The ecological role of the suspension feeding bivalve, *Austrovenus stutchburyi*, in estuarine ecosystems

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Abstract

Suspension feeding bivalves are described as key species in many aquatic ecosystems, where they can influence primary productivity and nutrient dynamics, are food for higher trophic levels, and may be harvested in commercial or recreational fisheries. In many areas where bivalve populations have declined, substantial changes to ecosystem structure and function have occurred. High-density beds of the infaunal suspension feeding bivalve, *Austrovenus stutchburyi*, are a dominant feature on intertidal flats in many New Zealand estuaries, but populations are declining in some areas, likely due to anthropogenic stressors such as overharvesting and sedimentation. This thesis examines the influence of *Austrovenus* on estuarine ecosystem function using laboratory, field and modelling studies.

The effects of bed density and flow speed on boundary layer dynamics and *Austrovenus* clearance rates (CR) were investigated in annular flumes. Bed shear stress increased with increasing bivalve density, and under certain conditions was also increased when *Austrovenus* were feeding, compared to when they were not. The bed roughness and siphonal currents generated by the bivalves may therefore influence food supply to the bed. Both individual and bed CR were significantly greater at the high flow speed. Bed CR did not scale proportionally with density, in part because individual CR decreased with increasing density, but also because the proportion of bivalves actively feeding decreased at high densities. Thus, scaling up individual CR obtained from animals at low densities will significantly overestimate population filtration capacity.

The effect of *Austrovenus* on ecosystem function was examined at two sites, one sandy, the other composed of muddy-sand, to determine whether sedimentary environment alters this key species’ role. Gross primary production (likely corresponding to microphytobenthos production) and ammonium uptake were significantly increased, and denitrification potential was also elevated, when *Austrovenus* was added, relative to removed, at the sandy site. In contrast, there was no effect of *Austrovenus* on any of these variables at the muddy-sand site. These results reveal the importance of considering sedimentary environment when examining the effect of key species on ecosystem function, and suggest that even moderate levels of sedimentation may reduce the positive effect of *Austrovenus* on primary productivity.

A food-web model was used to quantify the interactions between *Austrovenus* and other estuarine species, and to determine the effect of reducing *Austrovenus* biomass on ecosystem properties. The model revealed an estuarine system dominated by benthic species, characterised as a developing, rather than a mature ecosystem. Detritus production and export were high, while transfer efficiency and internal recycling were low. Decreasing *Austrovenus* biomass decreased system maturity, suggesting that reductions in *Austrovenus* populations may decrease ecosystem stability. The model also confirmed that within these estuarine systems *Austrovenus* and microphytobenthos are key species which impact greatly on all other trophic levels.

This thesis demonstrates that *Austrovenus* populations exert considerable influence on benthic communities and processes, and play a key role in the functioning of estuarine ecosystems. Reductions in *Austrovenus* populations will likely negatively impact on microphytobenthos and higher trophic levels, and may also reduce ecosystem maturity and stability.

Intertidal flats, Raglan Harbour

Dedication

For my parents,
who showed me the sea

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Preface

The main body of this thesis comprises three research chapters (chapters 2 - 4), which have been published, or submitted for publication, in peer reviewed international scientific journals. Only work carried out by myself is presented, though I gratefully acknowledge the guidance and advice provided by my supervisors and co-authors, Conrad Pilditch, Karin Bryan, David Hamilton, Denise Bruesewitz and Drew Lohrer.

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CHAPTER 1

General Introduction

1.1 Motivation

The link between biodiversity and ecosystem functioning has been well established in many systems (e.g. Tilman et al. 1997, Loreau et al. 2001, Naeem 2002, Hooper et al. 2005). However, often it is certain functional groups or key species, rather than biodiversity *per se*, which have a disproportionate effect on ecosystem structure and function (e.g. Widdicombe & Austen 1998, Lohrer et al. 2004, Norling et al. 2007). The pervasive influence of humans on nearly every ecosystem on Earth is also well-known, and anthropogenic stressors can lead to declines in both biodiversity and the abundance of key species (e.g. Chapin et al. 1997, Vitousek et al. 1997, Pauly et al. 1998). This has generated considerable interest in the influence of biodiversity and key species on ecosystem function, in order to understand the potential consequences of their loss (e.g. Solan et al. 2004, Thrush et al. 2006).

Suspension feeding bivalves are often highly abundant in aquatic ecosystems, and can play a major role in ecosystem structure and function (Dame 1993, Newell 2004). They have been described as key species in many systems (e.g. Dame & Prins 1998), although their dominance tends to preclude them from being true “keystone species” as defined by Power et al. (1996), i.e. a species whose effect is both large, and disproportionately large relative to its abundance. Nonetheless, suspension feeding bivalve populations have been shown to exert substantial top-down control on phytoplankton, thus reducing the effects of eutrophication (e.g. Cloern 1982, Officer et al. 1982). By clearing seston from the water column, suspension feeding bivalves also reduce turbidity, which increases light penetration to the sediment surface, and may increase macroalgae and microphytobenthos productivity (Newell 2004, Porter et al. 2004). Furthermore, transfer of inorganic and organic material in faeces and pseudofaeces, collectively known as biodeposits, from the water column to the sediment surface enhances benthic-pelagic coupling (e.g. Dame 1993, Giles & Pilditch 2004). Nitrogen contained in biodeposits can be buried in underlying sediment, and under certain conditions, coupled nitrification-denitrification removes nitrogen from the system; therefore, the bivalves may also exert a bottom-up control on phytoplankton populations by reducing nutrient loads (Kaspar et al. 1985, Newell et al. 2002, Newell et al. 2005). Moreover, consumption of pre-settlement macrofauna larvae by suspension feeders can be an important structuring influence on benthic macrofaunal community composition (e.g. Woodin 1976, Dittmann 1990, Troost et al. 2009a).

Loss of suspension feeding bivalves from some systems has resulted in substantial changes to ecosystem structure and function. For example, in Chesapeake Bay (USA), loss of eastern oyster (*Crassostrea virginica*) beds has increased the incidence of phytoplankton blooms, sometimes resulting in the occurrence of deep-water hypoxia (Jackson et al. 2001, Kemp et al. 2005). In Great South Bay (USA), declining clam (*Mercenaria mercenaria*) abundance has altered both phytoplankton and zooplankton dynamics, likely leading to the appearance of “brown tides” of the phytoplankton *Aureococcus anophagefferens* (Lonsdale et al. 2007). Suspension feeder loss can also affect higher trophic levels; a reduction in both the abundance and quality of cockles (*Cerastoderma edule*) in the Dutch Wadden Sea due to shellfish dredging has been linked to the loss of red knots (*Calidris canutus islandica*) from the area (van Gils et al. 2006). Conversely, invasion of aquatic systems by non-native suspension feeding bivalves, such as by the Asian clam (*Potamocorbula amurensis*) in San Francisco Bay and the zebra mussel (*Dreissena polymorpha*) in many freshwater systems in the USA, has resulted in reduced phytoplankton biomass (e.g. Alpine & Cloern 1992, Barbiero et al. 2006).

A substantial proportion of research into the ecosystem services provided by suspension feeding bivalves has focused on epibenthic species, which can create substantial reef structures (e.g. Dame 1993, Smaal & Zurburg 1997, Manzouni et al. 1998, Asmus & Asmus 2005, Newell et al. 2005, Hewitt et al. 2006). The influence of infaunal species on ecosystem function may not necessarily be the same as for epifaunal species, however. Infaunal species do not create reefs, but tend to bioturbate surficial sediments, which increases both oxygen penetration into the sediment, and sediment resuspension, facilitating the dispersal of nutrient-rich biodeposits (e.g. Widdows et al. 1998b, Ciutat et al. 2007). Moreover, many issues considered in previous research (and reviewed by

Newell 2004), such as occurrence of deep-water hypoxia after a phytoplankton bloom and organic matter remineralisation in the sediment around bivalves, were in deep, frequently stratified systems. However, deep-water hypoxia is unlikely in shallow, well-mixed estuaries. In this type of system, biodeposits are likely to be carried away from bivalve beds by tidal and wind driven currents, and may even be advected into the open coastal environment. Thus, there is a need to focus attention on the precise role of infaunal bivalves in shallow estuarine systems.

Worldwide, infaunal suspension feeding bivalves dominate intertidal areas in many estuaries, although populations have declined in a number of these systems in recent decades (e.g. Piersma et al. 2001, Peterson 2002, Kraeuter et al. 2008). Infaunal bivalves, such as *Ruditapes philippinarum* and *Corbicula japonica* in Japan, *Mercenaria mercenaria* in North America, and *Cerastoderma edule* in Europe, have been shown to play a major role in benthic nutrient regeneration and stimulation of microphytobenthos production (e.g. Doering et al. 1986, Doering et al. 1987, Swanberg 1991, Yamamuro & Kioke 1993, Magni et al. 2000, Rossi et al. 2008). These animals also provide an important food source for higher trophic levels, such as shorebirds, and may be part of commercially or recreationally valuable fisheries (e.g. Norris et al. 1998, Wolff 2005).

In many New Zealand estuaries the dominant feature on intertidal flats are high-density beds (c. 1000 ind. m^{-2}) of the infaunal suspension feeding bivalve, *Austrovenus stutchburyi* (Hewitt et al. 1996, Cummings et al. 2007). Commonly known as the cockle, little-necked clam or tuangi, *Austrovenus* is shallow-burrowing (lives within 5 cm of the sediment surface), has very short siphons, and can grow up to 60 mm in length (although < 35 mm is more common in estuaries near urbanised areas, Hewitt & Norkko 2007). *Austrovenus* has been shown to influence solute fluxes and enhance microphytobenthos production (Sandwell et al. 2009, Lohrer et al. 2010a), and a study into the effects of the loss of this species from tidal flats clearly showed the potential for functional changes to occur to the ecosystem (Thrush et al. 2006).

Estuaries in New Zealand, as elsewhere, are under increasing pressure from coastal and catchment development, causing problems such as habitat loss of fringing wetlands, excessive nutrient and sewage inputs, accumulation of chemical contaminants, over-fishing and altered freshwater flows (reviewed by Kennish 2002). Furthermore, land-use change in surrounding catchments can cause accelerated sedimentation rates, which may alter habitat and biological communities (Thrush et al. 2004). Increased levels of suspended sediment can damage or clog the feeding structures of suspension feeders, and decrease the nutritional value of seston (e.g. Turner & Miller 1991, Cheung & Shin 2005). *Austrovenus* has been shown to be sensitive to repeated exposure to high levels of suspended sediments (Norkko et al. 2006), and *Austrovenus* abundance tends to decline with increasing estuarine mud content (Thrush et al. 2003b). Chemical contaminants, originating from inputs such as stormwater runoff, can accumulate in estuarine sediments and affect benthic animal behaviour, mortality and community structure (e.g. Nipper et al. 1998, Morrisey et al. 2003). Even if contamination levels are not high enough to cause mortality, sublethal stress may reduce reproductive potential and growth in bivalves such as *Austrovenus* (e.g. De Luca-Abbott 2001, Peake et al. 2006). In addition to the adverse effects of sedimentation and pollution, over-harvesting has caused a steady decline in *Austrovenus* populations in some areas (Cummings et al. 2007, Marsden & Adkins 2010). As *Austrovenus* has been, and is likely to be further impacted by these pressures, it is important to understand the role of this key species in estuarine ecosystems.

The role of suspension feeding bivalves in maintaining or enhancing estuarine water quality is often estimated by scaling up individual clearance rates to ecosystem level (e.g. Hily 1991, Smaal & Prins 1993, Dame & Prins 1998). However, published clearance rate data for *Austrovenus* is limited (McClatchie 1992), and it is generally accepted that laboratory derived clearance rates overestimate *in situ* rates because they do not incorporate environmental variability, such as flow speed, and seston quality and quantity (e.g. Wildish & Saulnier 1993, Cranford 2001, Newell et al. 2001). Bivalve growth rates tend to decline in high density beds (e.g. Vincent et al. 1994, Taylor et al. 1997, Zhou et al. 2006), but the effect of con-specifics on clearance rates has largely been ignored. There is a need therefore to investigate the effect of bed density and flow speed on *Austrovenus* clearance rates, which may be an important step towards deriving better estimates of population grazing pressure for ecosystem models.

The influence of *Austrovenus* on estuarine ecosystems is likely to be related to more than just their ability to exert top-down control on phytoplankton populations. New Zealand estuaries are typically shallow and have high water clarity; microphytobenthos production is almost certainly more important than pelagic phytoplankton production in these systems (e.g. Miller et al. 1996, Safi 2003). Previous research has established that microphytobenthos productivity increases with increasing *Austrovenus* density, (likely due to enhanced nutrient fluxes at high densities), but these experiments were limited in space and time (Thrush et al. 2006, Sandwell et al. 2009). The influence of key species on ecosystem function is likely to differ between habitat types (Needham et al. 2011), and although *Austrovenus* tends to be absent from very muddy sediments, high-density beds exist across a range of sediment types. Furthermore, previous experiments have typically used small (≤ 1 m^2) experimental plots, but results from these studies may be dominated by edge effects (Hewitt et al. 1997, Englund & Cooper 2003), as the estuarine intertidal is dynamic and subject to substantial bedload transport and sediment reworking rates (e.g. Grant et al. 1997). Large scale *in situ* experimental studies, replicated in time and in different habitat types, are therefore required to more comprehensively determine the effect of *Austrovenus* beds on nutrient dynamics and primary productivity.

Field and laboratory experiments can elucidate interactions between key species and biogeochemical processes (e.g. Widdicombe & Austen 1998, Thrush et al. 2006, Lohrer et al. 2010a), providing pieces of a bigger picture, but rarely include multiple trophic levels (but see Petchey et al. 2004). Modelling can provide a valuable quantitative tool with which to reveal interactions at ecosystem scales, describe system properties, identify gaps in current knowledge, and integrate the ‘pieces’ of information acquired in experimental studies (Jørgensen & Bendoricchio 2001). Process-based models tend to focus on lower trophic levels and require substantial spatially and temporally resolved datasets for calibration and validation; food-web models, however, can be used to explore the energy flow and interactions between multiple trophic levels, and can be parameterised using comparatively smaller datasets gathered for other purposes (e.g. Gaedke 1995, Fulton et al. 2003, Christensen et al. 2008). Ecopath is a mass-balance food-web model that is widely used in fisheries management and has previously been used to model the interactions between species in a wide range of coastal systems, including estuaries (Christensen & Pauly 1992, Christensen et al. 2008). There are no published Ecopath models for New Zealand estuaries however, despite the fact that these ecosystems are numerous and have high ecological, recreational and cultural value. Furthermore, a mass mortality event occurred recently (February 2009) on *Austrovenus* beds in Whangateau Harbour (North Island, New Zealand), with the loss of c. 60 of the population (C. Pilditch unpublished data; MFish 2009), but the effect of such an event on the wider ecosystem is largely unknown. Construction of an Ecopath model is required to quantify the interactions between *Austrovenus* and other species in the estuary, and assess the potential effects of a decline in the *Austrovenus* population on ecosystem properties.

The aim of this thesis is thus to determine the ecological role of *Austrovenus* in estuarine ecosystems, i.e. the grazing pressure exerted by *Austrovenus* populations, the influence of *Austrovenus* on nutrient dynamics and primary productivity, and the interactions between *Austrovenus* and other estuarine species.

1.2 Thesis outline

The main body of this thesis comprises three research chapters (chapters 2 – 4), in which I use a variety of methods, (i.e. laboratory and field experiments, and trophic modelling), to quantify the effect of *Austrovenus* populations on ecosystem structure and function.

I begin in chapter 2 by conducting laboratory experiments to investigate the influence of *Austrovenus* density and flow speed on clearance rates and near-bed hydrodynamics. The effect of con-specifics on bivalve clearance rates has largely been ignored; quantification of bed clearance rates may be an important step towards deriving better estimates of population grazing pressure.

In chapter 3 I examine the influence of *Austrovenus* beds on benthic nutrient fluxes, primary productivity and sediment denitrification rates in differing sedimentary environments, in winter and summer. Previous studies have been limited in space and time, and in the size of experimental plots used. I use large experimental plots to reduce confounding edge effects and to determine whether habitat influences this key species' role.

In chapter 4 I investigate the effect of *Austrovenus* on estuarine energy flow and ecosystem properties using a food-web model. This allows me to examine the impact of *Austrovenus* on other trophic levels, and the impact of a reduction in *Austrovenus* biomass on ecosystem properties.

In chapter 5 I scale the bed clearance rates obtained from my laboratory experiments up to ecosystem level, review the main findings from my research chapters, and end with some overall conclusions and suggestions for further research.

CHAPTER 2

Effects of *Austrovenus stutchburyi* density and flow speed on clearance rates and near-bed hydrodynamics

2.1 Introduction

Suspension feeding bivalves play a key role in aquatic ecosystems by controlling phytoplankton populations directly via grazing, contributing to benthic-pelagic coupling, and by providing a food source for higher trophic levels (see review by Newell 2004). Estimates of bivalve grazing rates are necessary to quantify effects on ecosystem processes and are often estimated by measuring individual clearance rates (CR; the volume of water cleared of seston per unit time), which are then scaled-up to ecosystem level (e.g. Hily 1991, Smaal & Prins 1993, Dame & Prins 1998, Prins et al. 1998). However, it has long been accepted that this approach overestimates *in situ* population filtration rates because laboratory derived CR are often made using algal monocultures and do not incorporate environmental variability (Doering & Oviatt 1986). Environmental variables such as seston quantity and quality (e.g. Navarro & Widdows 1997, Hawkins et al. 2001) and flow speed (e.g. Wildish & Saulnier 1993, Sobral & Widdows 2000, Newell et al. 2001) have a significant effect on CR but are typically not included simultaneously in laboratory studies. Moreover, individually determined CRs ignore potential competitive intraspecific interactions that would occur in dense beds.

To my knowledge the interactive effects of bivalve density and flow speed on clearance rates have not been investigated simultaneously. This is surprising because numerous studies have documented the density dependent effects of roughness generated by bivalve shells and siphonal jets on boundary layer dynamics, and on consequently food supply to the bed (e.g. Fréchette et al. 1989, O'Riordan et al. 1995, Green et al. 1998, van Duren et al. 2006, Ciutat et al. 2007). Furthermore, in high densities bivalve growth rate is reduced in both epifaunal (e.g. Taylor et al. 1997, Prins et al. 1998, Zhou et al. 2006) and infaunal (e.g. Peterson & Black 1987, Jensen 1992, Vincent et al. 1994) species, likely due to intraspecific competition for seston. In this study, I quantify the effects of bivalve density and flow speed on clearance rates for an infaunal clam, which may be an important step toward deriving better estimates of population filtration capacity for ecosystem models (e.g. Gerritsen et al. 1994, Bayne 1998, Cranford & Hill 1999, Duarte et al. 2003, Dowd 2005, Spillman et al. 2009).

In suspension feeding bivalves the expected response of CR to flow speed is unimodal. Initially, individual CR increases with flow speed as increasing flow compensates for seston depletion around the animal. At high flow speeds however, pressure differences can pass water through the mantle too quickly, causing a reduction, and eventually complete suppression of feeding (Wildish & Kristmanson 1997). Studies investigating the effect of flow speed on individual CR have shown that the actual response can vary between and even within species for both epibenthic (e.g. Wildish & Miyares 1990, Wildish & Saulnier 1993, Pilditch & Grant 1999, Widdows et al. 2002) and infaunal bivalves (e.g. Cole et al. 1992, Sobral & Widdows 2000, Fernandes et al. 2007, Widdows & Navarro 2007). Although conflicting data from CR studies have been explained as being the result of differing experimental set-ups (Jorgensen 1996, Riisgård 2001), or the effect of other variables such as food quantity and quality (Cranford 2001, Hawkins et al. 2001), the effect of con-specifics has largely been ignored. In a bivalve bed re-filtration occurs due to the formation of a concentration boundary layer (a seston depleted layer above a bivalve bed; Fréchette et al. 1989, O'Riordan et al. 1993, 1995, Dolmer 2000a, Jonsson et al. 2005), potentially reducing individual CR. Flow speed is likely to be an important factor influencing CR over dense beds as increasing flow speeds will replenish seston-depleted water and reduce re-filtration (Fréchette et al. 1989, Butman et al. 1994, Dolmer 2000b).

Seston-depleted water above bivalves can also be replenished by vertical mixing, which can be enhanced due to bed roughness generated by both the physical structure of a bivalve bed and bivalve siphonal currents (Butman et al. 1994, O'Riordan et al. 1995, Nikora et al. 2002). Although epifaunal species might have a greater impact on bed roughness height (Green et al. 1998, van Duren et al. 2006), infaunal species can also create roughness elements such as tracks and mounds by bioturbation activity, raising bed shear stresses compared to a smooth bed (Ciutat et al. 2007). Siphonal currents can also have a significant effect on boundary layer dynamics generating turbulence and increasing bed shear stress, which may reduce re-filtration, especially when current velocities are low relative to the siphonal jet velocity (Monismith et al. 1990, van Duren et al. 2006). The effects of bed roughness and siphonal currents on boundary layer dynamics are thus likely to be density and flow speed dependent, and to influence food supply to the bed and CR.

In this study, laboratory annular flumes were used to estimate CR and measure near-bed hydrodynamics over beds of differing densities of an infaunal clam, *Austrovenus stutchburyi*, from New Zealand. The specific aims were: 1) to quantify the effect of bivalve bed density on CRs, and 2) to quantify the effect of bed density on boundary layer dynamics (separating the effects of morphological changes to the sediment surface from those due to bivalve feeding activity), both as a function of flow speed. I hypothesised that CR would increase with increasing flow speed, but decrease with increasing bivalve density, and that a seston-depleted layer would occur at high densities and low flow speeds (although I expected enhanced bed roughness and shear stress over high densities so increased vertical mixing might reduce this effect).

2.2 Methods

2.2.1 Study Species

Austrovenus stutchburyi, (hereafter referred to as *Austrovenus*), is an infaunal suspension feeding clam found on intertidal mud and sand flats, usually aggregated in high density beds (up to 1200 individuals m^{-2}), in estuaries around New Zealand (Hewitt et al. 1996, Whitlatch et al. 1997). It has short siphons (< 1 cm), feeds at the sediment water interface and exhibits an endogenous circatidal rhythm whereby feeding is restricted to the four hours around high tide (Beentjes & Williams 1986). *Austrovenus* populations can represent a large proportion of total estuarine biomass and play a key role in nutrient dynamics and primary productivity (Sandwell et al. 2009).

2.2.2 Laboratory flumes

Austrovenus beds of differing densities were established in annular flumes to examine the effects on bed clearance rate (bed CR; L h^{-1} m^{-2}), individual clearance rate (CR; L h^{-1} ind^{-1}), and on near-bed hydrodynamics as a function of flow speed. I used two identical annular flumes built to the same specifications as those at Plymouth Marine Laboratory (Widdows et al. 1998a). Briefly, the outer annulus has a diameter of 62 cm and the inner a diameter of 42 cm resulting in a channel width of 10 cm and a bed area of 0.17 m^2. The flumes have a maximum water depth of 30 cm (maximum vol. = 49 L) and water flow in the annulus is generated by a computer-controlled rotating lid.

2.2.3 Experimental treatments and setup

I chose three flow speeds (2, 5 and 15 cm s^{-1}) and seven *Austrovenus* density treatments (0, 29, 100, 247, 500, 747 and 1000 ind. m^{-2}) to span *in situ* ranges. A maximum flow speed of 15 cm s^{-1} was chosen because it is close to the mean velocities observed above *Austrovenus* beds on intertidal sand flats (Sandwell et al. 2009) and, importantly, because it was just below the entrainment threshold of the sand bed in the flume. I observed that once sand grains began to move, individuals ceased feeding. The other two flow speeds were selected based on expected changes in boundary layer dynamics. In a flume containing a smooth bed of sand without animals the flow was predicted to be fully turbulent at 15 cm s^{-1} with a Reynolds number of 5600 ($Re = UR/\nu$, where U = free-stream velocity, R = hydraulic radius and ν = kinematic viscosity). In contrast, at 2 cm s^{-1} ($Re \sim 700$) the flow should to be close to laminar and at 5 cm s^{-1} ($Re \sim 1800$) transitional between the two ($600 < Re < 2400$) (Boudreau & Jørgensen 2001). Because mean flow speed varied slightly with *Austrovenus* density due to changes in bed roughness (see results) I refer to flow treatments as low (2 cm s^{-1}), medium (5 cm s^{-1}) and high (15 cm s^{-1}). Bed CR experiments were duplicated at 0, 100, 500 and 1000 ind. m^{-2} at each flow speed, but for the other density treatments only one set of measurements were obtained. The flow speed/density combinations were randomised during the six week study period (May/June 2009).

Prior to each experimental run, *Austrovenus* individuals were collected from Raglan Harbour (37º48'S 174º52'E), North Island, New Zealand, on a morning low tide and transferred to the laboratory within one hour. Individuals between 20 to 25 mm shell height were selected (a range that typifies mid to lower intertidal regions where *Austrovenus* densities are greatest; C. Pilditch unpublished data) and scraped clear of any epibiota (e.g. barnacles, anemones). Each flume was filled with wet, clean sand (median grain size diameter 500 µm) to a depth of 5 cm and the surface smoothed. *Austrovenus* were spread evenly around the flume with their posterior end pressed gently into the sediment to encourage burial. A piece of ‘bubble wrap’ cut to the annulus dimensions was placed on the sediment surface and filtered artificial saltwater was carefully pumped onto the sheet which floated off without disturbing the sediment. The final water depth in the flume was 20 cm. The animals were left in the flume overnight to bury, at a flow speed of 5 cm s^{-1} and gentle aeration was provided by air stones. The following morning the flume was carefully drained without disturbing the sediment surface, animals that had failed to bury (usually only two or three in the high density treatments) were removed and the flume refilled with fresh seawater in preparation for the clearance rate measurements (by which time the animals had been starved for 24 h). Throughout the experiments natural light cycles were supplemented during the day with low level fluorescent light, and mean water temperature (14. 8 ± 1.7 °C) and salinity (31) in the flumes were maintained at a range similar to that observed at the collection beach (T = 13.1 - 15.9 °C, S = 31.4 - 31.6).

2.2.4 Bed clearance rate measurements

Bed CRs were determined by measuring the decline in phytoplankton chlorophyll *a* (chl *a*) concentration at regular intervals in the flumes. Based on preliminary measurements I varied the duration and sampling frequency of each experiment with *Austrovenus* density. For the high density (≥ 500 ind. m^{-2}) treatments chl *a* samples were collected every 5 min for a total of 30 min; for the mid density treatment (247 ind. m^{-2}) every 10 min for 60 min and for the low density treatments (≤ 100 ind. m^{-2}) every 15 min for 90 min. The advantage of taking time series measurements, as opposed to start and end points only, was that any fluctuation in bed CR due to reduced phytoplankton concentrations would have been readily apparent. To accommodate the circatidal rhythm in *Austrovenus* (Beentjes & Williams 1986) the midpoint of each experimental run coincided with the expected high tide in Raglan Harbour.

The microalga *Nannochloropsis* sp (cell dia. = 2 – 4 µm; Reed Instant Algae®) was added to the flumes at an initial chl *a* concentration of 25 ± 3 µg L^{-1}. This concentration is somewhat higher than typically found in New Zealand estuaries (~ 2 - 8 µg L^{-1}) but during phytoplankton blooms such concentrations are not uncommon (Vant 1990, Vant & Safi 1996). The algae were allowed to mix for 5 min at a flow speed of 5 cm s^{-1} before setting the flow speed for the experimental run and collecting the first set of samples. Fifty mL water samples were taken from sampling ports in the flume wall located 1, 2.5, 5, 10 and 15 cm above the bed and prefiltered through a 40 µm mesh to remove faeces and pseudofaeces before measuring *in vivo* fluorescence on a Turner Designs® Model 10-AU Fluorometer. Samples collected from the 5 cm port were filtered through a Whatman GF/C filter, frozen and later analysed for chl *a* following the methods of Parsons et al. (1984). The resulting regression between extracted chl *a* concentration (µg L^{-1}) and *in vivo* fluorescence ($r^2 = 0.89$, n = 83) allowed me to express *in vivo* measurements at the other sampling heights in terms of chl *a* concentration. Saltwater was added to the flume after each set of samples to replace the water removed and the dilution accounted for in CR calculations. At the end of each run five clams were measured, dried at 60 ºC for 24 h, and then ashed at 550 ºC for 5 h to obtain an estimate of dry weight (g DW) and ash free dry weight (g AFDW).

Bed CR (L m^{-2} h^{-1}) were calculated from the decline in chl *a* concentration using the following equation:

$$\text{Bed CR} = \frac{B * V(\ln C_1 - \ln C_2)}{t * N}$$

where, B = treatment (i.e. bed) density (ind. m^{-2}) , V = volume of water in the flume (L), C_1 and C_2 are the chl *a* concentrations at the start and end of each time increment respectively, t is the time (h) between measurements, and N is the number of animals in the flume (Widdows & Navarro 2007). Bed CR were corrected for phytoplankton settling/entrainment into the bed using data from runs without animals. I did not detect any variation in chl *a* concentration with height above the bed so readings were depth-averaged to derive C_1 and C_2. Chl *a* concentrations did not decrease below 7 µg L^{-1} and because successive bed CR estimates within a run did not decline I averaged the six readings. Individual clearance rate (L h^{-1} ind^{-1}) was obtained by removing B from the above equation.

At the beginning, middle and end of each run I counted the number of animals feeding (i.e. valves open and siphons extended); this allowed me to calculate individual CR as a function of the number of animals feeding (CR_f) as well as the total number of animals in the flume (i.e. feeding and non-feeding individuals; CR_b).

2.2.5 Near-bed hydrodynamics

I used a Sontek micro-Acoustic Doppler Velocimeter (ADV) to quantify the effects of bivalve feeding currents, bed density and flow speed on benthic boundary layer dynamics. Logistical constraints prevented me from making CR and hydrodynamic measurements concurrently; however the same experimental procedures were followed for both sets of measurements. The number of bed density treatments was reduced slightly for the hydrodynamic measurements (0, 29, 100, 500 and 1000 ind. m^{-2}) and replicated once at each flow treatment (low, medium and high). In an attempt to quantify the effects of feeding currents on near-bed hydrodynamics I made use of the bivalves' natural circatidal rhythm (Beentjes & Williams 1986). Measurements were made first at the time of low tide on the home beach when most animals in the flume were inactive and again at high tide in the presence of algae when the majority of animals were feeding. Hereafter, 'low tide' and 'high tide' data refer to measurements taken at the time of low or high tide on the home beach. The number of animals open with their siphons extended was counted three times during the hydrodynamic measurements to confirm that the numbers feeding were comparable with the numbers recorded during the clearance rate experiments.

A downward looking ADV was mounted mid-channel through the base of the flume on a vertical racking system. Previously, the spatial dimensions of the sampling volume had been carefully mapped to allow accurate positioning near the bed (e.g. Finelli et al. 1999). A velocity profile was recorded (sampling for 20 s at 25 Hz at nine elevations from 0.7 to 5 cm above the bed) and turbulence measurements (sampling at 25 Hz for 163 s) were made at 0.7 cm above the bed which was within the log layer (as determined by the velocity profiles), at the low, medium and high flow speeds. Turbulence measurements were used to calculate bed shear stress using the turbulent kinetic energy (TKE) method as described in

Kim et al. (2000) and Pope et al. (2006). TKE is the product of the absolute intensity of velocity fluctuations from the mean velocity

$$\mathrm{TKE} = \frac{1}{2}\rho\left(\overline{u'^2} + \overline{v'^2} + \overline{w'^2}\right)$$

where ρ is the density of the fluid, u′ is the fluctuating part of the flow in the stream-wise direction, (and v and w denote the cross channel and vertical components of the flow, respectively). The ratio of TKE to bed shear stress (τ_0) is constant

$$\tau_0 = C_1\mathrm{TKE}$$

where $C_1 = 0.19$ (Pope et al. 2006).

2.2.6 Statistical analysis

The number of *Austrovenus* feeding, and bed and individual clearance rates were compared among flow speed treatments using analysis of covariance (ANCOVA), with density as a covariate. Homogeneity of the regression slopes was tested by fitting a model that related the response variable to flow speed, density and the interaction between flow speed and density. If the interaction was not significant I proceeded with the ANCOVA. The assumptions of homogeneity of variances and normality were tested with Levene’s and Kolmogorov-Smironov tests. Where the assumptions were violated variables were $\log_{10}$ transformed. Tukey post-hoc tests were performed for significant ANCOVA results on adjusted means of flow speed. All statistical analyses were conducted using Statistica (Version 8).

2.3 Results

2.3.1 Number of animals feeding

Typically, the number of *Austrovenus* feeding varied little (by 0 to 20 %) during the course of each experimental run so the mean of the three counts (beginning, middle and end) was used to calculate the number feeding per m^2. Estimates of the number of animals feeding made during the hydrodynamic measurements and clearance rate measurements were comparable during high tide at the home beach and so the data sets were combined for analysis. A positive linear relationship between density and number feeding was observed from low to medium bed densities (29 to 500 ind. m^{-2}), but from medium to high bed densities (500 to 1000 ind. m^{-2}) the number feeding remained approximately constant (Figure 2.1A). At bed densities > 500 ind. m^{-2} a greater proportion (50 to 90 %) of animals were feeding at the high flow speed than at the low and medium flow speeds (30 to 60 %). A test for homogeneity of slopes on $\log_{10}$ transformed data revealed no significant interaction ($p > 0.05$; Figure 2.1B). ANCOVA results indicated that there was a significant effect of density and flow speed ($p < 0.001$) on number of animals feeding (Table 2.1). Tukey post-hoc tests revealed that there was no significant difference between the low and medium flow speeds ($p = 0.953$), but that number feeding was significantly greater at the high flow speed than at the low ($p < 0.01$) and medium flow speeds ($p < 0.01$). Adjusted means were 132, 138 and 186 ind. m^{-2} for the low, medium and high flow speed, respectively. During the hydrodynamic measurements the number of animals feeding at low tide was < 10 % of those feeding at high tide allowing me to potentially separate out the effects of bivalve induced changes to the bed morphology and their feeding currents on near-bed hydrodynamics.

Table 2.1: Analysis of covariance (ANCOVA) results testing the effects of flow speed on response variables, with *Austrovenus* density or $\log_{10}$ density as a covariate

Response variable	Source	df	MS	F	*p*	Tukey test†
Log$_{10}$ number feeding	Log$_{10}$ density	1	4.63	515	**<0.001**	
	Flow speed	2	0.063	7.05	**0.001**	L = M < H
	Error	23	0.009			
Log$_{10}$ bed clearance rate	Log$_{10}$ density	1	1.68	31.0	**<0.001**	
	Flow speed	2	1.00	18.5	**<0.001**	L = M < H
	Error	23	0.054			
Individual clearance rate (CR$_f$)	Density	1	0.777	24.1	**<0.001**	
	Flow speed	2	0.681	21.1	**<0.001**	L = M < H
	Error	23	0.032			

†Tukey post-hoc test results for significant differences between flow speeds (L = low, M = medium and H = high) are shown at $p < 0.05$.

