Effect of black swan foraging on seagrass and benthic invertebrates in western Golden Bay

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science in Ecology

Massey University, Palmerston North,
New Zealand

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2009

Table of contents

Thesis Abstract

Waterfowl are known to be capable of influencing wetland ecology in a number of ways, sometimes to the detriment of other species that also inhabit this type of environment. Western Golden Bay including Farewell Spit is one of the largest areas of intertidal sand flat habitat in New Zealand and supports a wide array of species including internationally important populations of bar-tailed godwits (*Limosa lapponica*) and red knot (*Calidris canutus*). These species, particularly red knot, have declined in number over the last the 25 years at this site. Another numerous species at this site, the black swan (*Cygnus atratus*), has been suggested as a possible contributor to the observed decline in wader numbers through their impact on the habitat. This thesis presents the findings of a research project on the role of black swans in the tidal seagrass (*Zostera muelleri*) ecosystem in western Golden Bay carried out between October 2007 and October 2008.

In an effort create a clear picture of what role the black swans play in this environment the project focused on four major aspects of swan-ecosystem interactions. The first of these looked at the activity patterns of black swan. This showed the swans' activity is largely dictated by the tidal cycle with foraging occurring during the intertidal period when the seagrass is accessible while roosting is mostly confined to around high and low tides.

The second part of the project explored the influence black swans have on the tidal seagrass landscape through their foraging habits. This showed that while swan foraging occurs across the tide flats it is concentrated on denser patches, on both small (meters) and large (hectares) scales. Experimental grubbings showed that the grubbing activity of swans is capable of forming and expanding bare sand patches within seagrass beds and that these bare patches can persist for at least two months.

The third part of the project focused on the direct impacts of swan foraging on the seagrass and associated benthic invertebrates. Exclusion plots showed that at some sites swan foraging can significantly reduce *Zostera* biomass and invertebrate biodiversity.

The final aspect examined was the role of swan in biomass and nutrient cycling. A faecal deposition survey showed swans consume 23.40 g DW ha^{-1} day^{-1} of *Zostera*. The average intake rate was 27.25 g DW ha^{-1} day^{-1}. Nutrient analysis of seagrass

showed that shoot material has significantly higher N, P, Ca and fibre than rhizome and that rhizome has significantly more soluble carbohydrates than shoots.

On the basis of the swans' direct and/or indirect influences on *Zostera muelleri* beds and the associated invertebrate fauna, swans could arguably be considered to be a major ecosystem engineer in the intertidal sandflats of Golden Bay.

1. General introduction

1.1 Project background

The tidal flats on the southern and eastern side of Farewell Spit within Golden Bay are one of New Zealand's principal wetlands, with around 95 square kilometres of tidal flat being exposed at low tide (Fig. 1.1). The area is highly productive and is rich in biodiversity including large numbers of both resident native and migratory bird species. Because of these factors Farewell Spit is classified as a Scientific Nature Reserve, the highest level of protection in the New Zealand reserves system, and a wetland of international importance under the Ramsar convention (Nelson/Marlborough conservancy office, 1990). In spite of the importance of Farewell Spit both nationally and internationally only little research has been carried out on the spit's tidal flats. These related mainly to the foraging ecology of the main shorebirds present (Battley, 1996) and the diversity and abundance of the benthos of the tidal flats (Battley *et al.*, 2005). These studies revealed that the seagrass *Zostera muelleri* is an important driver of invertebrate abundance and diversity; these in turn provide food for shorebirds (also known as waders).

Figure 1.1. Satellite image of Western Golden Bay, showing Farewell Spit and associated tidal and subtidal flats. Dark areas on the tidal flats represent dense seagrass beds.
Image: NASA.

The numbers of some wader species have changed significantly over the past few decades, particularly the red knot (*Calidris canutus*) which has declined by two thirds since the 1960s (Battley *et al.*, 2005). This decline has not been mirrored in other populations across New Zealand suggesting that local causes may be involved. One possibility raised by Battley et al. (2005) is that the suitable food supply or foraging habitat has deceased by changes brought about by the foraging behaviour of black swans (*Cygnus atratus*). Waterfowl in other wetland ecosystems are capable of drastically reducing aquatic vegetation that they forage on (Allin & Husband, 2003; Smith & Odum, 1981) and this has flow-on impacts on the associated invertebrate fauna (Marklund & Sandsten, 2002). As these invertebrates form an important part of the diet of many shorebirds it may be that excessive waterfowl foraging is detrimental to the shorebirds through the reduction in food supply (Bortolus *et al.*, 1998; Sherfy & Kirkpatrick, 2003).

This study explores whether black swans would be capable of such an effect on the tidal seagrass ecosystem in western Golden Bay through their foraging behaviour. To quantify the role of swan foraging four main approaches were used: (1) behavioural and foraging activity observations, (2) seagrass and feeding activity surveys and experimental disturbance, (3) analysis of seagrass biomass and invertebrate biodiversity when exposed and protected from swan foraging, and (4) swan seagrass consumption and nutrient turnover rates (see section 1.5 for more detail on study components).

1.2 Black swans

Farewell Spit supports up to between five and fifteen thousand black swans that inhabit the tidal flats and take advantage of the abundant seagrass meadows that grow there (see Figs. 1.2 and 1.3).

Species characteristics

Black swans are large (males 6 kg, females 5 kg; 110-140 cm in length (Marchant & Higgins, 1990)) waterfowl native to Australia. They are one of the most abundant waterfowl in New Zealand and are found throughout the country. Adult birds breed in

winter and early spring on permanent water bodies such as lakes and lagoons with sufficient aquatic vegetation to feed on (Sagar *et al.*, 1995).

