Sediment flux and bed level measurements from a macro tidal mudflat. *Estuarine, Coastal and Shelf Science* 49: 667-88.
- Cionco, R. M. 1985. Modeling windfields and surface layer wind profiles over complex terrain within vegetative canopies. *The Forest Atmosphere, International Proceedings of the Forest Environmental Measurement Conference* Dordrecht: Reidel Publishing.
- Clarisse, D., and C. Alzieu. 1993. Copper contamination as a result of antifouling paint regulations? *Marine Pollution Bulletin* 26: 395-97.
- Clarke, K. R. 1993. Non-metric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-43.
- Clarke, K. R., and R. M. Warwick. 2001. *Change in marine communities: An approach to statistical analysis and interpretation*. 2nd Edition ed. Plymouth: PRIMER-E .
- Clynick, B., and M. G. Chapman. 2002. Assemblages of small fish in patchy mangrove forests in Sydney Harbour. *Marine and Freshwater Research* 53: 669-77.
- Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: Decoupling cause and effect. *Ecology* 76: 486-92.
- Commito, J. A., C. A. Currier, L. R. Kane, K. A. Reinsel, and I. M. Ulm. 1995a. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. *Ecological Monographs* 65: 1-20.
- Commito, J. A., S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1995b. Dispersal dynamics in a wind-driven benthic system. *Limnology and Oceanography* 40: 1513-18.
- Connell, J. H. 1974. Field experiments in marine ecology. *Experimental Marine Biology*. Ed. R. Mariscal, 21-54. New York: Academic Press.
- Connell, J. H. 1978. Diversity in tropical rain-forests and coral reefs. *Science* 199: 1302-10.
- Connell, S. D., and T. M. Glasby. 1999. Do urban structures influence local abundances and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine and Environmental Research* 47: 373-87.
- Connolly, R. M. 1999. Saltmarsh as habitat for fish and nektonic crustaceans: challenges in sampling designs and methods. *Australian Journal of Ecology* 24: 422-30.
- Constable, A. J. 1991. The role of science in environmental protection. *Australian Journal of Marine and Freshwater Research* 42: 257-38.
- Cooper, W. S. 1926. The fundamentals of vegetation change. *Ecology* 7: 391-413.

- Coull, B. C., and S. S. Bell. 1979. Perspectives of marine meiofaunal ecology. *Ecological perspectives in coastal marine ecosystems*. Ed. R. Livingston, 189-216. New York: Plenum Press.
- Coops, H., R. Boeters, and H. Smit. 1991. Direct and indirect effects of wave attack on helophytes. *Aquatic Botany* 41: 333-52.
- Creed, J. C., and G. M. Amado Filho. 1999. Disturbance and recovery of the macroflora of a seagrass (*Halodule wrightii* Ascherson) meadow in the Abrolhos Marine National Park, Brazil: an experimental evaluation of anchor damage. *Journal of Experimental Marine Biology and Ecology* 235: 285-306.
- Crisp, D. J. 1974. Factors influencing the settlement of marine invertebrate larvae. *Chemoreception in marine organisms*. Eds. P. T. Grant, and A. M. Mackie, 177-265. New York: Academic Press.
- Daiber, F. C., D. Aurand, G. Brenum, and P. Clarke 1975. *Ecological effects upon estuaries resulting from lagoon construction, dredging, filling, and bulkheading*. Division of Fish and Wildlife, Delaware Department of Natural Resources and Environmental Control.
- Dales, R. P. 1952. The larval development and ecology of *Thoracophelia mucronata* (Treadwell). *Biological Bulletin of the Marine Biology Laboratory, Woods Hole* 102: 232-42.
- Dand, I. W. 1982. *Ship hydrodynamics and the design of port approach channels*. National Maritime Institute. October 1982.
- Danish Hydraulic Institute. 1996. *Technical investigation of wake wash from fast ferries*. Summary Report No 96-5012.
- Danish Maritime Authority. 1997. *Report on environmental impacts caused by fast ferries*. Unpublished Danish Maritime Authority Report, Copenhagen.
- Das, M. M., and J. W. Johnson. 1970. Waves generated by large ships and small boats. *Twelfth Coastal Engineering Conference, Proceedings* v3: 2281-86.
- Davidson, R.J. 1997. *Biological monitoring in relation to ferry wakes: 1996/97 season, Tory Channel and Charlotte Sound, Marlborough Sounds*. Research, Survey and Monitoring Report No. 149. Prepared by Davidson Environmental Limited for the Department of Conservation, Nelson/Marlborough.
- Davidson, R. J. 1996. *Biological monitoring of Tory Channel and Queen Charlotte Sound in relation to the effects from ferry wakes*. Research, survey and monitoring report number 107. Report prepared by R.J. Davidson (Davidson Environmental Consultants) for Director General of Conservation, Department of Conservation, Nelson/Marlborough Conservancy.
- Davies, I. M., and S. K. Bailey. 1991. The impact of tributyltin from large vessels on the dogwhelk *Nucella lapillus* (L.) populations around Scottish oil ports. *Marine and Environmental Research* 32: 202-11.
- Davis, G. E. 1977. Anchor damage to a coral reef on the coast of Florida. *Biological Conservation* 11: 29-34.

- Dawes, C. J., J. Andorfer, C. Rose, C. Uranowski, and N. Ehringer. 1997. Regrowth of the seagrass *Thalassia testudinum* into propeller scars. *Aquatic Botany* 59: 139-55.
- Day, J. H. 1951. The ecology of South African estuaries. Part 1. A review of estuarine conditions in general. *Transactions of the Royal Society of South Africa* 33: 53-91.
- Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351-89.
- Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45: 137-59.
- de Decker, H. P., and R. Bally. 1985. The benthic macrofauna of the Bot River estuary, South Africa, with a note on its meiofauna. *Transactions of the Royal Society of South Africa* 45: 379-96.
- de Jong, D. J., and V. N. de Jonge. 1995. Dynamics and distribution of microphytobenthic chlorophyll-*a* in the Western Scheldt estuary (SW Netherlands). *Hydrobiologia* 311: 21-30.
- de la Mare, W. K. 1986. Simulation studies on management procedures. *Reports of the International Whaling Commission* 36: 429-50.
- Dean, W. E. Jr. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Petrology* 44, no. 1: 242-48.
- Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76: 1446-1460
- Denley, E. J. 1981. *The ecology of the intertidal barnacle, Tesseropora rosea*. PhD Thesis, University of Sydney.
- Denley, E. J., and A. J. Underwood. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology* 36: 269-93.
- Denny, M. W. 1985. Wave forces on intertidal organisms: a case study. *Limnology and Oceanography* 30: 1171-87.
- Denny, M. W. 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecological Monographs* 65: 371-418.
- Denny, M. W. 1987. Life in the maelstrom: The biomechanics of wave-swept rocky shores. *Trends in Ecology and Evolution* 2: 61-66.
- Denny, M. W. 1998. *Biology and the mechanics of the wave-swept environment*. Princeton, New Jersey: Princeton University Press.
- Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. *Ecological Monographs* 55: 69-102.

- Denny, M. W., and M. F. Shibata. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *American Naturalist* 134: 859-89.
- Department of Urban Affairs and Planning. 1998. *Georges River Catchment*. Department of Urban Affairs and Planning, Canberra.
- Deutsch, W. G. 1980. Macroinvertebrate colonization of acrylic plates in a large river. *Hydrobiologia* 75: 65-72.
- Dexter, D. M. 1992. Sandy beach community structure: the role of exposure and latitude. *Journal of Biogeography* 19: 59-66.
- Dial, R., and J. Roughgarden. 1998. Theory of marine communities: the intermediate disturbance hypothesis. *Ecology* 79: 1412-24.
- Diaz, R. J., and L. C. Schaffner. 1990. The functional role of estuarine benthos. *Perspectives on the Chesapeake Bay, 1990. Advances in Estuarine Science*. Eds. M. Haire, and E. C. Krome, 25-56. Chesapeake Bay Program, Chesapeake Research Consortium Publication.
- Dobbs, F. C., and J. M. Vozarik. 1983. Immediate effects of a storm on coastal infauna. *Marine Ecology Progress Series* 11: 273-79.
- Dommasnes, A. 1968. Variation in the meiofauna of *Corallina officinalis* with wave exposure. *Sarsia* 34: 117-24.
- Donn, T. E., D. J. Clarke, A. McLachlan, and P. du Toit. 1986. Distribution and abundance of *Donax serra* Röding (Bivalvia: Donacidae) as related to beach morphology. I. Semilunar migrations. *Journal of Experimental Marine Biology and Ecology* 102: 121-31.
- Doyle, R. D. 2001. Effects of waves on the early growth of *Vallisneria*. *Freshwater Biology* 46: 389-97.
- Eagle, R. A. 1975. Natural fluctuations in a soft bottom benthic community. *Journal of the Marine Biology Association of the United Kingdom* 55: 865-78.
- Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography* 28: 241-57.
- Eckman, J. E. 1987. The role of hydrodynamics in recruitment, growth, and survival of *Agropecten irradians* (L.) and *Anomia simplex* (D'Orbigny) with eelgrass meadows. *Journal of Experimental Marine Biology and Ecology* 106: 165-91.
- Eckman, J. E., W. B. Savidge, and T. F. Gross. 1990. Relationship between duration of cyprid attachment and drag forces associated with detachment of *Balanus amphitrite* cyprids. *Marine Biology* 107: 111-18.
- Edgar, G. J. 1991. Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese Sargassum bed. *Hydrobiologia* 226: 111-18.
- Edgar, G. J. 1992. Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. *Journal of Experimental Marine Biology and Ecology* 157: 225-46.