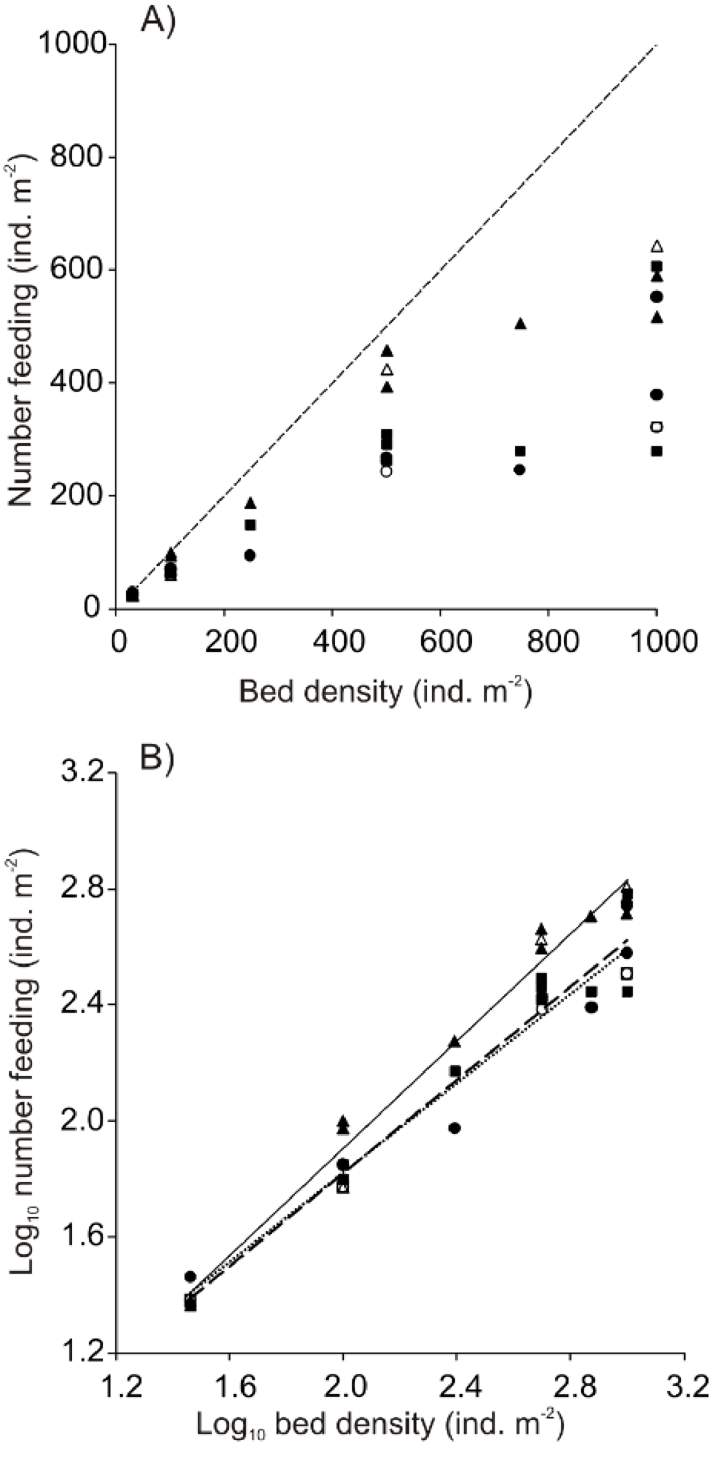

Figure 2.1: Number of *Austrovenus* feeding as a function of bed density and flow speed (circles = low, squares = medium, and triangles = high; closed symbols = data from clearance rate measurements and open symbols = data from high tide hydrodynamic measurements). In (A) the one to one relationship is indicated by the dotted line. The fitted lines in the log transformed data (B) are; low flow speed (dotted line) $y = 0.77x + 0.28$ ($r^2 = 0.97$, $p < 0.001$), medium flow speed (dashed line) $y = 0.80x + 0.21$ ($r^2 = 0.96$, $p < 0.001$), and for high flow speed (solid line) $y= 0.92x + 0.05$ ($r^2 = 0.98$, $p < 0.001$).

2.3.2 Near-bed hydrodynamics

Visual observations indicated that the scale of bed roughness (c. 1 cm) did not appear to alter with *Austrovenus* density, although the form of the roughness elements did. At low densities the clams created tracks in the sediment up to 20 cm long and 1 cm deep before burying. At high densities, although tracks were short or nonexistent (because the animals typically buried where they had been placed) c. 20 % of the animals were partially exposed.

Comparison of velocity profiles revealed that with increasing density there was a reduction in both near-bed and free-stream velocity at the low, medium and high flow speeds, regardless of whether or not *Austrovenus* were feeding (Figure 2.2). The height of the benthic boundary layer (BBL), as evidenced by a logarithmic velocity profile, decreased with increasing flow speed (low = 1.5 cm, medium = 1.25 cm, high = 1 cm) when measured over a smooth bed. There was little effect of *Austrovenus* density on BBL height at the low flow speed, but BBL height increased to 2 cm at the medium and high flow speeds at high *Austrovenus* densities. The effect of feeding on near-bed and free-stream velocity was minimal and inconsistent, except at the medium bed density (500 ind. m^{-2}) when velocities were slightly reduced over feeding animals at low, medium and high flow speeds (Figure 2.2).

Over smooth sediment (i.e. without clams) bed shear stress increased with flow speed (low = 0.0007, medium = 0.0038, high = 0.0314 N m^{-2}; Figure 2.3). Bed shear stresses also increased with *Austrovenus* density at low (regression $r^2 = 0.91$, $p < 0.05$), medium ($r^2 = 0.91$, $p < 0.05$), and high ($r^2 = 0.69$, $p = 0.08$) flow speeds (regressions used the average of the low and high tide shear stress estimates, n= 5). At low densities there was no clear effect of feeding activity on bed shear stress but at the highest density (1000 ind. m^{-2}), and at all flow speeds, bed shear stresses were higher in feeding compared to non-feeding *Austrovenus* beds. The relative magnitude of the increase in bed shear stress decreased with increasing flow speed. At the low flow speed bed shear stress increased by 78 % (from 0.00090 to 0.0016 N m^{-2}) when *Austrovenus* were feeding, but only by 40 % (from 0.0052 to 0.0073 N m^{-2}) and 29 % (from 0.072 to 0.093 N m^{-2}) at the medium and high flow speeds, respectively (Figure 2.3).

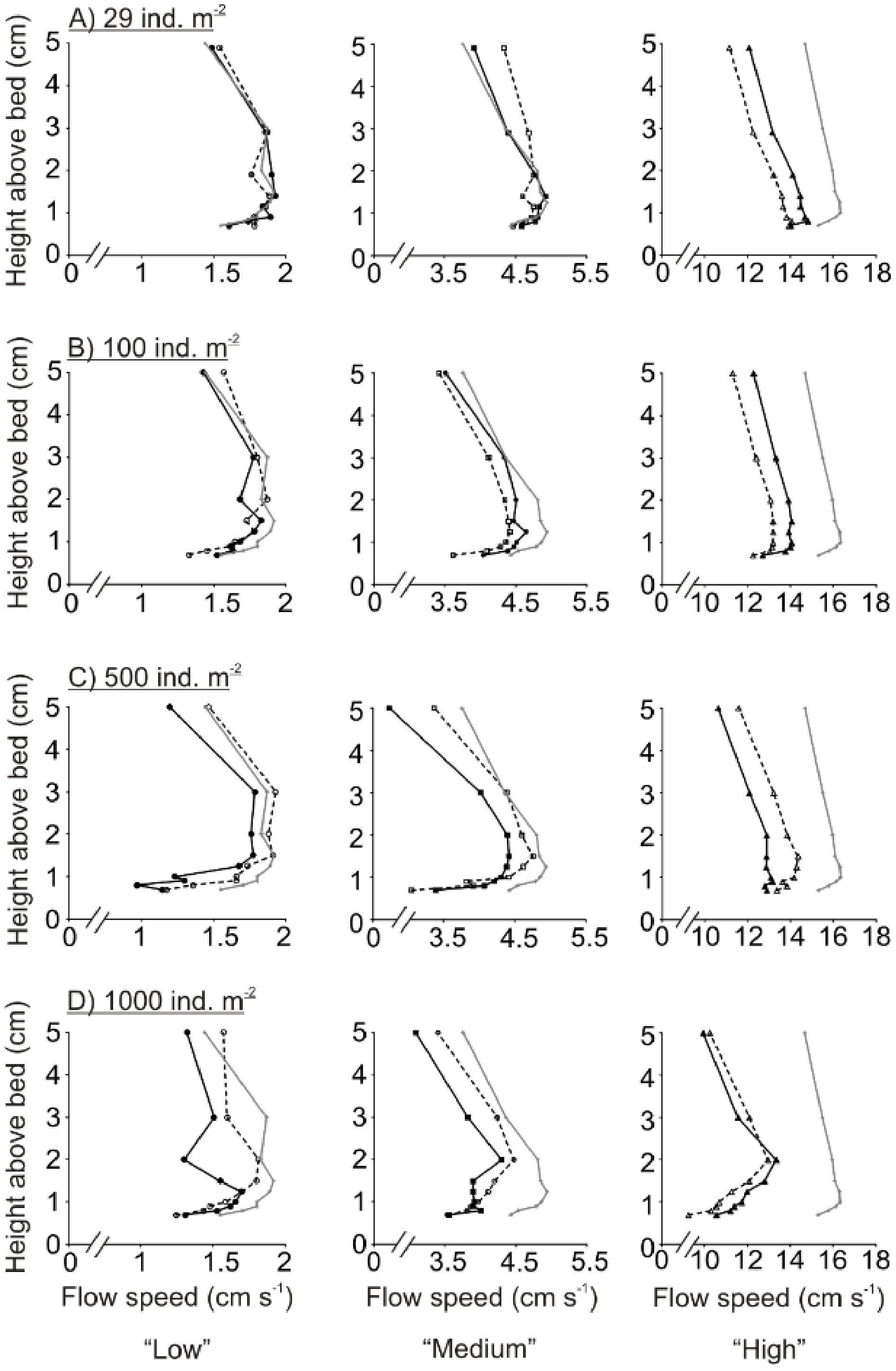

Figure 2.2: Flow speed as a function of height above the bed, for each treatment flow speed (left panel = low, middle panel = medium and right panel = high), and *Austrovenus* density (A - D). Measurements made when animals were feeding are represented by closed symbols and a solid black line and when not feeding by open symbols and a dashed line. Profiles recorded over a smooth bed (0 ind. m^{-2}) are included for comparison as a grey line.

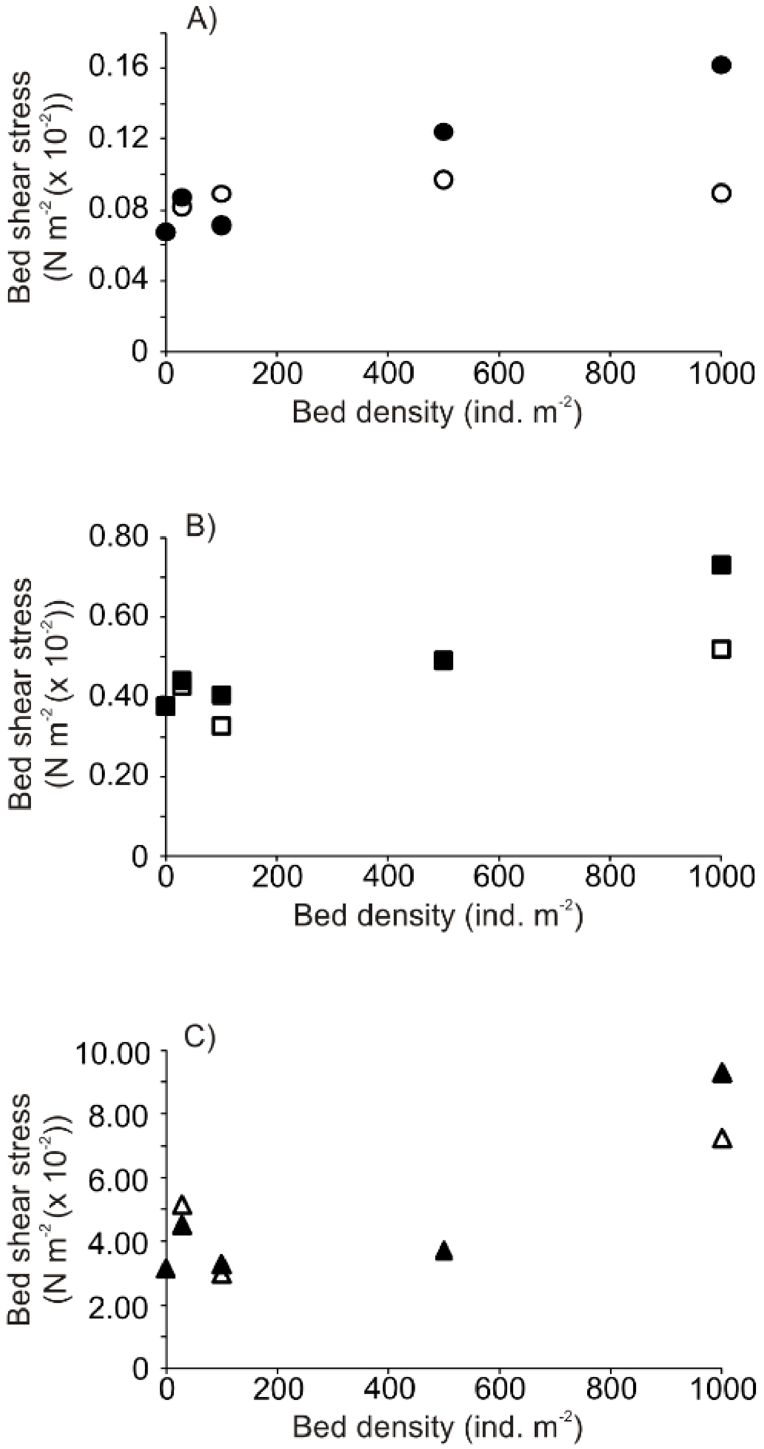

Figure 2.3: Bed shear stress as a function of *Austrovenus* density at low (A), medium (B) and high (C) flow speeds. Measurements made when animals were feeding are represented by closed symbols and when not feeding by open symbols. Note y axis scale varies amongst plots.

2.3.3 Clearance rates

Bed CR ranged from 20 to 420 L hr^{-1} m^{-2} across the flow speed and density treatments (Figure 2.4A). Bed CR increased with bed density from 29 to 500 ind. m^{-2}, but remained relatively constant from 500 to 1000 ind. m^{-2} (i.e. a similar trend to that seen in the number of animals feeding). A test for homogeneity of slopes on $\log_{10}$ transformed data revealed no significant interaction effect ($p = 0.10$; Figure 2.4B). ANCOVA results indicated that there was a significant effect of density and flow speed ($p < 0.001$) on bed CR (Table 2.1). Tukey post-hoc tests revealed a marginally significant difference between the low and medium flow speeds ($p = 0.071$), but bed CR was significantly greater at the high flow speed than at the low ($p < 0.01$) and medium flow speeds ($p < 0.001$). Adjusted means were 73.5, 40.8 and 187.0 L hr^{-1} m^{-2} for the low, medium and high flow speed, respectively.

Individual clearance rate based on the number of animals in the bed (CR_b) ranged from 0.03 to 1.3 L hr^{-1} ind.$^{-1}$. As with number feeding and bed CR, CR_b decreased rapidly with increasing bed density up to 500 ind. m^{-2} but remained relatively constant from 500 to 1000 ind. m^{-2} (Figure 2.5A). Individual clearance rate based on only the animals in the flume that were observed to be feeding (CR_f) ranged from 0.07 to 1.4 L hr^{-1} ind.$^{-1}$ and there was a linear relationship between CR_f and density (Figure 2.5B). A test for homogeneity of slopes revealed that there was no significant density x flow speed interaction ($p = 0.90$). ANCOVA results indicated that there was a significant effect of density and flow speed ($p < 0.001$) on CR_f (Table 2.1). Tukey post-hoc tests revealed that there was a marginally significant difference between the low and medium flow speeds ($p = 0.062$), and that CR_f was significantly greater at the high flow speed than at the low ($p < 0.01$) and medium flow speeds ($p < 0.001$). Adjusted means were 0.54, 0.34 and 0.88 L hr^{-1} ind.$^{-1}$ for the low, medium and high flow speed, respectively.

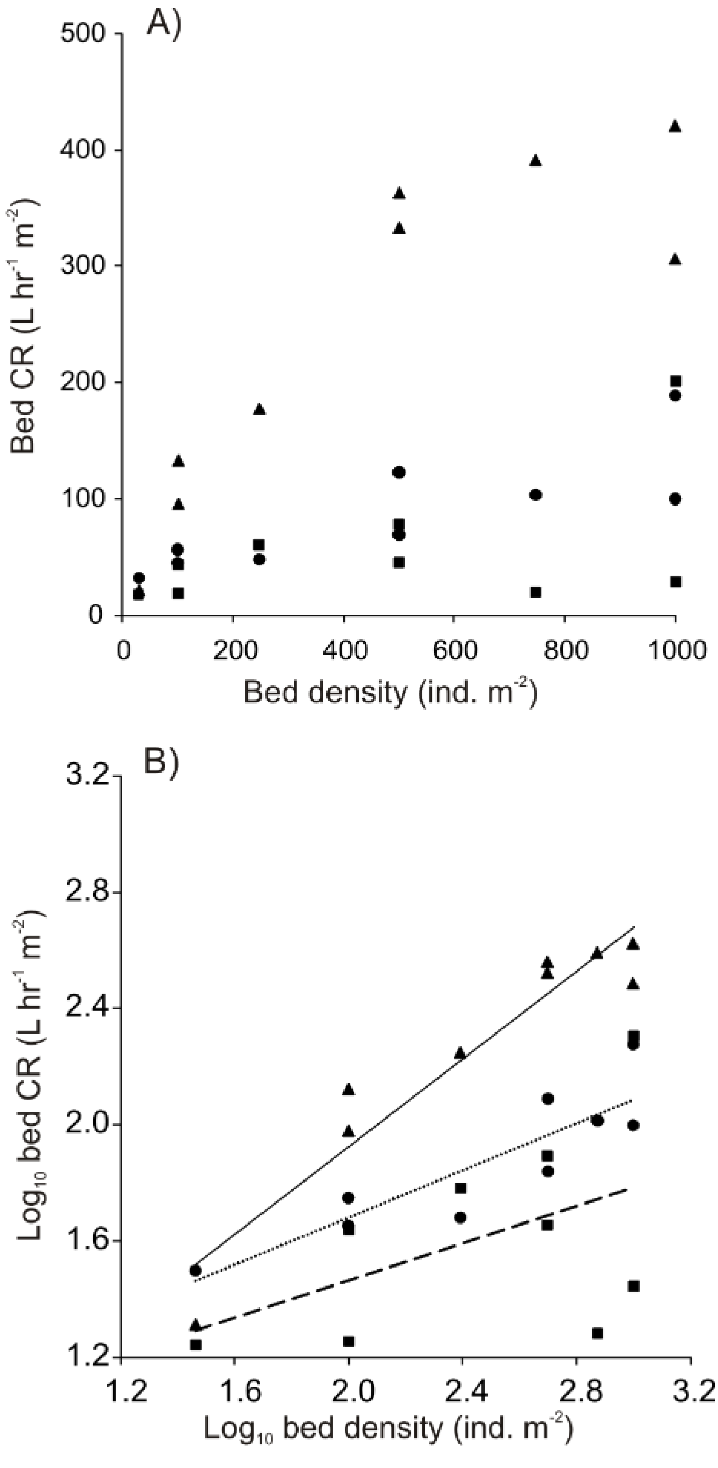

Figure 2.4: A) *Austrovenus* bed CR as a function of density and flow speed (circles = low, squares = medium and triangles = high). The fitted lines in the log transformed data (B) are; low flow speed (dotted line) y = 0.41x + 0.87 ($r^2 = 0.78$, $p < 0.01$), medium flow speed (dashed line) y = 0.32x + 0.82 ($r^2 = 0.24$, $p = 0.183$), and for high flow speed (solid line) y= 0.75x + 0.42 ($r^2 = 0.90$, $p < 0.001$).

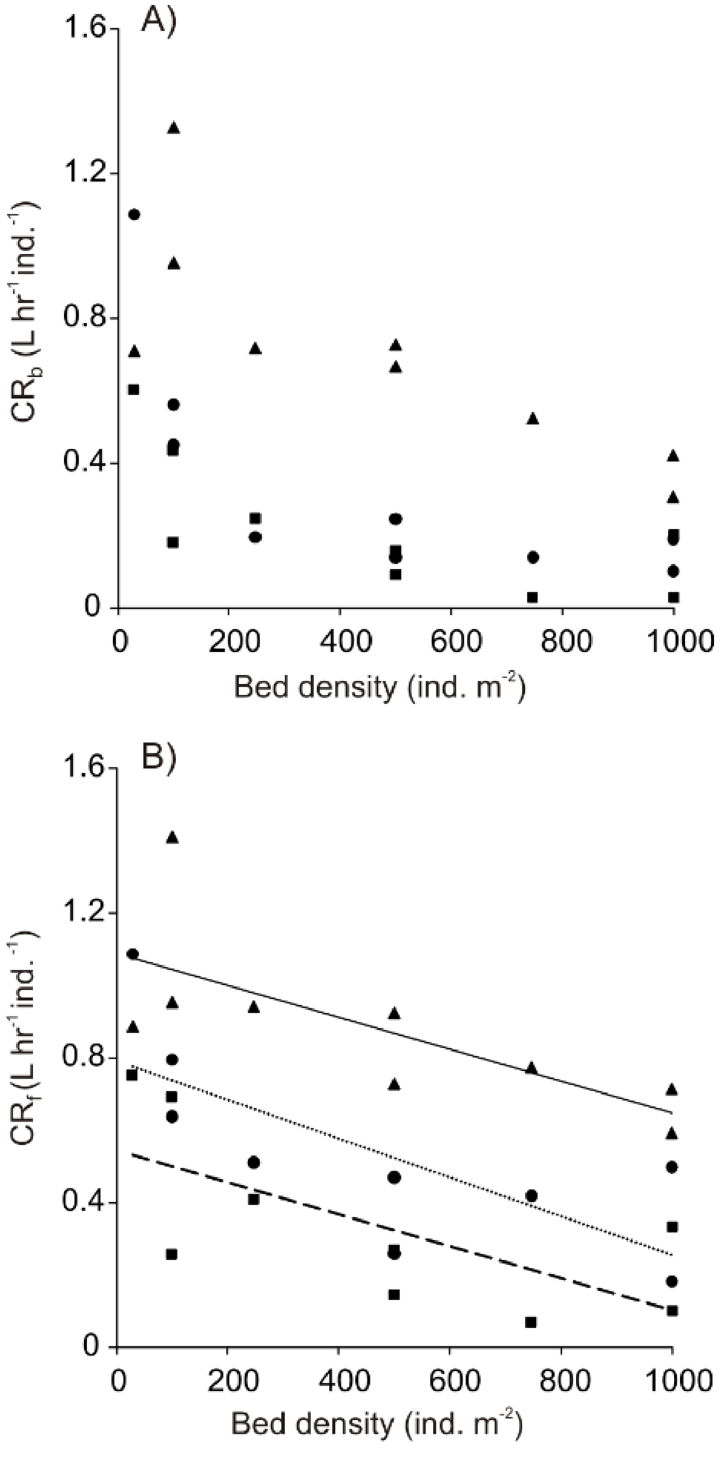

Figure 2.5: *Austrovenus* individual CR estimated by dividing the bed CR by (A) the total number of animals in the flume (CR_b) and (B) only the animals feeding (CR_f), as a function of bed density and flow speed (circles = low, squares = medium and triangles = high). The fitted lines in (B) are for; low flow speed (dotted lines) $y = 0.79 – 0.0005x$ ($r^2 = 0.55$, $p < 0.05$), medium flow speed (dashed line) $y = 0.54 – 0.0004x$ ($r^2 = 0.47$, $p < 0.05$), and for the high flow speed (solid line) $y = 1.08 – 0.0004x$ ($r^2 = 0.52$, $p < 0.05$).

2.4 Discussion

As I hypothesised, the bed roughness generated by this infaunal species (c. 1 cm) was less than that of an epifaunal species such as *Mytilus edulis* (c. 2.5 to 3 cm; van Duren et al. 2006) and *Atrina zelandica* (c. 15 to 20 cm; Green et al. 1998). However, it was still capable of reducing flow speeds, increasing the height of the benthic boundary layer, and increasing bed shear stress. My hydrodynamic measurements also suggest that siphonal currents may be able to influence vertical mixing and food supply to the bed under certain conditions, i.e. high bivalve density and low flow speed. I showed that bed clearance rates (CR) were significantly greater at the high flow speed compared to lower current velocities, and that individual CR decreases with increasing bed density. The latter result suggests that bed filtration rates may be overestimated if scaled up from individual CR obtained using animals at low densities. Using the data from this study, bed CR at 1000 ind. m^{-2} estimated by scaling up individual CR obtained at low densities would be 700 to 1300 L hr^{-1} m^{-2}, but I estimated bed CR to be two to three times less than that (i.e. 300 to 400 L hr^{-1} m^{-2}) in my 1000 ind. m^{-2} treatment. Furthermore, I found that both density and flow speed affected the proportion of animals in the bed that were actively feeding. This appears to be the first time that a feeding parameter has been measured and incorporated into a CR study despite acknowledgement in previous research that not all individuals in a bed may be feeding at the same time (Dolmer 2000b, Strohmeier et al. 2009, Troost et al. 2009b).

The proportion of animals that were actively feeding decreased as bed density increased, so that only 28 to 61 % of individuals (dependent on flow speed) were feeding at high densities. *In situ*, *Austrovenus* bed densities commonly exceed my highest density treatment (1000 ind. m^{-2}) (Hewitt et al. 1996) and bed density at the collection beach was c. 1500 ind. m^{-2} (author's unpublished data) so my density treatments are not unrealistic. If in high density beds *Austrovenus* cannot all feed at once, and because the animals only feed for c. 4 hours per high tide, then the reduction in feeding time or missed feeding opportunity for an entire high tide is likely to have important implications for energy acquisition.

Consistent with my expectations I observed increased roughness and bed shear stress with increasing bivalve density, especially at high densities and when

Austrovenus were feeding. This will increase vertical mixing, thus enhancing food supply to the bed and perhaps compensate for the reduced feeding opportunity. However, my individual CR estimates suggest that *Austrovenus* does not derive any benefit in high density beds. I found that individual CR deceased with increasing density (at low densities individual CR was up to 3 times greater than at high densities), most likely due to high re-filtration rates at high densities (O'Riordan et al. 1995, Prins et al. 1998, Yu & Culver 1999, Zhou et al. 2006). Therefore, it is likely that other advantages are afforded to *Austrovenus* that exist in high density beds, compensating for the reduction in CR. Recent research has described the importance of mussel bed structure to food supply by increasing resuspension of microphytobenthos (Widdows et al. 2009), and for providing protection from predation and resistance to wave disturbance (Widdows et al. 2002, van de Koppel et al. 2005). Microphytobenthos (MPB) are important primary producers in New Zealand's shallow estuaries, and high densities of *Austrovenus* have been shown to increase MPB production (Sandwell et al. 2009). Bioturbation activity by the clams will resuspend MPB, potentially providing the bivalve bed with a substantial food source.

In addition I found that the number of *Austrovenus* feeding, and individual and bed CRs, were significantly greater at the high flow speed than at the low or medium flow speed. An increase in flow speed increases vertical mixing and seston supply to the bed (O'Riordan et al. 1993, Wildish & Kristmanson 1997, Newell et al. 2001), thereby allowing more animals to feed and CRs to increase. A similar effect was measured *in situ* for mussel (*Mytilus edulis*) beds – 39 to 66 % of mussels were filtering at flow speeds of 1.2 to 2.1 cm s^{-1}, but at 3.9 to 6.5 cm s^{-1} this increased to 75 to 83 % – attributed to an increase in food supply at the higher flow speeds (Dolmer 2000b). Although other studies have demonstrated a decline in bivalve CR at high flow speeds (e.g. Sobral & Widdows 2000, Fernandes et al. 2007), it has typically been observed at speeds much greater (up to 45 cm s^{-1}) than my "high" flow speed (i.e. 15 cm s^{-1}). It is possible that *Austrovenus* CR may decline at flow speeds > 15 cm s^{-1} but my intention was to measure the individual and population response in CR to flow speeds commonly experienced by these bivalves *in situ.*

In this study, individual CRs were marginally (p = 0.06) greater at the low flow speed compared with the medium flow speed, but the number of animals feeding did not vary between the low and medium flow speeds. In a previous study with *Austrovenus* an increase in flow from 1.1 to 6.3 cm s^{-1} (i.e. similar to my low and medium flow speeds) also depressed CRs from c. 1.8 to 1.4 L hr^{-1} $ind.^{-1}$ (Heggie 2008). There is a complex relationship between bivalve siphonal currents and boundary layer flow. Previous research suggests that the relationship between the degree of re-filtration and flow speed may not be linear, but is related to the ratio between siphonal jet velocity and current velocity (Monismith et al. 1990, O'Riordan et al. 1995, Jonsson et al. 2005). To confound the issue, roughness elements may increase turbulent mixing and shear stress (O'Riordan et al. 1993, van Duren et al. 2006), or may cause skimming flow, which reduces turbulent mixing in the boundary layer (e.g. Eckman 1983, Green et al. 1998, Friedrichs et al. 2000, Coco et al. 2006). Based on the rather limited number of hydrodynamic measurements made during this study I might speculate that siphonal jets can affect vertical mixing at the low flow speed, but not at the medium flow speed. As *Austrovenus* experience low flow speeds whilst feeding around slack water at high tide, enhanced vertical mixing rates caused by feeding activity during this period would be advantageous, especially as this species has a limited feeding opportunity. However, further measurements are needed to elucidate this, in particular measurements of the boundary layer dynamics over *Austrovenus* beds *in situ*.

My weight standardised CRs of 0.5 – 7 L hr^{-1} g DW^{-1} are very similar to those obtained for another infaunal bivalve species (*Cerastoderma edule;* 0 – 7 L hr^{-1} g DW^{-1}) in a flume study (Fernandes et al. 2007). Previous CR studies have often incorporated flow but CR estimates obtained from laboratory experiments (which often use high food concentrations), are likely to be greater than *in situ* rates because seston quantity and quality can be significant factors affecting CR (e.g. Hawkins et al. 1999, Cranford 2001, Hawkins et al. 2001). For example, CRs based on laboratory experiments with algal cell diets were 320 to 1365 % higher than *in situ* rates (Cranford & Hill 1999). In my study the animals were starved for 24 hours prior to running the experiments and were fed a relatively high concentration of pure phytoplankton, not the mix of inorganic and organic particles found in estuarine seston, so I accept that the CRs calculated in my study are also likely to be overestimates. In addition, other environmental variables such as salinity, temperature, and pollution can affect bivalve CR (e.g. Bayne 1998, Widdows 2001), but the effect of these on *Austrovenus* CR were beyond the scope of my study.

The formation of a concentration boundary layer (i.e. a phytoplankton depleted region) over bivalve beds has been well documented *in situ* (Fréchette et al. 1989, Dolmer 2000a, Jonsson et al. 2005, Jones et al. 2009), and in laboratory studies (O'Riordan et al. 1993, Butman et al. 1994, O'Riordan et al. 1995) for both epifaunal and infaunal species. However, in this study vertical profiles of chl *a* concentration always showed the water column to be well mixed. Even at the low flow speed I did not observe a chlorophyll depleted layer over the bivalves, a feature described in some clearance rate studies using annular flumes (Sobral & Widdows 2000, Widdows & Navarro 2007), but not in others (Fernandes et al. 2007). The reason why I did not detect such a layer is unclear. Current velocities < 2 cm s^{-1} (i.e. lower than my “low” flow speed) may have been required to produce a concentration boundary layer (in previous studies in which it was detected flow speeds were typically ≤ 2 cm s^{-1}). Alternatively, my ability to detect that feature may have been limited because the bed roughness generated by my study species (1 cm) was similar to the height of the benthic boundary layer (1 to 2 cm) and the height of my lowest sampling port (1 cm). It is also possible that the siphonal jets created enough vertical mixing to prevent the formation of a layer of chlorophyll depleted water, suggested by the increase in bed shear stress over feeding *Austrovenus* at high densities.

I recognise that annular flumes generate a benthic boundary layer that is vertically compressed compared with other types of flume (e.g. straight or racetrack; Jonsson et al. 2006, Fernandes et al. 2007). However, larger flumes are subject to measurement error due to the small test section area relative to total water volume, and so are less appropriate for feeding experiments. Also, as hydrodynamic conditions change constantly on intertidal flats due to tidal forces and wind driven currents, and as water depths are shallow (between 0 and 2 m) over *Austrovenus* beds *in situ*, flumes that produce a larger logarithmic boundary layer are not necessarily representative of field conditions. It is thought that field conditions are properly represented in laboratory studies when bed shear stress, mean flows and bottom roughness values are matched to field values (Monismith et al. 1990, Jonsson et al. 2006). A recent study has demonstrated that for a range of naturally occurring flow speeds the Plymouth annular flumes generate a similar level of bed shear stress to that observed *in situ* on intertidal flats (Pope et al. 2006).

Bed clearance rates at average *Austrovenus* bed densities, c.700 ind. m^{-2} (Hewitt et al. 1996), were between c. 300 and 400 L m^{-2} h^{-1} at my high flow speed, and between c. 20 and 200 L m^{-2} h^{-1} at my low and medium flow speeds. Though I accept that my results are likely to overestimate actual CRs, these rates are of a similar magnitude to the population filtration rates calculated for a mussel (*Mytilus edulis*) bed *in situ*, i.e. 280 - 950 L m^{-2} h^{-1}, at bed density of c. 470 ind. m^{-2} and velocities similar to my low and medium flow speeds (Dolmer 2000b). My results show that bed CR did not scale proportionally with density (i.e. bed CR at 1000 ind. m^{-2} were only 2 to 3 times those at 100 ind. m^{-2}). Dolmer (2000b) also found that actual population filtration rates were a fraction (27 to 98 %) of population filtration capacity because not all mussels in the bed were feeding at the same time. However, I have provided evidence that it is the negative effect of density on individual CR, as well as on the percentage of animals feeding that is responsible for the disproportionate effect of density on bed CR.

The capacity of bivalve populations to control phytoplankton biomass in coastal ecosystems has often been estimated based on the assumption the bivalves filter continuously at a maximum rate (e.g. Officer et al. 1982, Hily 1991, Dame 1993, Dame & Prins 1998). The problem with this approach is that there is a growing body of evidence to show that CRs are regulated in response to environmental variables such as changes in flow speed (e.g. Dolmer 2000b, Sobral & Widdows 2000, Fernandes et al. 2007), and seston quantity and quality (e.g. Navarro & Widdows 1997, Dolmer 2000a, Hawkins et al. 2001). Although most of these studies have been conducted in the laboratory, *in situ* studies have also shown that population filtration rates are often much less than population filtration capacity (Cranford & Hill 1999, Dolmer 2000b). My results support those studies by showing that bed density and flow speed can significantly affect CR and the proportion of bivalves in a bed that are actively feeding. Both variables need to be considered when estimating the impact of *Austrovenus* populations on estuarine ecosystems.