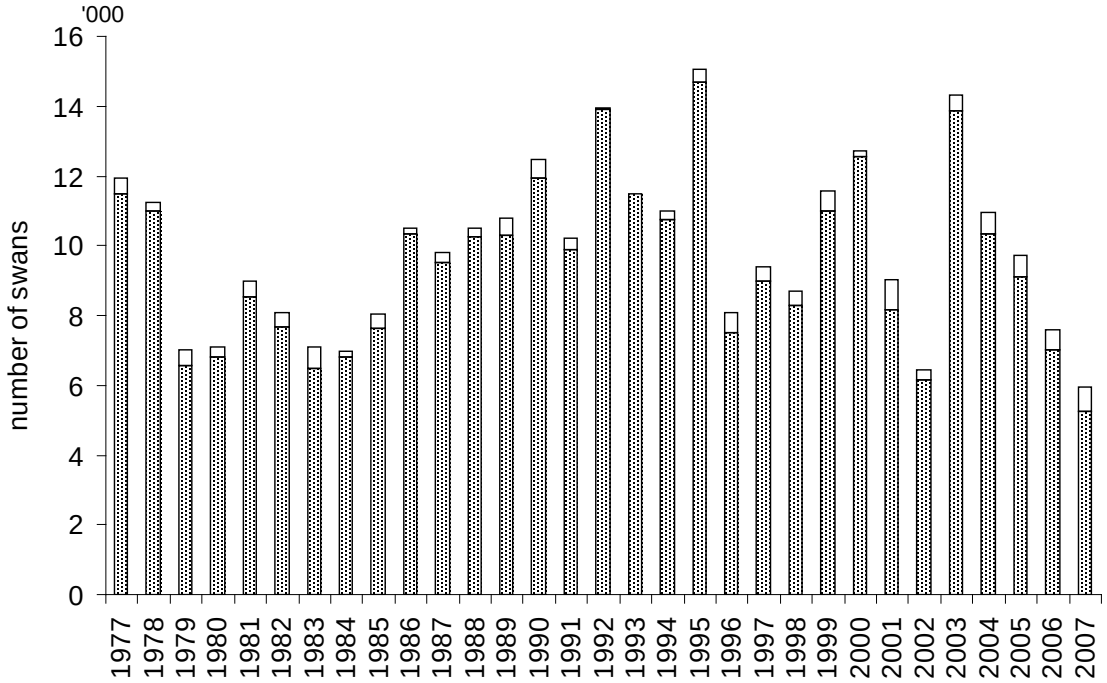


Figure 1.2. Total numbers of black swans counted in aerial surveys of Farewell Spit (filled bars) and the nearby Whanganui Inlet (white bars) in January from 1977-2007. Data from Fish and Game New Zealand.

Nesting pairs are very territorial and will drive non-breeding swans away. This is possibly a cause of the extensive national migration movements and the arrival of the first of the spring birds on Farewell Spit (Potts, 1982). Apart from a few pairs on small dune lakes black swans do not breed on Farewell Spit; given the small surface area of many of these lakes this may represent the carrying capacity for breeding pairs for Farewell Spit. Over summer many swans arrive from other parts of central New Zealand to moult (Byrom & Davidson, 1992).

History in New Zealand and on Farewell Spit

Black swans in New Zealand today are descendants of birds introduced from Australia in the last half of the nineteenth century for park beautification and waterweed control, and possibly swans that self-introduced around the same time and subsequently (Sagar *et al.*, 1995). Sub-fossil bones of a native New Zealand swan have been found that are

indistinguishable from the equivalent ones in modern Australian black swans so it is most likely that the New Zealand swan was, at most, a subspecies of the black swan and probably occupied a very similar ecological niche (Holdaway *et al.*, 2001). The native swan appears to have gone extinct since the arrival of humans. This is important when considering the role the swans have in the ecosystem from a management and conservation perspective, as effects observed now may represent a return to a pre-human state.

Figure 1.3. Black swan in the hand (left) and feeding along the water's edge in Golden Bay, Northwest Nelson (right). All photos by the author unless specified.

Role of swans in tidal seagrass ecosystems

As large herbivores, swans consume a large amount of plant material that is relatively low in nutritional value to meet their energy and nutritional requirements (Thayer *et al.*, 1984). Published information on swan foraging on the Farewell Spit flats suggested that swans were grazers, taking only seagrass leaves (Sagar *et al.*, 1995); this implies that their main potential impacts would be through overgrazing and through increased nutrient cycling. However, evidence of swan grubbing for rhizomes in this study suggests this position needs revision. Given that seagrass beds are known to harbour high diversity and abundances of invertebrates, swans could have both indirect (through nutrient cycles) and direct (through grubbing and physical modification of the habitat) impacts on seagrass and its associated communities. These could, in theory at least, flow on to impacts at higher trophic levels through changes in levels of invertebrate prey available to carnivorous shorebirds.

Blacks swans are not the only waterfowl present in western Golden Bay – Canada goose (*Branta canadensis*), paradise duck (*Tadorna variegata*), Australasian shoveler (*Anas rhynchotis*), mallard (*Anas platyrhynchos*), grey duck (*Anas superciliosa*), and grey teal (*Anas gracilis*) were also recorded during this study. All of these species were far less numerous than black swans however. Moreover, of these, the Canada goose is the only species that could potentially play a similar ecosystem role as black swans on tidal flats, but given their far lower numbers (maximum 80) and their spending a large portion of their time grazing on adjacent pastures, the impact of geese on tidal flats is probably insignificant. Of the duck species only paradise ducks were observed feeding on live seagrass (pers. obs.); as they were only rarely seen in flocks (maximum of 30 individuals) their impact on seagrass is also most likely negligible.

1.3 Seagrass

Species characteristics and habitat

While there has been some debate in the past regarding the taxonomic status of seagrass in New Zealand, the current consensus based on genetic and morphological evidence is that there is just one species, the small eelgrass *Zostera muelleri* (Jones *et al.*, 2008; Les *et al.*, 2002). The plant consists of a network of roots and subsurface rhizomes with shoots branching off these. Shoots contain 2-6 leaves up to 15 cm in length. *Z. muelleri* grows in patches ranging from just a few shoots up to beds of hundreds of m^2 and can be sparse or totally cover the substrate (Fig. 1.4), with the densest cover being along channel edges. The main mode of colonization is mostly through vegetative elongation rather than seed propagation (Ramage & Schiel, 1999). *Z. muelleri* is found throughout New Zealand where suitable habitat exists. This is principally sheltered estuarine tidal flats but also includes pools on rock platforms. It can grow on a range of soft shore substrate types from coarse sand to mud (Inglis, 2003).

Figure 1.4. *Zostera muelleri* in Golden Bay. Left – sparse cover on a sandflat; right – dense beds with standing pools of water.

Threats to seagrass

Nationally, seagrass is at risk from human development and has declined in some tidal areas adjacent to urban areas (Inglis, 2003; Turner & Schwarz, 2006a). While the seagrass habitat within the Farewell Spit Nature Reserve is largely unaffected by direct human disturbance (because of restricted access to the tidal flats), broader-scale influences such as increased turbidity and nutrient levels in the water may have impacts (Orth *et al.*, 2006). At Te Rae (see Fig. 1.6) there are several potential human threats as the public and commercial operators use the tidal flats for recreation and cockle harvesting. The flats are also flanked by dairy farms that could contribute additional nutrients to the ecosystem. The seagrass habitat of Whanganui inlet (an enclosed inlet on the west coast) faces less of a human threat as the surrounding landscape is predominantly forested and there is little urban development around the periphery. However there is some farming and recreational use of the inlet.