- Edgar, G. J., and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* 194: 83-106.
- Edwards, D. C. 1969. Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. *American Zoologist* 9: 399-417.
- Eggleston, D. B., L. L. Etherington, and W. E. Elis. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 223: 111-32.
- Eleftheriou A., and Holme N.A. 1984. Macrofauna techniques. *Methods for the study of marine benthos*. Eds. N. A. Holme, and A. D. McIntyre, 140-216. Oxford: Blackwell Scientific.
- Elmgren, R., S. Ankar, B. Marteleur, and G. Ejdung. 1986. Adult interference with postlarvae in soft sediments: the *Pontoporeia-Macoma* example. *Ecology* 67: 827-36.
- Emerson, C. W., and J. Grant. 1991. The control of the soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnology and Oceanography* 36: 1288-300.
- Emson, R. H., and R. J. Faller-Fritsch. 1976. An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton):Gastropoda: Prosobranchia. *Journal of Experimental Marine Biology and Ecology* 23: 285-97.
- Etter, R. J. 1996. The effect of wave action, prey type and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 196: 341-56.
- Etter, R. J., and J. F. Grassle. 1992. Pattern of species diversity in deep sea as a function of sediment particle size diversity. *Nature* 360: 576-78.
- Evans, L. J., and R. H. Norris. 1997. Prediction of benthic macroinvertebrate composition using microhabitat characteristics derived from stereo photography. *Freshwater Biology* 37: 621-33.
- Evans, S. M., A. Hutton, M. A. Kendall, and A. M. Samosir. 1991. Recovery in populations of dogwhelks *Nucella lapillus* (L.) suffering from imposex. *Marine Pollution Bulletin* 22: 331-33.
- Fager, E. W. 1964. Marine sediments: Effects of a tube-building polychaete. *Science* 143: 356-59.
- Faust, M. A. 1982. Contribution of pleasure boats to fecal bacteria concentrations in the Rhode River estuary, Maryland, U.S.A. *Science of the Total Environment* 25: 255-62.
- Fenchel, T., and S. Kolding. 1979. Habitat selection and distribution of five species of the amphipod genus *Gammarus*. *Oikos* 33: 316-22.

- Fenwick, G. D. 1976. The effect of wave exposure on the amphipod fauna of the alga *Caulerpa brownii*. *Journal of Experimental Marine Biology and Ecology* 25: 1-18.
- Field, J. G. 1971. A numerical analysis of changes in the soft-bottom fauna along a transect across False bay, South Africa. *Journal of Experimental Marine Biology and Ecology* 7: 215-53.
- Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.
- Fincham, A. A. 1970. Amphipods in the surf plankton. *Journal of the Marine Biological Association of the United Kingdom* 50: 177-98.
- Fincham, A. A. 1972. Rhythmic swimming and rheotropism in the amphipod *Marinogammarus marinus* (Leach). *Journal of Experimental Marine Biology and Ecology* 8: 19-26.
- Florence, T. M., G. D. Moody, and G. J. Whitelaw. 1999. *An assessment of the health of the Georges River, July 1999*. The Georges River Combined Councils Riverkeeper Program, Sydney, NSW.
- Folk, R. L. 1974. *Petrology of sedimentary rocks*. Austin, Texas: Hemphill Publishing Company.
- Fonseca, M. S., and S. S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina USA. *Marine Ecology Progress Series* 171: 109-21.
- Fonseca, M. S., and J. A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine, Coastal and Shelf Science* 35: 565-76.
- Fonseca, M. S., J. S. Fisher, J. C. Zieman, and G. W. Thayer. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine and Coastal Shelf Science* 15: 351-64.
- Fonseca, M. S., and W. J. Kenworthy. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* 27: 59-78.
- Fonseca, M. S., J. C. Zieman, G. W. Thayer, and J. S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine and Coastal Shelf Science* 17: 367-80.
- Friberg, N., B. Kronvang, H. O. Hansen, and L. M. Svendsen. 1998. Long-term, habitat-specific response of a macroinvertebrate community to river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8: 87-99.
- Frid, C. L. J. 1989. The role of recolonization processes in benthic communities, with special reference to the interpretation of predator-induced effects. *Journal of Experimental Marine Biology and Ecology* 126: 163-71.
- Furukawa, K., E. Wolanski, and H. Mueller. 1997. Currents and sediment transport in mangrove forests. *Estuarine, Coastal and Shelf Science* 44: 301-10.
- Gaines, S. D., and M. D. Bertness. 1993. Measuring juvenile dispersal: why field ecologists must learn to integrate. *Ecology* 74: 2430-2435.

- Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology* 74: 1677-92.
- Gaines, S. D., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the rocky intertidal zone. *Proceedings of the National Academy of Sciences* 82: 3707-11.
- Gallivan, L. B., and R. A. Jr Davis. 1981. Sediment transport in a microtidal estuary: Matanzas River, Florida, U.S.A. *Marine Geology* 40: 69-83.
- Gaylord, B, C. A. Blanchette, and M. W. Denny. 1994. Mechanical consequences of size in wave-swept algae. *Ecological Monographs* 64: 287-313.
- Gilbert, W. H. 1968. Distribution and dispersion patterns of the dwarf tellin clam, *Tellina agilis*. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole* 135: 419-20.
- Gilmore, G., and L. Trent. 1974. *Abundance of benthic macroinvertebrates in natural and altered estuarine areas*, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration.
- Glasby, T. M., and S. D. Connell. 2001. Orientation and position of substrata have large effects on epibiotic assemblages. *Marine Ecology Progress Series* 214: 127-35.
- Glasby, T. M, and A. J. Underwood. 1996. Sampling to differentiate between pulse and press perturbations. *Environmental Monitoring and Assessment* 42: 241-52.
- Gosselink, J. G., G. P. Shaffer, L. C. Lee, D. M. Burdick, D. L. Childers, N. C. Leibowitz, S. C. Hamilton, R. Boumans, D. Cushman, S. Fields, M. Koch, and J. M. Visser. 1990. Landscape conservation in a forested wetland watershed: Can we manage cumulative impacts? *BioScience* 40: 588-600.
- Graham, M. H. 1997. Factors determining the upper limit of the giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *Journal of Experimental Marine Biology and Ecology* 218: 217-149.
- Grant, J. 1980. A flume study of drift in marine infaunal amphipods (Haustoriidae). *Marine Biology* 56: 79-84.
- Grant, J. 1981. Sediment transport and disturbance on an intertidal sandflat: infaunal distribution and recolonization. *Marine Ecology Progress Series* 6: 249-55.
- Grant, W. D., and O. S. Madsen. 1982. Moveable bed roughness in unsteady oscillatory flow. *Journal of Geophysical Research* 87: 469-81.
- Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. 32: 253-84.
- Gray, J. S. 1974. Animal-sediment relationships. *Oceanography and Marine Biology: an Annual review* 12: 223-61.
- Gray, J. S. 1981. *The ecology of marine sediments. An introduction to the structure and function of benthic communities*. Cambridge: Cambridge University press.

- Gray, J. S., M. Aschan, M. R. Carr, K. R. Clarke, R. H. Green, T. H. Pearson, R. Rosenberg, and R. M. Warwick. 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Marine Ecology Progress Series* 46: 151-65.
- Gray, J. S., K. R. Clarke, R. M. Warwick, and G. Hobbs. 1990. Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. *Marine Ecology Progress Series* 66: 285-99.
- Grayson, J. E., M. G. Chapman, and A. J. Underwood. 1999. The assessment of restoration of habitat in urban wetlands. *Landscape and Urban Planning* 43: 227-36.
- Green, R. H. 1979. *Sampling design and statistical methods for environmental biologists*. Chichester, England: Wiley InterScience.
- Gucinski, H. 1981. *Sediment suspension and resuspension from small-craft induced turbulence*, Chesapeake Bay Program, U.S. Environmental Protection Agency, 401 Severn Avenue, Annapolis, MD 21401.
- 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.
- Hall, M. O., and S. S. Bell 1988. Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. *Journal of Marine Research* 46: 613-30.
- Hamer, M. 1999. Solitary killers. *New Scientist* 163: 18-19.
- Hammer, R. M., and R. C. Zimmerman. 1979. Species of demersal zooplankton inhabiting a kelp forest ecosystem off Santa Catalina Island, California. *Bulletin of the Southern California Academy of Science* 78: 199-206.
- Harlin, M. M., and J. M. Lindbergh. 1977. Selection of substrata by seaweeds: optimal surface relief. *Marine Biology* 40: 33-40.
- Hartley, J. P., and B. Dicks. 1987. Macrofauna of subtidal sediments using remote sampling. *Biological Surveys of Estuaries and Coasts*. Eds. J. M. Baker, and W. J. Wolff, 106-30. Blackwell Scientific Publications.
- Hastings, K, P Hesp, and G. A. Kendrick. 1995. Seagrass loss associated with boat moorings at Rottneet Island, Western Australia. *Ocean and Coastal Management* 26: 225-46.
- Hay, D. 1968. Ship waves in navigable waterways. *Proceedings of the Eleventh Coastal Engineering Conference*, 1472-87 New York: American Society of Civil Engineers.
- Hayworth, A. M., and J. F. Quinn. 1990. Temperature of limpets in the rocky intertidal zone: Effects of caging and substratum. *Limnology and Oceanography* 35: 967-70.
- Heck, K. L., and G. S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4: 135-42.
- Hessle, C. 1924. Bottenbonintering i inre Östersjön. *Meddelanden Från Kungliga Lantbroksstyrelsen Stockholm* 250: 1-52.