CHAPTER 3

Sedimentary environment influences the effect of *Austrovenus stutchburyi* on estuarine ecosystem function

3.1 Introduction

Estuaries are highly productive ecosystems that play a major role in biogeochemical cycles, but are subject to multiple stressors that will likely be exacerbated by climate change and expanding human habitation of coastal areas (Gray 1997, Levin et al. 2001, Kennish 2002). Although the effects of contaminants, invasive species, coastal alteration and development might be restricted to estuaries near large population centres, enhanced sedimentation rates threaten many estuaries, even when there have been only moderate levels of catchment development (Kennish 2002). Deposition of large amounts of terrestrial sediments during storm events smother benthic communities, and elevated levels of suspended sediments reduce primary productivity and detrimentally affect suspension feeders (e.g. Ellis et al. 2002, Norkko et al. 2002, Norkko et al. 2006). More pervasive and perhaps less obvious is the long term degradative change in the form of increasing muddiness that alters estuarine habitats and communities (Thrush et al. 2003b, Thrush et al. 2004).

If habitat change does lead to decreasing biodiversity, then that alone may cause shifts in ecosystem structure and function (Loreau et al. 2001, Naeem 2002, Hooper et al. 2005). However, in many cases it has been shown in estuarine systems that certain key species, rather than biodiversity *per se*, can have a disproportionate effect on indicators of ecosystem functioning such as nutrient cycling and productivity (e.g. Widdicombe & Austen 1998, Lohrer et al. 2004, Thrush et al. 2006). Although the loss of key species likely has important implications, many estuarine species exist across a range of sediment types (Thrush et al. 2003b). Habitat change may not necessarily then cause species loss but might more subtly affect ecosystem function by alteration of a species' functional role. For example an estuarine bioturbating crab (*Austrohelice crassa*) displays functional plasticity, acting as a bioturbator in sandy sediments and as a bioirrigator in muddy cohesive sediments (Needham et al. 2010). Thus, the influence of this species on biogeochemical exchange and microbial communities is likely to differ between habitat types (Needham et al. 2011). However, most studies to date are restricted temporally and spatially making it difficult to understand the effects of habitat change on a key species' influence on ecosystem function. In this study I examined the effect of a suspension feeding bivalve on ecosystem function at two sites with contrasting sediment properties, in winter and in summer. As sedimentation alters estuarine habitats by increasing sediment mud content I used a site with muddy-sand sediments as a proxy for habitat change, to compare with a site comprising only sandy sediment.

Suspension feeding bivalves can act as key species in estuarine ecosystems by exerting top-down control on phytoplankton populations, affecting rates of nutrient regeneration, contributing to benthic-pelagic coupling, and providing an important food source for higher trophic levels (reviewed by Newell 2004). Furthermore, accumulation of biodeposits and altered redox environments in sediments underlying bivalve beds may enhance sediment denitrification rates, the microbial reduction of NO_3^- to N_2 gas, which permanently removes fixed nitrogen from an ecosystem; thus, suspension feeding bivalves can also exert a bottom-up control on phytoplankton populations (e.g. Newell et al. 2002). Loss of suspension feeding bivalve populations has resulted in large shifts in ecosystem structure and function. For example, in Chesapeake Bay, USA, loss of eastern oyster (*Crassostrea virginica*) beds has substantially increased the incidence of phytoplankton blooms, sometimes resulting in the occurrence of deep-water hypoxia (e.g. Jackson et al. 2001, Kemp et al. 2005). Conversely, invasion of aquatic systems by non-native suspension feeding bivalves, such as by the Asian clam (*Potamocorbula amurensis*) in San Francisco Bay and the zebra mussel (*Dreissena polymorpha*) in many freshwater systems in the USA, has resulted in reduced phytoplankton biomass (e.g. Alpine & Cloern 1992, Barbiero et al. 2006).

In New Zealand estuaries the dominant suspension feeding bivalve is the native clam *Austrovenus stutchburyi* (hereafter *Austrovenus*), which commonly exists in high-density beds covering large areas of intertidal flats; typical bed densities average c. 1000 ind. m^{-2}, although peak densities may be 2000 - 3000 ind. m^{-2} in some areas (Hewitt et al. 1996, Whitlatch et al. 1997). *Austrovenus* is an infaunal species that bioturbates surficial sediments through vertical and horizontal movement, but has very short siphons and so lives close to the sediment surface (< 5 cm). *Austrovenus* beds are found across a range of sediment types, although very high levels of sedimentation adversely affect abundance (Thrush et al. 2003b). *Austrovenus* has been shown to be a key species influencing sediment stability, solute fluxes and macrofauna community structure as well as enhancing microphytobenthos productivity (Thrush et al. 2006, Sandwell et al. 2009). However, populations are declining in some areas likely due to chronic sedimentation, pollution and over-harvesting (De Luca-Abbott 2001, Norkko et al. 2006, Cummings et al. 2007).

In this study I manipulated the presence or absence of *Austrovenus in situ* at two estuarine sites, both with nearby high-density *Austrovenus* beds, but with contrasting sediment properties. My aim was to see if the role of this key species in ecosystem functioning was the same at a sandy site (a proxy for a habitat unimpacted by sedimentation) and at a muddy-sand site (a proxy for a habitat affected by a moderate level of sedimentation). In winter and summer, light and dark benthic chambers were used to quantify the effect of *Austrovenus* on O_2 and nutrient (NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}) fluxes, and to estimate gross primary production and nutrient uptake rates. Additionally, denitrification enzyme activity (DEA) assays were used to quantify the effect of *Austrovenus* on maximum sediment denitrification potential. Previously, high *Austrovenus* densities have been shown to enhance ammonium efflux which supported higher rates of microphytobenthos (MPB) production (Sandwell et al. 2009). Additionally, I expected increased rates of primary production and nutrient cycling in summer compared to winter due to increases in macrofaunal, microbial and photosynthetic activity (Thrush et al. 2003b). Greater retention of bivalve biodeposits was predicted for the more sheltered muddy-sand site. Microbial decomposition of biodeposits may result in enhanced nutrient regeneration and a stimulation of primary production (Giles & Pilditch 2006). Alternatively, biodeposit decomposition can elevate denitrification rates through coupled nitrification-denitrification, thus reducing primary production (Newell et al. 2002). The use of large experimental plots (16 m^2) to reduce confounding edge effects (e.g. Thrush et al. 2006, Sandwell et al. 2009) will enhance our understanding of the relative importance of the dynamics of these different habitat types.

3.2 Methods

3.2.1 Study site and experimental set up

Tauranga Harbour is a large (200 km^2) barrier-enclosed estuary on the north-eastern coast of New Zealand. I manipulated the presence or absence of *Austrovenus* at two sites with differing sedimentary characteristics on lower-mid intertidal flats in the harbour (Figure 3.1). The sandy site (37°27.77’S 175°57.90’E) was located near the northern harbour entrance and was composed of medium sands with no mud content (defined as the silt/clay fraction < 63 µm grain size). The muddy-sand site (37°29.20’S 175°56.73’E) was located 3 km up the estuary in the entrance of a small inlet and was composed of fine sands with c. 13 % mud content. Mean tidal currents at the sandy site were 13.2 cm s^{-1} (peak flow was 35 cm s^{-1}), and at the muddy-sand site were 7.2 cm s^{-1} (peak flow was 18 cm s^{-1}), as determined by deployment of a FSI current meter that included a spring and a neap tidal phase. Tides in the harbour are semi-diurnal and the mean immersion period at each site is 8 h. Water temperature in Tauranga Harbour typically fluctuates between 13 °C in mid-winter (July/August) and 22 °C in mid-summer (January/February) (Greig et al. 1988).

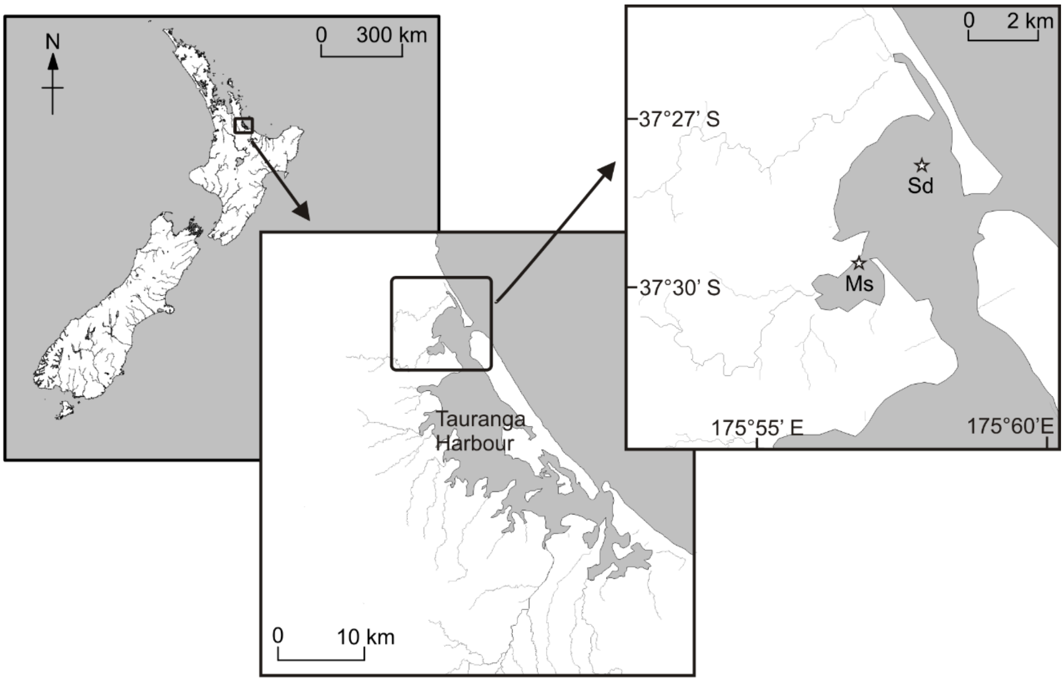

Figure 3.1: Location of sites (indicated by a star) in Tauranga Harbour, New Zealand. Sd = Sandy site, Ms = Muddy-sand site.

In June 2009, at both sites, six 4 m × 4 m plots separated by 1 m were established in a line parallel with the channel. *Austrovenus* addition and removal treatments were alternated along the transect. The experimental plots were established on areas of sandflat where ambient *Austrovenus* densities were low (c. 300 ind. m^{-2}), but were within 20 m of *in situ* high-density *Austrovenus* beds. Preliminary observations indicated that densities in the natural beds were c. 600 - 1200 ind. m^{-2} at the sandy site, and c. 2000 - 3000 ind. m^{-2} at the muddy-sand site. I noted however that *Austrovenus* individuals were larger at the sandy site. I intended to raise the density in addition plots so that so that densities were comparable with natural densities for the sites, and so that biomass (and therefore first order excretory and respiration contribution to solute fluxes) was comparable between sites. Therefore, to create the addition treatments (+AS) *Austrovenus* were collected from the nearby natural beds and transplanted to the plots during the same low tide to raise the density to c. 700 ind. m^{-2} at the sandy site and c. 2000 ind. m^{-2} at the muddy-sand site. Almost all the animals had buried into the sediment by the following day's low tide, and I observed no obvious *Austrovenus* mortality in the days and weeks following the transplants. To create the removal treatments (-AS) all *Austrovenus* were manually removed by finger plowing the sediment, minimising the impact of the manipulation on ambient macrofauna (Thrush et al. 2006), which was repeated the following day to ensure almost total removal. Plastic mesh fences (15 cm in height) were buried 10 cm into the sediment around the perimeter of each plot to prevent the migration of adult *Austrovenus*. The large mesh size (1 cm) and short height (5 cm above sediment) of the fencing was used to minimise effects on water flow (Miller & Gaylord 2007) and restrictions on the movement of smaller sized macrofauna. The *Austrovenus* manipulation was undertaken 6 weeks prior to the winter (August 2009) and summer (February-March 2010) benthic chamber incubations (see below) to allow the sediment and resident macrofauna to recover from the effects of the manipulation (Thrush et al. 2006).

3.2.2 In situ *chamber incubations*

To measure the response of the soft-sediment systems to the *Austrovenus* manipulations, O_2 and nutrient fluxes were measured in light and dark benthic chambers. One light and one dark chamber was deployed to each of the six plots per site on two consecutive days in both winter and summer. Chambers were placed at least 1 m inside each plot's fence to avoid edge artefacts (e.g. Hulberg & Oliver 1980, Hall et al. 1990). The four incubations per plot (1 light plus 1 dark on 2 consecutive days) came from four distinct locations so that the same sediments were never resampled. Benthic chamber incubations took place during midday high tides when benthic algal activity was expected to be high.

The incubation chambers (square chambers with domed lids enclosing 0.25 m^2 sediment and 35 L of mechanically-stirred overlying water) have been described previously (Lohrer et al. 2004). Chamber bases were deployed during the low tide just prior to the incubation, and lids were attached during the incoming tide when water depth was c. 0.5 m. Measurements commenced 2 h before high water and continued for 4 h; *Austrovenus* exhibits a circatidal rhythm whereby feeding is limited to this period (Beentjes & Williams 1986). Initially, and once per hour during the incubation, a 60 mL water sample was carefully collected from each chamber using a Luer Lok syringe, without allowing any air bubbles to enter the syringe. O_2 concentration was measured immediately with a hand held dissolved O_2 probe (PreSens Fibox 3 PSt3) and the water was then filtered through a Whatman GF/C filter, stored on ice in the dark and frozen that day for later analysis of nutrients (NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}) on a Thermo Scientific Aquakem 200 discrete analyzer. Water column effects on O_2 and nutrient concentrations were found to be negligible based on incubation of ambient water in light and dark water bottles (1 L) for the same length of time and at the same depth as the chamber incubations. O_2 and nutrient fluxes were calculated from the slope of the regression between concentration and incubation time, corrected for dilution of chamber water that occurred during each of the five 60 ml samplings. Additionally, HOBO® light meters and TidBit® temperature loggers were fitted to the outside of randomly selected chambers during the experiments.

After chamber deployment 16 surface sediment samples (1 cm depth) were taken from within each chamber footprint using a small syringe core (2.5 cm diameter). Samples were pooled and frozen for later analysis of pigments, grain size, organic matter, nitrogen and organic carbon content. One large core (13 cm diameter, 15 cm depth) was collected for macrofauna analysis, sieved on a 0.5 mm mesh and preserved in 70 % isopropyl alcohol with Rose-Bengal stain. A second large core was collected for sediment denitrification and DEA assays (see below) and an additional estimate of *Austrovenus* density (sieved on a 1 mm mesh). For light chamber cores only, the surficial 5 cm of sediment was placed in airtight bags, kept cool and transported to the laboratory that evening for denitrification assays.

3.2.3 Sediment denitrification assays

Sediment denitrification rates were quantified within 24 h of collection using the chloramphenicol-amended acetylene (C_2H_2) inhibition technique (Knowles 1990, Inwood et al. 2005, Bruesewitz et al. 2006). Although this technique results in underestimation of actual denitrification rates due to blocking of nitrification by the C_2H_2, it has proven reliable for comparison of denitrification activity between treatments, sites and seasons as well as measuring nutrient limitation of denitrification (e.g. Bernot et al. 2003, Bruesewitz et al. 2009). For each sediment sample (5 cm depth core from light chambers) 30 mL of homogenized sediment was combined with 25 mL unfiltered site water in preserve jars modified with an *n*-butyl rubber septa in the lids ($n = 6$ per treatment, per site, per season). Chloramphenicol was added to the jars to suppress *de novo* enzyme production and the jars were purged with ultra-pure helium for 10 min to ensure anoxic conditions. Pure C_2H_2 was added to the jar headspace to prevent the conversion of N_2O to N_2 and gas samples were collected hourly beginning 10 mins after the addition of the C_2H_2 for 4 h. To maintain a constant pressure the headspace was replaced with a mixture of helium and C_2H_2 after each sample. The gas samples were analysed for N_2O using a Varian CP 3800 gas chromatograph equipped with a HayeSep D column and electron capture detector. Denitrification rates were calculated from the linear increase in N_2O concentration over time, normalized to the sediment surface area. To determine whether sediment denitrification was limited by nitrate or carbon additional jars, prepared identically to those above, were amended with additional nitrate (as potassium nitrate 10 mg N L^{-1}), carbon (as glucose 12 mg C L^{-1}) or both nitrate (10 mg N L^{-1}) and carbon (12 mg C L^{-1}). The DEA measurements were determined from the rates measured in the samples amended with nitrate and carbon (+N+C). DEA provides a measure of maximum denitrification potential by providing optimized conditions in anoxic, +N+C-amended slurries, valuable for making across-site comparisons (Groffman et al. 2006, Bruesewitz et al. 2011).

3.2.4 Laboratory analyses

Sediment chlorophyll *a* (chl *a*) and phaeopigment content were determined by extraction in 90 % acetone and measurement of fluorescence before and after acidification on a Turner Designs 10-AU fluorometer (Arar & Collins 1997). Organic matter content (OM) was determined from dried (60 ºC for 24 h) and ashed (550 ºC for 4 h) sediment samples. Sediment grain size was measured on a Malvern Mastersizer-S after preparing the samples with 10 % hydrogen peroxide to remove OM, removal of the >1 mm fraction, and addition of calgon to disperse the particles (Singer et al. 1988). Organic carbon (OC) and total nitrogen (N) was measured on a LECO CHN analyser after removal of carbonate carbon from the samples by acidification with 1M hydrochloric acid (Ryba & Burgess 2002). Macrofauna samples were sorted into six broad taxonomic groups; *Austrovenus*, other bivalves, mudflat anemones (*Anthopleura aureoradiata)*, annelids, crustaceans and gastropods counted and weighed (blotted wet weight). The weight of the bivalves included their shells. *Austrovenus* density and biomass in each chamber was estimated from the mean of the two large sediment cores.

3.2.5 Data analysis

To eliminate pseudo-replication, one representative value for each chamber type per plot was obtained prior to statistical analysis by averaging the data from the two light and two dark chambers deployed per plot. Sediment O_2 and nutrient fluxes in the light and dark chambers were analysed separately. Net primary production (NPP) and sediment oxygen consumption (SOC) were defined as the O_2 flux in light and dark chambers respectively, and gross primary production (GPP) was estimated from NPP-SOC. GPP was standardised by the sediment chl *a* content to account for variations in microphytobenthos biomass. Nutrient uptake rates were estimated, (the difference between dark chamber flux and light chamber flux), to quantify usage by microbes and microphytes living in surficial sediments.

The response variables (NPP, SOC, GPP, nutrient fluxes and uptake, and sediment DEA) were analysed using 3-factor analysis of variance (ANOVA), with treatment (+AS, -AS), site (sandy, muddy-sand), and season (winter, summer) all considered as fixed factors. Any non-significant interaction terms of the highest order were removed and the analysis repeated. When the overall ANOVA was significant at $\alpha = 0.05$, pairwise comparisons were performed using Tukey post-hoc tests. For sediment denitrification, 2-factor ANOVA by presence or absence of nitrate (N) or carbon (C) was used to identify the limiting nutrient. Single nutrient limitation by N or C is identified with a significant result for that treatment, and co-limitation is identified by a significant interaction term (Tank & Dodds 2003). One-factor ANOVA were used to compare sediment properties, *Austrovenus* density and biomass between sites, seasons and treatments separately. In all tests, normality and homogeneity of variances were evaluated with Kolmogorov-Smironov tests and by plotting of residual versus predicted values. Variables were log or square root transformed where required. All statistical analyses were performed using Statistica (Version 8, Statsoft Inc., 2008).

3.3 Results

3.3.1 Macrofauna abundance and biomass

Austrovenus density in +AS plots ranged from c. 500 to 1000 ind. m^{-2} at the sandy site and from c. 1800 to 2500 ind. m^{-2} at the muddy-sand site (Figure 3.2). Small-scale spatial heterogeneity in *Austrovenus* density is characteristic of natural *Austrovenus* beds, as the adults tend to be aggregated rather than randomly or uniformly distributed (e.g. Hewitt et al. 1996). However, I expected the large size of my experimental plots (16 m^{2}) to affect the sediment biogeochemical environment at a scale larger than the chamber footprints (0.25m^{2}). Although I did not achieve total removal in -AS plots, *Austrovenus* density and biomass were at least an order of magnitude less than in the +AS plots.

Regardless of site or season, *Austrovenus* density and biomass were significantly greater in +AS compared to -AS plots (1-factor ANOVA, $p < 0.001$). Densities in +AS plots were equivalent to planned densities, i.e. mean *Austrovenus* density in +AS plots was significantly lower at the sandy site (700 ind. m^{-2}) compared to the muddy-sand site (2000 ind. m^{-2}, $p < 0.001$). Mean *Austrovenus* shell length (± SD) was significantly greater at the sandy site, 23.3 (± 1.0) mm, compared to the muddy-sand site, 17.7 (± 1.1) mm, ($p < 0.001$). Thus, as expected, mean biomass in +AS plots (c. 2300 g ww m^{-2}) was not significantly different between the two sites ($p > 0.05$). There was no significant seasonal difference in *Austrovenus* density, size or biomass at either site ($p > 0.05$).

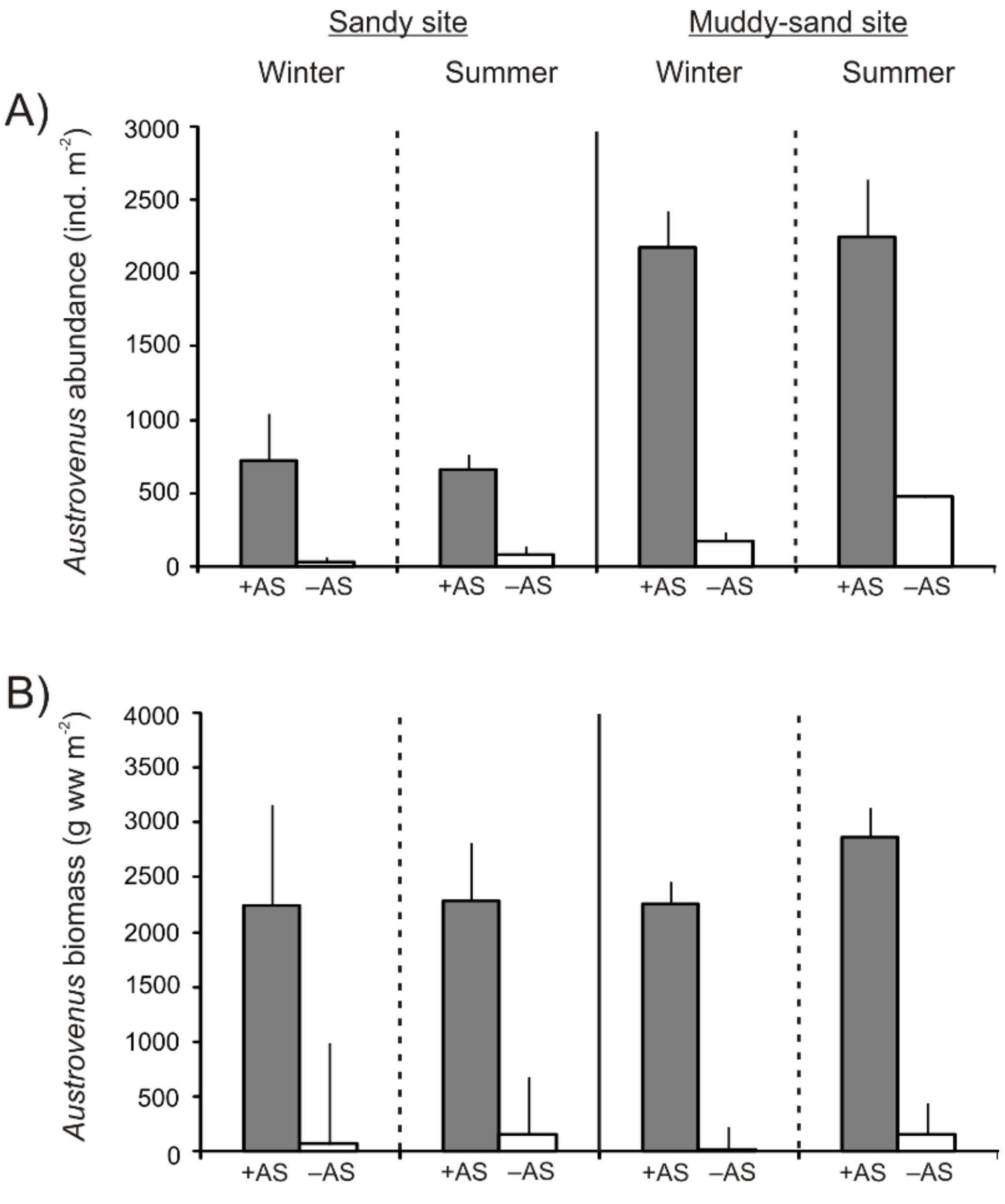

Figure 3.2: Mean (+ 1 SD; n = 3) *Austrovenus* abundance (A) and biomass (B) in *Austrovenus* addition (+AS; grey fill) and removal (–AS; no fill) plots as a function of site and season.

Abundance of other macrofaunal groups was dominated by annelids, *Anthopleura aureoradiata* (mudflat anemones, attached to the *Austrovenus* shells) and crustaceans (mostly barnacles, also attached to the *Austrovenus* shells) at the sandy site; annelids and other bivalves dominated at the muddy-sand site (Figure 3.3A). *Austrovenus* comprised c. 90 % of the mean total macrofaunal biomass in the +AS plots. Other than *Austrovenus* the biggest contributors to macrofaunal biomass were *Anthopleura* in +AS plots at the sandy site, other bivalves in -AS plots at the sandy site, and other bivalves in both +AS and -AS plots at the muddy-sand site (Figure 3.3B).

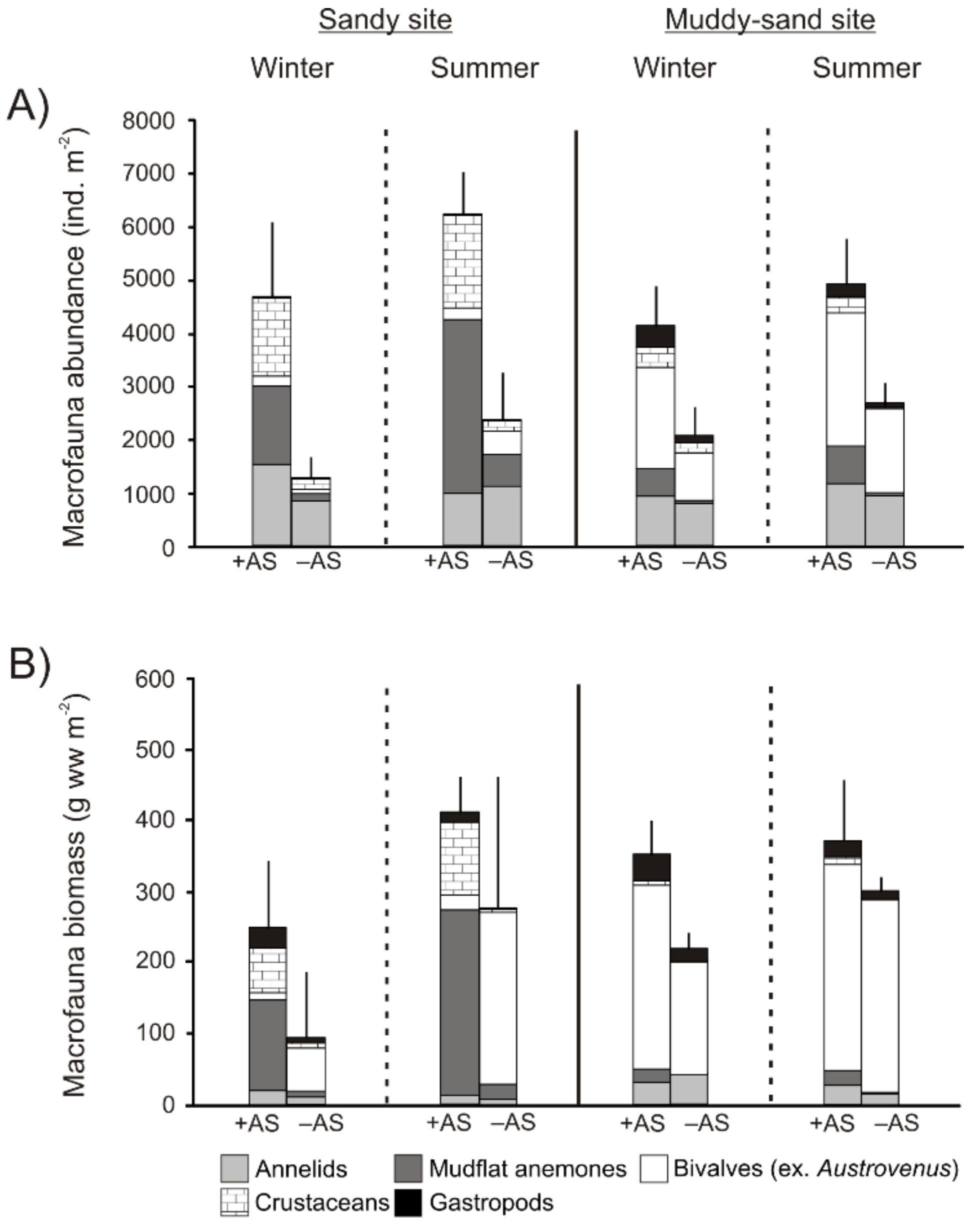

Figure 3.3: Mean (+ 1 SD; n = 3) macrofauna abundance (A) and biomass (B) in *Austrovenus* addition (+AS) and removal (–AS) plots as a function of site and season.

3.3.2 Environmental variables

There were large differences in water temperature and photosynthetically active radiation (PAR) between winter and summer, but little difference between sites in either season. Conversely, there were large differences in sediment properties between sites, but not between winter and summer (Table 3.1). Water temperature was greater in summer (c. 22 °C) than in winter (c. 14 °C). Levels of PAR were also much greater in summer (c. 1370 µmol photons $m^{-2} s^{-1}$) than in winter (c. 80 µmol photons $m^{-2} s^{-1}$). Regardless of season or *Austrovenus* treatment, median grain size was significantly lower at the muddy-sand site (c. 220 µm), compared to the sandy site (c. 420 µm, 1-factor ANOVA, $p < 0.001$). Mud, OM, OC, N, chl *a* and phaeopigment content were all significantly greater at the muddy-sand site ($p < 0.001$). I did not detect a significant effect ($\alpha = 0.05$) of *Austrovenus* treatment on any sediment properties at the sandy site. However, at the muddy-sand site, in both winter and summer, grain size was greater ($p < 0.05$) and mud content was lower ($p < 0.05$) in +AS than -AS plots. Also at the muddy-sand site, OM content was lower in +AS plots than in -AS plots, although the effect was only marginally significant ($p = 0.088$ in winter, $p = 0.075$ in summer).

Table 3.1: Environmental variables as a function of site, season and treatment

Environmental variable	Treatment	Sandy Site		Muddy-sand site	
		Winter	Summer	Winter	Summer
Median grain size (µm)	+AS	447 (38)	393 (20)	222 (8)	262 (14)
	–AS	463 (50)	389 (62)	195 (15)	221 (14)
Silt/clay (%)	+AS	0.0 (0.0)	0.0 (0.0)	10.8 (0.4)	9.1 (1.2)
	–AS	0.0 (0.0)	0.6 (1.0)	17.0 (2.0)	13.6 (2.1)
Organic matter (%)	+AS	1.1 (0.1)	1.0 (0.1)	3.7 (0.3)	3.2 (0.1)
	–AS	1.2 (0.2)	1.1 (0.3)	4.2 (0.3)	3.4 (0.1)
Chlorophyll *a* (µg g dw^{-1})	+AS	8.4 (0.5)	8.5 (1.9)	23.7 (1.3)	17.7 (0.7)
	–AS	8.6 (0.6)	8.2 (3.6)	22.0 (1.6)	14.5 (1.8)
Phaeopigment (µg g dw^{-1})	+AS	2.5 (0.2)	1.4 (0.5)	14.3 (0.4)	7.3 (0.4)
	–AS	2.5 (0.2)	1.6 (1.0)	15.9 (1.9)	6.0 (0.7)
Organic carbon (%)	+AS	0.15 (0.00)	0.17 (0.01)	0.37 (0.02)	0.31(0.01)
	–AS	0.16 (0.01)	0.18 (0.02)	0.45 (0.07)	0.34(0.04)
Nitrogen (%)	+AS	0.08 (0.00)	0.09 (0.00)	0.14 (0.01)	0.12(0.01)
	–AS	0.08 (0.01)	0.09 (0.01)	0.14 (0.01)	0.12(0.01)
OC:N	+AS	2.0 (0.1)	2.0 (0.2)	2.6 (0.2)	2.7 (0.1)
	–AS	2.1 (0.2)	2.1 (0.0)	3.2 (0.4)	2.8 (0.2)
Water temperature (°C)		13.9 (13.5 – 14.2)	21.4 (21.0 – 21.6)	14.7 (14.2 – 15.0)	22.6 (22.0 – 23.1)
PAR (µmol photons m^{-2} s^{-1})		82 (58 – 105)	1330 (560 – 2100)	81 (68 – 93)	1410 (1330 – 1490)

+AS = *Austrovenus* addition, –AS = *Austrovenus* removal, PAR = photosynthetically active radiation, OC:N = organic carbon to nitrogen ratio. For water temperature and PAR data represent mean with range measured during chamber incubations in parentheses. For sediment properties data represent mean (n = 3) with SD in parentheses.

3.3.3 O_2 fluxes and GPP

In dark chambers there was always an influx of O_2 into the sediments, indicating sediment oxygen consumption (SOC), however, in light chambers there was always an efflux of O_2 from the sediments which indicated that net primary production (NPP) was greater than zero (Figure 3.4A). There was a significant treatment effect on SOC which was 1.5 × higher in +AS plots compared to -AS plots (3-factor ANOVA, $p < 0.001$, Table 3.2). Post-hoc analysis of the site*season interaction ($p < 0.001$) revealed that SOC was significantly greater (by 2.5 ×) in summer than in winter at the sandy site but that there was no significant difference between seasons at the muddy-sand site. Comparisons between sites within seasons demonstrated that SOC was significantly higher (by 1.7 ×) at the sandy than at the muddy-sand site in summer only (in winter there was no significant difference). For light chamber O_2 fluxes, there was a marginally significant site*treatment interaction ($p = 0.086$). Closer examination suggested that NPP could be greater in +AS plots (compared to -AS plots) at the sandy site in summer. There was no indication of treatment effects on NPP in winter at the sandy site or at the muddy-sand site in either season. The site*season interaction was significant ($p < 0.05$) with NPP greater (by 2.4 ×) in summer than in winter at the sandy site. There was no significant seasonal effect on NPP at the muddy-sand site and no significant difference between the sites in either season.