Seagrass that accumulates on beaches around Puponga and Whanganui Inlet (Fig. 1.5) is collected by local gardeners for use as garden mulch. At Puponga seagrass collection is limited to the beach area directly adjacent to the Farm Park car park and is unlikely to have a major influence on the amount of seagrass detritus available to the rest of the tidal ecosystem due to the small scale and intermittency of collection.

Role of seagrass in tidal and coastal ecosystems

Seagrasses worldwide are an important component of the inshore marine environment performing a range of ecosystem functions (Duarte, 2002). The structure of the seagrass plant itself provides a number of microhabitats for invertebrates both above and below ground and acts as a refuge for juvenile fish (Heck *et al.*, 2003; Heck & Wetstone, 1977). Seagrass effectively stabilizes the substrate and reduces erosion by reducing water current speeds and allowing the settlement of fine particles in the water column (Heiss *et al.*, 2000). Another important function of seagrass is as a source of primary production that provides organic carbon and other nutrients to the wider tidal ecosystem (Borum *et al.*, 2004). The native New Zealand seagrass *Z. muelleri* is no exception and plays a central role in tidal ecosystems where it is present (Inglis, 2003).

Figure 1.5. Seagrass leaves on the tide line at Puponga, Golden Bay. Photo: Alastair Robertson.

Other tidal vegetation

While *Zostera* dominates the bulk of the tide flats several other vascular plants are present along the upper edge of the tide range, including sea rush *Juncus kraussii*, knobby clubrush *Isolepis nodosa*, jointed wire rush *Apodasmia similis*, sea primrose *Samolus repens* and Selliera *Selliera radicans*. A number of macroalgae species were observed across the tidal flats. The most conspicuous of these were *Ulva*, *Enteromorpha* and *Codium* species with a variety of smaller red seaweeds also noted.

1.4 Study sites

General location

This study was conducted at three sites in western Golden Bay: Puponga, Te Rae and Whanganui Inlet. These sites were selected to capture a range of intertidal *Zostera* habitat to allow a degree of contrast and comparison. Suitability for carrying out observations, setting up long term experiments and accessibility were also important considerations when selecting the study sites. While only the Puponga site is in the Farewell Spit Nature Reserve and then only at its western extremity the invertebrate community and seagrass distribution suggests wider extrapolation may not be unwarranted. Most work was carried out at Puponga and Te Rae. The Whanganui Inlet site was only included for the exclusion experiment and paired sampling.

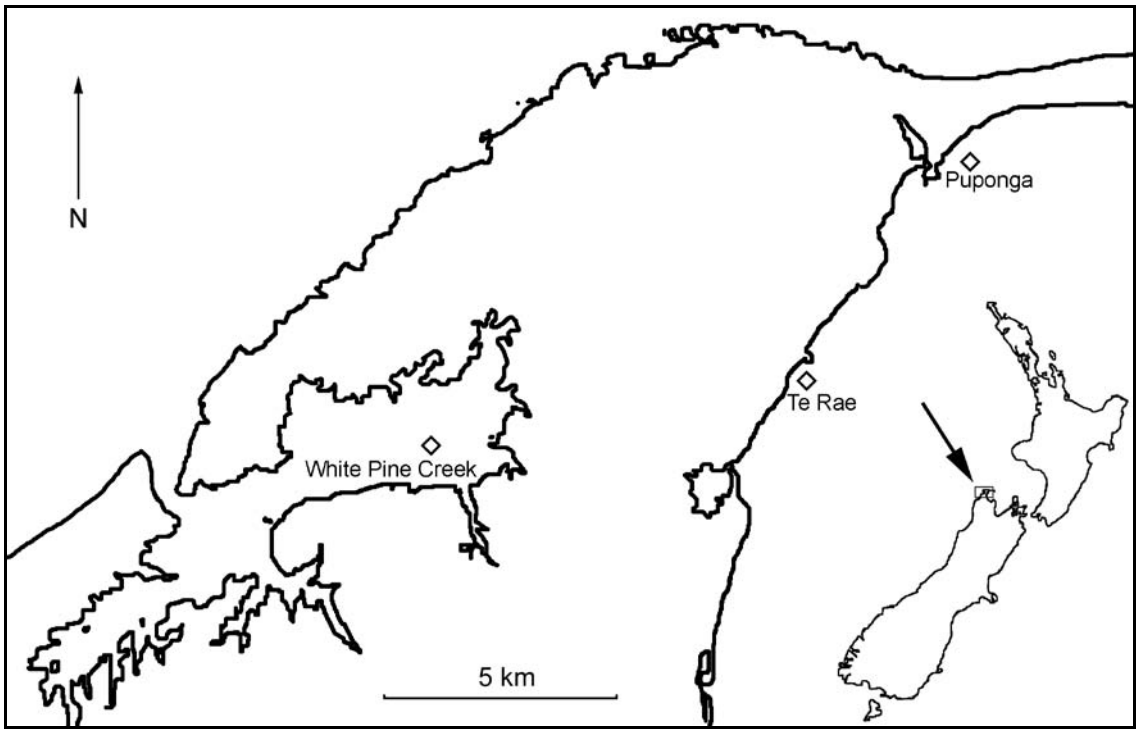


Figure 6. Location of study sites in western Golden Bay, Northwest Nelson.

Puponga

The Puponga site is situated at the western extremity of the Farewell Spit Nature Reserve, adjacent to Puponga Farm Park (40°31'20"S 172°44'32"E). The site covers approximately 6 km^2 of gently sloping tidal flat dominated by *Z. muelleri* beds. The tide recedes up to 2 km from the high water mark and the sand flat is drained by three small

channels. The substrate is mostly sandy with small shell banks and patches of mud in some dense *Zostera* beds near channels. *Zostera* forms a wide band across the flats with only the highest and lowest ~100m being completely devoid of it; there do not appear to be any subtidal *Zostera* beds. There are no major fresh water inflows into the area apart from the mouth of the Puponga inlet on the western boundary and a small drain from the farm houses and car park area. Even though this site is not enclosed, intense wave action is rare as the predominant winds are westerly rather than easterly and Farewell Spit provides shelter from northerly aspect winds. Swan numbers at this site vary considerably from a low of 35 during the winter to just over 2000 in mid to late summer. The annual average swan density was 1.58 per hectare, ranging from 0.07 to 5.08 per hectare. Because of the consistently large population and relatively consistent conditions, most of the flock observations were conducted here.