- Highsmith, R. C. 1982. Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology* 63: 329-37.
- Hilborn, R., and C. J. Walters. 1981. Pitfalls of environmental baseline and process studies. *EIA Review* 2: 265-78.
- Hilton, J, and G. L. Phillips. 1982. The effect of boat activity on turbidity in a shallow broadland river. *Journal of Applied Ecology* 19: 143-50.
- Hiura, T. 1995. Gap formation and species diversity in Japanese beech forests: A test of the intermediate disturbance hypothesis on a geographical scale. *Oecologia* 104: 265-71.
- Hoagland, K. E. 1978. Protandry and the evolution of environmentally mediated sex exchange: a study of the Mollusca. *Malacologia* 17: 365-91.
- Hobday, A. 1995. Body-size variation exhibited by an intertidal limpet: Influence of wave exposure, tidal height and migratory behavior. *Journal of Experimental Marine Biology and Ecology* 189: 29-45.
- Hobson, E. S., and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fisheries Bulletin* 74: 567-98.
- Holling, C. S., Ed. 1978. *Adaptive environmental assessment and management*. New York: John Wiley.
- Hopkinson, C. S., and F. A. Hoffman. 1984. The estuary extended - A recipient-system study of estuarine outwelling. *The Estuary as a Filter*. Ed. V. Kennedy, 313-30. Academic Press.
- Howard, R. K. 1985. Measurements of short-term turnover of epifauna within seagrass beds using an *in situ* staining method. *Marine Ecology Progress Series* 22: 123-68.
- Hurlberg, L. W., and J. S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedentary habitat modifications. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 1130-1139.
- Huston, M. 1994. *Biological Diversity. The Coexistence of Species on Changing Landscapes*. Cambridge: Cambridge University Press.
- Hutchings, P. A., and L. C. Collett. 1997. *Guidelines for the Protection and Management of Estuaries and Estuarine Wetlands*. Australian Marine Sciences Association.
- Hutchinson, G. E. 1975. *A Treatise of Limnology*. Vol. 3. Limnological Botany. New York: Wiley.
- Hyde, R., H. R. Malfroy, and G. N. Watt. 1983. Meteorology and brown haze in Sydney. *The urban atmosphere - Sydney, a case study*. Eds. J. N. Carras, and G. M. Johnson, 109-23. Melbourne: CSIRO.
- Irlandi, E. A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how seagrass landscapes influence rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98: 176-83.

- Irlandi, E. A. 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. *Journal of Marine Research* 54: 161-85.
- Irlandi, E. A., W. G. Ambrose Jr., and B. A. Orlando. 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. *Oikos* 72: 307-13.
- Irlandi, E. A., and C. H. Peterson. 1991. Modification of an animal habitat by large plants: mechanisms by which seagrasses influence clam growth. *Oecologia* 87: 307-18.
- Ishikawa, K. 1989. Relationship between bottom characteristics and benthic organisms in the shallow water of Oppa Bay, Miyagi. *Marine Biology* 102: 265-73.
- Jackson, G. A., and C. D. Winant. 1983. Effects of a kelp forest on coastal currents. *Continental Shelf Research* 2: 75-80.
- James, R. J., M. P. Lincoln Smith, and P. G. Fairweather. 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series* 118: 187-98.
- Jansson, B. O., and C. Källander. 1968. On the diurnal activity of some littoral and peracarid crustaceans in the Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 2: 24-36.
- Jernakoff, P., and J. Nielsen. 1998. Plant-animal associations in two species of seagrasses in Western Australia. *Aquatic Botany* 60: 359-76.
- Johnstone Environmental Technology Pty Ltd. 1987. *Geotechnical investigations and recommendations for rehabilitation at the Rhodes chemical factory site of Union Carbide Australia Ltd.*
- Jones, A. R., and J. Frances. 1988. Sublittoral zoobenthic communities of Homebush, Ermington and Bray's Bays, Parramatta River, NSW. *Wetlands (Australia)* 8: 16-20.
- Jones, N. S. 1950. Marine bottom communities. *Biological Reviews* 25: 283-313.
- Jones, W. E., and A. Demetropoulos. 1968. Exposure to wave action: measurements of an ecological parameter on rocky shores of Anglesey. *Journal of Experimental Marine Biology and Ecology* 2: 46-63.
- Jumars, P. A., and A. R. M. Nowell. 1984. Fluid and sediment dynamic effects on marine benthic community structure. *American Zoologist* 24: 45-55.
- Junoy, J., and J. M. Vieitez. 1990. Macrozoobenthic community structure in the Ria de Foz, an intertidal estuary (Galicia, Northwest Spain). *Marine Biology* 107: 329-39.
- Kalejta, B., and P. A. R. Hockey. 1991. Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. *Estuarine, Coastal and Shelf Science* 33: 175-91.
- Kaplan, E. H., J. R. Walker, and M. G. Kraus. 1974. Some effects of dredging on populations of macrobenthic organisms. *Fishery Bulletin* 72.

- Kautsky, L. 1987. Life-cycles of three populations of *Potamogeton Pectinatus* L. at different degrees of wave exposure in the Askoe area, Northern Baltic proper. *Aquatic Botany* 27: 177-86.
- Kautsky, L, and H. Kautsky. 1989. Algal species diversity and dominance along gradients of stress and disturbance in marine environments. *Vegetatio* 83: 259-67.
- Keddy, P. A. 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aquatic Botany* 14: 41-58.
- Keddy, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: Effects of exposure on zonation patterns. *Ecology* 64: 331-44.
- Keddy, P. A. 1985. Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora. *Canadian Journal of Botany* 63: 656-60.
- Kennelly, S. J. 1983. An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. *Journal of Experimental Marine Biology and Ecology* 68, no. 3: 257-76.
- Keough, M. J., and K. P. Black. 1996. Predicting the scale of impacts: understanding planktonic links between populations. *Detecting ecological impacts: concepts and applications in coastal habitats*. Eds. R. J. Schmitt, and C. W. Osenberg, 199-234. San Diego: Academic Press.
- Keough, M. J., and G. P. Quinn. 1991. Causality and the choice of measurements for detecting human impacts in marine environments. *Australian Journal of Marine Freshwater Research* 42: 539-54.
- Kikuchi, T., and J. M. Pérés. 1977. Consumer ecology of seagrass beds. *Seagrass ecosystems: A scientific perspective*. Eds. C. P. McRoy, and C. Helfferich, 147-93. New York: Marcel Dekker.
- Kimber, A., and J. W. Barko. 1994. *A literature review of the effects of waves on aquatic plants*. Kinne, O. 1971. Salinity. Animal-invertebrates. *Marine Ecology*. Ed. O. Kinne, 821pp. Vol. Vol.1 (Part 2). London: Wiley-Interscience.
- Kinne, O. 1971. Salinity. *Marine Ecology. A comprehensive, integrated treatise on life in oceans and coastal waters*. Ed. O. Kinne, 683-1244. London: Wiley.
- Kirk, R. M., and M. B. Single. 2000. Coastal impacts of new forms of transport: The case of the interisland fast ferries. *Environmental Planning and Management in New Zealand*. Eds. P. A. Memon, and H. PerkinsPalmerston North, New Zealand: Dunmore Press.
- Kirkegaard, J., N. Hojtvad, and H. O. H. Kristensen. 1998a. Fast ferry operation in Danish waters. *Proceedings of the 29th International Navigation Congress* International Navigation Association.
- Kirkegaard, J., H. Kofoed-Hansen, and B. Elfrink. 1998b. Wake wash of high speed craft in coastal areas. *Proceedings of the 26th International Coastal Engineering Conference*, 325-37 American Society of Civil Engineers.

- Klumpp, D. W., R. K. Howard, and D. A. Pollard. 1989. Trophodynamics and nutritional ecology of seagrass communities. *Biology of seagrasses*. Eds. A. W. D. Larkum, A. J. McComb, and S. A. Shepherd, 394-457. Amsterdam: Elsevier.
- Kobayashi, N., A. W. Raichle, and T. Asano. 1992. Wave attenuation by vegetation. *Journal of Waterway, Port, Coastal and Ocean Engineering, ASCE* 119: 30-48.
- Koch, E. W., and G. Gust. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 184: 63-72.
- Koehl, M. A. R. 1986. Seaweeds in moving water: Form and mechanical function. *On the Economy of Plant Form and Function*. Ed. T. J. Givnish, 603-34. Cambridge: Cambridge University Press.
- Koehl, M. A. R., and R. S. Alberte. 1988. Flow, flapping, and photosynthesis of *Nereocystis luetkeana*: a functional comparison of undulate and flat blade morphologies. *Marine Biology* 99: 435-44.
- Kofoed Hansen, H., and A. C. Mikkelsen. 1997. Wake wash from fast ferries in Denmark. *Proceedings of the 4th International Conference on Fast Sea Transportation*, 471-78 Baired Publications.
- Krebs, C. J. 1978. *Ecology: The Experimental Analysis of Abundance and Distribution*. New York: Harper and Row.
- Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1-27.
- Laegdsgaard, P., and C. R. Johnson. 1995. Mangrove habitats as nurseries: Unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Marine Ecology Progress Series* 126-3: 67-81.
- Lake, P. S. 1990. Disturbing hard and soft bottom communities: A comparison of marine freshwater environments. *Australian Journal of Ecology* 15: 477-88.
- Lancellotti, D. A., and R. G. Trucco. 1993. Distribution patterns and coexistence of six species of the amphipod genus *Hyale*. *Marine Ecology Progress Series* 93: 1131-141.
- Langston, W. J., G. R. Burt, and M. Zhou. 1987. Tin and organotin in water, sediments, and benthic organisms of Poole Harbour. *Marine Pollution Bulletin* 18: 634-39.
- Larsen, P. F. 1974. *Quantitative studies of the macrofauna associated with the mesohaline oyster reefs of the James River, Virginia*. 181 pp.
- Laughlin, R. A. 1982. Feeding habits of the blue crab *Callinectes sapidus* Rathbun, in the Apalachicola Estuary, Florida. *Bulletin of Marine Science* 32: 807-22.
- Laxton, J. H. 1991. *Water quality in the upper Parramatta River: analysis of data collected during 1990*. Parramatta, NSW: Upper Parramatta River Trust.
- Leber, K. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* 66: 1951-64.