Mean GPP ranged from 2.1 to 7.4 mmol O_2 m^{-2} h^{-1} at the sandy site, but the range was much smaller at the muddy-sand site (3.1 to 3.8 mmol O_2 m^{-2} h^{-1}). When normalised by sediment chl *a* content (a proxy for primary producer biomass), GPP at the sandy site was consistently greater (0.24 to 0.90 mmol O_2 µg chl *a* g^{-1} m^{-2} h^{-1}) than at the muddy-sand site (0.13 to 0.22 mmol O_2 µg chl *a* g^{-1} m^{-2} h^{-1}, Figure 3.4B). There were significant site*season and site*treatment interaction effects on normalised GPP (3-factor ANOVA, $p < 0.05$, Table 3.2). Post-hoc analysis showed that normalised GPP was higher in +AS plots compared to –AS plots at the sandy site, (by 1.4 × in winter and by 1.5 × in summer), but there was no significant difference between the treatments at the muddy-sand site in either season. Between sites within season comparisons demonstrated that normalised GPP was greater at the sandy site in both winter (by 2.1 ×) and summer (by 3.4 ×). Comparison between seasons within sites demonstrated that normalised GPP was greater at the sandy site in summer compared to winter (by

2.6 ×), but there was no significant difference between winter and summer at the muddy-sand site.

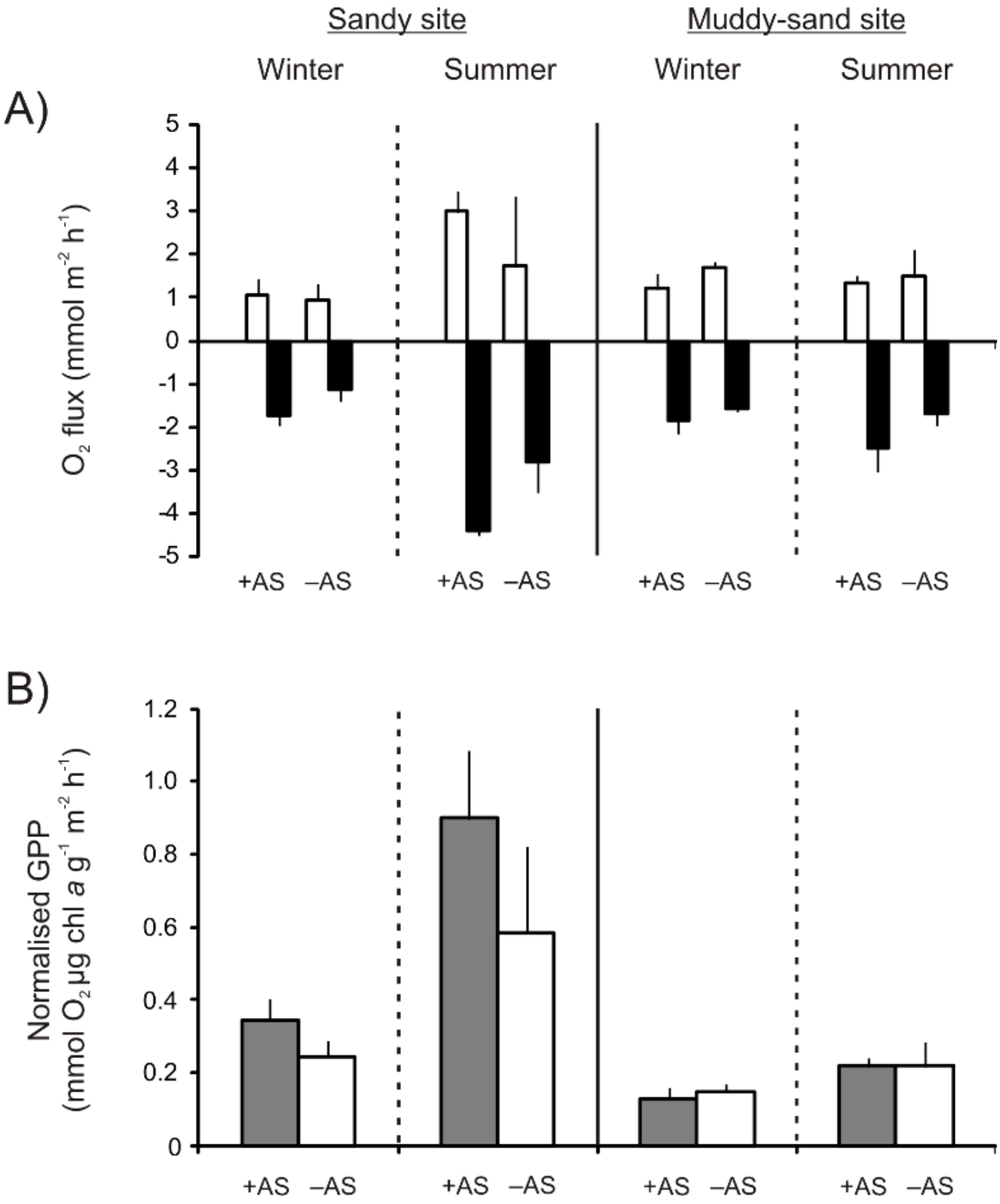

Figure 3.4: (A) Mean (+ 1 SD; n = 3) O_2 fluxes in light (no fill) and dark (black fill) chambers in *Austrovenus* addition (+AS) and removal (–AS) plots, as a function of site and season. Positive values represent an efflux out of the sediment, and negative values represent an influx into the sediment. (B) Mean (+ 1 SD; n = 3) normalised GPP (light minus dark chamber O_2 flux) in +AS (grey fill) and –AS (no fill) plots, as a function of site and season.

Table 3.2: 3-factor ANOVA (analysis of variance) results for sediment oxygen consumption (SOC; dark chamber O_2 flux), net primary production (NPP; light chamber O_2 flux) and gross primary production normalised by sediment chl *a* content (GPP/chl *a*)

Variable	Source	d.f.	MS	F	*p*	Significant Tukey post-hoc test		
						Site	Season	Treatment
SQRT SOC	Site	1	0.170	12.9	**0.002**			
	Season	1	1.02	78.2	**< 0.001**			
	Treatment	1	0.422	32.2	**< 0.001**			+AS > –AS
	Site*Season	1	0.482	36.8	**< 0.001**	Su: Sd > Ms	Sd: Wi < Su	
	Site* Treatment	1	0.0287	2.19	0.157			
	Season* Treatment	1	0.0455	3.47	0.080			
	Error	17	0.0131					
NPP	Site	1	0.364	0.800	0.383			
	Season	1	2.65	5.83	**0.027**			
	Treatment	1	0.205	0.451	0.511			
	Site*Season	1	2.96	6.51	**0.021**		Sd: Wi < Su	
	Site* Treatment	1	1.51	3.32	0.086			
	Season* Treatment	1	0.917	2.02	0.174			
	Error	17	0.455					
SQRT GPP/chl *a*	Site	1	0.457	86.3	**< 0.001**			
	Season	1	0.246	46.4	**< 0.001**			
	Treatment	1	0.024	4.61	**0.047**			
	Site*Season	1	0.071	13.5	**0.002**	Su & Wi: Sd > Ms	Sd: Wi < Su	
	Site* Treatment	1	0.035	6.60	**0.020**	+AS & –AS: Sd > Ms		Sd: +AS > –AS
	Season* Treatment	1	0.006	1.17	0.295			
	Error	17	0.005					

Factors are site (Sd = Sandy, Ms = Muddy-sand), season (Wi = Winter, Su = Summer) and treatment (+AS = *Austrovenus* addition, –AS = *Austrovenus* removal). Values in bold are significant at $p < 0.05$. Tukey post-hoc tests for significant differences between site, season and treatment are shown at $\alpha = 0.05$. SOC and GPP/chl *a* were square root (SQRT) transformed.

3.3.4 Nutrient fluxes and uptake

In dark and light chambers there was nearly always a net efflux of ammonium (NH_4^+) from the sediment, the only exception being some light chambers in the +AS plots at the sandy site in summer, when there was a small influx (Figure 3.5A). There was a significant treatment effect on dark chamber NH_4^+ flux which was 2.6 × greater in +AS plots compared with –AS plots (3-factor ANOVA, $p < 0.001$, Table 3.3). Post-hoc analysis of the site*season interaction ($p < 0.05$) showed that dark chamber NH_4^+ flux was greater in summer than in winter at both sites (by 1.8 × at the muddy-sand site, and by 3.6 × at the sandy site). Comparisons between sites within seasons demonstrated that dark chamber NH_4^+ flux was greater (by 2.3 ×) at the muddy-sand site than at the sandy site in winter only (in summer there was no significant difference). The effect of *Austrovenus* treatment on light chamber NH_4^+ flux was not consistent across sites and seasons (3-factor ANOVA, $p < 0.05$, Table 3.3). Post-hoc analysis of the site*season*treatment interaction revealed that light chamber NH_4^+ flux was significantly greater (by 11.8 ×) in +AS compared to -AS plots at the muddy-sand site in summer, but there was no significant difference between treatments in winter or at the sandy site in either season. Comparison between sites within seasons and treatments revealed that in +AS plots in summer light chamber NH_4^+ flux was significantly greater at the muddy-sand site; at the sandy site NH_4^+ flux was negative (-0.52 µmol m^{-2} h^{-1}) indicating a small influx into the sediment, but at the muddy-sand site NH_4^+ flux was positive (74.6 µmol m^{-2} h^{-1}) indicating a large efflux out of the sediment. In contrast, in +AS plots in winter and in -AS plots in both seasons, there was no significant difference between the sites.

NH_4^+ uptake exhibited a far greater range at the sandy (6 to 105 µmol NH_4^+ m^{-2} h^{-1}) compared to the muddy-sand site (-9 to 49 µmol NH_4^+ m^{-2} h^{-1}; Figure 3.5B). The effect of *Austrovenus* treatment on NH_4^+ uptake was inconsistent across sites and seasons (3-factor ANOVA, $p < 0.05$, Table 3.3). Post-hoc analysis of the site*season*treatment interaction demonstrated that NH_4^+ uptake was significantly increased (by 8 ×) in +AS compared to -AS plots at the sandy site in summer, but there was no significant difference between treatments in winter. At the muddy-sand site there was no treatment effect in either season. Comparison between seasons within treatments and sites revealed that in +AS plots at the sandy site NH_4^+ uptake was significantly greater (by 10 ×) in summer compared to winter, but there was no significant difference between the seasons in -AS plots. At the muddy-sand site there was no significant difference between the seasons in +AS or -AS plots. Comparison between sites within treatments and seasons revealed that NH_4^+ uptake was significantly greater (by 3.4 ×) at the sandy site in +AS plots in summer, but there was no significant difference between the sites in +AS plots in winter. There was also no significant difference between the sites in -AS plots in either season.

NH_4^+ is the form of dissolved inorganic nitrogen (DIN) most readily taken up by microphytobenthos (MPB) and, as is typically the case in New Zealand estuaries, comprised the majority (c. 80 %) of DIN in my samples (Thrush et al. 2006, Sandwell et al. 2009, Lohrer et al. 2010a). I measured high variation in NO_3^- and PO_4^{3-} fluxes (Figure 3.6). Additionally, chamber nutrient concentrations were often near instrument detection limits, particularly for NO_2^- (0.005 µmol L^{-1}), and this led to uncertainty in flux estimates (mean $r^2 < 0.3$). There were no obvious treatment effects and no further analyses were conducted for NO_3^-, NO_2^- or PO_4^{3-} fluxes.

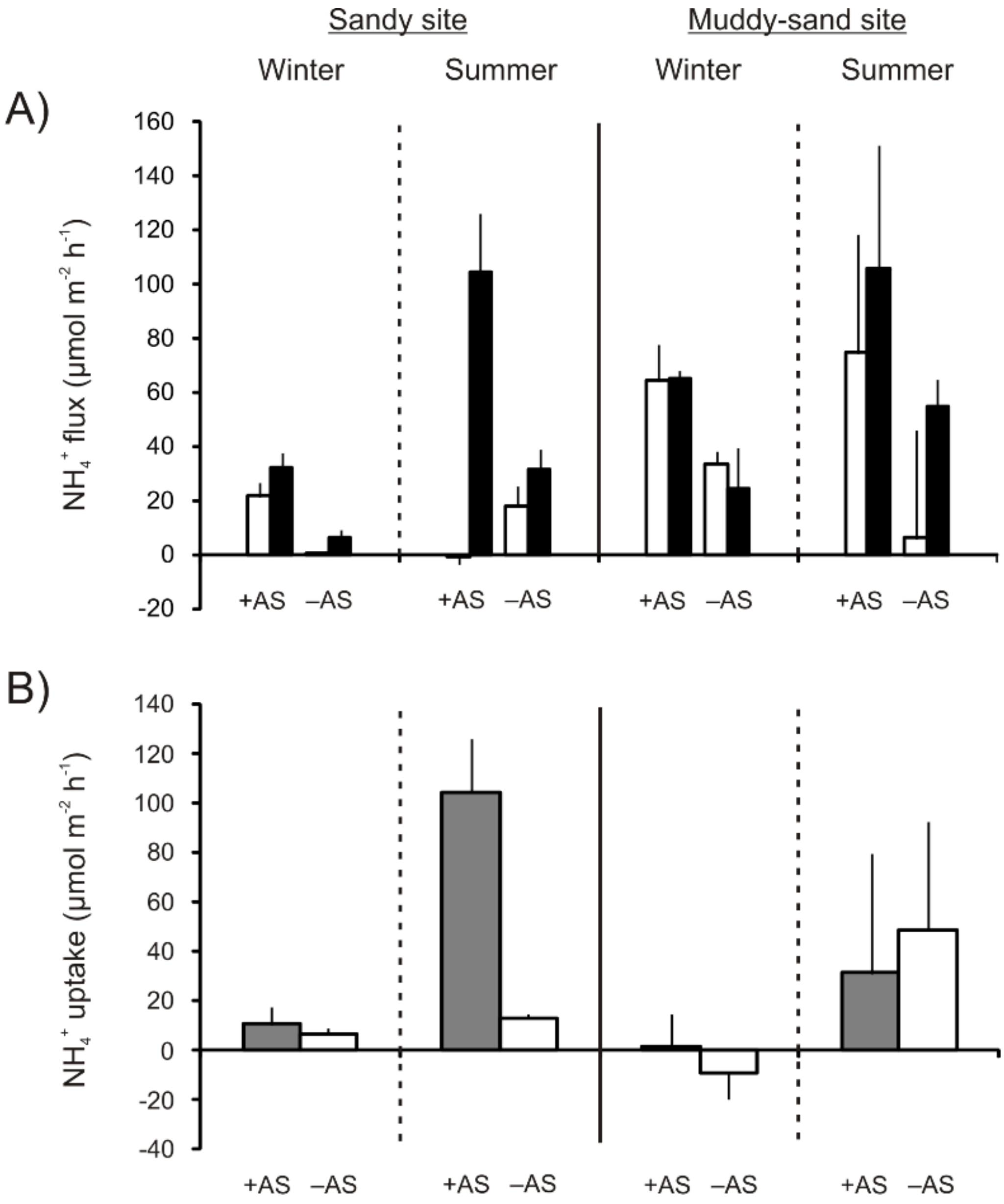

Figure 3.5: (A) Mean (+ 1 SD; n = 3) NH_4^+ fluxes in light (no fill) and dark (black fill) chambers in *Austrovenus* addition (+AS) and removal (–AS) plots, as a function of site and season. Positive values represent an efflux out of the sediment, and negative values represent an influx into the sediment. (B) Mean (+ 1 SD; n = 3) NH_4^+ uptake (dark minus light chamber NH_4^+ flux) in +AS (grey fill) and –AS (no fill) plots, as a function of site and season.

Table 3.3: 3-factor ANOVA (analysis of variance) results for dark and light chamber NH_4^+ flux and NH_4^+ uptake

Variable	Source	d.f.	MS	F	p	Significant Tukey post-hoc test		
						Site	Season	Treatment
Log$_{10}$ Dark NH_4^+	Site	1	0.464	16.4	< **0.001**			
	Season	1	1.24	44.0	< **0.001**			
	Treatment	1	1.52	53.7	< **0.001**			+AS > –AS
	Site*Season	1	0.161	5.70	**0.029**	Wi: Sd < Ms	Sd & Ms: Wi < Su	
	Site* Treatment	1	0.105	3.72	0.071			
	Season* Treatment	1	0.078	2.75	0.116			
	Error	17	0.028					
Light NH_4^+	Site	1	7190	15.3	**0.001**			
	Season	1	172	0.366	0.554			
	Treatment	1	3850	8.19	**0.011**			
	Site*Season	1	58.7	0.125	0.728			
	Site* Treatment	1	3470	7.39	**0.015**			
	Season* Treatment	1	2.55	0.005	0.942			
	Site*Season*Treatment	1	2290	4.88	**0.042**	+AS Su: Sd < Ms		Ms Su: +AS > –AS
	Error	16	470					
NH_4^+ uptake	Site	1	1430	2.28	0.151			
	Season	1	13400	21.4	< **0.001**			
	Treatment	1	2950	4.69	**0.046**			
	Site*Season	1	66.0	0.110	0.749			
	Site* Treatment	1	3980	6.32	**0.023**			
	Season* Treatment	1	1320	2.09	0.168			
	Site*Season* Treatment	1	4990	7.92	**0.012**	+AS Su: Sd > Ms	+AS Sd: Wi < Su	Sd Su: +AS > –AS
	Error	16	629					

Factors are site (Sd = Sandy, Ms = Muddy-sand), season (Wi = Winter, Su = Summer) and treatment (+AS = *Austrovenus* addition, –AS = *Austrovenus* removal). Values in bold are significant at $p < 0.05$. Tukey post-hoc tests for significant differences between site, season and treatment are shown at $\alpha = 0.05$. Dark NH_4^+ flux was log$_{10}$ transformed.

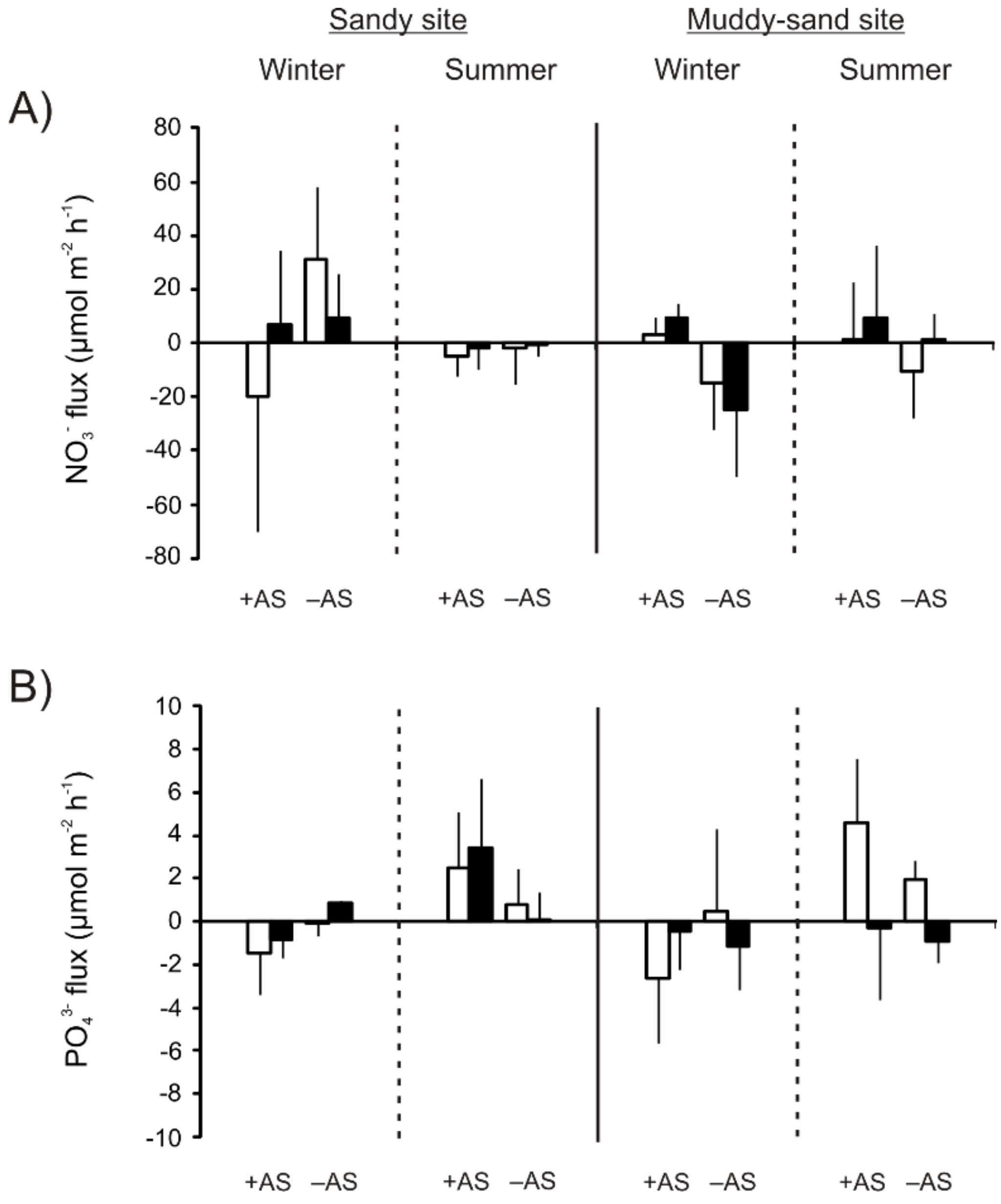

Figure 3.6: Mean (+ 1 SD; n = 3) NO_3^- (A) and PO_4^{3-} (B) fluxes in light (no fill) and dark (black fill) chambers in *Austrovenus* addition (+AS) and removal (–AS) plots, as a function of site and season. Positive values represent an efflux out of the sediment, and negative values represent an influx into the sediment.

3.3.5 Sediment denitrification rates

Non-amended denitrification rates (0 to 30 µmol N m^{-2} h^{-1}) were lower than the sediment denitrification potential (38 to 164 µmol N m^{-2} h^{-1}), which was determined from samples amended with nitrate and carbon (DEA). Two-way ANOVA revealed a significant effect of nitrate addition at both sites in winter and in summer, indicating that denitrification was always N limited, regardless of site or season (Table 3.4).

As with GPP and NH_4^+ uptake, the range in sediment denitrification potential was greater at the sandy site (55 to 164 µmol N m^{-2} h^{-1}) compared to the muddy-sand site (38 to 48 µmol N m^{-2} h^{-1}; Figure 3.7). Denitrification potential did trend towards an increase in +AS compared to -AS plots at the sandy site, especially in summer, although the treatment effect was only marginally significant (3-factor ANOVA, $p = 0.078$, Table 3.5). There was a significant site*season interaction ($p < 0.001$) and post-hoc analysis demonstrated that denitrification potential was significantly greater (by 2.4 ×) in summer compared to winter at the sandy site, but there was no significant seasonal effect at the muddy-sand site. Also, denitrification potential was significantly greater (by 3 ×) at the sandy site than at the muddy-sand site in summer, but there was no significant difference between the sites in winter.

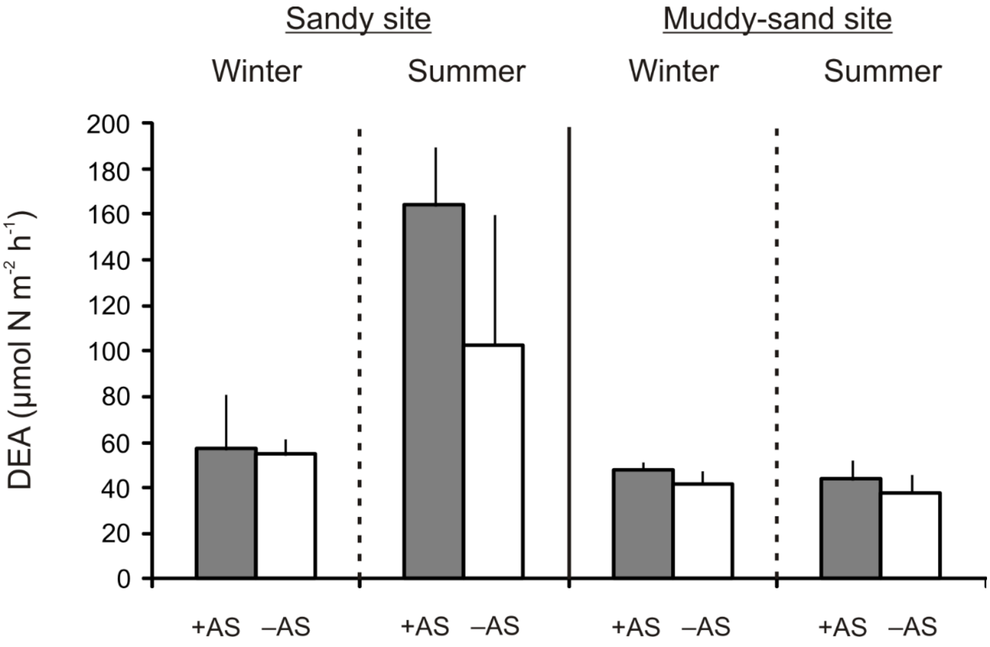

Figure 3.7: Mean (+ 1 SD; n = 3) sediment denitrification assay (DEA), i.e. sediment denitrification potential, in *Austrovenus* addition (+AS; grey fill) and removal (–AS; no fill) plots as a function of site and season.

Table 3.4: 2-factor ANOVA (analysis of variance) results determining whether nitrogen, carbon or both nutrients are limiting denitrification rates

Site/Season	Source	d.f.	MS	F	*p*	Significant Tukey post-hoc test	
						Nitrogen	Carbon
Sandy site in winter	Nitrogen	1	189	193	**< 0.001**		
	Carbon	1	8.05	8.23	**0.009**		
	Nitrogen*Carbon	1	6.74	6.89	**0.016**	+C & –C: +N > –N	–N: –C > +C
	Error	20	0.980				
Sandy site in summer	Nitrogen	1	92000	97.8	**< 0.001**	+N > –N	
	Carbon	1	548	0.582	0.454		
	Nitrogen*Carbon	1	548	0.582	0.454		
	Error	20	942				
Muddy-sand site in winter	Nitrogen	1	256	447	**< 0.001**	+N > –N	
	Carbon	1	5.61	9.77	**0.005**		–C > +C
	Nitrogen*Carbon	1	0.226	0.394	0.537		
	Error	20	0.574				
Muddy-sand site in summer	Nitrogen	1	8640	291	**< 0.001**	+N > –N	
	Carbon	1	56.5	1.90	0.183		
	Nitrogen*Carbon	1	56.5	1.90	0.183		
	Error	20	29.7				

Factors are nitrogen (N) and carbon (C). Values in bold are significant at $p < 0.05$. Tukey post-hoc tests for significant differences between presence/absence (+/–) of nitrogen and carbon are shown at $\alpha = 0.05$.

Table 3.5: 3-factor ANOVA (analysis of variance) results for $\log_{10}$ transformed DEA (denitrification enzyme activity; i.e. sediment denitrification potential)

Variable	Source	d.f.	MS	F	*p*	Significant Tukey post-hoc test		
						Site	Season	Treatment
Log_{10} DEA	Site	1	0.486	34.8	**< 0.001**			
	Season	1	0.145	10.4	**0.005**			
	Treatment	1	0.049	3.52	0.078			
	Site*Season	1	0.242	17.3	**< 0.001**	Su: Sd > Ms	Sd: Wi < Su	
	Site* Treatment	1	0.004	0.310	0.585			
	Season* Treatment	1	0.023	1.62	0.220			
	Error	17	0.014					

Factors are site (Sd = Sandy, Ms = Muddy-sand), season (Wi = Winter, Su = Summer) and treatment (+AS = *Austrovenus* addition, –AS = *Austrovenus* removal). Values in bold are significant at $p < 0.05$. Tukey post-hoc tests for significant differences between site, season and treatment are shown at $\alpha = 0.05$.

3.4 Discussion

At the sandy site, there were significant increases in many response variables (i.e. SOC, NPP, GPP, NH_4^+ uptake and denitrification potential) in summer, compared to winter. In contrast, for the same variables at the muddy-sand site, there was no significant difference between winter and summer measurements. Similarly, the effect of *Austrovenus* treatment on response variables was inconsistent between sites and seasons. Although both SOC and dark chamber NH_4^+ fluxes increased significantly in +AS plots regardless of site and season, GPP (and NPP to a lesser extent) were increased in +AS plots only at the sandy site. An increase in GPP indicates increased MPB productivity as water column primary production was negligible. My results suggest that increased availability of NH_4^+ drives this increase in MPB productivity as NH_4^+ uptake was higher in +AS plots at the sandy site, especially in summer. There was also a trend for greater denitrification potential in +AS sandy site plots in summer. At the muddy-sand site there was no significant effect of *Austrovenus* on GPP, NH_4^+ uptake or denitrification potential. Furthermore, GPP and denitrification potential were both significantly lower than at the sandy site.

As for other suspension feeding bivalves in coastal systems worldwide, resuspended MPB are an important component of *Austrovenus*' diet, especially as water column primary productivity is typically low in New Zealand estuaries (Kang et al. 1999, Safi 2003, Kang et al. 2006). Previous research with *Austrovenus* and other large bioturbating macrofauna has also observed an increase in MPB productivity even though MPB are often a major food source for the animals (Lohrer et al. 2004, Thrush et al. 2006, Sandwell et al. 2009). However, this study suggests that the positive effect of *Austrovenus* on MPB productivity is not consistent across habitat types, and that there can be substantial temporal variability in GPP. At both sites, the lower rates of GPP in winter are likely to be caused by limited MPB and bivalve activity. MPB photosynthetic activity was likely limited by wintertime water temperatures and reduced levels of PAR, while the reduced dark chamber NH_4^+ fluxes in the wintertime *Austrovenus* addition treatments provided evidence of reduced metabolic rates (i.e. less NH_4^+ excretion during the colder winter period). More surprising are the low rates of GPP in summer, and lack of an effect of *Austrovenus* on GPP, at the muddy-sand site. As dark chamber NH_4^+ fluxes in +AS plots were similar between the two sites it seems unlikely that the reason for low MPB productivity at the muddy-sand site was nutrient limitation.

Muddy sediments, despite often having higher microalgal biomass, can be less productive (in terms of rates of photosynthesis and oxygen evolution) than sandy sediments (Billerbeck et al. 2007). Resuspension of fine sediments, causing light limitation at the benthos, is more likely in muddy sediments, but I did not observe higher levels of turbidity at my muddier site on the days that I sampled. However, productivity can be enhanced in sandy sediments because light can penetrate further into the sediment column (as there is greater interstitial space between sediment grains). This increased sediment permeability can enhance solute flux (by permitting pore-water advection), and more frequent resuspension can cause a higher turnover of algal biomass (Middelburg et al. 2000, Blanchard et al. 2001, Billerbeck et al. 2007). Furthermore, sediment grain size can affect microbial composition and activity, and thus organic matter remineralisation, nutrient availability and MPB productivity (Middelburg et al. 2000). In fact, I found normalised GPP was significantly increased at the sandy site compared to the muddy-sand site even in -AS plots, although the effect was enhanced in +AS plots.

At the sandy site other macrofaunal abundance and biomass in +AS plots was dominated by mudflat anemones (*Anthopleura aureoradiata*). Previous work has described a mutualistic relationship between *Austrovenus* and *A. aureoradiata* whereby the anemones use the living bivalves as hard substrate for attachment and the bivalves gain protection from parasitic infection (Mouritsen & Poulin 2003). The anemones may also benefit from greater NH_4^+ availability in *Austrovenus* beds as endosymbiotic zooxanthellae can uptake NH_4^+ from surrounding water (Morar et al. 2011). It is probable that mudflat anemones significantly contribute to, and complicate, nutrient recycling and productivity at the sandy site, by both excretion and uptake of NH_4^+, but further work is needed to determine whether this species is a net source or sink of NH_4^+, and its effect on system productivity. Barnacles were also supported on *Austrovenus* shells at the sandy site. It is therefore possible that the positive effect on productivity measured in +AS plots at the sandy site is not attributable to *Austrovenus* alone, but to the combination of *Austrovenus* and the macrofaunal communities they support.

In contrast, at the muddy-sand site other macrofaunal abundance and biomass was dominated by other bivalves (mostly the deposit feeders *Nucula hartvigiana* and *Macomona liliana*). I expected OM content to increase in +AS plots at this site, due to retention of biodeposits in the lower energy environment, but instead found the reverse to be true. Deposit-feeder abundance and biomass was higher in +AS plots and they may have utilised the increased supply of OM. Alternatively, decreased mud content and increased grain size in +AS plots suggests that *Austrovenus* bioturbation enhanced fine sediment and OM transport by destabilising the sediment (Davis 1993, Ciutat et al. 2007). Furthermore, there was no difference in sediment C, N and C:N ratio between +AS and -AS plots. Typically, these parameters are found to increase under epifaunal bivalve beds, particularly so under longline mussel farms (Stenton-Dozey et al. 2001, Bruesewitz et al. 2006, Giles et al. 2006). Although biodeposition rates would almost certainly be lower for an infaunal bivalve bed than for a three dimensional epifaunal bed/longline my results suggest that *Austrovenus* biodeposits do not accumulate at either site. It is probable that OM is dispersed by currents at the sandy site, and quickly utilised by deposit feeders and/or resuspended by bivalve bioturbation at the muddy-sand site.

Unamended sediment denitrification rates were nil or low, likely because sediment nitrification may be a major source of NO_3^- for denitrification and coupled nitrification-denitrification is inhibited by the method used here (e.g. Seitzinger 1988). This is further reinforced by the low measured NO_3^- fluxes into the sediment. My expectation was that increased N from *Austrovenus* biodeposits (at the more sheltered muddy-sand site especially) would fuel coupled nitrification-denitrification but I found that OM content was not increased in +AS plots, and denitrification remained N limited regardless of site, season or addition/removal of *Austrovenus.* However, sediment denitrification potential (as measured with excess nitrate and carbon) did trend towards an increase in +AS plots at the sandy site in summer. Although *Austrovenus* biodeposits may not accumulate at the sandy site, bivalve bioturbation and excretion may have enhanced NH_4^+ availability, thus providing a source of nitrogen for nitrification (Gardner et al. 2001, Bruesewitz et al. 2008). NH_4^+ uptake was significantly increased in +AS plots at the sandy site in summer, which may have been partly due to increased nitrification. Without measuring sediment nitrification rates, however, it is not possible to separate uptake by nitrifiers from that by MPB (and perhaps anemones also). Nitrifiers are known to be poor competitors for nitrogen (Sundback et al. 2000, Risgaard-Petersen 2003), but oxygen production by benthic photosynthesis may enhance rates of coupled nitrification-denitrification when NH_4^+ is not limiting (An & Joye 2001). My results suggest that increased availability of NH_4^+ at the sandy site in summer as a result of *Austrovenus* activity likely increases both MPB productivity and sediment denitrification, though concurrent measurements of GPP, nitrification and denitrification would be needed to confirm this.

A possible confounding factor influencing the interpretation of my results is the difference in *Austrovenus* size between the two sites. Individuals were significantly larger at the sandy site (c. 23 mm shell length) than at the muddy-sand site (c. 18 mm shell length). Previous research has indicated that *Austrovenus* condition is enhanced in sandy compared to muddier sediments (Norkko & Thrush 2006), and the bivalves in my experimental plots had been transplanted from nearby beds at each site so represented a natural size for the habitat type. As biomass was comparable between sites I would not expect first order excretion rates to be substantially different between sites. However, the size difference might affect the degree to which *Austrovenus* bioturbation alters sediment chemistry. Bioturbation by macrofauna that mix surficial sediments, such as *Austrovenus*, can facilitate the release of solutes from sediment porewater (Lohrer et al. 2010a). Previous experiments have shown that *Austrovenus* tend to be retained in unfenced high-density plots, i.e. individual bivalves display minimal horizontal movement through surface sediments when in high-density beds (Whitlatch et al. 1997, Sandwell et al. 2009). The main effect of *Austrovenus* bioturbation in bivalve beds is therefore likely to be small-scale (< 2 - 3 cm) vertical movement as the bivalves move to the sediment-water interface to feed around high tide, and thereafter retreat to just below the sediment surface. The larger bivalves at the sandy site may have reworked sediment to a greater depth than the smaller individuals at the muddy-sand site. However, solute gradients are likely to be steeper in sediments at the muddy-sand site, potentially offsetting the size difference, and making it difficult to speculate on size-specific bioturbation effects on solute fluxes.