Te Rae

Te Rae is located approximately halfway between Pakawau and Puponga at the mouth of Billy King Creek (40°34'00"S 172°42'10"E). The site covers about 3 km^2 of tidal flat composed largely of bare sand swales interspersed with *Zostera* beds. Up to 800 m of flat are exposed at low tide, with water draining into a channel formed by Billy King Creek. Sand is the dominant substrate with small areas of shell bank, and mud in the densest *Zostera* patches. This site is within an area used for cockle harvesting, which occurs in bare sand areas. During storms this site is exposed to quite intense wave action. At this site swans numbers can vary on a daily basis, but numbers are generally fairly low (0-274 recorded during surveys) relative to Puponga. The average density of swans was 0.81 per hectare across the whole year and ranged from 0 to 2.59 per hectare. Most of the individual behavioural observations were carried out here as the site allowed close observation.

White Pine Creek, Whanganui Inlet

Whanganui Inlet is a large, enclosed inlet up to 12 km long and 3 km wide on the west coast of Northwest Nelson. At its closest point it is just c. 4.5 km from Golden Bay. The study site is located adjacent to the mouth of White Pine creek on the southern side of the inlet (40°35'00"S 172°36'20"E), around 1.5 km from shore within the most significant *Zostera* bed in the estuary. The entire Whanganui Inlet is largely drained at

low tide with the exception of a few large deep permanent channels. This leaves a large expanse of tidal flat uncovered at low tide. The substrate at the study site is entirely clay and silty mud and supports approximately 860 ha of dense, largely continuous *Zostera* beds intersected with small channels and pools of bare mud (Davidson, 1990). As Whanganui Inlet is only open to the sea by a narrow mouth this site is subject to relatively little wave action. Swan numbers at this site are difficult to gauge accurately as the study site was set within the wider estuary without distinct boundaries and because there is no satisfactory vantage point from which to count. The counts taken from White Pine Creek Bridge and Muddy Creek Bridge in early summer consistently numbered around 250. Aerial counts conducted by Fish and Game in mid-summer (Fig 1.2) show an average of 406 swans in the Inlet. Assuming they stay within the areas where *Zostera* is present their density would be 0.47 swans per hectare. It is unlikely swans breed in the estuary proper given its tidal nature but a few pairs most probably nest in peripheral standing water bodies.

1.5 Study Components

This study investigates the effect of black swans on seagrass and the associated invertebrate fauna, focusing on four aspects of this interaction: the foraging behaviour and activity of black swans, the role of swans in the creation and maintenance of patches in the eelgrass landscape, the impact of swan grazing on *Zostera* biomass and invertebrate abundance/diversity, and the swans' diet and rates of nutrient cycling.

Chapter 2. *Swan foraging behaviour*

This chapter describes the feeding behaviour and routines of swans in the western Golden Bay intertidal zone, based on observations of individual birds and the flock as a whole. Swan numbers were tracked over a year and density estimates made for the two study sites used: Puponga and Te Rae. Feeding modes and rates were assessed in relation to the stage of the tide cycle. This gives an indication of the amount of time spent feeding. This information provides background information that is used in the following chapters.

Chapter 3. *Seagrass patchiness and swan grubbing*

As the presence or absence of *Zostera* has a large bearing on the invertebrate infauna found in a given area, the grazing and grubbing of feeding swans that reduces or removes *Zostera* are likely to drive some of this variation. A large-scale survey of the tidal flats quantified the patchiness of the *Zostera* and the extent of swan feeding in a spatial context. To evaluate the potential for swan foraging to be active agents in creating seagrass patchiness, holes mimicking swan grubbing were created and monitored at set intervals to record changes in shape, size and persistence. Paired samples in *Zostera* patches and bare sand were used to quantify difference in the invertebrate fauna in each habitat type.

Chapter 4. *Impacts of swan foraging on seagrass and invertebrates*

Exclosure experiments were conducted at three sites, excluding swans from foraging over dense seagrass beds for 2-6 months. Comparisons of *Zostera* size and structure (shoot number, above versus below-ground biomass), and invertebrate abundance and community structure, were made between experimental and control plots to determine if removal of swan foraging has a discernible impact on the benthic environment and fauna.

Chapter 5. *Diet and nutrient cycling of swans*

Observations and faecal analyses were used to confirm *Zostera* is the major food and determine the relative proportions of rhizome and shoot in the swans' diet. Swans make available through their droppings the nutrients in *Zostera* that would otherwise take much longer to enter the tidal environment. They also sequester a portion of these nutrients into their own bodies for growth and metabolic function. Varying amounts of nutrients in different parts of the *Zostera* plant may lead to preferential targeting of those parts with the highest nutritional value. This was examined via nutrient analysis of seagrass rhizomes (which may be grubbed by swans) and shoots (which may be grazed), and of swan faeces (the components being returned into the environment and made available to other species).

2. Intertidal activity and foraging of black swans in western Golden Bay

Abstract

The foraging activity of waterfowl can have a major impact on the habitat in which they live. This activity often is dictated by environmental cycles both daily and seasonally. This chapter characterizes the foraging behaviour of black swans in western Golden Bay and their foraging activity over the tidal cycle. Swan abundance and density were tracked over a year from October 2007 to October 2008 and varied greatly over time, being highest (maximum 4193) in summer and early autumn and lowest in winter and early spring (minimum 147). Swans employed an array of foraging behaviours depending on the location of the patch they were foraging on and the depth of the water at the time. The foraging activity of the swans was closely linked to the tide cycle – high and low tide are dominated by roosting with foraging occurring during the intertidal period.