- Lee, R. F., B. Dornseif, F. Gonsoulin, K. Tenore, and R. Hanson. 1981. Fate and effects of heavy fuel oil spill on a Georgia salt marsh. *Marine Environmental Research* 5: 125-43.
- Lee, R. F., and D. S. Page. 1997. Petroleum hydrocarbons and their effects in subtidal regions after major oil spills. *Marine Pollution Bulletin* 34: 928-40.
- Lee, S. Y., C. W. Fong, and R. S. S. Wu. 2001. The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. *Journal of Experimental Marine Biology and Ecology* 259: 23-50.
- Leigh, E. G., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave energy and intertidal productivity. *Proceedings of the National Academy of Sciences, USA* 84: 1314-18.
- Lenihan, H. S., and J. S. Oliver. 1995. Anthropogenic and natural disturbances to marine benthic communities in Antarctica. *Ecological Applications* 5: 311-26.
- Lenihan, H. S., J. S. Oliver, and M. A. Stephenson. 1990. Changes in hard bottom communities related to boat mooring and tributyltin in San Diego Bay: a natural experiment. *Marine Ecology Progress Series* 60: 147-59.
- Levin, L. A. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65: 1185-200.
- Levin, L. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-67.
- Levitan, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* 181: 261-68.
- Lewis, F. G. 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. *Marine Ecology Progress Series* 19: 101-13.
- Lewis, F. G., and A. W. Stoner. 1981. An examination of methods for sampling macrobenthos in seagrass meadows. *Bulletin of Marine Science* 31: 116-24.
- Lewis, F. G., and A. W. Stoner. 1983. Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. *Bulletin of Marine Science* 33: 296-304.
- Li, M. Z., and C. L. Amos. 1999. Field observations of bedforms and sediment transport thresholds of fine sand under combined waves and currents. *Marine Geology* 158: 147-60.
- Lincoln-Smith, M. P. 1991. Environmental impact assessment: the roles of predicting and monitoring extent of impacts. *Australian Journal Marine Freshwater Research* 42: 603-14.
- Lively, C. M., P. T. Ramandi, and L. Y. Delph. 1993. Intertidal community structure: space-time interactions in the northern Gulf of California. *Ecology* 74: 162-73.
- Longbottom, M. R. 1970. The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. *Journal of Experimental Marine Biology and Ecology* 5: 138-57.

- López Gappa, J. J., A. Tablado, and N. H. Magaldi. 1990. Influence of sewage pollution on a rocky intertidal community dominated by the mytilid *Brachidontes rodriguezii*. *Marine Ecology Progress Series* 63: 163-75.
- Lopez-Jamar, E., G. Gonzalez, and J. Mejuto. 1986. Temporal changes of community structure and biomass in two subtidal macrofaunal assemblages in La Coruna Bay, NW Spain. *Long-term changes in coastal benthic communities*. Eds. C. Heip, B. F. Keegan, and J. R. Lewis, 137-50. Dordrecht: Junk.
- Loucks, O. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* 10: 17-25.
- Lu, L., and S. S. Wu. 2000. An experimental study on recolonization and succession of marine macrobenthos in defaunated sediment. *Marine Biology* 136: 291-302.
- Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* 59: 67-94.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260: 17,36.
- Madsen, J. D., J. A. Bloomfield, J. W. Sutherland, L. W. Eichler, and C. W. Boylen. 1996. The aquatic macrophyte community of Onondaga Lake: Field survey and plant growth bioassays of lake sediments. *Lake Research and Management* 12: 73-79.
- Madsen, T. V., and E. Warnacke. 1983. Velocities of currents around and within submerged aquatic vegetation. *Archives of Hydrobiology* 89: 389-394.
- Malanson, G. P. 1984. Intensity as a third factor of disturbance regime and its effect on species diversity. *Oikos* 43: 411-13.
- Marcus, J. M., and T. P. Stokes. 1985. Polynuclear aromatic hydrocarbons in oyster tissue around three coastal marinas. *Bulletin of Environmental Contamination and Toxicology* 25: 835.
- Maritime and Coastguard Agency. 1998. Research project 420: *Investigation of high speed craft (HSC) on routes near to land or enclosed estuaries*, Marine and Coastguard Agency, Southampton, England.
- Massel, S. R., K. Furukawa, and R. M. Brinkman. 1999. Surface wave propagation in mangrove forests. *Fluid Dynamics Research* 24: 219-49.
- Matthiessen, G. C. 1960. Intertidal zonation in populations of *Mya arenaria*. *Limnology and Oceanography* 5: 381-88.
- McCabe, D. J., and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* 124: 270-279.
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *Journal of Marine Research* 35: 221-66.

- McCall, P. L. 1978. Spatial-temporal distributions of Long Island Sound infauna: the role of bottom disturbance in a nearshore habitat. *Estuarine Interactions. Proceedings of the Fourth International Estuarine Research Conference.*, Ed. Wiley M.L. 191-219NY: Academic Press.
- McCook, L. J., and A. R. O. Chapman. 1991. Community succession following massive ice scour on an exposed rocky shore - effects of *Fucus* canopy algae and mussels during late succession. *Journal of Experimental Marine Biology and Ecology* 154: 137-69.
- McCook, L. J. and A. R. O. Chapman. 1993. Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. *Journal of Experimental Marine Biology and Ecology* 154: 137-69.
- McCook, L. J., and A. R. O. Chapman. 1997. Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology and Ecology* 214: 121-47.
- McDermott, J. J. 1983. Food web in the surf zone of an exposed sandy beach along the mid-Atlantic coast of the United States. *Sandy beaches as ecosystems*. Ed. A. McLachlan, and T. Erasmus, 529-38. The Hague: Junk.
- McGee, B. L., C. E. Schlekat, D. M. Boward, and T. L. Wade. 1995. Sediment contamination and biological effects in a Chesapeake Bay marina. *Ecotoxicology* 4: 39-59.
- McGuinness, K. A. 1987. Disturbance and organisms on boulders: I. Patterns in the environment and the community. *Oecologia* 71: 409-19.
- McIntosh, A. 1991. Trace metals in freshwater sediments: a review of the literature and an assessment of research needs. *Metal ecotoxicology: current concepts and applications*. Eds. M. C. Newman, and A. McIntosh, 243-60. Lewis Publishers, Inc.
- McLusky, D. S. 1981. *The estuarine ecosystem*. New York: Halsted Press.
- McMahon, P. J. P. 1989. The impact of marinas on water quality. *Water Science and Technology* 21: 39-43.
- McQuaid, C. D., and G. M. Branch. 1984. Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Marine Ecology Progress Series* 19: 145-51.
- McQuaid, C. D., and G. M. Branch. 1985. Trophic structure of rocky intertidal communities: response to wave action and implication for energy flow. *Marine Ecology Progress Series* 22: 153-61.
- Meadows, P. S., and J. I. Campbell. 1972. Habitat selection by aquatic invertebrates. *Advances in Marine Biology* 10: 271-382.
- Menge, B. A. 1978a. Predation intensity in a rocky intertidal community: effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia* 34: 17-35.
- Menge, B. A. 1978b. Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental harshness. *Oecologia* 34: 1-16.

- Menge, B. A., L. R. Ashkens, and A. Matson. 1983. Use of artificial holes in studying community development in cryptic marine habitats in a tropical rocky intertidal region. *Marine Biology* 77: 129-42.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* 130: 730-735.
- Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctula*. *Oecologia* 17: 293-316.
- Miller, D. C., and R. W. Sternberg. 1988. Field measurements of the fluid and sediment-dynamic environment of a benthic deposit feeder. *Journal of Marine Research* 46: 771-96.
- Mills, E. L. 1967. The biology of an ampeliscid amphipod crustacean sibling pair. *Journal of the Fisheries Research Board of Canada* 24: 305-55.
- Möller, P. L., L. Pihl, and R. Rosenberg. 1985. Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. *Marine Ecology Progress Series* 27: 109-21.
- Moore, P. G. 1973. The kelp fauna of north east Britain I. Function of the physical environment. *Journal of Experimental Marine Biology and Ecology* 13: 97-125.
- Morrisey, D. J., L. Howitt, A. J. Underwood, and J. S. Stark. 1992. Spatial variation in soft-sediment benthos. *Marine Ecology Progress Series* 81: 197-204.
- Moverley, J., and A. Hirst. 1999. Estuarine health assessment using benthic macrofauna. National River Health Program, Urban Sub Program, Report No 11, LWRRDC Occasional Paper 18/99. Canberra: Land and Water Resources Research and Development Corporation.
- Mukai, H., M. Nishihira, H. Kamisato, and Y. Fujimoto. 1986. Distribution and abundance of the sea-star *Archaster typicus* in Kabira Cove, Ishigaki Island, Okinawa. *Bulletin of Marine Sciences* 38: 366-83.
- Myers, A. A., and T. Southgate. 1980. Artificial substrates as a means of monitoring rocky shore cryptofauna. *Journal of the Marine Biological Association of the United Kingdom* 60: 963-75.
- Nagelkerken, I., M. Dorenbosch, W. C. E. P. Verberk, E. Cocheret de la Morinière, and G. van der Velde. 2000a. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns of biotope association, community structure and spatial distribution. *Marine Ecology Progress Series* 202: 175-92.
- Nagelkerken, I., G. van der Velde, M. W. Gorissen, G. J. Meijer, T. van't Hof, and C. den Hartog. 2000b. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* 51: 31-44.
- Nagle, J. S. 1968. Distribution of the epibiota of macroepibenthic plants. *Contributions in Marine Science at the University of Texas* 13: 105-44.