It is well documented that denitrification is often highly variable over small spatial and temporal scales in estuaries, due to variable O_2 profiles, nitrate and OM availability in the sediment (Groffman et al. 2006, Seitzinger et al. 2006). This is caused by a variety of processes such as frequent wetting/drying due to the tides or macrofauna activity (especially bioturbation and burrow building) which create denitrification microsites and make collection of a large number of replicates crucial (Seitzinger et al. 2006). More sophisticated (but more expensive) techniques, such as isotope-pairing techniques using Membrane Inlet Mass Spectrometry, can quantify denitrification rates without blocking nitrification, which may help to resolve the complicated interactions among macrofauna, such as *Austrovenus*, MPB and microbial communities (e.g. Kana et al. 1998, An et al. 2001). My work shows that these interactions are likely to be further complicated by context (i.e. spatial and temporal variability), so future studies should be mindful of this.

There is typically a trade-off between the size of experimental plots and the number of replicates that can be established. I recognise the low levels of replication (n = 3 per treatment) inherent in my experiments, but my efforts were focused on using relatively large plots as the estuarine intertidal is dynamic and subject to substantial bedload transport and sediment reworking rates (e.g. Grant et al. 1997); consequently results from experiments using smaller-scale manipulations may be dominated by edge effects (Hewitt et al. 1997, Englund & Cooper 2003). Furthermore, modifications of sediment stability associated with the addition or removal of macrofauna are often scale and/or density dependent (Thrush et al. 1996, Friedrichs et al. 2000, Coco et al. 2006). I recognise also that there are limitations associated with using benthic chambers to measure solute fluxes, such as stirring-induced pressure gradients that affect rates of porewater exchange (Glud et al. 1996), or altered boundary layer dynamics (Tengberg et al. 2004). However, in sediments colonised by large bioturbating or bioirrigating macrofauna and by patchy MPB communities (as in this study) there is considerable small-scale spatial and temporal heterogeneity in solute distribution. Benthic chambers have the advantage of integrating fluxes over a large sediment surface area, and in this study my intention was to identify any differences in relative fluxes between the sites, seasons and treatments, rather than quantifying absolute fluxes.

In summary, *Austrovenus* enhanced primary productivity and sediment denitrification potential at the sandy site, whereas there was no effect of *Austrovenus* on these variables at the muddy-sand site, leading me to hypothesise that increasing estuarine mud content may limit the influence of this key species on ecosystem function. However, there is a need to sample across a gradient of increasing muddiness to further explore these relationships. Similarly, there is a need for more comprehensive sampling to better resolve temporal variability. Previous research has established that high levels of sedimentation are likely to reduce *Austrovenus* populations (Thrush et al. 2003b), but my results indicate that moderate levels of sedimentation may reduce the positive effect of this species on system productivity even when they persist. Furthermore, my results suggest that denitrification potential is lower in muddy-sand compared to sandy sediments so moderate levels of sedimentation may also limit the system's ability to counteract the effects of eutrophication. These experiments reveal that it is important to consider context, i.e. the range of conditions inhabited by a particular species, in order to assess the effect of key species on ecosystem function. It appears that it is not just the loss of key species, but alteration of those species' habitats (even without substantial changes in biomass), that has the potential to alter ecosystem function.

CHAPTER 4

Modelling the effect of *Austrovenus stutchburyi* on energy flow and ecosystem properties in a shallow estuary

4.1 Introduction

Suspension feeding bivalves can act as key species in estuarine ecosystems by contributing to benthic-pelagic coupling and affecting rates of nutrient regeneration, but also due to their position in the food web, by exerting considerable top down control on phytoplankton populations and providing a substantial food source for higher trophic levels (reviewed by Newell 2004). In many systems, previous research has often emphasised the role of suspension feeding bivalves as a 'natural eutrophication control' because estimates of grazing pressure have shown that populations may be capable of filtering the entire volume of a system within a few days (Cloern 1982, Hily 1991, Smaal & Prins 1993, Dame & Prins 1998). Indeed, the loss of suspension feeders has resulted in an increased incidence of phytoplankton blooms for some ecosystems, e.g. following reductions in eastern oyster (*Crassostrea virginica*) beds in Chesapeake Bay, USA (Jackson et al. 2001, Kemp et al. 2005), or clams (*Mercenaria mercenaria)* in Great South Bay, NY, USA (Lonsdale et al. 2007). However, in shallow systems with short water residence times, it is likely that even large and dense aggregations of suspension feeders will have little effect on phytoplankton populations (e.g. Dame & Prins 1998). In shallow estuaries with large areas of intertidal flats then, these bivalves may not then be important as an eutrophication control, but may impact primarily on the ecosystem as a food source for higher trophic levels, such as shorebirds. For example, a reduction in both the abundance and quality of cockles (*Cerastoderma edule*) in the Dutch Wadden Sea due to shellfish dredging has been linked to the loss of red knots (*Calidris canutus islandica*) from the area (van Gils et al. 2006).

Estuarine systems are dynamic and complex habitats subject to increasing pressure from expanding coastal populations; however, understanding the consequences of anthropogenic or natural impacts often requires knowledge of the functioning of the entire system (e.g. Levin et al. 2001, Kennish 2002, Hooper et al. 2005). Although field and laboratory experiments may elucidate interactions between estuarine species and biogeochemical processes (e.g. Widdicombe & Austen 1998, Thrush et al. 2006, Lohrer et al. 2010a), providing pieces of a bigger picture, they rarely included multiple trophic levels (but see Petchey et al. 2004). Modelling can provide a valuable quantitative tool with which to reveal interactions at ecosystem scales, describe system properties, identify gaps in current knowledge and integrate the ‘pieces’ of information acquired in experimental studies (Jørgensen & Bendoricchio 2001). Here we adopted a modelling approach to understand the role of a suspension feeding bivalve in the food web of a shallow estuary.

Process-based models tend to focus on lower trophic levels and require substantial spatially and temporally resolved datasets for calibration and validation; food-web models, however, can be used to explore the energy flow and interactions between multiple trophic levels, and can be parameterised using comparatively smaller datasets gathered for other purposes (e.g. Gaedke 1995, Fulton et al. 2003, Christensen et al. 2008). Ecopath is a mass-balance food-web model that is widely used in fisheries management and has previously been used to model the interactions between species in a wide range of coastal systems, including estuaries (Christensen & Pauly 1992, Christensen et al. 2008). Output from Ecopath can be used to quantify certain ecosystem properties, (e.g. the degree of internal recycling, food web complexity, or realised growth and development), which can characterise ecosystem maturity (sensu Odum 1969) and may be related to ecosystem stability (e.g. Vasconcellos et al. 1997).

Worldwide, infaunal suspension feeding bivalves dominate intertidal areas in many estuaries, although populations have declined in a number of these systems in recent decades (e.g. Piersma et al. 2001, Peterson 2002, Kraeuter et al. 2008). In New Zealand estuaries, a dominant feature on intertidal flats is large, high-density (c. 1000 ind. m^{-2}) beds of the infaunal suspension feeding bivalve, *Austrovenus stutchburyi* (Dobbinson et al. 1989, Whitlatch et al. 1997). *Austrovenus* is known to be a key species in these systems, capable of influencing microphytobenthos productivity and nutrient cycling, as well as providing a food source for shorebird and ray species (Thrush et al. 1991, Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011a). *Austrovenus* populations are declining in some areas, however, likely due to adverse effects associated with sedimentation, pollution and over-harvesting (De Luca-Abbott 2001, Norkko et al. 2006, Cummings et al. 2007).

I constructed an Ecopath model for a shallow estuary (Whangateau Harbour, North Island, New Zealand) which is representative of a relatively unimpacted (in terms of nutrient enrichment) system with high water quality (typically low nutrient, chlorophyll *a* and suspended sediment concentrations, and high dissolved oxygen concentration (Scarsbrook 2008)) and containing an abundant *Austrovenus* population (Pawley 2011). The objectives were to gain an overview of the functioning of the entire system, in terms of energy flow between species, and to assess the potential effects of a decline in the *Austrovenus* population on the ecosystem. I hypothesised that *Austrovenus* would be a key species in the system, exerting considerable influence on both higher and lower trophic levels. I also aimed to determine the sensitivity of the model to changes in *Austrovenus* biomass, and the implications of changes in *Austrovenus* biomass for other species in the system and for ecosystem maturity and stability.

4.2 Methods

4.2.1 Model description

Ecopath with Ecosim (EwE v 6.1 (Christensen et al. 2008)) is derived from the Ecopath program of Polovina (1984) to estimate the biomass and food consumption of species or groups of species in an ecosystem. It has since been modified to base parameterization on an assumption of mass-balance over an arbitrary period (typically one year), and combined with approaches from theoretical ecology for the analysis of flow (i.e. transfer of energy) between species or groups of species (Ulanowicz 1986, Christensen & Pauly 1992, Christensen et al. 2008). Parameterization is based on two governing equations; the first describes production for each group *i* (which may be a single species, or a group of species that share a functional role), whereby prey mortality equates to consumption for a predator:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

where P_i is production, Y_i is total fishery catch, B_i is biomass, $M2_i$ is total predation, E_i is net migration (emigration – immigration), BA_i is biomass accumulation, and EE_i is ‘ecotrophic efficiency’, which is the proportion of production that is utilized in the system. The term given by $P_i \cdot (1 - EE_i)$ is also described as ‘other mortality’ ($M0_i$).

Ecopath consists of linear equations for each group in the system, which it solves for one of the following four parameters: biomass (B_i), production/biomass ratio (P_i/B_i), consumption/biomass ratio (C_i/B_i), or ecotrophic efficiency (EE_i). The other three parameters, along with catch, net migration, biomass accumulation, assimilation and diet composition, must be entered for each group. After ensuring mass balance between groups the energy balance within a group is ensured using the second governing equation:

$$C_i = P_i + R_i + UA_i$$

where C_i is consumption, P_i is production, R_i is respiration and UA_i is unassimilated consumption. A balanced model is defined as one in which $EE < 1$ for all model groups. If $EE \geq 1$ for one or more groups, the model is deemed unbalanced (because consumption of a group cannot be greater than its production), and the input parameters must be adjusted to obtain a balanced solution (Christensen & Walters 2004). Abbreviations used for model parameters, groups and ecosystem indices are listed in Table 4.1.

Table 4.1: List of abbreviations

Abbreviation	Denotes	Units
Model parameters		
B	Biomass	g C m^{-2}
P	Production	g C m^{-2} yr^{-1}
C	Consumption	g C m^{-2} yr^{-1}
R	Respiration	g C m^{-2} yr^{-1}
A	Assimilation	g C m^{-2} yr^{-1}
EE	Ecotrophic efficiency	
UA	Unassimilated consumption	
Model groups		
Bir	Birds	
Ray	Rays	
FPi	Piscivorous fish	
FIn	Invertebrate feeding fish	
FPl	Planktivorous fish	
FHe	Herbivorous fish	
BCa	Carnivorous benthic invertebrates	
Aus	*Austrovenus stutchburyi*	
BSu	Benthic suspension feeding invertebrates	
BDe	Benthic deposit feeding invertebrates	
Zoo	Zooplankton	
Mac	Macrophytes	
MPB	Microphytobenthos	
Phy	Phytoplankton	
Det	Detritus	
Summary statistics and ecosystem indices		
TPP	Total primary production	g C m^{-2} yr^{-1}
TR	Total respiration	g C m^{-2} yr^{-1}
TB	Total biomass	g C m^{-2}
TST	Total system throughput	g C m^{-2} yr^{-1}
TL	Trophic level	
TE	Transfer efficiency	%
MTI	Mixed trophic impact	
A	Ascendency	flowbits
Ca	Development capacity	flowbits
O	Overhead	flowbits
A/Ca	Relative ascendency	%
CI	Connectance index	
SOI	System omnivory index	
FCI	Finn's cycling index	%

4.2.2 Study area

Whangateau Harbour is located on the north-east coast of New Zealand (36°19'S, 174°46'E), 60 km north of the city of Auckland (Figure 4.1). It was chosen as the model system because it is representative of a common estuary type in New Zealand (Hume et al. 2007), and has been the focus of a relatively large number of studies, which provide a substantial amount of data suitable for model parameterisation (see reviews by Kelly 2009, Townsend et al. 2010). Whangateau is a small barrier-enclosed lagoon (area 7.5 km^2, mean depth 1.6 m), which has extensive intertidal sandflats (comprising 85 % of total estuary area), is well-flushed (the tidal prism is 81 % of total estuary spring-tide volume), and receives little freshwater input (Hume et al. 2007). Substrate transitions from sand in the main body to mud in the sheltered parts of the arms, and the resulting complex and varied habitat supports diverse benthic macrofauna and fish communities (e.g. Francis et al. 2005, Alfaro 2006). A recent (February 2009) mass mortality event resulted in the loss of c. 60 % of the *Austrovenus* population on shellfish beds in the harbour (MFish 2009; C. Pilditch unpublished data). The event was attributed to a combination of infection by a coccidian parasite and a mycobacterium, and high temperatures coinciding with midday low tides (MFish 2009; K. Tricklebank, pers. comm.). Surveys conducted on the shellfish beds before and after the event provided an opportunity to compare the observed changes in *Austrovenus* biomass with the Ecopath model sensitivity.

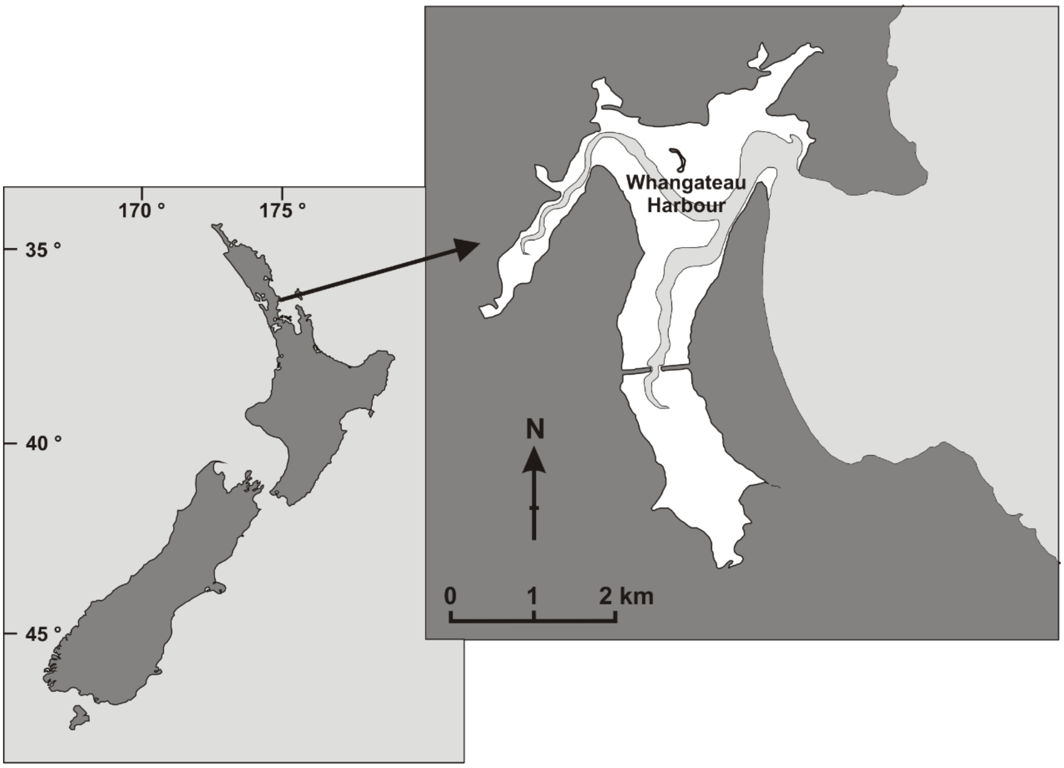

Figure 4.1: Whangateau Harbour, New Zealand. Land is shaded dark grey, intertidal flats are white, and subtidal areas are light grey.

4.2.3 Model groups and input

The food web of Whangateau Harbour was defined as having 15 groups, based on available information on functional role and diet composition for species known to inhabit the estuary (Appendix 1). *Austrovenus* was placed in a group separate from other benthic suspension feeders; previous research has established that *Austrovenus* impacts greatly on estuarine ecosystem function, and dominates benthic macrofaunal biomass over large areas of intertidal flats (Jones et al. 2011a, Thrush et al. 2006, Sandwell et al. 2009, Lohrer et al. 2010a). All available information on biomass, P/B and C/B ratios, and diet composition for each of the model groups were assembled from scientific articles, reports, theses and unpublished data, and converted into the model currency, i.e. g carbon m^{-2} for biomass and g carbon m^{-2} yr^{-1} for production and consumption. Quantitative data on diet composition for each of the species/groups in this model were extremely scarce. Where only qualitative estimates were available it was assumed that the proportion of prey in the diet of a group was proportional to the fraction that its biomass contributed to the total biomass of all the prey items for the group. Unassimilated consumption (i.e. the fraction of food that is egested and directed to detritus) was assumed to be 0.4 for zooplankton, 0.3 for herbivores, and 0.2 for carnivores (Christensen et al. 2008). Recreational *Austrovenus* harvest was also included as a fishery in the model, but there are no data available for harvest of other species. The origin of the input data and the methods used to convert biomass (often reported as wet weight or dry weight) to carbon are given in Appendix 1. Input parameters and diet composition are summarised in Table 4.2.

Table 4.2: (a) Balanced model input and output (in bold) parameters, and diet matrix (b) where numbers represent percentage prey (rows) taken by predators (columns).

Group	a) Input and output parameters										b) Diet Matrix										
	TL	B	P/B	C/B	EE	P/C	UA	R/A	P/R	R/B	Bir	Ray	FPi	FIn	FPl	FHe	BCa	Aus	BSu	BDe	Zoo
Bir	**3.035**	0.00457	0.2	35	**0.000**	**0.006**	**0.2**	**0.993**	**0.007**	**27.8**											
Ray	**3.006**	0.128	0.35	2.40	**0.000**	**0.146**	**0.2**	**0.818**	**0.223**	**1.57**											
FPi	**3.748**	0.017	0.33	2.99	**0.000**	**0.110**	**0.2**	**0.862**	**0.160**	**2.06**											
FIn	**3.001**	0.132	0.75	5	**0.383**	**0.150**	**0.2**	**0.813**	**0.231**	**3.25**	1.9		68.7								
FPl	**3.000**	0.010	1.07	7.87	**0.247**	**0.136**	**0.2**	**0.830**	**0.205**	**5.23**			5.2								
FHe	**2.050**	0.031	1.61	11.38	**0.164**	**0.141**	**0.3**	**0.798**	**0.253**	**6.36**			16.1								
BCa	**2.986**	0.11	1.60	9	**0.083**	**0.178**	**0.2**	**0.778**	**0.286**	**5.60**	1.7	0.5		1.6							
Aus	**2.001**	3.38	2.18	10	**0.160**	**0.218**	**0.3**	**0.689**	**0.452**	**4.82**	49.5	85.0		49.0			50.1				
BSu	**2.001**	0.17	2.18	10	**0.050**	**0.218**	**0.3**	**0.689**	**0.452**	**4.82**		0.7		1.0			1.0				
BDe	**2**	3.20	3	13	**0.095**	**0.231**	**0.3**	**0.670**	**0.492**	**6.10**	46.9	13.8	8.0	46.8	20.0		47.4				
Zoo	**2**	0.022	20	80	**0.268**	**0.250**	**0.4**	**0.583**	**0.714**	**28.0**			2.0	0.1	80.0	5.0		0.1	0.1		
Mac	**1**	**0.186**	18		0.100											95.0					
MPB	**1**	3.00	53.3		**0.237**													80.0	80.0	20.0	65.0
Phy	**1**	0.11	260		**0.130**													10.0	10.0		10.0
Det	**1**	151			**0.196**									1.5			1.5	9.9	9.9	80.0	25.0

TL = trophic level, B = biomass (g C m^{-2}), P = production (g C m^{-2} yr^{-1}), C = consumption (g C m^{-2} yr^{-1}), EE = ecotrophic efficiency, UA = unassimilated consumption, R = respiration (g C m^{-2} yr^{-1}), A = assimilation (g C m^{-2} yr^{-1}). For group name abbreviations see Table 4.1.

4.2.4 Diagnostic tests

Prior to balancing the model several diagnostic tests were performed to evaluate the validity of the input data. These pre-balancing tests (Link 2010) allow identification of issues with model structure and data quality by examining the conformity of input data to simple ecological and physiological rules. Biomass, “vital rates” (i.e. production, consumption and respiration), vital rate ratios and biomass to total primary production (TPP) ratios were plotted against the model groups in order of decreasing trophic level (Figure 4.2). Although not a required Ecopath input parameter, respiration is useful in diagnostic tests and was estimated as 65 % of assimilated consumption for each functional group (Link et al. 2006).

Biomass, vital rates and vital rate ratios should increase with decreasing trophic level and be within acceptable limits, i.e. P_i/C_i should be less than 0.5, $P_i/R_i < 1$, $B_i/TPP < 1$ and $C_i > P_i$ (Link 2010). When these rules were not met parameters were corrected by increasing or decreasing by a multiple of 0.2, 0.5, or 1.333 until the parameter conformed to the expectations of the diagnostic test (Byron et al. 2011). The tests revealed that P/C values for bird and fish groups were too low, and so the initial estimates for P/B and C/B were adjusted accordingly. Reasonable P/C ratios for fish groups range from 0.1 for piscivorous fish to 0.15 for herbivorous and invertebrate feeders; P/C ratios for birds are typically less than 0.1 (Christensen et al. 2008, Byron et al. 2011).

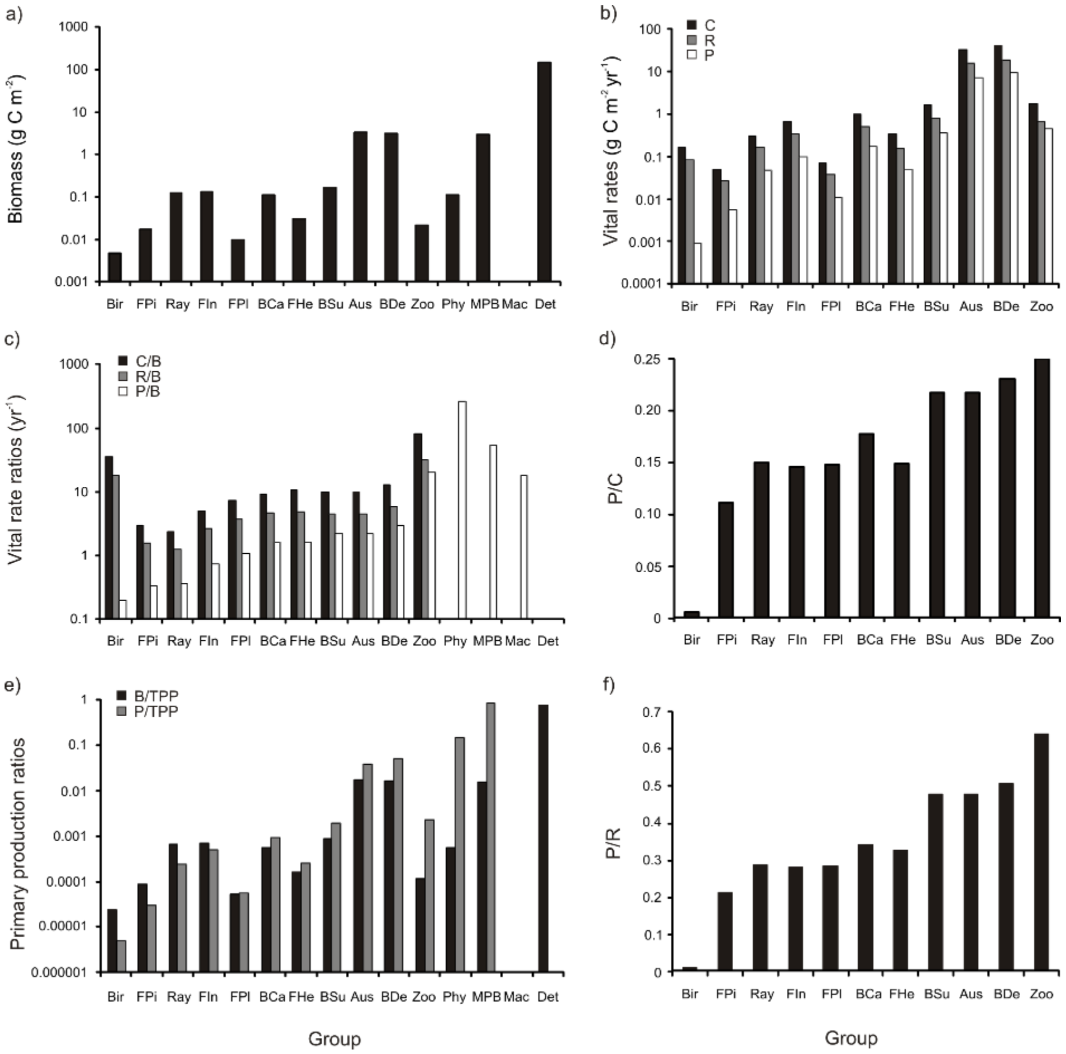

Figure 4.2: Input parameters adjusted after pre-balancing diagnostic tests. Groups arranged on x-axes in order of decreasing trophic level to depict trophic decline in (a) biomass, (b) vital rates, (c) vital rate ratios, (d) P/C, (e) biomass and production relative to primary production, and (f) P/R. For group name and parameter abbreviations see Table 4.1.

4.2.5 Model balancing

The input parameters for biomass, P/B and C/B did not need adjusting to balance the model as ecotrophic efficiency (EE) was less than one for all groups (Table 4.2). Ecopath provides output for predation mortality, showing which predators contribute most to a prey's mortality, and electivity, a selection index describing a predator's preference for prey. Both were examined to ensure the predation pressures and preferences were reasonable. The diet compositions for two fish groups (planktivores and herbivores) were adjusted slightly to bring the preferences into line with what was expected based on available literature

(Appendix 1). Ecopath also provides output for consumption, respiration and assimilation, allowing the user to check that ratios are within acceptable limits. A number of these rates had already been checked during pre-balance diagnostic tests, but examination of model output was necessary to ensure the balanced model values were within realistic ranges. Ratios of P/C < 0.3, and P/R < 1. Ratios of respiration to assimilation (R/A) were also less than one, and decreased with trophic level. Ratios of respiration to biomass (R/B), which are an expression of the activity level of a group, were also within the ranges reported in the literature (Bradford-Grieve et al. 2003, Jiang & Gibbs 2005, Christensen et al. 2008).

4.2.6 Model outputs

Ecopath provides a number of outputs that can be used to characterise the trophic structure and energy flow in a modelled system. Fractional trophic levels (TLs) are assigned to each model group; producers and detritus have, by definition, a TL of 1 and TL for consumers is calculated as 1 + the weighted average of the preys' TLs (Christensen et al. 2008). The components of the modelled system are also aggregated into discrete trophic levels, allowing calculation of trophic transfer efficiencies, i.e. the fraction of throughput at each trophic level that is transferred to the next trophic level (Lindeman 1942). Summary statistics provide overall measures of consumption, respiration, export and flows to detritus, as well as total and primary production, and gross efficiency of any fisheries (i.e. catch / net primary productivity). Ecosystems have a tendency to internalise flows, and to increase control system feedback, compartment specialisation and diversity as they develop and mature (Odum 1969). Some of these attributes of ecosystem development are quantified by Ecopath using indices such as total system throughput, ascendency, system omnivory index, Finn's cycling index and mean path length (Christensen et al. 2008).

Total system throughput (TST) is a measure of the size of a system, and is calculated as the sum of all flows through each group. Ascendency (A) is a measure of system organisation, scaled by system size (i.e. TST), and is measured in "flow bits" (where bit is an information unit and flow in this model is g C m^{-2} yr^{-1}). The upper limit on A is the development capacity (Ca); the difference between *A* and *Ca* is system overhead (*O*), which is the energy in reserve with which a system can deal with perturbations. The *A*/*Ca* ratio quantifies a system's realised growth, organisation and development (Ulanowicz 1986). The connectance index (CI) compares the number of actual links between groups in the system to the number of possible links; mature systems tend to have more web-like food chains, whilst developing systems are more linear (Christensen & Walters 2004). An omnivory index for each consumer is calculated as the variance in the trophic level of its prey groups, (a value of 0 indicates specialised feeding, a large value indicates the consumer feeds on many trophic levels); the system omnivory index (SOI) is the average omnivory index of all consumers weighted by the biomass consumed (Christensen 1995). Finn's cycling index (FCI) is the proportion of total system throughput that is recycled, and the mean path length is the average number of groups that an inflow or outflow passes through (Finn 1976). *A*, SOI, FCI and path length have all been shown to be correlated with ecosystem stability (Vasconcellos et al. 1997, Morissette 2007) ,, which is consistent with Odum's theory that greater internal cycling is a feature of a mature system.

Ecopath provides a form of "uncertainty analysis" in the mixed trophic impact (MTI) routine, which evaluates the impact that a very small increase in biomass of one group will have on other groups in the system (Christensen et al. 2008). Also, the "keystoneness" of each group in the system is calculated from the total impact of a group on all the others (based on MTI analysis) and the group biomass (Libralato et al. 2006). Finally, an overall measure of model quality is provided by the pedigree index, which is calculated based on categorisation of input data sources. Input parameters estimated from local data sources are scored higher than those derived from elsewhere or other models. The overall index scales from 0 (data not derived from local data) to 1 (data fully derived from local sources). As the index is partly a function of the number of groups in a system then a measure of fit, t*, is also provided (Pauly et al. 2000). Examining the quality of input data is crucial when building ecosystem models as the pedigree has been shown to be correlated with system stability (when expressed as the resilience of a system, i.e. the speed and degree of recovery to perturbations (Morissette 2007)).

4.2.7 *Calculating minimum and maximum possible* Austrovenus *biomass*

Using the original balanced Ecopath model the effect of a reduction of *Austrovenus* biomass on the ecosystem was investigated by adapting a process that has previously been used to calculate ecological carrying capacity for harvested shellfish in other systems. In these instances, shellfish biomass is increased in consecutive models until the model is no longer balanced (i.e. EE for one or more groups is greater than 1), and the point just prior to this is defined as the ecological carrying capacity (Jiang & Gibbs 2005, Byron et al. 2011). For this study, *Austrovenus* biomass was instead decreased in consecutive models until the model was no longer balanced. Two scenarios were defined. In the first scenario, recreational *Austrovenus* harvest (0.022 g C m^{-2} yr^{-1}) was maintained at levels measured in 1999, i.e. before the 2009 mass mortality event (Kearney 1999). The second scenario simulated the closure of the shellfish beds by reducing harvest to zero. *Austrovenus* biomass after the mass-mortality event was estimated to be 1.58 g C m^{-2} (see Appendix 1), which can be compared with the minimum *Austrovenus* biomass required to keep the model balanced.

Historical *Austrovenus* populations in estuaries around New Zealand were likely to have been greater than they have been in recent decades, due to habitat degradation, sedimentation and over-fishing (e.g. Cummings et al. 2007, Marsden & Adkins 2010). Therefore, as a third scenario, ecological carrying capacity was calculated by increasing *Austrovenus* biomass in consecutive models to quantify the maximum *Austrovenus* biomass the system might be able to support. Furthermore, summary statistics and network analysis indices were compared between the three scenarios and the original model to investigate the effect of this key species' biomass on energy flow and ecosystem properties.

4.2.8 *Sensitivity analysis*

A sensitivity analysis was employed to examine the degree to which biomass of model groups could vary without unbalancing the model (i.e. by pushing EE $\geq$ 1), over a range in *Austrovenus* biomass. *Austrovenus* biomass (g C m^{-2}) was changed by a factor of 0.001, 0.1, 0.2, 0.5, 2, 5, 10 and 100 of the original value and for each of these models, one at a time, biomass for each of the other groups (g C m^{-2}) was changed by a factor of 0.001 to 100 of its original value (Byron et al. 2011). Colour maps (plots of EE for *Austrovenus* biomass vs.

biomass of each other group) were used to assess the sensitivity of the model to changes in the biomass of other groups across a range in *Austrovenus* biomass.

4.3 Results

4.3.1 Model description and summary statistics

The trophic model of Whangateau Harbour is depicted in Figure 4.3. In terms of biomass, detritus was by far the largest group in the system with 151 g C m^{-2}; in contrast the total biomass of all living groups was 10.5 g C m^{-2} (Tables 4.3 and 4.4). The largest living groups were *Austrovenus* (3.38 g C m^{-2}), deposit feeding benthic invertebrates (3.20 g C m^{-2}) and microphytobenthos (MPB; 3.00 g C m^{-2}), and the smallest was shorebirds (0.005 g C m^{-2}). The benthic groups made up 96 % of total living biomass and the pelagic groups only 4 %. Of the primary producers, MPB were by far the largest group, making up 91 % of total primary producer biomass, (macrophytes made up 6 % and phytoplankton 3 %). Total primary production (192 g C m^{-2} y^{-1}) made up 91 % of all production (210 g C m^{-2} yr^{-1}; Table 4.4). Microphytobenthos also accounted for the majority of primary production (160 g C m^{-2} yr^{-1}; 83 % of total), whereas phytoplankton production was 29 g C m^{-2} yr^{-1} (15 % of total) and macrophyte production was only 3.3 g C m^{-2} yr^{-1} (2 % of total). Consumption by the benthic groups (78 g C m^{-2} y^{-1}) far outweighed that of the pelagic groups (3 g C m^{-2} y^{-1}). Consumption by *Austrovenus* totalled 33.8 g C m^{-2} y^{-1}, which was exceeded only by that of deposit feeding benthic invertebrates (41.6 g C m^{-2} y^{-1}). Consumption of *Austrovenus* totalled 1.2 g C m^{-2} y^{-1}, split between birds (7 %), rays (22 %), invertebrate feeding fish (28 %) and carnivorous benthic invertebrates (43 %).

Ecotrophic efficiencies (EE) were low (< 0.4) for all groups, indicating high flows to detritus (total 190 g C m^{-2} y^{-1}) , and the low EE for detritus indicated that much more flow was entering the detritus compartments than leaving it (Table 4.3, Figure 4.3). Closer examination of model output revealed that of the total flow into detritus, 37.1 g C m^{-2} yr^{-1} was consumed and 152.9 g C m^{-2} yr^{-1} exported from the system. The only other export from the system was the *Austrovenus* harvest which was far smaller at 0.022 g C m^{-2} yr^{-1}. Total system throughput was 463 g C m^{-2} yr^{-1} (235 g C m^{-2} yr^{-1} from primary producers and 228 g C m^{-2} yr^{-1} from detritus), 18 % of which was consumed, 8 % respired, 41 % flowed to detritus, and 33 % exported (Table 4.3).