2.1 Introduction

Globally, millions of waterfowl rely on a range of wetland systems at some stage of their annual cycles or daily routines, including marine or estuarine habitats. In areas where large herbivorous species such as geese or swans occur in high numbers, they have been shown to be capable of modifying their food supply and habitat extensively. Mute swan (*Cygnus olor*) on the eastern seaboard of the USA have undergone rapid growth since 1960s and are now causing habitat degradation through their foraging mode and high densities, and as they are non-migratory this foraging pressure is maintained throughout the year (Tatu *et al.*, 2007b). The effect of this foraging on the aquatic vegetation is dramatic with biomass reduced by 95% at some sites (Allin & Husband, 2003). Swans foraging in flocks were more destructive than territorial pairs (Tatu *et al.*, 2007a). The aquatic vegetation provides an important habitat and food source to other native species so the impact of the swans' foraging extend beyond that seen to the vegetation itself (Perry *et al.*, 2004). The foraging habits and life history of mute swans are having a significant impact on the ecology of this environment, raising issues regarding management to maintain the value of the habitat for native species (Ellis & Elphick, 2007).

The effects of black swan foraging activity on their habitat have not been widely studied in New Zealand. McKinnon and Mitchell (1994) found a clear negative relationship between winter black swan density and macrophyte abundance on a number of small South Island lakes. However, on these lakes variation in macrophyte levels was attributed to differing sediment types and prevalence of phytoplankton blooms rather than the effect of swan foraging. On Hawksbury Lagoon in Otago the impact of swan foraging on aquatic vegetation was minimal even though the density reached 25 swans per hectare (Mitchell & Wass, 1996). In some parts of New Zealand black swans have been known to feed on farm pasture, sometimes to damaging levels; this behaviour has been recorded mostly when aquatic vegetation is in short supply (Sagar *et al.*, 1995). The study of black swan behavioural patterns by Byrom and Davidson (1992) provides the only baseline information available for foraging and behavioural activity in a tidal *Zostera* habitat. They outlined individual swan behaviour, swan density and the influence of the tidal cycle on swan activity. From their observations they concluded that swans at Puponga and Whanganui Inlet feed only on *Zostera* leaves and do not eat the rhizome.

This chapter describes the variation in swan number and density over a 12-month period, the foraging methods of swans and their activity pattern over a 12-hour tide cycle. This information tests the assertion by Byrom and Davidson (1992) that swans do not forage on *Zostera* rhizome and expands on the outline of black swan foraging behaviour presented by Sagar *et al*. (1995). It also provides foundation knowledge for the following chapters of this thesis.

Figure 2.1. Swans feeding on a *Zostera* patch at low tide at Te Rae.

2.2 Methods

Weekly swan counts

From 31 October 2007 to 31 October 2008 counts of swans were made weekly from ten vantage points between Tamatea Point at Pakawau and the Farewell Spit access gate at Puponga (Fig. 2.3). From these vantage points all swans along this stretch of coastline could be counted. Time, tide stage and wind direction and strength were recorded during each survey. Nikon 10x25 'sportstar' field binoculars were used for the counts. An eight compass point division was used to estimate wind direction i.e. N, NW, W, SW, S, SE, E, NE. This was coupled with a four point scale for wind strength, 0, W1, W2, W3, corresponding to no wind, light wind, medium wind and strong wind respectively.

Surveys were conducted as near to high tide as possible as this was when the swans were closer to shore, increasing the accuracy of the counts. The entire count took 30-45 minutes depending on swan numbers and weather conditions.

Figure 2.2. The author in the field.

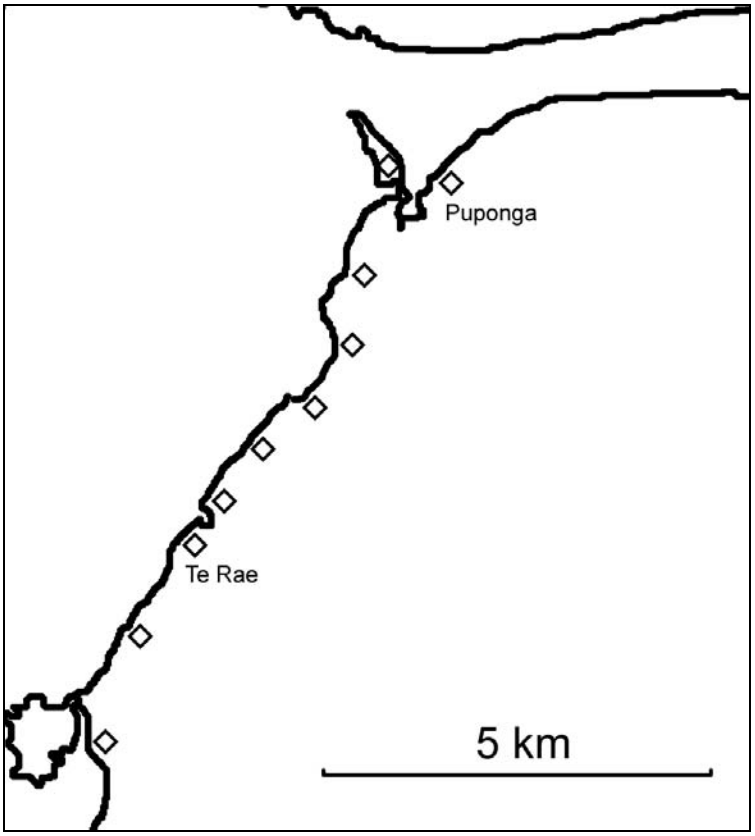


Figure 2.3. Map of vantage points used in weekly swan counts with behaviour observation points. The main study sites for this thesis are labelled.

Swan density

Monthly swan density per hectare was estimated for Puponga and Te Rae using the swan numbers recorded for Te Rae and Puponga in weekly counts divided by the area of each site. The area of each site was determined from a 1:50,000 NZ grid topographical map.

Behavioural observations

Behavioural observations were carried out over the summer and autumn months of 2008, at Puponga for flock observation or Te Rae for individual feeding behaviour. Pentax PF-80ED and Carton 880 spotting scopes, field binoculars, and unassisted observation were used to observe swan behaviours.

Foraging methods

Individual swan foraging was observed and a list of behaviours was compiled to characterize individual modes of foraging. Observations of individual swan's feeding behaviour were carried out mainly at the Te Rae because the site allowed closer viewing of birds than at Puponga. The swans' behaviours were assigned codes and categorized. Feeding event times on water were recorded.