- Nanson, G. C., A. von Krusenstierna, and E. A. Bryant. 1994. Experimental measurements of river-bank erosion caused by boast generated waves on the Gordon River, Tasmania. *Regulated Rivers: Research and Measurement* 9: 1-14.
- Nelson, W. G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. *Marine Ecology Progress Series* 5: 141-49.
- Notini, M. 1978. Long-term effects of an oil spill on *Fucus* macrofauna in a small Baltic bay. *Journal of the Fisheries Research Board of Canada* 35: 745-53.
- [NRC] National Research Council. 1981. *Testing for effects of chemicals on ecosystems*. Washington, DC: National Academy Press.
- [NRC] National Research Council. 1995. *Understanding marine diversity: A research agenda for the nation*. Washington, DC: National Academy Press.
- [NSW DLWC] NSW Department of Land and Water Conservation. 2000a. *Estuaries of NSW: Estuaries* URL <http://www.dlwc.nsw.gov.au/care/water/estuaries/estuaries.html>
- [NSW DLWC] NSW Department of Land and Water Conservation. 2000b. *Parramatta River. Estuarine Fact Sheet*.
- [NSW DLWC] NSW Department of Land and Water Conservation. 2000c. *Narrabeen Lake, Dee Why, Curl Curl and Manly Lagoons. Estuarine Fact Sheet*.
- [NSW DLWC] NSW Department of Land and Water Conservation. 2000d. *Georges River. Estuarine Fact Sheet*.
- NSW Fisheries. 1998. *Policy and guidelines: aquatic habitat management and fish conservation*, Eds. A. K. Smith, and D. A. Pollard. NSW Fisheries, Sydney.
- Ólafsson, E. B., C. H. Peterson, and W. G. Ambrose Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft-sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology: an Annual Review* 32: 65-109.
- Oliver, H. R. 1971. Wind profiles in and above a forest canopy. *Quarterly Journal of the Royal Meteorological Society* 97: 548-53.
- Olsgard, F., and J. S. Gray. 1995. A comprehensive analysis of the effects of offshore oil and gas exploration and production on the benthic communities of the Norwegian continental shelf. *Marine Ecology Progress Series* 122: 277-306.
- Orth, R. J. 1975. Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. *Chesapeake Science* 16: 205-8.
- Orth, R. J. 1977. The importance of sediment stability in seagrass communities. *Ecology of marine benthos*. Ed. B. C. Coull, 281-300. Columbia: University of South Carolina Press.

- Orth, R. J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. *Plant-animal interactions in the marine benthos*. Eds. D. M. John, S. J. Hawkins, and J. H. Price, 147-64. Oxford: Clarendon Press.
- Orth, R. J., K. L. Heck Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7: 339-50.
- Osenberg, C. W., R. J. Schmitt, S. J. Holbrook, K. E. Abu-Saba, and A. R. Flegal. 1994. Detection of environmental impacts: natural variability, effect size and power analysis. *Ecological Applications* 4: 16-30.
- Orth, R. J., and J. van Montfrans. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquatic Botany* 18: 43-69.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93-120.
- Palumbi, S. R. 1984. Measuring intertidal wave force. *Journal of Experimental Marine Biology and Ecology* 81: 171-79.
- Pardy, B. 1995. Fast ferries: new equilibrium versus ecological sustainability. *New Zealand Law Journal* 202: 302-4.
- Parnell, K. E. 1996. *Monitoring effects of ferry wash in Tory Channel and Queen Charlotte Sound*. Unpublished report to Marlborough District Council and the Director General of Conservation, Marlborough, New Zealand.
- Parnell, K. E., and H. Kofoed-Hansen. 2001. Wakes from high-speed ferries in confined waters: management approaches with examples from New Zealand and Denmark. *Coastal Management* 29: 217-37.
- Patterson Britton and Partners. 1999a. *Progress Report #3. Parramatta River long-term shoreline monitoring program*, Waterways Authority of New South Wales.
- Patterson Britton and Partners. 1999b. *HarbourCat wave measurements in upper river. Parramatta River long-term shoreline monitoring study*, Waterways Authority of New South Wales.
- Patterson Britton and Partners. 2000a. *Progress report #5. Parramatta River long-term shoreline monitoring study*, Waterways Authority of New South Wales.
- Patterson Britton and Partners. 2000b. *Progress Report #6. Parramatta River long-term shoreline monitoring study*, Waterways Authority of New South Wales.
- Patterson Britton and Partners. 2000c. Letter to Waterways Authority of New South Wales, 24 March 2000.
- Pawlik, J. R. 1986. Chemical induction of larval settlement and metamorphosis in the reef-building tube worm *Phragmatopoma californica* (Sabellariidae: Polychaeta). *Marine Biology* 91: 59-68.

- Pearson, R.G. 1981. Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* 4: 105-22.
- Pearson, T. H., and R Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual review* 16: 229-311.
- Peckarsky, B. L., and M. A. Penton. 1990. Effects of enclosures on stream microhabitat and invertebrate community structure. *Journal of the North American Benthological Society* 9: 249-61.
- Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biological Bulletin* 169: 417-30.
- Petersen, C. G. J. 1918. The sea bottom and its production of fish food. *Reports of the Danish Biological Station* 25: 1-62.
- Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. *Ecological Processes in Coastal and Marine Systems*. Ed. R. J. Livingston, 233-64. New York: Plenum Press.
- Peterson, C. H. 1986. Enhancement of *Merenaria mercenaria* densities in seagrass beds: Is patterns fixed during settlement season or altered by subsequent differential survival? *Limnology and Oceanography* 31: 200-205.
- Peterson, C. H. 1991. Intertidal zonation of marine invertebrates in sand and mud. *American Scientist* 79: 236-49.
- Peterson, C. H. 1993. Improvement of environmental impact analysis by application of principles derived from manipulative ecology: lessons from coastal marine case histories. *Australian Journal of Ecology* 18: 21-52.
- Peterson, C. H., and R. Black. 1994. An experimentalist's challenge: when artifacts of intervention intercat with treatments. *Marine Ecology Progress Series* 111: 289-97.
- Peterson, C. H., and H. C. Summerson. 1992. Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. *Marine Ecology Progress Series* 90: 257-72.
- Pezeshki, S. R., S. W. Matthews, and R. D. Delaune. 1991. Root cortex structure and metabolic responses of *Spartina patens* to soil redox conditions. *Environmental and Experimental Botany* 31: 91-97.
- Pfitzenmyer, H. T. 1975. *The effects of shallow-water channel dredging on the community of benthic animals and plants. Phase I*. Center for Estuarine and Environmental Studies, University of Maryland, Chesapeake Biological Laboratory, Solomons, MD 20688.
- Pfitzenmyer, H. T. 1978. *The effects of shallow-water channel dredging on the community of benthic animals and plants. Phase II*. Center for Estuarine and Environmental Studies, University of Maryland, Chesapeake Biological Laboratory, Solomons MD 20688.

- Phillips, J. C., G. A. Kendrick, and P. S. Lavery. 1997. A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. *Marine Ecology Progress Series* 153: 125-38.
- Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: a synthesis. *The Ecology of Natural Disturbance and Patch Dynamics*. Pickett, S. T. A and P. S. White, 371-84. New York: Academic Press.
- Plazait, J. C. 1975. Mollusc distribution and its value for recognition of ancient mangroves. *Proceedings of the International Symposium on the Biology and Management of Mangroves*, Eds. G. Walsh, S. Snedekar, and H. Teas, 456-68.
- Ponder, W., P. Hutchings, and R. Chapman. 2002. *Overview of the conservation of Australian marine invertebrates*. A report for Environment Australia. July 2002. Sydney: Australian Museum.
- Posey, M. H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69: 974-83.
- Posey, M, W Lindberg, T Alphin, and F Vose. 1996. Influence of storm disturbance on an offshore benthic community. *Bulletin of Marine Science* 59: 523-29.
- Prescott, A. M. 1984. *Sydney ferry fleets*. Magill, SA: Parsons.
- Pritchard, D. W. 1967. What is an estuary, physical viewpoint. *Estuaries*. Ed. G. H. Lauf. Washington D.C.: American Association for the Advancement of Science.
- Probert, P. K. 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities. *Journal of Marine Research* 42: 893-921.
- Qian, P-Y, and F-S Chia. 1992. Effects of diet type on the demographics of *Capitella* sp. (Annelida: Polychaeta): lecithotrophic development vs. planktotrophic development. *Journal of Experimental Marine Biology and Ecology* 157: 159-79.
- Rachor, E., and A. Gerlach. 1978. Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. *Rap. P.-V. Cons. Int. Explor. Mer* 172: 418-31.
- Raimondi, P. T., and D. C. Reed. 1996. Determining the spatial extent of ecological impacts caused by local anthropogenic disturbances in coastal marine habitats. *Detecting ecological impacts: concepts and applications in coastal habitats*. Eds., R. J. Schmitt, and C. W. Osenberg, 179-98. San Diego: Academic Press.
- Remane, A. 1934. Brackwasserfauna. *Zoologischer Anzeiger*: 34-74.
- Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. *Oceanography and Marine Biology: an Annual review* 12: 263-300.
- Rhoads, D. C., and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28: 150-178.
- Ricciardi, A, and E Bourget. 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Marine Ecology Progress Series* 185: 21-35.

- Robbins, B. D., and S. S. Bell. 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends in Ecology and Evolution* 9: 301-4.
- Robertson, A. I. 1984. Trophic interactions between the fish fauna and macrobenthos of an eelgrass community in Western Port, Victoria. *Aquatic Botany* 18: 135-53.
- Robertson, A. I., and N. C. Duke. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Marine Biology* 96: 193-205.
- Rosenberg, R. 1972. Benthic faunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. *Oikos* 23: 92-108.
- Rosenberg, R. S. 1973. Succession in benthic macrofauna in a Swedish fjord subsequent to the closure of a sulphite pulp mill. *Oikos* 24: 244-58.
- Rosenberg, R. 1976. Benthic faunal dynamics during succession following pollution abatement in a Swedish estuary. *Oikos* 27: 414-27.
- Rosenberg, D. M., and V. H. Resh. 1982. The use of artificial substrates in the study of freshwater benthic macroinvertebrates. *Artificial substrates*. Ed. J. Jr. Cairns, 175-235. Ann Arbor, Michigan: Ann Arbor Science Publishers Inc.
- Rosenberg, D. M., and V. H. Resh. 1993. Introduction to freshwater biomonitoring using benthic macroinvertebrates. *Freshwater biomonitoring and benthic macroinvertebrates*. Eds. D. M. Rosenberg, and V. H. Resh, 1-9. New York: Chapman and Hall.
- Royse, C. F. 1970. *An introduction to sediment analysis*. Arizona: Arizona State University.
- Ruiz, J. M., G. Bachelet, P. Caumette, and O. F. X. Donard. 1996. Three decades of tributyltin in the coastal environment with emphasis on Arcachon Bay, France. *Environmental Pollution* 93: 195-203.
- Ruuskanen, A., S. Back, and T. Reitalu. 1999. A comparison of two cartographic exposure methods using *Fucus vesiculosus* as an indicator. *Marine Biology* 134: 139-45.
- Ryan, T. A. 1959. Multiple comparisons in psychological research. *Psychological Bulletin* 56: 26-47.
- Sánchez-Jerez, P., C. B. Cebrián, and A. A. R. Esplá. 1999. Comparison of the epifaunal spatial distribution in *Posidonia oceanica*, *Cymodocea nodosa* and unvegetated bottoms: importance of meadow edges. *Acta Oecologica* 20: 391-405.
- Sammot, M., and G. Nickless. 1978. Petroleum hydrocarbons from marine sediments and animals from the island of Malta. *Environmental Pollution* 16.
- Sanders, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. *Diversity and Stability in Ecological Systems*. Eds G. M. Woodwell, and Smith H.H., 71-81. Upton, NY: Brookhaven National Laboratory.