4.3.2 Trophic levels and transfer efficiency

Fractional trophic levels ranged from 1 for primary producers to 3.7 for piscivorous fish (Table 4.2). When aggregated into five discrete trophic levels, transfer efficiencies (TE) between the trophic levels ranged from 2.8 to 1.1 %, and overall TE was 2 %. The greatest proportion (65 %) of living biomass was in level II (herbivores), level I (the primary producers) accounted for 31 % of biomass, and only 4 % of total living biomass was in levels III and above (Figure 4.4). Input into level II was split almost equally between primary producers (41.9 g C m^{-2} y^{-1}) and detritus (37.3 g C m^{-2} y^{-1}).

4.3.3 Ecosystem indices

Ecosystem indices are summarised in Table 4.3. Briefly, the system omnivory index (SOI) was low (0.009) indicating that feeding for most groups was focused on a single trophic level, and the connectance index (CI) was 0.205. Finn's cycling index (FCI) was also low at 5.03 % of TST, and mean path length was 2.42. Ascendency (*A*) was 36 % of the total capacity (*Ca*).

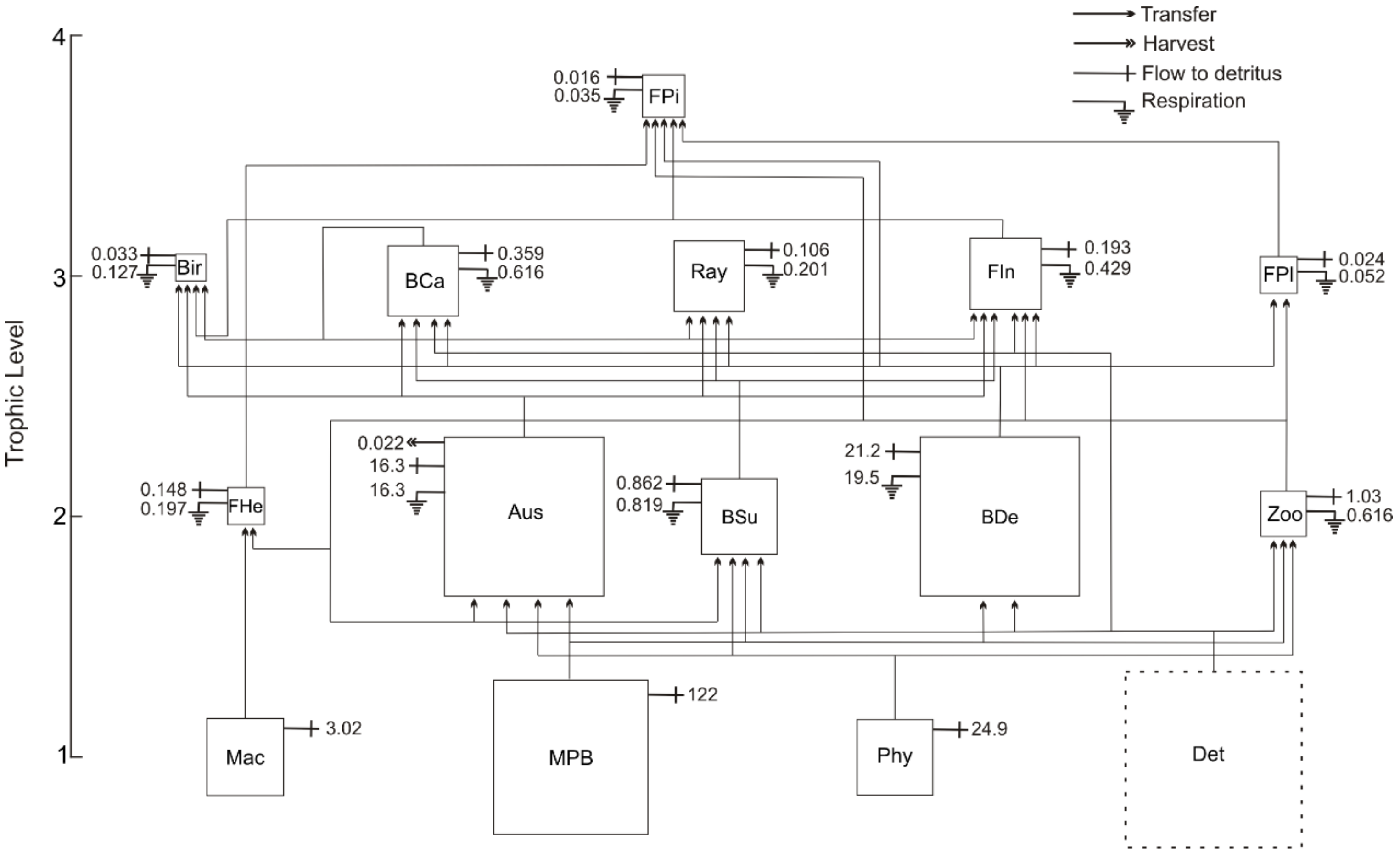

Figure 4.3: Trophic model for Whangateau Harbour. Box size is proportional to the square root of the group biomass (except for detritus). Flows are in g C m^{-2}. For group name abbreviations see Table 4.1.

Table 4.3: Ecosystem properties for balanced models representing: original model for Whangateau Harbour; the estuary at minimum *Austrovenus* biomass, with harvest maintained at 0.022 g C m^{-2} yr^{-1}, and with no harvest; the estuary at ecological carrying capacity.

Parameter	Original balanced model	Min. *Austrovenus* biomass	Min. *Austrovenus* biomass, no harvest	Ecological carrying capacity	Units
Sum of all consumption	81.5	53.5	53.1	234	g C m^{-2} year^{-1}
Sum of all exports	153	166	167	79.6	g C m^{-2} year^{-1}
Sum of all respiratory flows	38.9	25.4	25.2	112	g C m^{-2} year^{-1}
Sum of all flows into detritus	190	201	201	132	g C m^{-2} year^{-1}
Total system throughput (TST)	463	446	446	557	g C m^{-2} year^{-1}
Sum of all production	210	204	204	243	g C m^{-2} year^{-1}
Mean trophic level of the catch	2.001	2.001	2.001	2.001	
Gross efficiency (catch/net primary production)	0.000115	0.000115	0	0.000631	
Total primary production (TPP)	192	192	192	192	g C m^{-2} year^{-1}
Total primary production/total respiration (TPP/TR)	4.93	7.55	7.61	1.71	
Net system production	153	166	167	79.6	g C m^{-2} year^{-1}
Total primary production/total biomass (TPP/TB)	18.3	24.9	25	7.46	year^{-1}
Total biomass/total throughput (TB/TST)	0.0227	0.0173	0.0172	0.0461	
Total biomass (excluding detritus)	10.5	7.70	7.66	25.7	g C m^{-2}
Total catches	0.0220	0.0220	0	0.121	g C m^{-2} year^{-1}
Connectance index (CI)	0.205	0.205	0.205	0.205	
System omnivory index (SOI)	0.00871	0.00921	0.00923	0.00834	
Finn’s cycling index (FCI)	5.03	4.78	4.78	8.65	% of TST
Finn’s mean path length	2.42	2.33	2.33	2.91	
Ascendency (*A*)	509	490	490	724	flowbits
Overhead (*O*)	889	662	657	1030	flowbits
Capacity (*Ca*)	1398	1152	1147	1753	flowbits
A/*Ca*	0.364	0.425	0.427	0.413	
Ecopath pedigree index	0.353	0.353	0.353	0.353	
Measure of fit, t*	1.31	1.31	1.31	1.31	

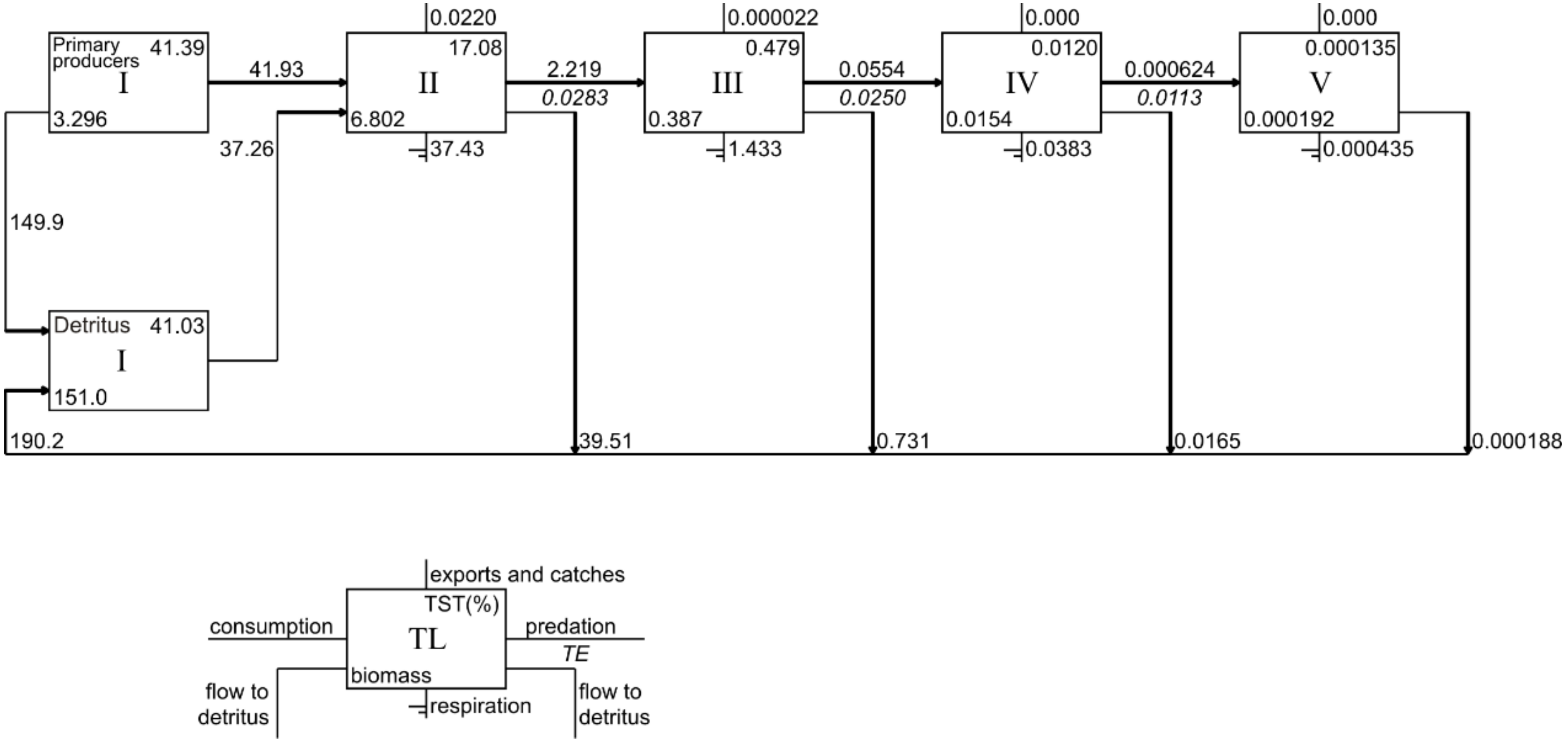

Figure 4.4: Lindeman spine showing flows between discrete trophic levels (I to V) in Whangateau Harbour. Biomass is in g C m^{-2} and flows are in g C m^{-2} y^{-1}. TL = trophic level, TST = total system throughput, TE = transfer efficiency.

4.3.4 Mixed trophic impacts and keystoneness

The mixed trophic impact analysis shows the impact a small increase in the biomass of one group has on all other groups (Figure 4.5). Of the top predators, birds and rays had little impact on any other group (except for a small negative impact on carnivorous benthic invertebrates and *Austrovenus*). Piscivorous fish, however, had a large negative impact on their prey, and a positive impact on carnivorous benthic invertebrates, zooplankton and macrophytes. Negative impacts on prey species were obvious, e.g. on zooplankton by planktivorous fish, on macrophytes by herbivorous fish, and on phytoplankton and MPB by *Austrovenus*. Microphytobenthos had a positive impact on most groups, especially *Austrovenus*, other benthic-suspension feeders, and the *Austrovenus* harvest. *Austrovenus* had relative large impacts (either negative or positive) on most other groups. All groups had a negative impact on themselves, except for the *Austrovenus* harvest, which was so small as to have little impact on itself or any other groups.

The keystoneness index shows highest values for piscivorous and invertebrate feeding fish, *Austrovenus* and MPB (Figure 4.6). *Austrovenus* had the highest total impact, but due to its large biomass its keystoneness index was reduced compared to that for groups with lower biomass (i.e. the piscivorous and invertebrate feeding fish). In contrast, phytoplankton, birds and rays had low values for the keystoneness index, despite the low biomass of these groups.

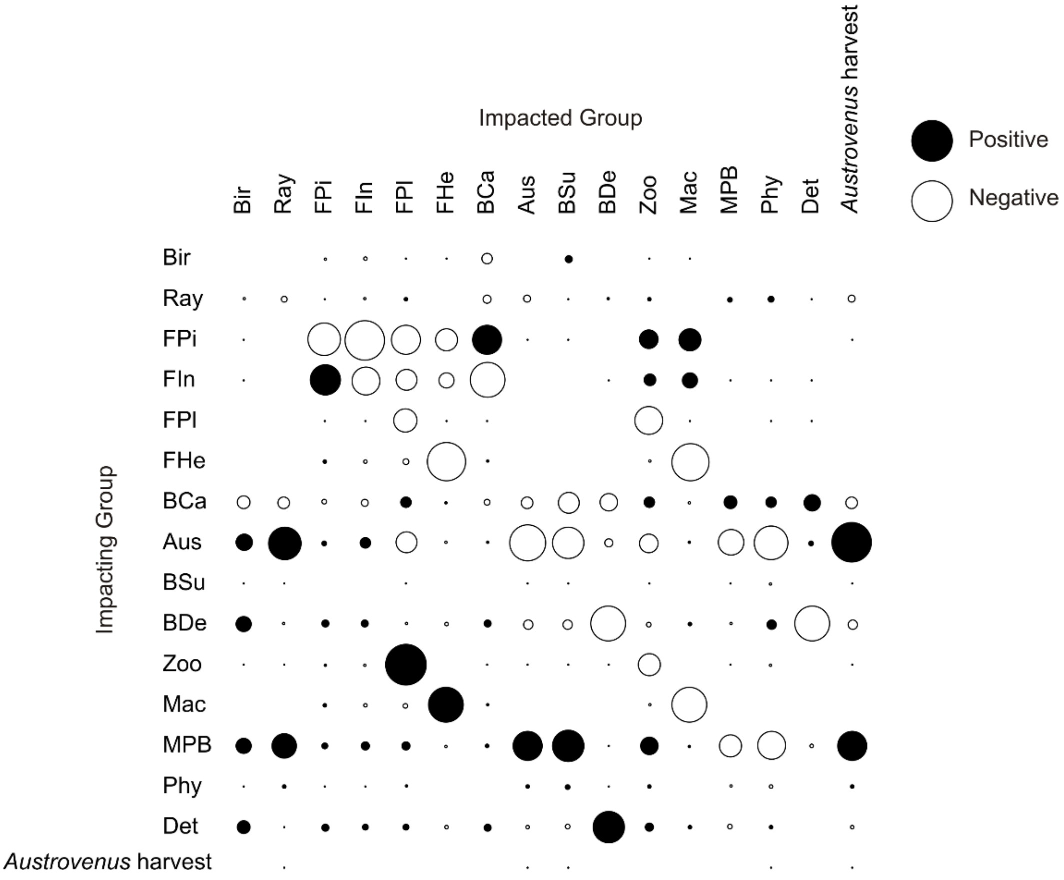

Figure 4.5: Mixed trophic impact analysis of Whangateau Harbour model. Direct and indirect impacts of a small increase in the biomass of one group (vertical axis) on all other groups (horizontal axis) are shown. Positive impacts are shown in black and negative in white. Impacts are relative and circle size is proportional to the size of the impact. See Table 4.1 for group name abbreviations.

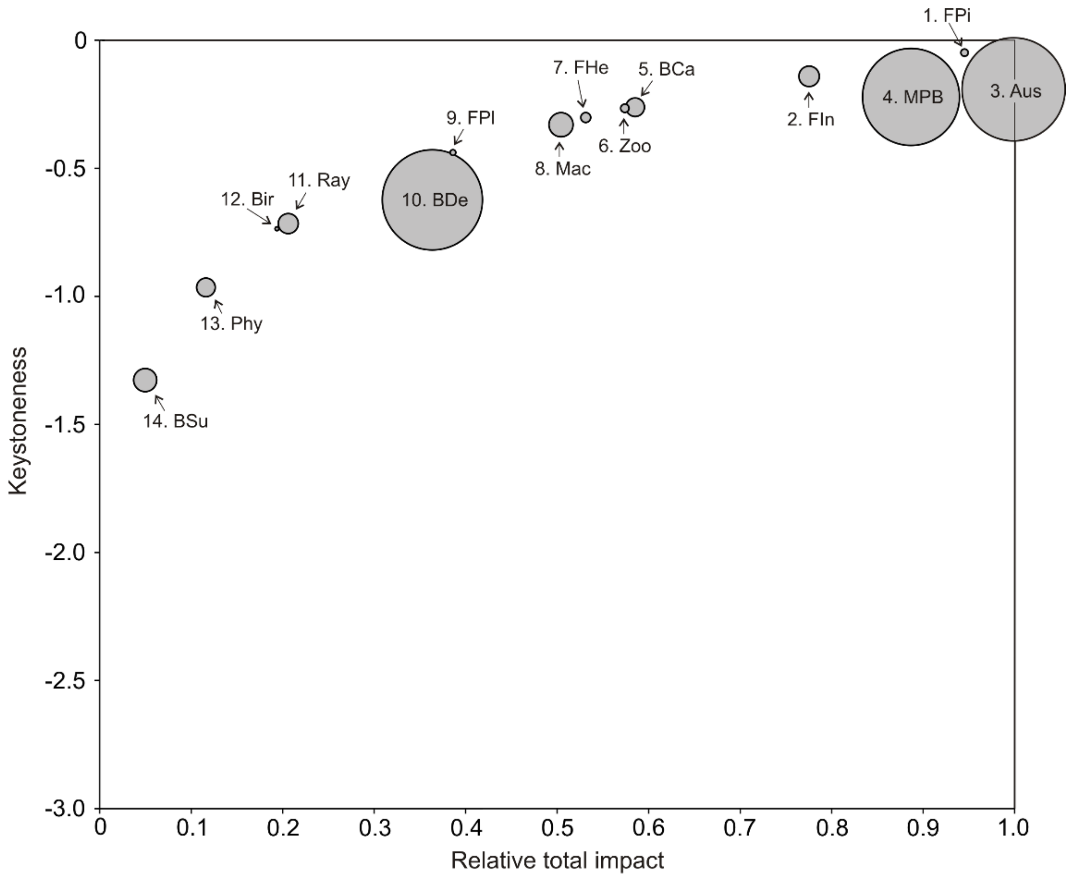

Figure 4.6: "Keystoneness" for the groups in the Whangateau Harbour model. Keystoneness is plotted against total impact (which is relative to the maximum impact and thus scaled between 0 and 1). The groups are numbered in order of decreasing keystoneness and circle size is proportional to group biomass. See Table 4.1 for group name abbreviations.

4.3.5 Austrovenus

Austrovenus biomass was decreased in small increments from the original model value of 3.38 g C m^{-2} until the model became unbalanced (i.e. EE greater than one), to calculate the minimum possible biomass (Table 4.4). Under the first scenario (with harvest pressure left as it was before the mass mortality event) biomass needed to be decreased by 83 % to 0.58 g C m^{-2} before predation pressure on *Austrovenus* was too great. With the fishery closed (i.e. zero harvest) the biomass could be decreased a little further (to 0.54 g C m^{-2}) before the model was unbalanced. *Austrovenus* biomass following the 2009 mass mortality event (i.e. 1.58 g C m^{-2}; Appendix 1) was nearly three times greater than the minimum possible biomass, as determined in this analysis.

Increasing *Austrovenus* biomass in small increments suggests that the biomass could increase 5.5 times to 18.6 g C m^{-2} without exceeding the ecological carrying capacity of Whangateau Harbour (Table 4.4). When biomass was increased further than this the grazing pressure on MPB was too great, with EE exceeding one. Under this scenario, *Austrovenus* harvest was also increased 5.5 times to 0.121 g C m^{-2} yr^{-1}, which is the equivalent of 154 tonnes wet weight (Appendix 1).

Total system throughput decreased slightly (by c. 4 %) when *Austrovenus* biomass was reduced to the minimum possible, but increased by 20 % when *Austrovenus* biomass was increased to ecological carrying capacity (Table 4.3). The sum of all exports increased by c. 10 % at minimum *Austrovenus* biomass, but decreased by c. 50 % at ecological carrying capacity (mostly due to the increased value for EE for detritus). Ratios of total primary production to respiration, and to total biomass, increased at minimum *Austrovenus* biomass, and decreased at ecological carrying capacity; the reverse was true for the ratio of total biomass to total throughput, Finn's cycling index and mean path length. Ascendency increased slightly at both minimum and maximum *Austrovenus* biomass compared to the original model.

Table 4.4: Effect of changes in *Austrovenus* biomass on Whangateau Harbour model under three scenarios: (1) decreasing biomass whilst maintaining harvest at 0.022 g C m^{-2} yr^{-1}, (2) decreasing biomass with no harvest to represent closure of the fishery, (3) increasing biomass (and harvest) to calculate ecological carrying capacity.

Multiplier	Biomass g C m^{-2}	Harvest g C m^{-2} yr^{-1}	Mass-balance changes
Original model representing estuary before mass mortality event			
1	3.38	0.022	
Scenario 1: biomass decreased and harvest maintained at 0.022 g C m^{-2} yr^{-1}			
0.8	2.70	0.022	Balances
0.6	2.03	0.022	Balances
0.467	1.58*	0.022	Balances
0.2	0.68	0.022	Balances
0.18	0.61	0.022	Balances
0.17	0.58	0.022	Balances
0.16	0.54	0.022	*Austrovenus* EE = 1.002
0.15	0.51	0.022	*Austrovenus* EE = 1.069
0.1	0.34	0.022	*Austrovenus* EE = 1.604
Scenario 2: biomass decreased and no harvest			
0.2	0.68	0	Balances
0.18	0.61	0	Balances
0.17	0.58	0	Balances
0.16	**0.54**	0	Balances
0.15	0.51	0	*Austrovenus* EE = 1.049
0.1	0.34	0	*Austrovenus* EE = 1.574
Scenario 3: biomass (and harvest) increased to calculate ecological carrying capacity			
2	6.76	0.044	Balances
5	16.90	0.110	Balances
5.5	**18.59**	0.121	Balances
6	20.28	0.132	MPB EE = 1.082
7	23.66	0.154	MPB EE = 1.251
10	33.80	0.220	MPB EE = 1.759, Phytoplankton EE = 1.194

Minimum and maximum *Austrovenus* biomass are highlighted in bold and *Austrovenus* biomass after 2009 mass mortality event is indicated by *.

4.3.6 Sensitivity analysis

Colour maps show the possible range in biomass for each model group over a range in *Austrovenus* biomass (Figure 4.7). The greyscale indicates the maximum EE for each model run (and thus whether or not the model was balanced), with black/grey indicating EE < 1, and therefore the possible biomass range. In contrast, white indicates EE ≥ 1, and therefore that the biomass was outside of the possible range. The plots show that with *Austrovenus* biomass left unchanged (i.e. at its original value) the model was robust to small (2-fold) changes in biomass of all groups, and was robust to large (100-fold) changes in detritus, decreases in apex predators and increases in primary producers. The model was most sensitive to changes in the biomass of *Austrovenus* and planktivorous fish as only a moderate (10-fold) change in the biomass of those groups unbalanced the model.

At minimum *Austrovenus* biomass the model was most constrained by invertebrate feeding fish, as a small increase or a moderate decrease in the biomass of that group unbalanced the model (Figure 47). In contrast, when at maximum *Austrovenus* biomass, the model was constrained by decreases in MPB, phytoplankton and zooplankton, but was very robust to changes in biomass of birds and rays.

4.3.7 Parameter quality

The overall pedigree index for the Whangateau Harbour model was 0.35 and the measure of fit was 1.3 (Table 4.3). Highest confidence was placed in biomass estimates, most of which had been derived from local data sources, reflected in their relatively high index values (c. 0.7). Ratios of P/B and C/B ratio were mostly derived from empirical relationships or other models so confidence in these estimates was lower (index values: 0.2 - 0.5). Diet compositions were mostly estimated from general knowledge about the groups/species, and so confidence in these estimates was also low (index values: c. 0.2).

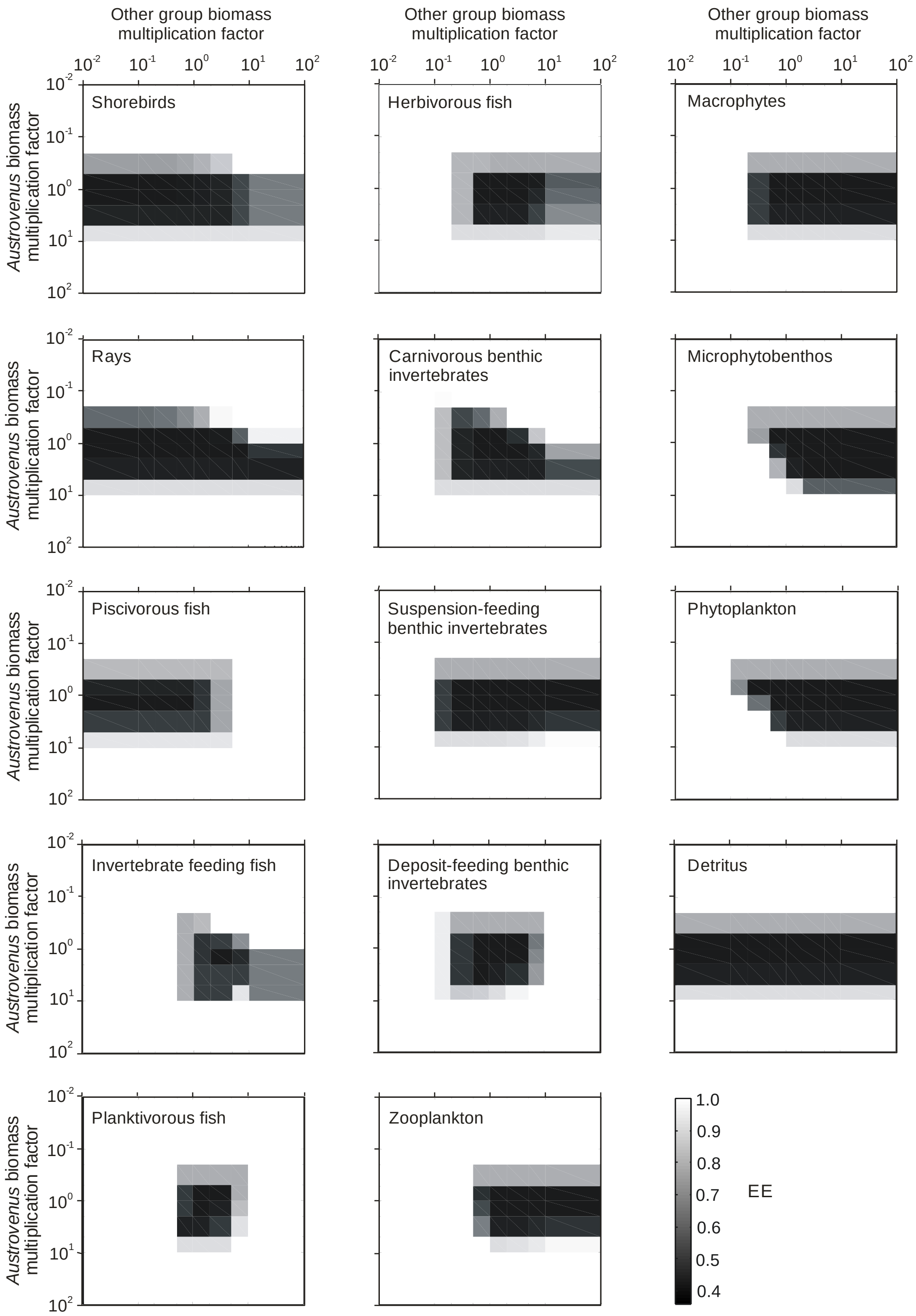

Figure 4.7: Results of sensitivity analysis. Colour maps depicting the effect of *Austrovenus* and other groups' biomass on ecotrophic efficiency (EE). Biomass for each group was multiplied by a factor of 10^{-2} to 10^{2}. White indicates EE ≥ 1 (i.e. unbalanced model). Grey/black indicates EE < 1 (i.e. balanced model) and thus the possible biomass range for each group.

4.4 Discussion

The Ecopath model for Whangateau Harbour shows a system dominated by the benthic groups, particularly *Austrovenus*, deposit feeding benthic invertebrates and microphytobenthos (MPB). The latter group was the most important primary producer, in terms of biomass and productivity, and *Austrovenus* and deposit feeding benthic invertebrates were responsible for the vast majority of total consumption. The model shows a system characterised by high flows to detritus for all groups, high detritus export, low trophic transfer efficiency and limited internal recycling. Other coastal lagoon systems overseas show similar characteristics, e.g. high MPB productivity, and significant export of organic material to the open ocean from Wilson Inlet, Western Australia (Haese & Pronk 2011), and high flows to detritus and dominance of benthic groups in Laguna de Rocha, Uruguay (Milessi et al. 2010). Whangateau shows characteristics of a shallow, oligotrophic system, with low water column biomass and primary production dominated by MPB. The model suggests that in this type of estuary suspension feeding bivalves are not important as a “natural eutrophication control”, but do play an important role facilitating the transfer of energy from MPB to other species such as invertebrate feeding fish and birds.

Estuaries such as Whangateau Harbour, barrier-enclosed lagoons with extensive intertidal flats and a tidal prism that makes up a large proportion of total volume, are widespread in New Zealand (Hume et al. 2007). The model highlights the important role of MPB, as opposed to pelagic phytoplankton, in these systems. Removal of MPB from the model reveals that phytoplankton and detrital production alone are not enough to sustain the consumer groups (i.e. a balanced solution was not obtained with benthic invertebrates and zooplankton feeding only on phytoplankton and detritus). It seems that the short residence time and shallow nature of these estuaries limits the importance of pelagic phytoplankton to benthic consumers, but high water clarity and large areas of intertidal flats allow high MPB productivity and biomass (Cahoon & Safi 2002). Previous research has shown that resuspended MPB may be an important food source for benthic suspension feeders such as *Austrovenus* (Safi 2003, Kang et al. 2006), which in turn enhance MPB productivity through excretion of ammonium (Sandwell et al. 2009, Jones et al. 2011a). High values for the keystoneness index and relatively large impacts on numerous other groups for both MPB and *Austrovenus* confirm that these groups are important components of the system, sustaining higher trophic levels. Reductions in MPB productivity and/or *Austrovenus* populations are therefore likely to impact greatly on the entire estuarine system. In particular, long-term degradation in sediment composition, in the form of increasing mud content, is likely to reduce MPB productivity by enhancing turbidity in the water column, as well as reducing the photic zone within the sediment and reducing pore-water nutrient fluxes due to decreased sediment permeability (Middelburg et al. 2000, Blanchard et al. 2001, Billerbeck et al. 2007). As well as other stressors such as pollution and over-harvesting (De Luca-Abbott 2001, Cummings et al. 2007), increasing mud content can also directly adversely affect *Austrovenus* populations; abundance is decreased in very muddy sediments and increased suspended sediment concentrations reduce feeding efficiency (Thrush et al. 2003b, Norkko et al. 2006).

The impact of *Austrovenus* harvesting on the Whangateau Harbour ecosystem appears to be relatively minor as mixed trophic impacts analysis suggests that it has little effect on other model groups. Furthermore, the gross efficiency of the harvest (ratio of catch to primary productivity) is very low (0.0115 %), indicating that the majority of ecosystem production is not removed from the estuary by harvesters. It should be noted however, that quantification of recreational shellfish harvesting is notoriously difficult (Hartill et al. 2005) and the input data used in this model was based on only one study (Kearney 1999). Furthermore, recreational harvest of other species, such as pipi (*Paphies australis*), occurs in the estuary but could not be incorporated into the model due to lack of data. The model output therefore likely underestimates recreational harvest pressure and its effect on other groups. Currently, shellfish beds in Whangateau Harbour are closed to harvesting to allow recovery from the mass mortality event (MFish 2009), but if/when harvesting resumes more effort may be needed to quantify and limit harvest pressure to prevent over-exploitation of this key species (Hartill et al. 2005).

The model produced low EE values for all model groups and flows to detritus made up 41 % of total system throughput, suggesting that a significant fraction of production is not consumed directly but enters the detrital pool. This is not uncommon in Ecopath models of coastal systems, especially well-flushed lagoons (Tomczak et al. 2009, Byron et al. 2011). Furthermore, the low EE calculated for detritus suggests that a large proportion (c. 80 %) is not used by the system components included in the model. This 'detritus export' (153 g C m^{-2} yr^{-1}) includes detritus that is buried in the sediment, decomposed by bacteria, and physically exported out of system. Reliable estimates of microbial biomass, production and respiration are scarce so bacteria were not included explicitly in the model, but were assumed to be part of detritus (Christensen et al. 2008). Therefore microbial activity will account for some of the 'detritus export'. It is also possible that some detritus is buried as the estuary is infilled by catchment-derived sediment. Sedimentation rates in Whangateau Harbour are likely to be relatively low across most of the estuary due to the small size and limited development of the catchment, and the well flushed nature of the estuary (Kelly 2009). However, mangrove expansion indicates that sedimentation is occurring in the more sheltered reaches of the estuary, and suggests that detritus burial is likely in these areas at least (Townsend et al. 2010). It is not possible to quantify, with the present model, the relative importance of microbial activity, burial in the sediment and physical export to the 'detritus export', but it may be that the latter is particularly significant in well-flushed estuaries such as Whangateau.

The tidal prism in Whangateau Harbour is 80 % of the total estuary volume, indicating that a substantial amount of detritus produced in the estuary may be advected to the coastal environment. The estuary is ebb-dominated (Grace 1972), also suggesting that the system conforms to the "outwelling hypothesis" (Odum et al. 1979), acting as a source of material to the coastal ocean (Childers et al. 2000). The flux of organic matter from Whangateau has not been measured directly, but comparison with studies from other estuaries reveals that an export of c. 150 g C m^{-2} yr^{-1} (as determined by this Ecopath model application and equivalent to 1100 tonnes yr^{-1}) is not unreasonable. In Manukau Harbour (80 km south of Whangateau), net export was estimated to be between 50 and 80 g C m^{-2} yr^{-1} from the inner to the outer estuary (Vant et al. 1998). In the few studies that have directly measured material flux at the estuarine-ocean interface the net export, although dependent on a number of biological and hydrological factors, has been calculated to be of a similar order of magnitude to this study, e.g. 453 g C m^{-2} yr^{-1} for North Inlet, South Carolina (Dame et al. 1986), and c. 320 g C m^{-2} yr^{-1} for Swartkops Estuary, South Africa (Baird et al. 1987). This export of organic material to the coastal ocean is likely to provide an energy source for plankton and benthic consumers, which may significantly influence coastal productivity in some systems (Dame & Allen 1996, Schlacher et al. 2009).