Activity patterns

Observations of flock behaviour in relation to tide were carried out at Puponga. This site was used because there were always swans present and because it provided a good vantage point from which to observe the whole flock. The entire flock was counted then scanned using a scope and the number of swans exhibiting each behaviour category was recorded. This was converted to a percentage of the total flock number. The behaviour categories used were foraging, roosting, preening, and moving. Foraging was divided into foraging onshore and foraging on water. These behaviour categories were adapted from Mathers and Montgomery (1996) who conducted a similar study on Brent geese (*Branta bernicla*) in Ireland and from black swan behaviours observed by Bimler (1983) and Byrom and Davidson (1992). Observations were made every 10 minutes across the whole 12-hour tide cycle. As day length, and often weather, precluded observing the full 12-hour tide cycle at one time, observations were carried out on multiple occasions. This meant that most of the 10 minute segments across the tide range were observed on several occasions. One night-time observation was carried out between 11:00 pm and 2:00 am on 21/03/2008 when the moon was full and tide was high and receding.

In calculating daily activity budget of swans, the behaviour of the flock was used as a proxy for individual behaviour. For example if >50% of the flock was roosting this was classified as time spent roosting. While these percentages give an indication of swan activity in relation to the tide cycle the activity pattern of individual swans may vary from that of the flock as a whole.

The tide stage was calculated from the nearest high or low tide time for Collingwood as printed in a tide table. These times proved to be reasonably accurate for Puponga too although there was some variability in tide size depending on wind direction.

2.3 Results

Swan numbers

The number of swans between Pakawau and Puponga varied over the course of the year (Fig. 2.4). Numbers increased from the initial count of 799 at the end of October 2007 to a maximum of 4193 in early April then declined rapidly to around 5% of this by the beginning of July and reaching a low of 147 in early September before beginning to rise steeply again in October 2008. Wind direction and strength did not have a major effect on overall numbers or where they were found along the coast other than that in particularly strong wind the swans would come closer to or onto shore.

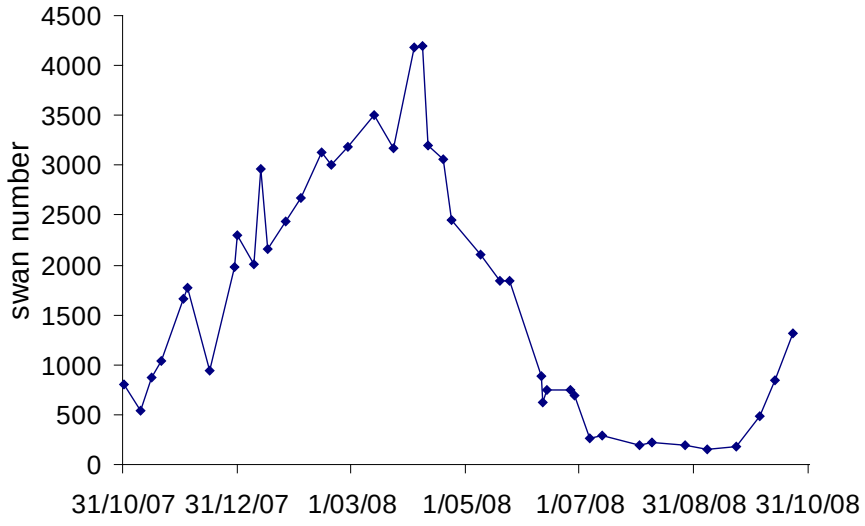


Figure 2.4. Swan numbers between Pakawau and Puponga from October 2007 to October 2008.

Swan density

Monthly swan density at both sites followed the pattern of numbers along the whole stretch of coast with maximum densities from February to April and minimum densities from July to September (Fig. 2.5). Swan density was higher at Puponga than Te Rae every month except for July and reached 3.9 swans ha^{-1} in February and dropped to 0.07 swans ha^{-1} in July. The annual average swan density at Puponga was 1.64 swans ha^{-1}, double the density at Te Rae. The highest density at Te Rae was 1.9 swans ha^{-1} in March, the lowest density was 0.05 swan ha^{-1} in September, and the annual average swan density at this site was 0.81 swan ha^{-1}.

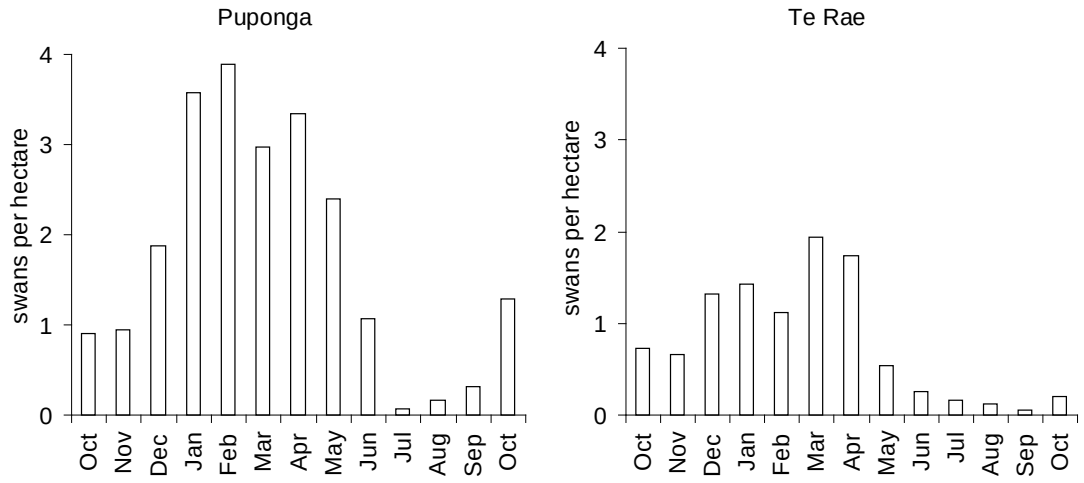


Figure 2.5. Monthly average swan density at Puponga and Te Rae from 31/10/07 to 31/10/08.

Foraging methods

A number of discrete foraging behaviours were identified (see list below). Of these, the most common feeding mode employed by the swans was number 5 – head and neck submerged while floating on the water. This involved dipping the head and neck underwater for 10-15 seconds then raising the head for 2-5 seconds, often just exposing the nostrils before dipping down again. Swans would either stay in one spot for several minutes before moving to another or feed and move at the same time. Most food appeared to be consumed under water but *Zostera* material was often brought to the surface and consumed there.

<u>Observed foraging behaviours</u>

1- *Dabbling*: pecking at *Zostera* shoots floating on water surface while swimming, usually when tide is high and swans could not reach the bottom to feed or opportunistically while transiting.

2- *Head down*: face under while on water. Occurred usually in shallow water where the swan was in just enough water to float.