- Sanders, H. L., J. F. Grassle, G. E. Hampson, L. S. Morse, S. Garner-Price, and C. C. Jones. 1980. Anatomy of an oil spill: long term effects from the grounding of the barge Florida off West Falmouth, Massachusetts. *Journal of Marine Research* 8: 265-380.
- Schaffner, L. C., R. J. Diaz, C. R. Olsen, and I. L. Larsen. 1987. Faunal characteristics and sediment accumulation processes in the James River Estuary, Virginia. *Estuarine, Coastal and Shelf Science* 25: 211-26.
- Scheltema, R. S. 1974. Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavica* 10: 263-69.
- Schmidt, G. H., and G. F. Warner. 1984. Effects of caging on the development of a sessile epifaunal community. *Marine Ecology Progress Series* 15: 251-63.
- Schoellhamer, D. H. 1996. Anthropogenic sediment resuspension mechanisms in a shallow microtidal estuary. *Estuarine, Coastal and Shelf Science* 43: 533-48.
- Scholer, H. A. 1974. "Hawkesbury River; the effects of speedboat activities on river banks, Appendix 3." *Hawkesbury River report on effects of water ski-ing*, Public Works Department of New South Wales, Sydney.
- Seapy, R. R., and M. M. Littler. 1978. The distribution, abundance, community structure, and primary productivity of macroorganisms from two central California rocky intertidal habitats. *Pacific Science* 32: 293-314.
- Seed, R., and T. H. Suchanek. 1992. Population and community ecology of *Mytilus*. *The mussel Mytilus: ecology, physiology, genetics and cultur*. Ed. E. Gosling. Amsterdam: Elsevier Science Publishers.
- Segerstråle, 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 Biologicae Societas Scientiarum Fennica* 24: 1-26.
- Segerstråle, S. G. 1973. Results of bottom fauna sampling in certain localities in the Tvärminne area (inner Baltic), with special reference to the so called *Macoma-Pontoporeia* theory. *Commentationes Biologicae Societas Scientiarum Fennica* 67: 1-12.
- Shaw, D. W., and G. W. Minshall. 1980. Colonization of an introduced substrate by stream macroinvertebrates. *Oikos* 34: 259-71.
- Shaw, R. H., J. Travangar, and D. Ward. 1983. Structure of the Reynolds stress in a canopy layer. *Journal of Climatology and Applied Meteorology* 22: 1922-31.
- Shephard, R. N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. *Psychometrika* 27: 125-40.
- Sheridan, P. 1997. Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, U.S.A. *Estuarine, Coastal and Shelf Science* 44: 455-69.
- Shull, D. H. 1997. Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat. *Journal of Marine Research* 55: 153-79.

- Small, K. J. 1999. *Assemblages of macrofauna in sediments around outfalls surrounded by industrial and residential land-use*. BSc (Hons) Thesis, University of Sydney.
- Smith, D. 1990. *Environmental impact statement for the extension of ferry services on the Parramatta River, west of Silverwater Bridge*, New South Wales Department of Transport.
- Smith, J. D., and S. R. McLean. 1977. Spatially averaged flow over a wavy surface. *Journal of Geophysical Research* 84, no. 12: 1735-46.
- Smith, S. D. A. 2000. Evaluating stress in rocky shore and shallow reef habitats using the macrofauna of kelp holdfasts. *Journal of Aquatic Ecosystem Stress and Recovery* 7: 259-272.
- Snelgrove, P. V. R., and C. A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology: an Annual Review* 32: 111-77.
- Snelgrove, P. V. R., C. A. Butman, and J. P. Grassle. 1993. Hydrodynamic enhancement of larval settlement in the bivalve *Mulinia lateralis* (Say) and the polychaete *Capitella* sp. 1 in microdepositional environments. *Journal of Experimental Marine Biology and Ecology* 168: 71-109.
- Sogard, S. M., and K. M. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine and Coastal Shelf Science* 33: 501-19.
- Somerfield, P. J., and K. R. Clarke. 1995. Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* 127: 113-19.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Evolution and Systematics* 15: 353-91.
- Southward, A. J. 1958. The zonation of plants and animals on rocky sea shores. *Biological Reviews* 33: 137-77.
- Spaling, H., and B. Smit. 1993. Cumulative environmental change: conceptual frameworks, evaluation approaches, and institutional perspectives. *Environmental Management* 17: 587-600.
- [SPCC] State Pollution Control Commission. 1987. *Pollution control in Sydney's waterways*, State Pollution Control Commission, Sydney.
- Spence, D. N. H. 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* 12: 37-125.
- Stachowitsch, M. 1991. Anoxia in the Northern Adriatic Sea: rapid death, slow recovery. *Modern and ancient continental shelf anoxia*. Eds. R. V. Tyson, and T. H. Pearson, 119-29. Vol. 58. London: Geological Society Special Publication.
- Stander, G. H., and J. A. V. Venter. 1968. Oil pollution in South Africa. *International conference on oil pollution of the sea. Report of Proceedings.*, 231-59.

- Stanhope, H. S., W. C. Banta, and M. T. Temkin. 1982. Size-specific emergence of the marsh snail, *Littorina irrorata*: Effect of predation by blue crabs in a Virginia salt marsh. *Gulf Coast Research Report* 7: 179-82.
- Stark, J. S. 1996. *Heavy metal pollution and assemblages in estuarine soft-sediments*. MSc Thesis, University of Sydney.
- State Transit. 1993. *A ferry to Parramatta*. December 1993
- Steichen, D. J., S. J. Holbrook, and C. W. Osenberg. 1996. Distribution and abundance of benthic and demersal macrofauna within a natural hydrocarbon seep. *Marine Ecology Progress Series* 138: 71-82.
- Stoner, A. W. 1980. The role of the seagrass biomass in the organization of benthic macrofaunal assemblages. *Bulletin of Marine Science* 30: 537-51.
- Ström, K., and F. Ziegler. 1998. *Miljöeffekter av svallvågor från höghastighetsfärjor*. Miljöförvaltningen i Göteborg.
- Stumbo, S, K Fox, F Dvorak, and L Elliot. 1999. The prediction, measurement and analysis of wake wash from marine vessels. *Marine Technology* 36: 248-60.
- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 31: 105-20.
- Summerson, H. C., and C. H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Marine Ecology Progress Series* 15: 63-77.
- Summerson, H. C., and C. H. Peterson. 1990. Recruitment failure of the bay scallop, *Argopecten irradians concentricus*, during the first red tide, *Ptychodiscus brevis*, outbreak recorded in North Carolina. *Estuaries* 13: 322-31.
- Sutherland, T. F., C. L. Amos, and J. Grant. 1998. The effect of carbohydrate production by the diatom *Nitzschia curvileata* on the erodibility of sediment. *Limnology and Oceanography* 43: 65-72.
- Tabachnik B.G., and L. S. Fidell. 1989. *Using multivariate statistics*. 2nd ed. Harper and Row.
- Tagatz, M. E. 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. U. S. *Fisheries and Wildlife Services, Fisheries Bulletin* 67: 17-33.
- Tamaki, A. 1987. Comparison of restivity to transport by wave action in several polychaete species on an intertidal sand flat. *Marine Ecology Progress Series* 37: 181-89.
- Tansley, A.G., Adamson, R.S., 1925. Studies on the vegetation of the English chalk. III. The chalk grasslands of the Hampshire-Sussex border. *Journal of Ecology* 13: 177-223.
- Tararam, A. S., and Y. Wakabara. 1981. The mobile fauna - especially Gammaridea - of *Sargassum cymosum*. *Marine Ecology Progress Series* 5: 157-63.
- Taylor, R. B. 1998. Short-term dynamics of a seaweed epifaunal assemblage. *Journal of Experimental Marine Biology and Ecology* 227: 67-82.