Trophic transfer efficiencies (TE) decreased with increasing trophic level, due to increased respiration at higher trophic levels, but average TE (2 %) was well below the value of 10 % that is generally considered to be the case for most ecosystems (Lindeman 1942, Christensen & Pauly 1993). Values of TE vary widely in other Ecopath models, however, dependent on the type of ecosystem, and even the model configuration; for example, high P/C ratios lead to high TE (Christensen & Pauly 1993). Furthermore, estuarine systems tend to have TE < 10 %, and in other highly flushed lagoons TE has been reported to be 5 %, due to the high production and low utilisation of detritus in these types of systems (e.g. Manickchand-Heileman et al. 1998, Wolff et al. 2000, Rybarczyk & Elkaim 2003, Christian et al. 2005, Taylor et al. 2008, Tomczak et al. 2009, Byron et al. 2011). The low TE is in agreement with the low value (5 %) calculated for the Finn's cycling index (FCI), which indicates limited internal cycling, but is within the range reported in the literature for this type of ecosystem. Both TE and FCI tend to be higher in models of estuarine systems that include bacteria (Byron et al. 2011).

Other indices are also suggestive of the Whangateau Harbour as a developing, rather than a mature system. The total primary production to total respiration ratio (TPP/TR) was high at 4.93, although respiration was likely underestimated due to omission of bacteria from the model. This ratio tends to be close to 1 in mature systems (Christensen & Pauly 1993, Christensen 1995). The connectance (CI) and system omnivory indices (SOI) suggest only a moderate number of links between groups, and that consumers tend to feed only on a single trophic level. The relative ascendency, at 36 %, suggests that the system has realised a moderate level of growth and development. Other models also tend to suggest that many estuary and bay systems are not mature (e.g. Rybarczyk & Elkaim 2003, Tomczak et al. 2009), but estuaries are by their very nature likely to be maintained in an early stage of ecosystem development, due to the repeated replenishment of nutrients by tidal or fluvial input (Odum 1969). Other research suggests that several of the indicators of ecosystem development, especially FCI and ascendency, reflect eutrophication status rather than maturity; for example, FCI will be low in less stressed estuaries, and high in polluted estuaries (Baird &

Ulanowicz 1993). The low FCI and moderate ascendency for Whangateau Harbour could therefore reflect the relatively pristine nature (i.e. high water quality) of the system (Kelly 2009). It seems that these indices are, to some degree, system specific and so may be best used to assess the effect of change on ecosystem properties within a particular system (as in e.g. Heymans et al. 2007, Baird 2009), rather than as a comparative measure across estuaries.

In this study, a possible range for *Austrovenus* biomass was established to assess the effect of this key species on ecosystem properties and other species/groups. I found that *Austrovenus* biomass was able to be substantially decreased, to 17 % of its original value, without unbalancing the model. The minimum biomass (0.54 g C m^{-2}) was less than the *Austrovenus* biomass estimated for the estuary after the mass-mortality event (1.58 g C m^{-2}), suggesting that the system is able to tolerate such a reduction in the biomass of a key species. Closure of the shellfish beds to harvesting after the mass mortality event may have been prudent, however, to enable the bivalve populations to recover, as another mortality event or overharvesting could reduce the biomass further to the critical minimum level of 0.54g C m^{-2} identified in this Ecopath model application. However, as the sensitivity analysis shows, the model is fairly insensitive to changes in biomass of all groups, and incorporating spatial and temporal dynamics into the modelling process (e.g. using Ecosim and Ecospace) might reveal that the system is more sensitive than the current results suggest.

The high MPB biomass in the system allowed the maximum *Austrovenus* biomass (i.e. ecological carrying capacity) to be 5.5 times greater than the pre-mass mortality event level, perhaps supporting anecdotal evidence of historically larger individual bivalves and bivalve populations (Marsden & Adkins 2010). In other systems detritus has been shown to make up a significant proportion of suspension feeding bivalves' diet (Kang et al. 1999, Decottignies et al. 2007). If detritus were to be a more important component in *Austrovenus* diet (than is assumed in this model) then there is the potential for even greater ecological carrying capacity due to the current low utilisation of detritus. However, as a substantial amount of detritus, phytoplankton and resuspended MPB is likely to be removed from the estuary by tidal flushing ecological carrying capacity calculations should be viewed with caution.

Comparison of the ecosystem indices across the original, minimum and maximum *Austrovenus* biomass models indicates that maturity increases as *Austrovenus* biomass increases. At minimum *Austrovenus* biomass, TPP/TR and TPP/TB increased, and TB/TST and FCI decreased. The reverse occurred at ecological carrying capacity; for example TPP/TR was close to 1 and FCI increased. Ratios of TPP/TR are considerably greater or less than 1 in developing ecosystems and close to 1 in mature ecosystems, TPP/TB is high in immature systems and diminishes as they mature, and TB/TST tends to increase as a system matures (Christensen 1995). Also, FCI is positively correlated with ecosystem maturity and stability (Vasconcellos et al. 1997). The results of this study therefore suggest that reductions in *Austrovenus* biomass may decrease the stability and resilience of the ecosystem.

Ecosystem complexity has also been shown to be correlated with stability, thought to be due to the increased numbers of linkages between species in complex or highly diverse systems affording a degree of resilience to perturbations (e.g. Eklof & Ebenman 2006, Thebault & Loreau 2006, Morissette 2007). CI, SOI and ascendency provide measures of complexity, but comparison of these indices across the original, minimum and maximum *Austrovenus* biomass models reveals little. This is because in Ecopath, ecosystem complexity is largely a function of model complexity, i.e. the number of model groups, aggregation of species into those groups, and links between groups as defined in the diet matrix. Model pedigree has also been found to be correlated with system stability, i.e. higher quality models tend to perform better at predicting changes in biomass than poor quality ones (Morissette 2007) . The pedigree index for the Whangateau model (0.35) indicates that the input data was of moderate quality, although there is considerable scope for improvement (Morissette 2007). Thus, it may be sensible to focus future effort on improving data quality, and increasing model complexity, before more detailed scenario testing is undertaken with a temporally dynamic simulation such as Ecosim (Walters et al. 1997, Walters et al. 2000).

The sensitivity analysis revealed that the original model could withstand moderate changes in the biomass of all groups, suggesting that the system is fairly robust to perturbations (although incorporating temporal dynamics into the model would be necessary to confirm this). As would be expected, the model is most constrained by increases in predators (rays, invertebrate feeding fish, carnivorous benthic invertebrates), or decreases in prey (microphytobenthos, phytoplankton), at minimum and maximum *Austrovenus* biomass, respectively. A sensitivity analysis can also reveal for which groups it is critical to obtain high quality input data (Christensen & Walters 2004). The relatively narrow range of possible biomass values for the fish groups (particularly the planktivores) suggests that as the model is sensitive to changes in these parameters, accurate biomass estimates are important for these groups. Quantitative data on fish abundance/biomass in New Zealand estuaries is very scarce and the abundance data for this model were mostly taken from one study (Morrison & Carbines 2006) conducted in Mahurangi Harbour (located 20 km south of Whangateau Harbour). Fish usage of Mahurangi Harbour may be quite different to Whangateau, as Mahurangi is a larger and deeper estuary; Mahurangi Harbour area at high tide is 24.6 km^2, of which 51 % is intertidal, and mean depth is 2.74 m *cf.* Whangateau Harbour area of 7.46 km^2, of which 85 % is intertidal, and mean depth is 1.56 m (NIWA 2011). The sensitivity analysis seems to highlight the uncertainty around the input parameters for the fish groups and the need for input data derived from the modelled system.

Finally, as this model suggests that a large proportion of system throughput is exported (as detritus) it may be advantageous to increase the modelled area to include the open coast. Systems modelled using Ecopath need to be fairly self-contained, i.e. the interactions occurring within the system should exceed the import and export from a system (Christensen et al. 2008). Although this was the case in this study, (export was less than half TST), there is substantial exchange between estuaries and connected environments. Apart from export of organic matter, a number of fish species migrate to and from estuaries, or use estuarine habitats as nursery grounds before dispersing to open coast environments (Morrison et al. 2002, Francis et al. 2005). However, a model of this complexity would require much more data, especially on fish usage and abundance, and the exchange of detrital material between the estuary and the coast, than is currently available.

In summary, the Ecopath model application to Whangateau Harbour reveals that it is a developing, rather than a mature system, with low trophic transfer efficiencies, high flows to detritus and high detritus export. The model confirms that *Austrovenus* is a key species in these systems, which represents a large proportion of total biomass and impacts greatly on all other trophic levels. Furthermore, the model reveals that phytoplankton and detritus production alone are not sufficient to support consumers, highlighting the important role of MPB in these systems. Previous research has established that *Austrovenus* enhance MPB productivity by increasing nutrient availability (Sandwell et al. 2009, Jones et al. 2011a). Thus, reductions in *Austrovenus* biomass will likely impact on MPB, and most other groups (e.g. birds and rays) in the estuary. Moreover, ecosystem indices calculated by the model suggest that reductions in *Austrovenus* biomass will reduce ecosystem maturity, which will likely reduce stability and resilience.

CHAPTER 5

General discussion and conclusions

The overall aim of this thesis was to quantify the effect of *Austrovenus* populations on ecosystem structure and function, i.e. the influence of *Austrovenus* on nutrient cycling and primary productivity, the interactions between *Austrovenus* and other species in estuarine systems, and the potential effects of a decline in *Austrovenus* population on ecosystem properties. Additionally, I aimed to quantify *Austrovenus* clearance rates (CR) at bed densities and flow speeds equivalent to *in situ* conditions, so that I could scale up *Austrovenus* grazing rates to ecosystem level. The bed CR obtained from the experiments in chapter 2 allows me to ascertain the grazing pressure exerted by *Austrovenus* in Whangateau Harbour (the same estuarine system modelled using Ecopath in chapter 4).

5.1 *Austrovenus* grazing pressure in Whangateau Harbour

Suspension feeding bivalves have long been described as a ‘natural eutrophication control’ as they are thought to be capable of exerting considerable top-down control on phytoplankton populations (Officer et al. 1982). Estimates of bivalve grazing pressure, typically calculated by scaling up individual clearance rates (CR) to the ecosystem level, have shown that in some cases the suspension feeders are capable of filtering the entire volume of a system within a few days (Cloern 1982, Hily 1991, Smaal & Prins 1993, Dame & Prins 1998). However, this approach may overestimate grazing pressure as laboratory derived CR tend to overestimate *in situ* rates, which are affected by environmental variables such as seston quantity and quality (e.g. Navarro & Widdows 1997, Hawkins et al. 2001) and flow speed (e.g. Wildish & Saulnier 1993, Sobral & Widdows 2000, Newell et al. 2001, Jones et al. 2011b).

In chapter 2 I showed bivalve bed density also has a significant effect on CR, and quantified *Austrovenus* CR over a range of densities and flow speeds. *Austrovenus* density has been surveyed in Whangateau Harbour for a number of years, allowing me to use my CR data to estimate the grazing pressure exerted by *Austrovenus* in that system. Scaled up grazing rates can be used to calculate bivalve clearance time (CT; days), which is the theoretical time needed for the bivalve population of a system to clear seston from a volume of water equivalent to the total system volume (Dame & Prins 1998). This can be compared with two other ecosystem scale parameters, water residence time and phytoplankton production time, to assess the potential for the bivalve population to control phytoplankton biomass (Dame & Prins 1998, Duarte et al. 2005). Water residence time (RT; days) is the theoretical time is takes for the water volume of a system to be exchanged with water from outside the system. Phytoplankton production time (PT; days) is the ratio of phytoplankton biomass to phytoplankton primary production.

Bivalve grazing pressure in Whangateau Harbour was calculated by dividing the *Austrovenus* population into two areas, high-density shellfish beds and low-density areas covering the rest of the intertidal, which were then combined to calculate total population CR (Table 5.1). Methodology used to calculate mean density in these areas was consistent with the Ecopath study in chapter 4. Ministry of Fisheries survey data was used to estimate mean density and size for the high-density beds, and the mean density for the rest of the intertidal area was assumed to be 50 ind. m^{-2} (Walshe et al. 2006, Pawley & Ford 2007, Pawley 2011). Also, the data was split into two periods, before and after the 2009 mass mortality event to quantify its effect on the population CR.

Bed CR was calculated for each area, using the equations derived in chapter 2, for three flow speeds (2, 5 and 15 cm s^{-1}, i.e. “low”, “medium” and “high”, respectively), which are representative of *in situ* flow speeds. Other environmental variables are also likely to affect CR, and my calculations are likely to overestimate grazing pressure because of the relatively high concentration of phytoplankton used in the CR experiments, not the mix of inorganic and organic material found in estuarine seston (Cranford 2001). Bivalve size can also affect CR; unsurprisingly, larger animals tend to have higher absolute CR (e.g. Sylvester et al. 2005). The mean size (shell length) of *Austrovenus* before the mass mortality event (23.4 mm) was equivalent to the size of the animals used in the CR experiments in chapter 2, so the equations are likely to be valid for this period. After the mass mortality event, however, mean size in the high-density beds was reduced to 20.5 mm. Individual CR is known to be an allometric function of individual biomass, and biomass is an allometric function of shell length (Bayne 1998). The relationship between shell length and biomass for *Austrovenus* is given by:

$$M = a \cdot L^{b}$$

where M is ash free dry weight (g AFDW), L is shell length (cm), and a and b are coefficients determined to be 6×10^{-7} and 3.788, respectively (author's unpublished data; $r^2 = 0.93$, $n = 140$). Though there are no data available for *Austrovenus*, the relationship between CR and biomass for the European cockle, *Cerastoderma edule*, is given by:

$$CR = c \cdot M^{d}$$

where CR is clearance rate ($m^3\ d^{-1}\ ind^{-1}$), M is g AFDW, and c and d are coefficients determined to be 0.041 and 0.61, respectively (Smaal et al. 1997). Using these relationships for *Austrovenus* in Whangateau Harbour suggests that the mean size (shell length) decrease from 23.4 mm to 20.5 mm results in a 22 % decrease in CR. Bed CR in the high-density beds after the mass mortality event was thus reduced by 22 % to account for the reduction in bivalve size. To calculate population CR, bed CR were scaled by the area, (641,500 m^2 for the high-density beds, 4,780,000 m^2 for the low-density area), and converted to the volume of water cleared per tidal cycle, based on the assumption that the bivalves feed for 4 hours per tide (Beentjes & Williams 1986).

My calculations indicate that before the mass mortality event the total volume of water cleared by *Austrovenus* per tidal cycle was between 565,100 and 1,653,300 m^3, depending on flow speed (Table 5.1). After the mass mortality event, the population CR was reduced slightly to between 529,600 and 1,391,500 m^3. Averaged across the three flow speeds the water cleared by *Austrovenus* before the mass mortality event (1,055,100 m^3) was equivalent to c. 9 % of total harbour volume (i.e. 11,663,589 m^3; Table 5.2). After the mass mortality event this was reduced to 931,300 m^3 (or c. 8 % of total harbour volume).

Table 5.1: Whangateau Harbour *Austrovenus* population clearance rates calculated for three flow speeds (2, 5 and 15 cm s^{-1}, i.e. "low", "medium" and "high", respectively)

Harbour area	Density	Size	Bed clearance rate (L hr^{-1} m^{-2})[†]			Population clearance rate per tidal cycle (m^3)‡			
	(ind. m^{-2})	(mm)	Low	Medium	High	Low	Medium	High	Average
Before mass mortality event									
High-density beds	495	23.4	94.4	48.1	276.0	242000	123400	707700	357700
Low-density areas	50	23.4	36.9	23.1	49.5	704800	441700	945600	697400
Total			131.2	71.2	325.5	946800	565100	1653300	1055100
After mass mortality event									
High-density beds*	372	20.5	65.5	34.3	173.8	168000	87900	445900	233900
Low-density areas	50	23.4	36.9	23.1	49.5	704800	441700	945600	697400
Total			102.3	57.4	223.2	872800	529600	1391500	931300

[†] Bed clearance rate (BCR) at each flow speed calculated from equations derived in chapter 2, i.e. at low flow speed, $\log_{10}(BCR) = 0.41(\log_{10}(\text{bed density})) + 0.87$; at medium flow speed, $\log_{10}(BCR) = 0.32(\log_{10}(\text{bed density})) + 0.82$; and at high flow speed, $\log_{10}(BCR) = 0.75(\log_{10}(\text{bed density})) + 0.42$.

‡ Population clearance rate calculated by scaling BCR by area (641,500 m^2 for high density beds and 4,780,000 m^2 for low density areas) and assuming *Austrovenus* feed for 4 hours per tidal cycle.

* BCR reduced by 22 % for high-density beds after mass mortality event to account for reduction in mean size.

Individual CR for *Austrovenus* has previously been estimated to be c. 1 L hr^{-1} (Heggie 2008, Kainamu 2010) and at low densities (i.e. ≤ 100 ind. m^{-2}) I found individual CR to be c. 0.7 L hr^{-1} (averaged across the three flow speeds). Using this individual CR to scale up grazing rates for Whangateau Harbour yields a population CR of c. 1,643,000 m^3 per tidal cycle (based on the pre- mass mortality event *Austrovenus* population of 557 million individuals, i.e. 495 ind. m^{-2} over 641,500 m^2 and 50 ind. m^{-2} over 4,780,000 m^2). This is 55 % greater than that calculated using bed CR and illustrates the degree to which bivalve grazing pressure can be overestimated using CR derived at low densities.

Table 5.2: Ecosystem scale parameters for Whangateau Harbour

Physical characteristics and turnover rates	Value	Units
Estuary volume at spring tide[†]	11663589	m^3
Spring tidal prism[†]	9491105	m^3
Austrovenus population clearance rate per tidal cycle		
Before mass mortality event	1055000	m^3
After mass mortality event	961200	m^3
Clearance time (estuary volume / volume of water cleared)		
Before mass mortality event	5.54	days
After mass mortality event	6.07	days
Residence time (estuary volume / volume of water exchanged)	0.61	days
Phytoplankton production time (biomass / primary production)	1.40	days

[†] Source: http://wrenz.niwa.co.nz/webmodel/coastal (NIWA Coastal Explorer)

The volume of water cleared by the *Austrovenus* population each tidal cycle is much less than the tidal prism (9,491,105 m^3), and the ecosystem scale parameters reveal that the bivalve clearance time (c. 6 days) is much greater than both the water residence and phytoplankton production times (0.61 and 1.4 days, respectively; Table 5.2). This suggests that *Austrovenus* do not exert a top-down control on phytoplankton in the harbour.

In systems where pelagic phytoplankton populations are low (as in this system), but there is limited top-down control, then bottom-up control on phytoplankton productivity may be more important (Prins et al. 1998). Bottom-up controls include light and nutrient availability, and it is highly likely that phytoplankton growth is limited by the latter in Whangateau Harbour. Nutrient concentrations in estuaries similar to Whangateau tend to be low (NH_4^+ and NO_3^- concentrations are typically < 0.01 mg/L), and it is unlikely that light is limiting pelagic phytoplankton growth in such a shallow estuary with a highly abundant and productive microphytobenthos (MPB) community (see chapter 4). This highlights the functionally important link between benthic macrofauna, such as *Austrovenus*, and MPB. The macrofauna provide a source of nutrients, which would otherwise be limiting, to the MPB, directly by excretion of NH_4^+, or indirectly by facilitating the release of pore-water nutrients through bioturbation (e.g. Thrush et al. 2006, Sandwell et al. 2009, Lohrer et al. 2010a). Therefore, in this type of system suspension feeding bivalves are not a ‘natural eutrophication control’; rather they perform the opposite function by stimulating primary production.

5.2 Summary

5.2.1 Austrovenus *clearance rates and grazing pressure*

In chapter 2 of this thesis I showed that bivalve bed density and flow speed are significant factors affecting *Austrovenus* CR, and even the proportion of animals in the bed that are actively feeding. Furthermore, the bed roughness generated by *Austrovenus* is capable of influencing near-bed flow speeds and bed shear stress, and their siphonal currents appear to influence near-bed hydrodynamics under certain conditions, (i.e. at high bivalve densities and low flow speeds).

Both individual CR and the proportion of animals feeding were depressed at high densities. This suggests that other advantages, such as protection from predation or wave disturbance, may be afforded to *Austrovenus* in high-density beds, compensating for the reduction in CR and feeding opportunity (Widdows et al. 2002, van de Koppel et al. 2005). Additionally, the enhanced bed roughness over *Austrovenus* beds is likely to increase resuspension of microphytobenthos, potentially providing the bed with a substantial food source (Widdows et al. 2009).

Bed filtration rates can therefore be substantially overestimated if scaled up using CR obtained from animals at low densities, but may also be affected by assumptions made about *in situ* flow speeds. My experiments showed that individual and bed CR, and the proportion of animals feeding, were increased at a relatively high flow speed, compared to lower flow speeds. An increase in flow speed increases vertical mixing and seston supply to the bed (O'Riordan et al.

1993, Wildish & Kristmanson 1997, Newell et al. 2001), thereby allowing more animals to feed and CRs to increase.

Calculation of population grazing rates therefore requires data on *in situ* bivalve density and the current velocity, but other environmental variables can significantly affect CR (e.g. Bayne 1998, Hawkins et al. 1999, Hawkins et al. 2001, Widdows 2001). The accurate scaling up of bivalve filtration rates to ecosystem level is thus reliant on a large amount of bivalve- and system-specific information. Taking into account the effect of density and flow speed, my population CR calculations for Whangateau Harbour reveal that *Austrovenus* populations are unlikely to exert a top-down control on pelagic phytoplankton. But chapters 3 and 4 of this thesis show that *Austrovenus* have a significant effect on benthic communities and processes.

5.2.2 Effect of Austrovenus *on nutrient cycling and primary productivity*

Previously, *Austrovenus* has been shown to be a key species in estuarine ecosystems, which enhances MPB productivity, and influences nutrient fluxes and macrofauna community structure (Thrush et al. 2006, Sandwell et al. 2009, Lohrer et al. 2010b). However, my experiments suggest that the positive effect of *Austrovenus* on primary productivity is not consistent across habitat types, and that there is substantial temporal variability in primary production (chapter 3). Whilst *Austrovenus* enhanced primary productivity and sediment denitrification potential at a sandy site, there was no effect of *Austrovenus* on these variables at a muddy-sand site. Furthermore, at both sites primary productivity was low in wintertime, likely caused by reduced water temperatures, PAR, and bivalve metabolic rates.

Accelerated sedimentation rates are considered a major threat to estuarine communities and ecosystem function (e.g. Ellis et al. 2002, Thrush et al. 2003a, Thrush et al. 2004, Norkko et al. 2006). Increasing estuarine mud content is likely to reduce *Austrovenus* populations (Thrush et al. 2003b), but my results show that it may also reduce the positive effect of this species on system productivity and denitrification potential even when they persist. Moreover, these experiments highlight the importance of considering context, i.e. the range of conditions inhabited by a particular species, when attempting to assess the effect of key species on ecosystem function.

A substantial proportion of research into the ecosystem services provided by suspension feeding bivalves has focused on epibenthic species, such as mussels and oysters (see review by Newell 2004). High biodeposition rates for these three dimensional structures, particularly for longline mussel farms, result in substantial nitrogen enrichment of underlying sediments, significantly affecting nutrient recycling (Stenton-Dozey et al. 2001, Bruesewitz et al. 2006, Giles et al. 2006). However, my study suggests that biodeposits do not accumulate in the sediments around *Austrovenus* beds, thus the effect of these infaunal bivalves on ecosystem services cannot be directly inferred from studies of epibenthic species. Increased sediment denitrification potential in the *Austrovenus* beds at the sandy site indicate that although nitrogen enrichment from biodeposits is negligible, enhanced NH_4^+ availability may provide a source of nitrogen for nitrification (Gardner et al. 2001, Bruesewitz et al. 2008).

5.2.3 Effect of Austrovenus *on ecosystem properties and other trophic levels*

An Ecopath model for Whangateau Harbour revealed that the system is dominated by benthic groups, and is characterised by high detritus production and export, low transfer efficiency and limited internal recycling. *Austrovenus* and MPB biomass accounted for c. 60 % of total living biomass and the model highlighted the important role of MPB, as opposed to pelagic phytoplankton, in these systems (i.e. phytoplankton and detrital production alone were not sufficient to sustain the benthic groups). High values for the keystoneness index and relatively large impacts on numerous other groups for both MPB and *Austrovenus* confirmed that these are important components of the system, underpinning higher trophic levels.

The model was fairly robust to changes in biomass for all groups and *Austrovenus* biomass was able to be reduced to 17 % of its original value without unbalancing the model. The minimum biomass was less than the *Austrovenus* biomass estimated for the harbour after the 2009 mass mortality event, indicating that the system is able to tolerate such a reduction in the biomass of a key species. However, incorporating spatial and temporal dynamics into the modelling process might reveal that the system is more sensitive than these results suggest.

Ecosystem property indices suggest that, as with other estuarine systems, Whangateau Harbour is a developing, rather than a mature ecosystem (e.g.

Rybarczyk & Elkaim 2003, Tomczak et al. 2009, Byron et al. 2011). However, with decreasing *Austrovenus* biomass, maturity also decreases, suggesting that reductions in *Austrovenus* populations may decrease the stability and resilience of the ecosystem (Christensen 1995, Vasconcellos et al. 1997).

5.3 Conclusions and recommendations for future research

In summary, I have shown that *Austrovenus* is a key species in estuarine ecosystems, but its influence is different to that of suspension feeding bivalves in overseas systems (reviewed by Newell 2004). In New Zealand's shallow estuaries *Austrovenus* populations are unlikely to exert considerable grazing pressure on pelagic phytoplankton, but instead enhance MPB productivity by increasing nutrient availability. In turn, MPB are highly likely to be an important component of *Austrovenus*' diet and enhanced turbulence over high-density bivalve beds may increase resuspension of MPB, thus providing the bivalves with a substantial food source. *Austrovenus* populations represent a large proportion of total biomass in these systems and impact greatly on all other trophic levels. Reductions in *Austrovenus* biomass will therefore likely impact not only on MPB, but most other groups in the estuary, and may also reduce ecosystem maturity and stability.

Results from this thesis indicate that increasing estuarine mud content, caused by accelerated sedimentation rates, may be a considerable threat to estuarine ecosystem functioning. The Ecopath model highlights the very important role of MPB and *Austrovenus* in these systems, but previous research has shown that both are adversely affected by sedimentation. MPB productivity is reduced in muddy sediments compared to sandy sediments, and is likely to be light limited during inundation if turbidity is enhanced due to increased suspended sediment concentrations (e.g. Billerbeck et al. 2007). Although *Austrovenus* are found in areas with moderate levels of sedimentation, *Austrovenus* beds tend to be absent from very muddy sediments (Thrush et al. 2003b). Furthermore, my experiments suggest that the positive effect of *Austrovenus* on MPB productivity and sediment denitrification rates are limited at sites with moderate levels of sedimentation. Thus, even small increases in estuarine mud content have the potential to impact on system productivity, with further increases in mud content likely to have multiple and cumulative effects.

Further research is needed to quantify the effect of *Austrovenus* bed density on sediment stability and resuspension of MPB. Bioturbators such as *Austrovenus* tend to enhance resuspension of sediment (and associated MPB), thus reducing stability of surficial sediments, but effects may be scale- or habitat-dependent. In the large (16 m^2) plots constructed for my experiments in chapter 3 *Austrovenus* appeared to enhance sediment stability at the sandy site; sediment level was raised in *Austrovenus* addition plots compared to removal plots and sand ripples were clearly visible in removal plots, but not in addition plots (author's pers. obs.). High-density beds are a dominant feature on intertidal flats but are particularly likely to be targeted by harvesters, or affected by mass mortality events, thus reductions in *Austrovenus* populations are likely to manifest primarily in these large structures. Recent research has identified spatial self-organisation in mussel (*Mytilus edulis*) beds that affects sediment dynamics and ecosystem productivity (van de Koppel et al. 2005, van de Koppel et al. 2008, Widdows et al. 2009). The effect of spatial self-organisation on ecosystem structure and functioning is likely to be different for infaunal bivalves, however, and future studies should address the role of *Austrovenus* beds in sediment dynamics.

Future work could also focus on improving the complexity of ecosystem modelling, which should improve the accuracy of predictions on the effect of declining *Austrovenus* populations on estuarine ecosystems. Spatial and temporal dynamics can be incorporated into the Ecopath model using Ecosim and Ecospace (Christensen & Walters 2004). Alternatively, a process-based ecological model could be linked to a 3D hydrodynamic model to investigate the coupling of physical and biological processes in estuarine environments (e.g. Spillman et al. 2008). Both methods require more, and higher quality, input data than is currently available but are a logical next step in elucidating the role of *Austrovenus*, and the impact of declining *Austrovenus* populations, on ecosystem function.

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APPENDIX 1

Data collation for Whangateau Harbour Ecopath model

The species and groups considered in the Whangateau Harbour Ecopath model are listed in Table A1.1 and the origin of input data (biomass, production and consumption rates, and diet composition) for each of the groups are described in the following sections.

A1.1 Shorebirds

Whangateau Harbour provides feeding, roosting and breeding habitat for many shorebirds (c. 25 species), including populations of nationally vulnerable and declining species such as the New Zealand dotterel (*Charadrius obscures*) and banded dotterel (*Charadrius bicinctus*) (Kelly 2009). The shorebird biomass estimate was based on the species thought to be the most numerous, based on observations made around the harbour and knowledge of common species in nearby estuaries.

Mangatawhiri Spit which encloses Whangateau Harbour is an important breeding and flocking site for the New Zealand dotterel, with a post-breeding flock arriving in January and maximum numbers occurring in February to March. Non-resident birds leave for their breeding grounds from April to September, with a small number of birds (c. 10 pairs) staying resident and breeding at the spit (Dowding & Chamberlin 1991). Variable oystercatchers (*Haematopus unicolor*) are resident year round; gulls (black-backed *Larus dominicanus* and red-billed *Larus scopulinus*) and pied shag (*Phalacrocorax varius varius*) are also likely to be common in the harbour. Banded dotterels, South Island pied oystercatchers (*Haemotopus ostralegus finschi*) and pied stilt (*Himantopus himantopus*) winter in the harbour, returning to their breeding grounds in summer. Bar-tailed godwits (*Limosa lapponica baueri*) spend the summer in the harbour, returning to Alaska to breed (Thrush et al. 1994).

Table A1.1: Species and groups considered in Whangateau Harbour model

Group name	Common name	Scientific name
Shorebirds	New Zealand dotterel	*Charadrius obscurus*
	Banded dotterel	*Charadrius bicintus*
	Pied oystercatcher	*Haematopus ostralegus*
	Variable oystercatcher	*Haematopus unicolor*
	Bar-tailed godwit	*Limosa lapponica baueri*
	Pied stilt	*Himantopus himantopus*
	Black-backed gull	*Larus dominicanus*
	Red-billed gull	*Larus scopulinus*
	Pied shag	*Phalacrocorax varius varius*
Rays	Short tailed stingray	*Dasyatis brevicaudata*
	Eagle ray	*Myliobatis tenuicaudatus*
Piscivorous fish	Kahawai	*Arripis trutta*
	Spotted stargazer	*Genyagnus monopterygius*
	Kingfish	*Seriola lalandi*
	Barracouta	*Thyrsites atun*
	John dory	*Zeus faber*
Invertebrate feeding fish	Rock cod	*Acanthoclinus fuscus*
	Yellow eyed mullet	*Aldrichetta forsteri*
	Red moki	*Cheilodactylus spectabilis*
	Red gurnard	*Chelidonichthys kumu*
	Hiwihiwi	*Chironemus marmoratus*
	Common triplefin	*Forsterygion lapillum*
	Variable triplefin	*Forsterygion varium*
	Spotty	*Notolabrus celidotus*
	Banded wrasse	*Notolabrus fucicola*
	Snapper	*Pagrus auratus*
	Leatherjacket	*Parika scaber*
	Small bastard red cod	*Pseudophycis breviuscula*
	Yellow belly flounder	*Rhombosolea leporina*
	Sand flounder	*Rhombosolea plebeia*
	Clingfish	*Trachelochismus melobesia*
	Goatfish	*Upeneichthys lineatus*
Planktivorous fish	Koheru	*Decapterus koheru*
	Trevally	*Pseudocaranx dentex*
	Blue maomao	*Scorpis violacea*
Herbivorous fish	Parore	*Girella tricuspidata*
	Piper	*Hyporhamphus ihi*
Carnivorous benthic invertebrates	Whelks	*Cominella spp.*
	Oyster borer	*Lepsiella scobina*
Austrovenus	Clam	*Austrovenus stutchburyi*
Suspension feeding benthic invertebrates	Pipi	*Paphies australis*
Deposit feeding benthic invertebrates	Mud crab	*Austrohelice crassa*
	Wedge shell	*Macomona liliana*
	Nut shell	*Nucula hartvigiana*
	Polychaete worms	
	Amphipods	
	Benthic copepods	
	Echinoderms	
Zooplankton		
Macrophytes	Flapjack	*Carpophyllum flexuosum*
	Sea lettuce	*Ulva* sp.
	Neptune's necklace	*Horomosira banksii*
	Coralline algae	*Corallina* spp.
Microphytobenthos		
Phytoplankton		
Detritus		

Observations made around Whangateau Harbour from 1998 to 2002 and published by the Ornithological Society of New Zealand (OSNZ) provide population estimates for several of these species: 70 NZ dotterels, 80 banded dotterels, 400 pied oystercatchers, 50 variable oystercatchers and 400 bar-tailed godwits (Parrish 2000, 2001, 2002, 2006). It is hard to obtain estimates for other species, most likely because the observations made by the OSNZ were focused on the spit and not on the intertidal flats in the estuary. In Manukau Harbour (80 km south of Whangateau Harbour) shorebird densities range from c. 90 to 120 ind. km^{-2} through the year (Thrush et al. 1994), suggesting than in a harbour the size of Whangateau (i.e. 7.5 km^{2}) total population size is likely to be c. 800 shorebirds. Accounting for the fact that a number of the species for which there are data are only resident for half the year, other species (i.e. pied stilt, gulls, etc) were expected to make up approximately 250 individuals. To estimate the biomass of birds in a study region Lunquist and Pinkerton (2008) used the following equation:

$$B = ((N \cdot W \cdot C)/A) \cdot (S/100) \cdot (M/12)$$

where B = effective biomass (g C m^{-2}), N = number of birds in local population, W = average wet weight of bird (g WW), C = carbon:wet weight ratio (g C g^{-1} WW), A = study area (m^{2}), S = proportion of foraging area covered by the study region (%), and M = months spent in the foraging area per year. Average bird weights were obtained from Heather and Robertson (2000). Carbon biomass of birds is approximately 10% of wet weight (Lundquist & Pinkerton 2008). Biomass was estimated for each species and total shorebird biomass was estimated to be 0.00457 g C m^{-2} (Table A1.2).

In previous Ecopath models for New Zealand coastal systems P/B for bird groups is typically 0.1 – 0.3 yr^{-1} and C/B is 35 – 90 yr^{-1} (Bradford-Grieve et al. 2003, Jiang & Gibbs 2005, Pinkerton et al. 2008), so initial estimates were be taken to be in the middle of these ranges.