3- *Foot grubbing*: a forceful side-to-side rocking motion as legs are used to fan sand away from *Zostera* rhizome. Seen in conjunction with 4.

4- *Half neck down:* half neck under while on water, in water half a neck-length deep. Occurred particularly as the tide receded.

5- *Neck down*: neck fully submerged while on water. This was the most common mode of feeding, observed throughout the tide cycle.

6- *Upending*: when feeding in water deeper than the neck plus half the body length, displayed by swans further offshore or by the first swans to start feeding after high tide. This behaviour was rare.

7- *Head down on shore*: face under water while standing when feeding on flats in or at the edge of shallow pools and channels.

8- *Half neck down*: feeding neck half under water while standing in leg-depth water.

9- *Pool edge grubbing standing:* head above water, working along pool or channel edges while standing.

10- *Pool edge grubbing on water*: head above water, working along pool or channel edge while floating on water.

11- *Tugging at Zostera rhizome*: forceful neck tugging/twisting at *Zostera* rhizome.

12- *Plucking at Zostera shoots*: less forceful tugging to break off shoots.

13- *Gentle head shaking*: to loosen/break up *Zostera* rhizome and shoots, usually while on water in conjunction with other feeding behaviours - 4, 5, 6.

14- *Neck/body jerking with head/neck submerged*: most probably equivalent to 11 and 12 but underwater.

15- *Washing plucked Zostera*: after a beak full of *Zostera* was plucked from 'dry' ground it was then swished in nearby water before eating, possibly to remove sand and shell. Rarely seen.

Activity patterns

Swans followed an activity pattern that is controlled by the tide cycle (Fig. 2.6). On average swans spent 61% of the time foraging. In this study sleeping (roosting) dominated 16% of the time while a majority of swans were classed as moving 6% of the time. For the remaining 17% of time no one activity dominated. As the tide receded swans would begin by foraging on water once the *Zostera* was in reach (with the head submerged). As the tidal flats became exposed swans would increasingly forage on shore until mid-way between high and low tide then many would move out to the water edge and follow it out toward low tide. Once the low tide line passed beyond the lower limit of the *Zostera* the swans would stay on shore foraging. As the tide came back in, all foraging swans did was on water (Fig. 2.7). During the single night observation the swan activity recorded was similar to that seen at the same tide stage in daylight hours.

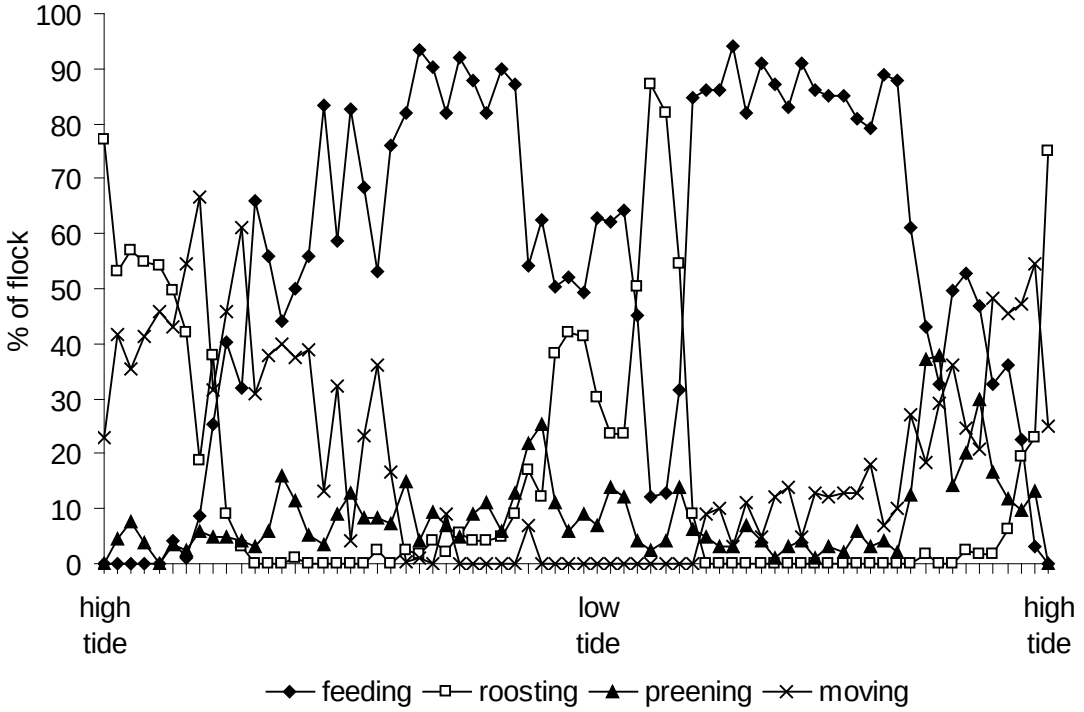


Figure 2.6. Percent of swans engaged in assigned behaviours over a 12-hour tide cycle measured at 10-minute intervals.