- ten Hallers-Tjabbes, C. C., J. F. Kemp, and J. P. Boon. 1994. Imposex in whelks (*Buccium undatum*) from the open North Sea: Relation to shipping traffic intensities. *Marine Pollution Bulletin* 28: 311-13.
- ter Braak, C. J. F. 1992. Permutation versus bootstrap significance tests in multiple regression and ANOVA. *Bootstrapping and related techniques*. Eds. K.-H. Jockel, G. Rothe, and W. Sendler, 79-86. Berlin: Springer-Verlag.
- Thain, J. E., and M. J. Waldcock. 1986. The impact of tributyltin (TBT) antifouling paints on molluscan fisheries. *Water Science and Technology* 18: 193-202.
- Thompson, J. K. 1982. Population structure of *Gemma gemma* (Bivalvia: Veneridae) in south San Francisco Bay, with a comparison to some northeastern United States estuarine populations. *The Veliger* 24: 281-90.
- Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). *Memoirs of the Geological Society of America*. 67: 461-534.
- Thrush, S. F. 1986. Community structure on the floor of a sea-loagh: are large epibenthic predators important? *Journal of Experimental Marine Biology and Ecology* 104: 171-83.
- Thrush, S. F., J. E. Hewitt, and R. D. Pridmore. 1989. Patterns in the arrangement of polychetes and bivalves in intertidal sandflats. *Marine Biology* 102: 529-35.
- Thrush, S. F., R. B. Whitlatch, R. D. Pridmore, J. E. Hewitt, V. J. Cummings, and M. R. Wilkinson. 1996. Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. *Ecology* 77: 2472-87.
- Tilmant, J. T., and G. P. Schmahl. 1981. A comparative analysis of coral damage on recreationally used reefs within Biscayne National Park, Florida. *The Reef and Man. Proceedings of the 4th International Coral Reef Symposium* .
- Total Environment Centre. 1996. *Sydney harbour and foreshores: environmental status and future*. Sydney: TEC.
- Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42: 938-49.
- Trussell, G. C., A. S. Johnson, S. G. Rudolph, and E. S. Gilfillan. 1993. Resistance to dislodgement: habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Marine Ecology Progress Series* 100: 135-44.
- Turner, S. J., J. E. Hewitt, M. R. Wilkinson, D. J. Morrissey, S. F. Thrush, V. J. Cummings, and G. Funnell. 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22: 1016-32.
- Turner, S. J., and M. A. Kendall. 1999. A comparison of vegetated and unvegetated soft sediment macrobenthic communities in the River Yealm, south western Britain. *Journal of the Marine Biological Association of the United Kingdom* 79: 741-43.

- Turner, S. J., S. F. Thrush, V. J. Cummings, J. E. Hewitt, M. R. Wilkinson, R. B. Williamson, and D. J. Lee. 1997. Changes in epifaunal assemblages in response to marina operations and boating activities. *Marine Environmental Research* 43, no. 3: 181-99.
- Turner, S. J., S. F. Thrush, R. D. Pridmore, J. E. Hewitt, V. J. Cummings, and M. Maskery. 1995. Are soft-sediment communities stable? An example from a windy harbour. *Marine Ecology Progress Series* 120: 219-30.
- Underwood, A. J. 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology* 51: 57-85.
- Underwood, A. J. 1989. The analysis of stress in natural populations. *Biological Journal of the Linnean Society* 7: 51-78.
- Underwood, A. J. 1990. Experiments in ecology and management: their logic, functions and interpretations. *Australian Journal of Ecology* 15: 365-89.
- Underwood, A. J. 1991. Beyond BACI: Experimental designs for selecting human environmental impacts on temporal variations in natural populations. *Australian Journal of Marine and Freshwater Research* 42: 569-87.
- Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology* 161: 145-78.
- Underwood, A. J. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Australian Journal of Ecology* 18: 99-116.
- Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications*: 3-15.
- Underwood, A. J. 1995. Ecological research and (and research into) environmental management. *Ecological Applications* 5: 232-47.
- Underwood, A. J. 1997. *Experiments in Ecology: Their logical design and interpretation using analysis of variance*. United Kingdom: Cambridge University Press.
- Underwood, A. J. 1998. Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. *Journal of Experimental Marine Biology and Ecology* 231: 291-306.
- Underwood, A. J. 1999. Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *Journal of Experimental Marine Biology and Ecology* 232: 125-40.
- Underwood, A. J., and M. G. Chapman. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107: 212-24.
- Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56: 202-19.

- Underwood, A. J., and P. G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* 4: 16-20.
- Underwood, A. J., and P. Jernakoff. 1984. The effects of tidal height, wave exposure, seasonality and rock-pools on grazing and the distribution of microalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology* 75: 71-96.
- Underwood, A. J., and C. H. Peterson. 1988. Towards an ecological framework for investigating pollution. *Marine Ecology Progress Series* 46: 227-34.
- [US EPA] US Environmental Protection Agency. 1983. *Results of the nationwide urban runoff program. Volume I final report.* Washington, DC: U.S. Environmental Protection Agency.
- Valkirs, A. O., P. F. Seligman, P. M. Stang, V. Homer, S. H. Lieberman, G. Vafa, and C. A. Dooley. 1986. Measurement of butyltin compounds in San Diego Bay. *Marine Pollution Bulletin* 17: 319-24.
- van Dolah, R. F., D. R. Calder, and D. M. Knott. 1984. Effects of dredging and open-water disposal on benthic macroinvertebrates in a South Carolina estuary. *Estuaries* 7: 28-37.
- van Katwijk, M. M., and D. C. R. Hermus. 2000. Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology Progress Series* 208: 107-18.
- Viejo, R. M., J. Arrontes, and N. L. Andrew. 1995. An experimental evaluation of the effect of wave action on the distribution of *Sargassum muticum*. *Botanica Marina* 38: 437-41.
- Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199-217.
- Virnstein, R. W. 1978. Predator caging experiments in soft sediments: caution advised. *Estuarine Interactions*. Ed. M. L. Wiley, 261-73. New York: Academic Press.
- Virnstein, R. W. 1979. Predation on estuarine infauna: Response patterns of component species. *Estuaries* 2: 69-86.
- Virnstein, R. W., and M. C. Curran. 1986. Colonization of artificial seagrass versus time and distance from source. *Marine Ecology Progress Series* 29: 279-88.
- Virnstein, R. W., W. G. Nelson, III F. G. Lewis, and R. K. Howard. 1984. Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained? *Estuaries* 7A: 310-330.
- Waldock, R., H. L. Rees, P. Matthiessen, and M. A. Pendle. 1999. Surveys of the benthic infauna of the Crouch Estuary (UK) in relation to TBT contamination. *Journal of the Marine Biological Association of the United Kingdom* 79: 225-32.
- Waldock, M. J., and J. E. Thain. 1983. Shell thickness in *Crassostrea gigas*: Organotin antifouling of sediment induced. *Marine Pollution Bulletin* 14: 411-15.
- Walker, D. I., R. J. Lukatelich, G. Bastyan, and A. J. McComb. 1989. Effect of moorings on seagrass beds near Perth, Western Australia. *Aquatic Botany* 36: 69-77.

- Walters, C. 1986. *Adaptive management of renewable resources*. New York: Macmillan.
- Warren, J. H. 1985. Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata*. *Journal of Experimental Marine Biology and Ecology* 89: 11-28.
- Warwick, R. M., and K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology* 172: 215-26.
- Watanuki, A., and H Yamamoto. 1990. Settlement of seaweeds on coastal structures. *Hydrobiologia* 204/205: 275-80.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1-22.
- Webster, P. J., A. A. Rowden, and M. J. Attrill. 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. *Estuarine, Coastal and Shelf Science* 47: 351-57.
- Weis, J. S., and P. Weis. 1992. Transfer of contaminants from CCA treated lumber to aquatic biota. *Journal of Experimental Marine Biology and Ecology* 161: 189-99.
- Wells, F. E. 1986. Distribution of molluscs across a pneumatophore boundary in a small bay in northwestern Australia. *Journal of Molluscan Studies* 52: 83-90.
- Widdows, J., P. Donkin, M. D. Brinsley, S. V. Evans, P. N. Salkeld, A. Franklin, R. J. Law, and M. J. Waldock. 1995. Scope for growth and contaminant levels in North Sea mussels *Mytilus edulis*. *Marine Ecology Progress Series* 127: 131-48.
- Wiens, J. A., and K. R Parker. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. *Ecological Applications* 5: 1069-83.
- Wildish, D. J., and D. D. Kristmanson. 1997. *Benthic suspension feeders and flow*. Cambridge: Cambridge University Press.
- Wildish, D. J., and D. Peer. 1983. Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 40, no. Suppl. 1: 309-21.
- Williams, D. D. 1980. Temporal patterns in recolonization of stream benthos. *Arch. Hydrobiol.* 90: 56-74.
- Williams, D. D., and K. A. Moore. 1986. Microhabitat selection by a stream-dwelling amphipod: a multivariate analysis approach. *Freshwater Biology* 16: 115-22.
- Williams, D. D., and K. A. Moore. 1989. Environmental complexity and the drifting behaviour of a running water amphipod. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1520-1530.
- Wilson, B. 1994. Letters: "RiverCat surge erodes foreshores". *Sydney Afloat*, No. 54. March, 1994.
- Wilson, S. D., and P. A. Keddy. 1985. The shoreline distribution of *Juncus pelocarpus* along a gradient of exposure to waves: an experimental study. *Aquatic Botany* 21: 277-84.

- Wilson, Jr. W. H. 1980. A laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychete larvae. *Journal of Experimental Marine Biology and Ecology* 46: 73-80.
- Wilson, W. H. Jr. 1991. Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics* 21: 221-41.
- Winer, B. J., D. R. Brown, and K. M. Michels. 1991. *Statistical principles in experimental design*. 3rd ed. ed. New York: McGraw-Hill.
- Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. *Marine Ecology Progress Series* 16: 259-68.
- Wolanski, E., and P. Ridd. 1986. Tidal mixing and trapping in mangrove swamps. *Estuarine, Coastal and Shelf Science* 23: 759-71.
- Woodin, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. *Ecology* 59: 274-84.
- Woodin, S. A. 1991. Recruitment of infauna; positive or negative cues? *American Zoologist* 31: 797-807.
- Wu, R. S. S., and P. K. S. Shin. 1997. Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. *Marine Biology* 128: 475-87.
- Yallop, M. L., D. M. Paterson, and P. Wellsbury. 2000. Interrelationships between rates of microbial production, exopolymer production, microbial biomass, and sediment stability in biofilms of intertidal sediments. *Microbial Ecology* 39: 116-27.
- Yeo, R. K., and M. J. Risk. 1979. Intertidal catastrophes: effects of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. *Journal of the Fisheries Research Board Canada* 36: 667-69.
- Young, D. K., and D. C. Rhoads. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts I. A transect study. *Marine Biology* 11: 242-54.
- Young, D. R., G. V. Alexander, and D. McDermott-Ehrlich. 1979. Vessel-related contamination of southern California harbors by copper and other metals. *Marine Pollution Bulletin* 10: 50-56.
- Zajac, R. N. 1986. Effects of intra-specific density and food levels on growth and reproduction in an infaunal polychaete, *Polydora ligni*. *Journal of Marine Research* 44: 319-29.
- Zajac, R. N., and R. B. Whitlatch. 1982a. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of intertidal recolonization. *Marine Ecology Progress Series* 10: 1-14.
- Zajac, R. N., and R. B. Whitlatch. 1982b. Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Marine Ecology Progress Series* 10: 15-27.
- Zieman, J. C. 1976. The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. *Aquatic Botany* 2: 127-39.