Table A1.2: Shorebird abundance and biomass estimates for Whangateau Harbour

Common name	Average individual wet weight (g)	No. of months in harbour	Population estimate	Biomass (g C m^{-2})
NZ dotterel (resident)	160	12	20	0.0000363
NZ dotterel (non-resident)	160	6	50	0.0000453
Banded dotterel	60	6	80	0.0000272
South Island pied	550	6	400	0.00125
Variable oystercatcher	725	12	50	0.000411
Bar-tailed godwit	325	6	400	0.000737
Pied stilt	200	6	200	0.000227
Black-backed gull	950	12	50	0.000538
Red-billed gull	300	12	50	0.00017
Pied shag	2000	12	50	0.00113

Shorebirds feed mostly on small fish and benthic invertebrates but quantitative estimates of the relative importance of the different groups to diet are rare. Oystercatchers in the Firth of Thames (North Island, New Zealand) are known to feed on pipi, whelks, wedge shells, *Austrovenus*, polychaetes and mud crabs (Battley et al. 2007). Dotterels feed mostly on benthic invertebrates, especially crabs, and small fish; red-billed gulls feed on plankton during summer, and benthic invertebrates and small fish; black-backed gulls are opportunistic feeders that will take a wide range of food including carcasses, invertebrates and fish; pied stilt and bar-tailed godwits feed mainly on benthic invertebrates; and pied shags feed mostly on live fish, such as flounder and mullet (Heather & Robertson 2000, Medway 2000).

A1.2 Fish

Approximately 40 species of fish are known to live in Whangateau Harbour; rare species were excluded from the model and data were collected on the 20 to 25 species that are classed as common or frequent (Grace 1972, Kelly 2009). Data on diet composition are available for many of these species from studies conducted nearby (Russell 1983, Le Port 2003, Usmar 2010), and elsewhere in New Zealand (Webb 1973, Curtis & Shima 2005). Both the short tailed stingray (*Dasyatis brevicaudata)* and the eagle ray (*Myliobatis tenuicaudatus*) are common in New Zealand estuaries, moving from channels to the intertidal flats at high tide where they feed on shellfish beds and other invertebrates (Thrush et al. 1991, 1994, Le Port 2003). *Austrovenus stutchburyi* likely comprise a substantial proportion of the eagle rays' diet in Whangateau Harbour as in the rays' foraging grounds *Austrovenus* has been found to comprise 85 % of total bivalve population (Le Port 2003). As important predators of *Austrovenus,* rays were placed in a separate group in order to better facilitate the examination of the effect of *Austrovenus* populations on energy flow in the system. Although adults tend to emigrate offshore, estuaries are likely to be particularly important to juvenile snapper (*Pagrus auratus*), which tend to feed on crustaceans and polychaetes, rather than hard shelled molluscs (Usmar 2010). Fish (other than rays) were placed into one of four functional groups primarily based on feeding mode: invertebrate feeders, herbivores, planktivores, piscivores. For some species, however, feeding mode is not limited to one type. For example, kahawai (*Arripis trutta*) are known to feed on fish, zooplankton and benthic invertebrates (Russell 1983). In these cases, the species were assigned to the group which accounted for the largest proportion of their diet.

Although stock assessments are carried out for species targeted by recreational and commercial fisheries in coastal areas, estimates of fish biomass in New Zealand estuaries are very scarce. Several studies have quantified the relative abundance of estuarine fish using beach seine and outrigger trawl but converting these data to absolute abundances is not possible as these methods catch only small species and juveniles of larger species (e.g. Morrison et al. 2002, Francis et al. 2005). However, a recent study in Mahurangi estuary, just south of Whangateau, obtained population estimate and size-frequency data for snapper and several other species using dropped underwater video (Morrison & Carbines 2006). Population size for those same species in Whangateau Harbour was estimated by scaling the population estimates from Mahurangi, based on the size (i.e. estuary area at high tide) of Whangateau compared to Mahurangi. Length-weight relationships allowed conversion of mean length (L) from Morrison and Carbines (2006) to mean weight (W):

$$W = a \cdot L^b$$

where a and b are constants available for many New Zealand fish species in Taylor and Willis (1998), Chubb et al. (1981), Francis (1988) and in Fishbase (Froese and Pauly, 2005). Where mean lengths were not available mean weight was estimated to be 33 % of maximum weight (calculated from maximum length), and biomass for each species was estimated assuming carbon was 8.3% of wet weight for fish (Lundquist & Pinkerton 2008). There is considerable uncertainty in these data as Mahurangi is larger and deeper than Whangateau (24.6 km^2 in area compared to 7.5 km^2, and 2.7 m mean depth compared to 1.6 m). Scaling based on estuary area therefore likely overestimates fish biomass for Whangateau. On the other hand, there were several species for which no biomass estimate could be obtained, potentially underestimating total group biomass.

Production for each fish species was estimated using an empirical relationship that relates maximum weight of the species to P/B:

$$P/B = 2.4 \cdot M^{-0.26}$$

where M is the maximum wet weight (g) of the species. M is taken to be equivalent to W_∞ (asymptotic weight in g; i.e. the mean weight fish of a given stock would reach if it were to grow for an infinitely long period) (Haedrich & Merrett 1992). As for biomass, length-weight relationships allowed the conversion of asymptotic lengths to asymptotic weights.

Consumption for each fish species was estimated using an empirical relationship derived by Palomares and Pauly (1998) that relates C/B to mortality, food type, fish morphometrics and temperature:

$$\mathrm{Log}(C/B) = 5.847 + 0.280\log Z - 0.152\log W_\infty - 1.360T' + 0.062A + 0.510h + 0.390d$$

where Z is an estimate of total mortality (yr^{-1}; equivalent to P/B), W_∞ is asymptotic weight (g), T’ = 1000/(temperature in Kelvin), A = aspect ratio of tail (ratio of tail height to surface area), h expresses food type (1 for herbivores, 0 for detritivores/carnivores) and d also expresses food type (1 for detritivores, 0 for herbivores/carnivores). Average annual water temperature in Whangateau Harbour is approximately 17.5 °C (Kelly 2009). Table A1.3 summarises the available data on food items, biomass, P/B and C/B for each fish species. For some species there was no data available to calculate P/B and/or C/B. In these cases data from other species in the group was used to provide an estimate for the initial input parameters. Data for C/B was lacking for both of the species in the ray group; as rays use their pectoral fins as the dominant means of propulsion C/B could not be estimated using Palomares and Pauly's equation. Other models that have included a ray/shark group have typically used C/B values of between 2.8 and 3.9 yr^{-1} (e.g. de Paula et al. 1993, Wolff et al. 1998, Jiang & Gibbs 2005). In groups with production and consumption data values were weighted by estimates of species abundance to obtain initial parameters. The initial P/B and C/B estimates for fish groups are within the ranges reported for similar species in other Ecopath models of New Zealand coastal systems (e.g. Jiang & Gibbs 2005, Pinkerton et al. 2008).

Table A1.3: Fish species, food items, biomass (B; g C m^{-2}), P/B (yr^{-1}) and C/B (yr^{-1}) estimates for Whangateau Harbour

Ecopath group	Species name	Common name	Food item[1]	B	P/B	C/B
Rays	*Dasyatis brevicaudata*	Short tailed stingray	*Austrovenus*, other benthic inverts	0.038	0.10	
	Myliobatis tenuicaudatus	Eagle ray	*Austrovenus*, other benthic inverts	0.090	0.12	
Fish (piscivores)	*Arripis trutta*	Kahawai	Fish, zooplankton, benthic inverts	0.016	0.31	5.02
	Genyagnus monopterygius	Spotted stargazer	Fish (demersal species)			
	Seriola lalandi	Kingfish	Fish	0.001	0.10	2.92
	Thyrsites atun	Barracouta	Fish		0.27	3.83
	Zeus faber	John dory	Fish e.g. koheru, triplefins, spotty, leatherjackets	< 0.001	0.34	4.18
Fish (invertebrate feeders)	*Acanthoclinus fuscus*	Rock cod	Benthic inverts (crustaceans and molluscs)			
	Aldrichetta forsteri	Yellow eyed mullet	Benthic invertebrates, detritus, algae	0.008	0.54	6.74
	Cheilodactylus spectabilis	Red moki	Benthic inverts		0.23	3.73
	Chelidonichthys kumu	Red gurnard	Benthic crustaceans, zooplankton	0.006	0.40	4.84
	Chironemus marmoratus	Hiwihiwi	Benthic inverts		0.43	6.04
	Forsterygion lapillum	Common triplefin	Small benthic inverts (ispods, amphipods, polychaetes)	< 0.001	1.45	14.69
	Forsterygion varium	Variable triplefin	Small benthic crustaceans, other benthic inverts	< 0.001	1.27	13.14
	Notolabrus celidotus	Spotty	Benthic inverts	0.005	0.73	8.85
	Notolabrus fucicola	Banded wrasse	Benthic inverts		0.40	5.48
	Pagrus auratus	Snapper	Benthic inverts, fish, zooplankton	0.095	0.22	3.99
	Parika scaber	Leatherjacket	Benthic inverts, macroalgae	0.002	0.36	4.52
	Pseudophycis breviuscula	Small bastard red cod	Benthic inverts		0.30	3.72
	Rhombosolea leporina	Yellow belly flounder	Benthic inverts, detritus	0.004	0.40	4.78
	Rhombosolea plebeia	Sand flounder	Benthic inverts, detritus	< 0.001	0.33	4.09
	Trachelochismus melobesia	Clingfish	Small benthic inverts			
	Upeneichthys lineatus	Goatfish	Small benthic inverts	0.02	0.50	8.82
Fish (planktivores)	*Decapterus koheru*	Koheru	Zooplankton	0.003		
	Pseudocaranx dentex	Trevally	Zooplankton, benthic inverts	0.005	0.36	7.23
	Scorpis violacea	Blue maomao	Zooplankton	0.003	0.44	6.74
Fish (herbivores)	*Girella tricuspidata*	Parore	Macroalgae	0.031	0.34	13.48
	Hyporhamphus ihi	Piper	Macroalgae, zooplankton			

[1] If more than one item in diet the food contributing the greatest proportion is listed first. (Fields left blank where no input data available).

A1.3 Benthic invertebrates

Benthic invertebrates were split into functional groups based on feeding mode, i.e. carnivores, deposit feeders and suspension feeders (which was further split into two groups: *Austrovenus stutchburyi* and other suspension feeders).

A1.3.1 Carnivorous benthic invertebrates

Feeding aggregations (c. 15 – 20 individuals) of predatory/scavenging whelks, (mostly *Cominella glandiformis* with smaller numbers of *C. adspersa*, *C. virgata*, *C. maculosa* and *Lepsiella scobina*), are common on intertidal flats in Whangateau Harbour (Stewart & Creese 2004). *Cominella* spp. are generally scavengers but are capable of drilling and/or chipping at the shells of their prey (mostly *Austrovenus stutchburyi*), whereas *L. scobina* is an active predator, particularly of smaller *Austrovenus* (Stewart & Creese 2004). Whelk abundance on shellfish beds on intertidal flats is c. 10 ind. m^{-2} (author's unpublished data; Ansell 2001, Hewitt 2008, Singleton 2010). Densities are likely to be less in areas where prey abundance is reduced, however. Based on the habitat map of Whangateau Harbour (which shows the extent of shellfish beds), density averaged over the whole harbour area is estimated to be 2.2 ind. m^{-2}. There are no data to convert number to biomass for *Cominella* spp., but based on the biomass of a similar animal, *Buccinulum* sp. (a rocky shore predatory gastropod in the same family as, but slightly larger than *Cominella*), average individual AFDW of *Cominella* spp. was estimated to be 0.1 g (Lundquist & Pinkerton 2008). One g AFDW is equivalent to 0.489 g C (Brey 2001) so biomass of predatory gastropods averaged over total harbour area was estimated to be 0.11 g C m^{-2}. Lundquist and Pinkerton (2008) estimated P/B and C/B for predatory gastropods to be 2.24 and 8.95 yr^{-1}, respectively; these values were used as initial input parameters in this study.

A1.3.2 Austrovenus stutchburyi

Austrovenus stutchburyi surveys were carried out in Whangateau Harbour for the Ministry of Fisheries (MFish) on four occasions between 2001 and 2006 (Walshe et al. 2006, Pawley & Ford 2007). The surveys took in 641,500 m^2 of tidal flats located in the northern part of Whangateau Harbour, and adjacent to the channel in the southern arm. Population estimates ranged from 2.53 × 10^8 (SE:

2.8×10^7) to 3.77×10^8 (SE: 4.1×10^7), equating to mean densities from 395 to 587 ind. m^{-2}, and mean individual shell length was from 22 to 24 mm. Measurements from *Austrovenus* gathered from Tauranga Harbour (author's unpublished data) provide the following relationship between shell length (L; mm) and ash-fee dry weight (AFDW; g):

$$AFDW = 0.0000006 \cdot L^{3.788} \ (r^2 = 0.93, n = 140)$$

Based on average shell length of 23 mm, average individual biomass is 0.09 g AFDW and 0.045 g C (based on Brey's (2001) conversion for bivalves whereby 1 g AFDW is equivalent to 0.5 g carbon). *Austrovenus* biomass in the areas surveyed by MFish is therefore equal to 22.5 g C m^{-2}, based on an average density of 500 ind. m^{-2}. The area surveyed does include the largest *Austrovenus* bed in Whangateau Harbour (Hartill et al. 2000), but *Austrovenus* are present at varying densities (10 to 400 ind. m^{-2}) throughout the estuary (Townsend et al. 2010); average density in these areas was conservatively assumed to be 50 ind. m^{-2} (equivalent to 2.25 g C m^{-2}). *Austrovenus* are unlikely to be found in sediments with high mud content (Thrush et al. 2003), such as that found under mangroves. Mangroves cover c. 15% of total harbour area (Hartill et al. 2000) so *Austrovenus* are likely to be found over 5.42 km^2 of intertidal flats. Combining the biomass estimates for the *Austrovenus* beds surveyed by MFish (22.5 g C m^{-2} over 0.64 km^2), and for the rest of the intertidal area that *Austrovenus* is likely to inhabit (2.25 g C m^{-2} over 4.78 km^2), then *Austrovenus* biomass averaged over the whole estuary (i.e. intertidal and subtidal) area was estimated to be 3.38 g C m^{-2}.

In an Ecopath model of Tasman and Golden Bays (South Island, New Zealand) Jiang and Gibbs (2005) calculated P/B and C/B ratios for *Austrovenus* to be 2.18 and 10 yr^{-1}, respectively; the same values were used for initial input parameters in this model.

A1.3.3 Other suspension feeding benthic invertebrates

Paphies australis (pipi) were also surveyed in Whangateau Harbour for MFish between 2001 and 2006 (Walshe et al. 2006, Pawley & Ford 2007). As for Austrovenus, the surveys took in 641,500 m^2 of tidal flats located in the northern part of Whangateau Harbour, and adjacent to the channel in the southern arm.

Population estimates ranged from 0.48×10^6 (SE: 0.08×10^6) to 1.18×10^7 (SE: 2.37×10^6), equating to mean densities from 0.75 to 18.46 ind. m^{-2}, and mean individual shell length was from 25 to 49 mm.

The area surveyed was intertidal but pipi beds are often prevalent subtidally, and therefore are likely to be outside the sampling extent. The MFish surveys cannot, therefore, be taken as a reasonable estimate of harbour pipi population. Juvenile pipi occur in the intertidal, whereas adults are found at high densities (up to 4400 m^{-2}) in main harbour channels. In addition, the MFish surveys show high inter-annual variability in intertidal pipi density in Whangateau Harbour, making it difficult to estimate average annual biomass from the limited data available. However, density of pipi in intertidal/subtidal beds in Whitianga Harbour was found to be c. 500 m^{-2} (Grant & Hay 2003). Assuming mean individual AFDW to be 0.045 g (i.e. similar to values for *Austrovenus* and *Macomona* (Cummings et al. 1997)), and that 1 g AFDW is equivalent to 0.5 g carbon in bivalves (Brey 2001), then pipi biomass in these high-density beds was estimated to be 11.25 g C m^{-2}.

Assuming that pipi beds cover 10% of the subtidal area (equivalent to *Austrovenus* coverage of the intertidal area), then the pipi biomass of 11.25 g C m^{-2} on the subtidal beds, averaged over total harbour area equals 0.17 g C m^{-2}. Initial estimates for P/B and C/B were taken to be the same as for *Austrovenus stutchburyi.*

A1.3.4 Deposit feeding benthic invertebrates

There are a number of deposit feeding invertebrate taxa known to inhabit New Zealand estuaries including bivalves, polychaetes, crabs, and amphipods. Available data on these taxa are described below:

Average density of the wedge shell (*Macomona liliana*) in Tauranga Harbour (North Island, New Zealand) was 30 and 400 ind. m^{-2} at a sandy and muddy site, respectively (author's unpublished data). Based on a survey of 15 intertidal sites covering a range of habitat types in the upper, mid and lower of Weiti Estuary (near Auckland, North Island, New Zealand) average density was c. 55 m^{-2} (Hewitt 2008). Cummings et al., (1997) estimated the mean individual ash-free dry weight (AFDW) for *Macomona* was 0.046 g, which is equivalent to 0.023

g C (Brey 2001). The average biomass of *Macomona* on intertidal flats was therefore estimated to be 1.27 g C m^{-2}.

The nut shell (*Nucula hartvigiana)* is abundant (500 to 1500 ind. m^{-2}) in sheltered muddy areas of New Zealand estuaries (Hewitt 2008, own unpublished data). As Whangateau is a relatively sandy estuary *Nucula* may be abundant over only 10 – 20 % of intertidal area (Kelly, 2009). The average size of adult *Nucula* is c. 5 mm, which is about one-tenth of the size of an adult *Austrovenus,* (based on approximate dimensions (W, H, D) of the two bivalves as follows: *Nucula* 5 x 5 x 2.5 mm, *Austrovenus* 20 x 8 x 4 mm), consequently AFDW is estimated to be c. 0.008 g ind.$^{-1}$. Based on the assumption that 1 g AFDW is equivalent to c. 0.5 g C for benthic macrofauna (Brey 2001) then a *Nucula* density of 1000 m^{-2} over 15% of the harbour equates to 0.6 g C m^{-2} over the whole harbour area.

Polychaete worms are one of the most abundant macrofaunal groups in intertidal areas, with densities averaging c. 1000 - 1500 m^{-2}; commonly occurring deposit feeding taxa include *Boccardia syrtis*, Cirratulidae, *Cossura consimilis, Heteromastus filiformis*, *Magelona dakini*, and *Prionospio aucklandia* (Hewitt 2008). Median wet weight for polychaetes is c. 2.3 mg (Lundquist & Pinkerton 2008). For polychaetes dry weight is approximately 20 % of wet weight and carbon is about 33 % of dry weight (Brey 2001). Based on the conversions a polychaete density of 1250 m^{-2} equates to a biomass of 0.19 g C m^{-2}.

Intertidal crab species in New Zealand estuaries are dominated by the mud crab (*Austrohelice crassa*) which inhabits a range of sediment types from silt to coarse sand (Needham et al. 2010). The number of mud crabs living on estuarine intertidal flats in the North Island of New Zealand has been found to range between 35 - 55 ind. m^{-2} in sand and 150 - 550 ind. m^{-2} in mud, with average size (carapace width) being c. 7 mm (Morrisey et al. 1999, Needham et al. 2010). Sediments in the main body of Whangateau Harbour are mostly sandy, with high proportions (> 10%) of mud only present in small areas that are sheltered, often associated with mangroves. Consequently crab densities are likely to be low over most of the intertidal area, but substantially higher in the muddier areas. Average crab density over the whole intertidal area was therefore estimated to be 80 ind. m^{-2}. The relationship between carapace width (CW) and dry weight (dw) has been described for *Chasmagnathus granulatus* (an Argentinean estuarine crab), a species similar to *Austrohelice crassa,* and is given by:

$dw = 7.3045 \cdot 10^{-5} \cdot CW^{3.2094}$ (César & Armendáriz 2007)

and for *Uca pugnax* and *U. minax* (North Carolina salt marsh fiddler crabs):

$dw = 0.000067 \cdot CW^{3.161}$ (Cammen et al. 1984).

Based on the above two equations the dry weight of *Austrohelice crassa* individuals with carapace width of 7 mm is c. 0.035 g. Carbon is assumed to comprise c. 35% of dry weight in brachyurans (Brey 2001), therefore the biomass of *Austrohelice crassa* was estimated to be 0.98 g C m^{-2} (i.e. 80 ind. m^{-2} at 0.012 g C $ind.^{-1}$).

Amphipods are also abundant, with densities c. 1000 ind. m^{-2}, on intertidal flats across a range of sediment types (Stevens et al. 2006). Median wet weight of amphipods is c. 1 mg, AFDW is 19 % of wet weight, and carbon is 50 % of AFDW (Lundquist & Pinkerton 2008) so amphipod biomass was estimated to be 0.095 g C m^{-2}. Additionally, Hicks (1985) described the benthic copepod (*Parastenhalia megarostrum*) as being an important prey item for young flatfish and estimated the biomass in Pautahanui Inlet, Poirua Harbour (North Island, New Zealand) to be 0.059 – 0.242 g C m^{-2}.

The total biomass of these six intertidal taxa (*Macomona liliana*, *Nucula hartvigiana*, polychaetes, *Austrohelice crassa*, amphipods and *Parastenhalia megarostrum)* in Whangateau estuary was estimated to be 3.20 g C m^{-2}. Subtidally, echinoderms such as *Echinoderm australe* and *Fellaster zelandiae* are likely to be abundant (Hewitt 2008) but biomass data for subtidal estuarine benthic invertebrates is scarce. The subtidal comprises only a small proportion (14%) of estuary area and it is assumed that the biomass of deposit feeding macrofauna is similar for the intertidal and subtidal parts of the estuary. The initial biomass for this group was therefore set at 3.20 g C m^{-2}.

P/B and C/B ratios for this group have varied between other Ecopath models, likely because the models span a range of climates, habitats and species in countries such as Mexico, France, Taiwan and New Zealand (Manickchand-Heileman et al. 1998, Rybarczyk & Elkaim 2003, Jiang & Gibbs 2005, Lin et al. 2007). Typically, the ratios tend to be higher for polychaete groups (P/B c. 4 – 9 yr^{-1}, and C/B c. 21 – 50 yr^{-1}) than for crabs and molluscs (P/B c. 2 – 4 yr^{-1}, and

C/B c. 13 – 15 yr^{-1}), and estimates in New Zealand systems for benthic invertebrates typically have P/B at c. 2 yr^{-1} and C/B at c. 8 yr^{-1} (Jiang & Gibbs 2005, Pinkerton et al. 2008). As the majority of the biomass in this group comprised crabs and molluscs the initial P/B and C/B values for this Ecopath model were set at 3 and 13 yr^{-1}, respectively.

A1.4 Zooplankton

A study of zooplankton abundance in Tauranga Harbour found that numbers peaked in late summer and early spring (< 250,000 ind. m^{-3}) and annual average abundance inside the harbour was c. 50,000 ind. m^{-3}. Copepods were numerically dominant and the study also noted that estuarine zooplankton feed on detritus as well as phytoplankton (Giles 2002). Data on zooplankton biomass in New Zealand estuaries is scarce, but zooplankton biomass in Cook Strait (between North and South Islands, New Zealand) has been found to range between 15 and 31 mg dry weight (dw) m^{-3}, with a mean of approximately 21 mg dw m^{-3} (Bradford-Grieve et al. 1993). If 1 g dw zooplankton is equivalent to 0.416 g C (Brey 2001), then mean biomass for Cook Strait zooplankton converted to units of carbon equals 8.74 mg C m^{-3}. However, zooplankton biomass may be substantially greater in estuaries than coastal waters due to higher nutrient levels and primary production rates in the shallow semi-enclosed systems. For example, annual average zooplankton biomass in Fukuyama Harbor, Japan was 39.1 mg C m^{-3}, and abundance was c. 110, 000 ind. m^{-3} (Uye & Liang 1998). This suggests that biomass in Tauranga Harbour would be equivalent to 17.78 mg C m^{-3} (i.e. approximately twice that of Cook Strait). Other studies indicate annual average estuarine zooplankton biomass tends to range between c. 8 mg C m^{-3} (Froneman 2001, Leandro et al. 2007) and 20 mg C m^{-3} (Fulton 1984, Lara-Lopez & Neira 2008). Taking an average value of 14 mg C m^{-3} and assuming mean depth in Whangateau Harbour to be 1.56 m (Hume et al. 2007), zooplankton biomass was estimated to be 0.022 g C m^{-2}. That this estimate is substantially lower than in models of other New Zealand coastal systems (Bradford-Grieve et al. 2003, Jiang & Gibbs 2005, Pinkerton et al. 2008) is unsurprising due to the shallow nature of Whangateau Harbour in comparison to the other coastal environments modelled, (where depth is 12 – 615 m).

Production and consumption rates for zooplankton were taken from other Ecopath models of New Zealand coastal systems (Jiang & Gibbs 2005, Pinkerton et al. 2008), both of which split zooplankton into large and small groups, although there was a substantial range in the values for small zooplankton. For large zooplankton P/B ranged between 15 and 17.8 yr^{-1} and C/B between 50 and 51.3 yr^{-1}, whereas for small zooplankton P/B ranged between 20 and 200 yr^{-1} and C/B between 80 and 626 yr^{-1}. Initial input parameters for this study were set to 20 yr^{-1} for P/B and 80 yr^{-1} for C/B.

A1.5 Primary Producers

Primary producers were split into 3 functional groups (macrophytes, microphytobenthos and phytoplankton). Mangroves and seagrass beds are also present in Whangateau Harbour, but contribute to the food web primarily through input to the detritus pool (Alfaro et al. 2006, Leduc et al. 2006), and so were not included as a separate group.

A1.5.1 Macrophytes

As with mangroves and seagrass, macroalgae are likely to contribute to the estuarine food web primarily as a source of detritus. Thus EE for macroalgae are typically low, i.e. 0.01 - 0.2 (e.g. Ortiz & Wolff 2002, Pinkerton et al. 2008, Taylor et al. 2008, Tomczak et al. 2009, Byron et al. 2011). However, macroalgae are also a significant food source for parore, known to be abundant in Whangateau Harbour, and therefore have been given a distinct functional group in the model. Data on macrophyte biomass in the harbour are scarce, but on subtidal reefs dense *Carpophyllum flexuosum* forests exist, which are used by juvenile and adult parore. *Horomosira banksii* (Neptune's necklace; also consumed by juvenile parore) and *Ulva* sp. are abundant throughout the harbour and coralline paint and turfing algae (*Corallina* spp.) are found on rocky substrates both intertidally and subtidally (Kelly 2009).

Pinkerton et al. (2008) split macroalgae into three functional groups (canopy, foliose and crustose) for their model of Te Tapuwae o Rongokako Marine Reserve (North Island, New Zealand). The P/B values in their balanced model were 2.84 yr^{-1} (canopy), 13.0 yr^{-1} (foliose) and 25 yr^{-1} (crustose) and ecotrophic efficiencies in the balanced model were very low (0.003 – 0.058). As macroalgal species in Whangateau Harbour span these three groups the initial P/B estimate for this study was 12.5 yr^{-1}. Due to the lack of biomass data EE was set to 0.1 and Ecopath was used to calculate macroalgal biomass.

A1.5.2 Microphytobenthos

Microphytobenthos biomass (chlorophyll *a*) in Manukau Harbour (North Island, New Zealand) ranged from 32.7 to 121.2 mg m^{-2} across a range of sediment types (mud to shelly sand), with the mean estimated to be at least 62.5 mg m^{-2} (Cahoon and Safi, 2002). Estuarine monitoring programmes in various locations in North Island New Zealand have found that sediment chl *a* content typically ranges from 6 to 25 µg g^{-1} dw across a range of sediment types (e.g. Halliday & Cummings 2009, Singleton 2010).Without a measure of sediment bulk density, however, it is not possible to convert µg g^{-1} dw to mg m^{-2}. However, sediment density was measured to be 1.51 g cm^{-3} in a study of Tauranga Harbour where sediment chlorophyll *a* at an exposed site (comprised of sand with no mud content) and a sheltered site (fine sands with 10 – 15 % mud content) were c. 8 and 20 µg g dw^{-1}, respectively (author’s unpublished data). These values convert to 128 and 336 mg m^{-2}. Based on these studies, average microalgal biomass was estimated to be 100 mg m^{-2} which, using a carbon to chl *a* mass ratio of 30: 1, converts to 3 g C m^{-2} (Gallegos & Vant 1996). This is almost double the estimate for benthic microphytes (1.6 g C m^{-2}) used in a model of Te Tapuwae o Rongokako Marine Reserve, a coastal marine ecosystem, (Lundquist & Pinkerton 2008), but benthic microalgal biomass is likely to be greater in the much shallower Whangateau Harbour. The model of Te Tapuwae o Rongokako also included ephiphytic algal biomass but data on the contribution of epiphytes to the estuarine food web or, even on biomass of epiphytes is limited, so have not been considered. Microphytobenthos production in the southern region of Manukau Harbour has been estimated at 100 g C m^{-2} yr^{-1} (Vant & Budd 1993). When divided by the average biomass estimate for that harbour this produces a P/B value of 53.3 yr^{-1}, similar to the value of 40 yr^{-1} given for benthic microphytes in Lundquist and Pinkerton (2008). Both biomass and production estimates are within the ranges indentified in a review of global microphytobenthos abundance and productivity (MacIntyre et al. 1996).

A1.5.3 Phytoplankton

There is little data available on phytoplankton biomass in Whangateau Harbour. Auckland Regional Council has a water quality site outside the harbour entrance at Ti Point, but that is of limited use as phytoplankton biomass at open water sites is typically lower than inside estuaries (Scarsbrook 2008). However, chlorophyll *a* (chl *a*) concentration has been monitored at several sites in nearby Mahurangi Harbour, yielding an annual average of 2.35 mg m^{-3} (Wilcock & Kemp 2003). This is lower than the annual average for southern Manukau Harbour, 5.3 mg m^{-3}, estimated by Vant and Safi (1996), but Manukau's catchment is dominated by urban development and is subject to enhanced wastewater input compared to both Mahurangi and Whangateau harbours. Due to the close proximity of the two harbours and similar levels of development in their catchments the chl *a* concentration from Mahurangi is taken to be an appropriate estimate for Whangateau. Based on an average depth in Whangateau of 1.56 m and using a carbon to chl *a* mass ratio of 30: 1 (Gallegos & Vant 1996), 2.35 mg m^{-3} converts to 0.110 g C m^{-2}. Direct comparison of biomass in g C m^{-2} with other Ecopath models is not possible as it is dependent on the average (euphotic) depth of the studied area.

Phytoplankton production in northern and southern regions of Manukau Harbour has been estimated to be 200 and 170 g C m^{-2} yr^{-1}, respectively (Vant & Budd 1993). In the same regions, mean chl *a* concentration was estimated to be 9 and 5.3 mg m^{-3}, which is equivalent to c. 0.8 and 0.4 g C m^{-2} (Vant & Safi 1996). This yields P/B estimates of between 255 and 425 yr^{-1}; P/B has ranged between 200 and 248 yr^{-1} in previous New Zealand Ecopath model applications (Bradford-Grieve et al. 2003, Jiang & Gibbs 2005, Pinkerton et al. 2008), so P/B was set to 260 yr^{-1}.

A1.6 Detritus

Carbon content of sediment in Whangateau Harbour is typically < 1%, although it can be up to 8 % underneath mangroves stands (Kelly 2009). Organic carbon content of sediment in Tauranga Harbour ranged from 0.15 to 0.4% (at an exposed, sandy site and a sheltered, muddier site); if carbon content of the sediment is assumed to average 1 % and based on a sediment density of 1.51 g cm^{-3} there will be 15,100 g C m^{-3} (author's unpublished data). Detritus biomass was estimated to be 151 g C m^{-2}, based on the assumption that only the upper 1 cm of the sediment will be available to the detritus feeders (Rybarczyk and Elkaim, 2003). This is somewhat lower than values used in some other Ecopath models, for example Bradford-Grieve et al. (2003) used 433 g C m^{-2} in their model of the Southern Plateau, New Zealand (but that was an oceanic system), and 423 g C m^{-2} in a model of the Seine estuary, France (Rybarczyk and Elkaim, 2003).

A1.7 Fisheries in Whangateau Harbour

Shellfish beds in the harbour are exploited by recreational harvesters, who travel from the surrounding region. The majority of harvesters come from Auckland and closure of beaches to shellfish harvesting in Auckland is thought to have contributed to increasing harvesting pressure in Whangateau Harbour (Kearney 1999). The annual harvest of *Austrovenus* from Lews Bay, a popular shellfish gathering location in the north of the harbour, has been estimated to be 28 tonnes wet weight, out of a possible 408 tonnes of harvestable biomass (i.e. > 30 mm shell length) (Kearney 1999). Average individual wet weight of *Austrovenus* in that area of the harbour has been measured to be 6.8 g (C. Pilditch, University of Waikato unpublished data). Twenty-eight tonnes is therefore equivalent to c. 165, 000 g C, or 0.022 g C m^{-2} (based on average individual biomass of 0.04 g C).

Paphies australis (pipi) are also an important recreational fishery resource and although catch has not been recorded for this species anecdotal evidence suggests that pipi populations are under significant pressure from harvesters (MFish 2009). Closure of the *Austrovenus* beds to harvesters in 2010 also included pipi as there was concern that if the harbour was closed for *Austrovenus* only then harvesters would focus effort on pipi, significantly increasing harvesting pressure on that species (MFish 2009). However, due to lack of data an estimate of pipi harvest has not been included in the model.

A1.8 Reduction in *Austrovenus* biomass following a mass mortality event

The Ministry of Fisheries surveyed shellfish beds in Whangateau Harbour in 2009 following a mass mortality event. Comparison of the 2009 survey with data from similar surveys carried out between 2001 and 2006 shows that

Austrovenus biomass decreased by 54 % after the mass mortality event (Table A1.4). There was a large decrease in the number of larger individuals as the proportion of the population with shell length ≥ 30 mm decreased from c. 16 % in 2001 to 2006, to 7 % in 2009. Following the methods outlined earlier in this appendix for estimating *Austrovenus* biomass the post-mass mortality event biomass was estimated to be 1.58 g C m^{-2} across the total estuary area (compared with 3.38 g C m^{-2} before the event).

Table A1.4: Ministry of Fisheries *Austrovenus* survey data for 2001 to 2009

Year	Population estimate (SE) × 10^6	Density ind. m^{-2}	Shell length (L) mm	% ≥ 30 mm length	Biomass g C m^{-2} *
2001	253.3 (27.6)	394.6	24.0	19.2	20.0
2003	376.7 (41.4)	587.2	23.0		25.4
2004	349.0 (57.9)	544.1	24.0	16.3	27.6
2006	290.0 (23.2)	452.0	22.4	13.7	17.7
2009	239.8 (17.3)	371.8	20.5	7.4	10.4

*Densities converted to biomass using: AFDW = $0.0000006 \cdot L^{3.788}$ (author's unpublished data; $r^2 = 0.93$, n = 140), and 1g AFDW = 0.5 g C in bivalves (Brey 2001)

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