Zimmerman, R., R. Gibson, and J. F. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. *Marine Biology* 54: 41-47.

APPENDIX I

PILOT STUDY FOR COLONIZATION EXPERIMENT (CHAPTER 6) - THE VERTICAL DISTRIBUTION OF INFAUNA

The homogenisation of sediment for the colonization experiment involved the mixing of sediment cores over their depth. Properties of sediment follow a gradient with depth below the sediment-water interface that is related to disturbance by waves and currents (e.g. de Jong and de Jonge, 1995). Mixing of sediment at the surface with sediment at depths of 10 cm will destroy this gradient and may result in sediment with characteristics far removed from those found naturally. This is not desirable for experiments examining the settlement of invertebrates, since there is evidence to suggest that settlement is related to properties of the sediment that vary with depth (e.g. Gray, 1974; Probert, 1984).

The top few centimeters of the sediment appear to be fairly well mixed *in situ* by wind and boat-generated waves (see Bell et al., 1997). Thus, the homogenization of sediment over a small vertical range may not grossly alter its profile. It was, therefore, decided to only use the top 4 cm of sediments in the colonization experiment. This meant that only the top 2 cm of fauna could be sampled, since it is advisable to leave a buffer zone adjacent to the container. Models and hypotheses were, however, based on observations of assemblages found in the top 10 cm of sediment.

Previous studies suggest that up to 95% of invertebrates are found in the top 2 cm of the sediment (Coull and Bell, 1979; Schaffner et al., 1987). It was proposed that this would also be the case along the Parramatta River, such that spatial patterns in assemblages and taxa would be comparable between samples collected to depths of 2 cm and those collected to depths of 10 cm.

To test these hypotheses, three cores of sediment, 10 cm-deep, and three cores of sediment, 2 cm-deep, were collected from each of the sites shown in Figure 6.2. These samples were processed using the methods described in Section 2.5.2.

Any difference between the assemblages of the 2 cm and 10 cm cores was tested for using a two-way NP-MANOVA of un-standardized data, with the factors, site and sampling unit. No significant difference was found (NP-MANOVA: $p > 0.05$; Fig. A1.1). Differences in assemblages between the 2cm and 10 cm cores did not appear to be any greater than differences between sites in locations. Similarly, no significant difference was found in the abundances of nereids, spionids or amphipods between the sampling units (ANOVA: $p > 0.05$, Fig. A1.2). *Xenostrobus securis*, surprisingly, appeared more abundant when sampled using the 2 cm-deep

cores (Fig. A1.2e). The abundance of capitellids was greater in the 10 cm cores than the 2 cm cores at W2(S1) and W2(S2) (ANOVA: $p < 0.01$, site x depth interaction; Fig. A1.2a).

Based on these results, it was concluded that the majority of infaunal organisms along the Parramatta River are found in the top 2 cm of the sediment, such that patterns in assemblages do not differ significantly between the two units of sampling. Models and hypotheses relating to distribution and abundance of these may therefore be evaluated by sampling with a 2 cm-deep core.

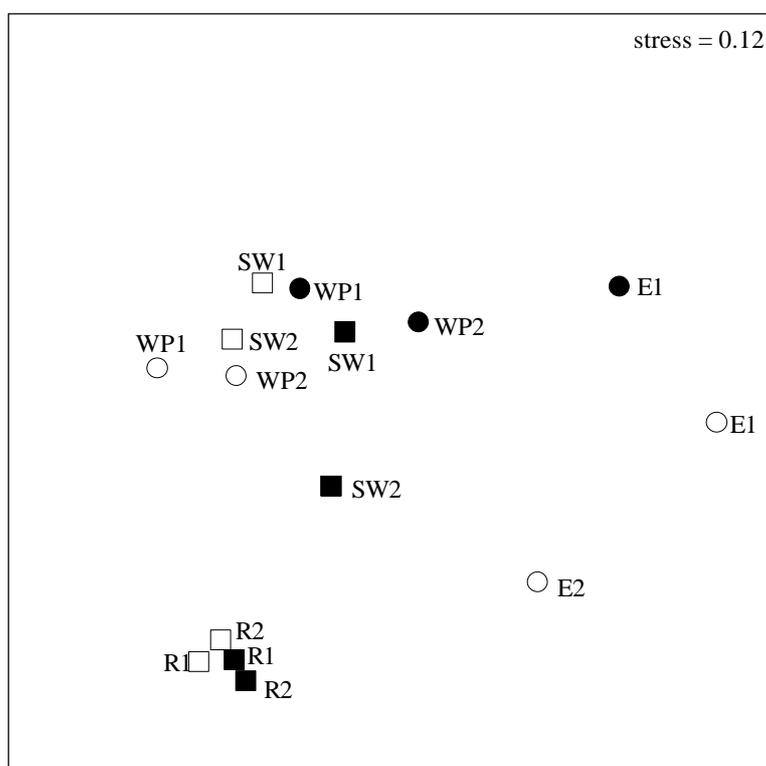


Figure A1.1 nMDS ordination of assemblages of macrobenthic infauna in sites of the upper Parramatta River, as determined using cores that were 2 cm deep (black) and 10 cm deep (white). Circles indicate sites within the wash zone and squares, sites within the no-wash zone. Points represent centroids of untransformed data. The centroid for 2 cm cores collected from E2 is not included due to the loss of a core. $n = 3$.

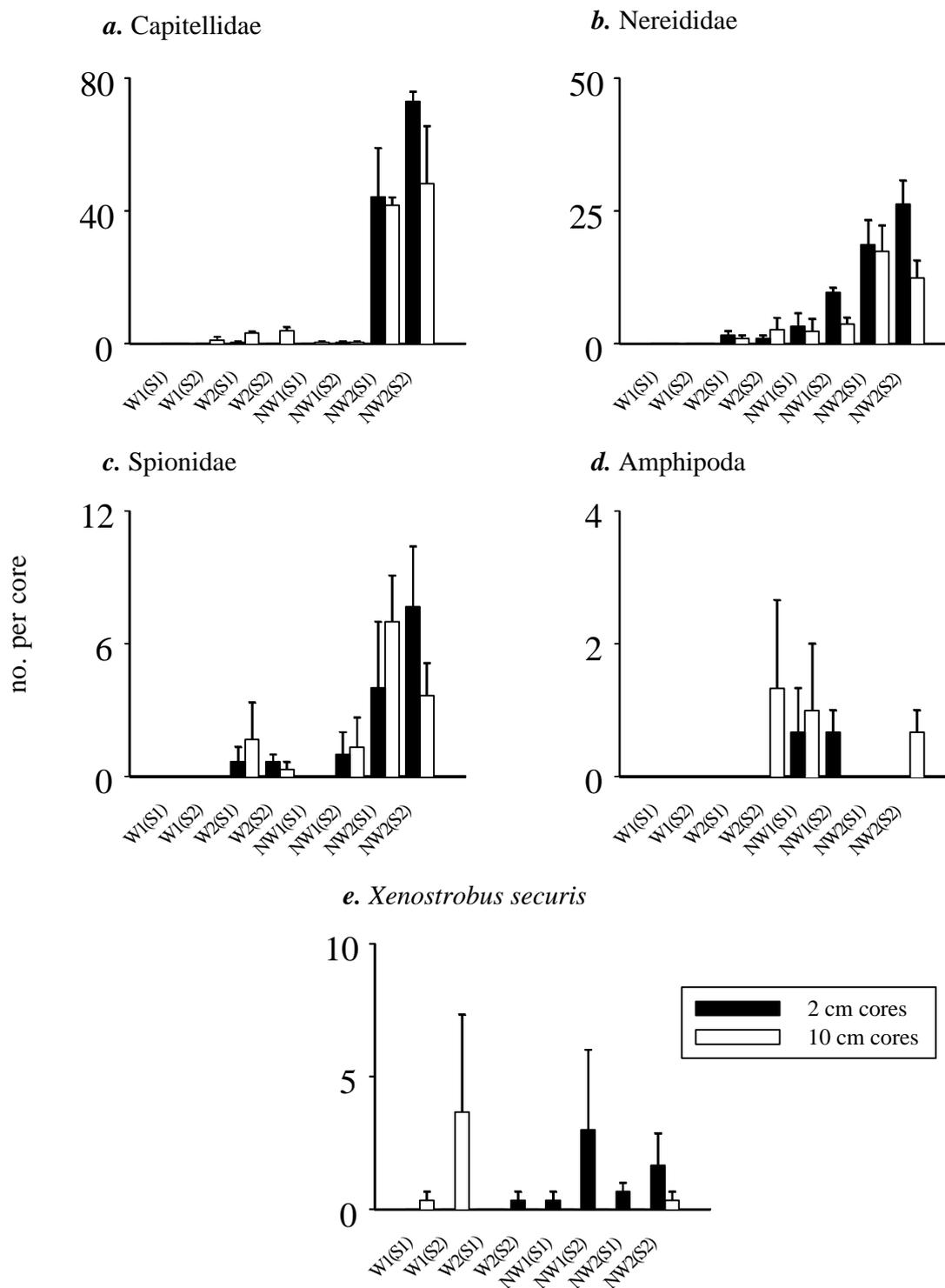


Fig. A1.2 Mean (+ S.E.) abundance of taxa of macrobenthic infauna in sites along the upper Parramatta River, as determined using cores that were 2 cm deep and 10 cm deep. $n = 3$.