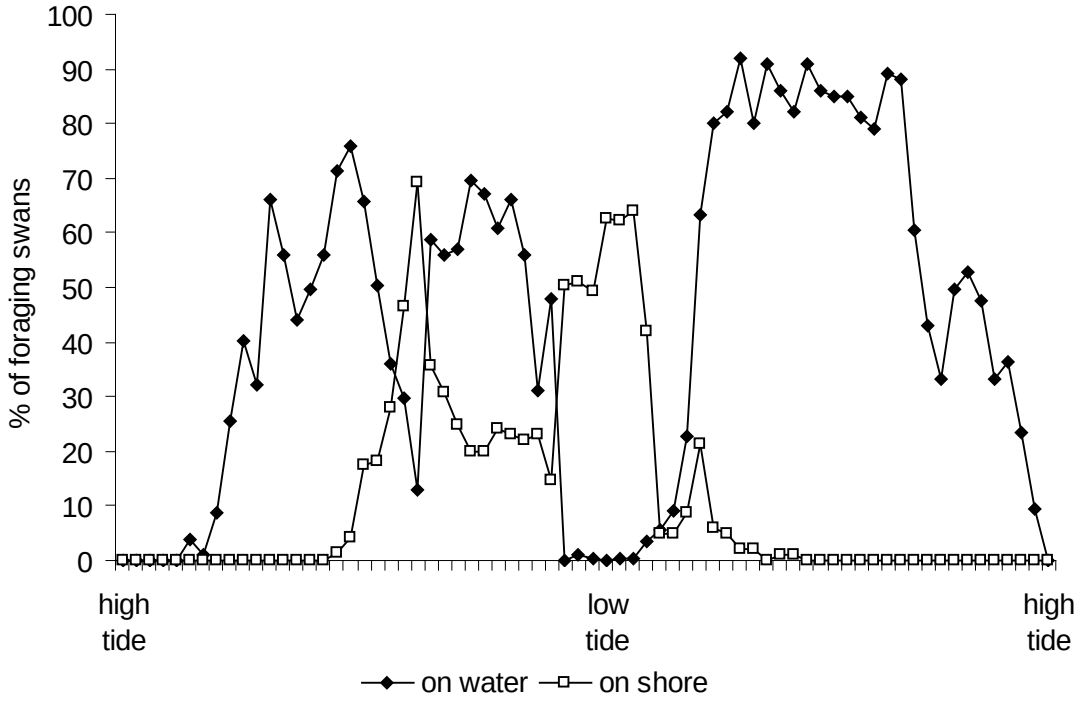


Figure 2.7. Percent of total swan flock foraging on water and on shore across a 12-hour tide cycle measured at 10-minute intervals.

2.4 Discussion

Swan number and density

The distinctive seasonal pattern seen in swan numbers in western Golden Bay, with low numbers in winter increasing to peak in late summer before declining again, supports patterns of annual change seen in other studies on black swans in New Zealand. The lowest number in this study occurred from July to September, the main period when breeding swans are nesting on permanent lagoons and freshwater lakes (Marchant & Higgins, 1990). Aggression by breeding swans in a freshwater wetland in the Manawatu forced non-breeding swans to leave in early spring (Potts, 1982); this coincides with when swan numbers in western Golden Bay begin to increase. The peak swan numbers in western Golden Bay in late summer/early autumn coincide with the fledging of juveniles from the previous breeding season (Marchant & Higgins, 1990).

The swan density observed at Puponga during January in this study (3.57 swans/ha) closely matches those reported by Byrom and Davidson (1992) (approximately 3.85 swan/ha) for this site in 1991. The total swan number on Farewell Spit in 1991 also closely matches the numbers present during this study (Fig 1.2, Chapter 1). The density observed in this study, however, was much lower than densities recorded on Hawksbury Lagoon where summer swan density was frequently above 10 swans/ha and occasionally reached as high as 20 swans/ha when aquatic macrophyte is abundant (Mitchell & Wass, 1995).

It is possible that the variation in swan numbers along the coast from Pakawau to Puponga is not an accurate reflection of the numbers across the whole of Farewell Spit so caution is needed when extrapolating the observed pattern beyond the study site itself. It may be that this stretch of coast has a more desirable food source in summer or provide more shelter from changing seasonal weather patterns. The total area of tidal flat on Farewell Spit is around 9000 hectares so 5000-15,000 swans over this area would give a density of 0.6-1.7 swans/ha. However the actual area that provides suitable foraging habitat is smaller than this so the effective swan density on *Zostera* patches is probably higher than this figure.

Foraging methods

Black swans on Farewell Spit feed on all parts of the *Zostera* plant by cropping the shoots and digging for rhizome with their bill and feet. This contrasts with observations made by Byrom and Davidson (1992) when they reported that the swans at Puponga did not feed on *Zostera* rhizomes. The prevalence of feeding while on water may be because it allows rhizome to be removed from the substrate and sand washed off rhizome more easily than on 'dry' flats. When *Zostera* is exposed at low tide the leaves lie flat on the sand and can form dense mats but once submerged the leaves 'float' upright. This may make access to both the leaves and the underlying rhizome easier. It may be that it is more efficient for swans to move from one food patch to another by swimming rather than walking, making water feeding a by-product of their movement pattern.

The swans used a number of feeding modes depending on whether they were feeding on water or on shore. The behaviours recorded during this study largely matched the feeding behaviours observed by Byrom and Davidson (1992), who were more focused on general black swan ecology, and Bimler (1983) who was more concerned with breeding behaviour but listed feeding behaviour as well.

Activity patterns

Swans followed an activity pattern that was synchronised with the daily tide cycle. Most swans roosted at high and low tides – at high tide most of the *Zostera* would be out of reach and at low tide the edge of the water recedes well below the lower limit of the *Zostera* beds, preventing the swans from using their preferred mode of foraging. Feeding occurred through out the rest of the cycle, either as a combination of onshore and on water as the tide receded or on water as the tide came in. The change-over between dominant activities was rapid, occurring in a matter of 15 to 30 minutes.

The observations of this study that show swans spent 61% of their time foraging closely match the findings of Byrom and Davidson (1992) who suggested that the swans at Puponga foraged about 60% of the time. In their study they classed the remaining 40% of the time as roosting, without differentiating between preening and sleeping activity. In this study sleeping (roosting) dominated 16% of the time while a majority of swans

were classed as moving 5.7% of the time. For the remaining 17% of time no one activity dominated.

While no firm inferences can be made on the basis of a single observation, that swans did not seem to alter their behaviour significantly at night agrees with night-time observations carried out by Byrom and Davidson (1992).

Conclusions

The size of the swan population in western Golden Bay varied greatly over a yearly cycle. This variation fits with what is known of their breeding and migration habits in other parts of New Zealand. The arrival of swans in western Golden Bay comes in two phases: those arriving in spring are probably non-breeding birds that have been driven off lakes and lagoons by breeding birds, while the birds arriving later in summer are likely to be breeding birds and newly fledged offspring.

The maximum swan density matches those seen at this site in a previous study but is much lower than densities observed on some permanent lakes. This is probably due to two main factors: firstly, the area of suitable swan habitat in western Golden Bay is large giving the swans space to spread out, and secondly the algae consumed on some lakes are a more plentiful and assimilable food source.

Individual swans showed a range of different modes of foraging but mostly fed by submerging their neck while floating on water, possibly because this allows easier removal of rhizome from the substrate or because movement on water is more energetically efficient than moving on land.

Because black swans cannot reach beyond about a meter below the surface of the water their access to their *Zostera* food supply is dictated by the tide cycle. Although the swans generally appear to prefer feeding on water to foraging on shore the direction of the tide flow influences the foraging mode they employ – on the incoming tide swans forage exclusively while on water but as the tide goes out swans forage both on water and onshore. This difference in foraging behaviour is probably simply because some swans are left ‘stranded’ as the water recedes from under them on the outgoing tide whereas the water pushes them towards shore as it comes back in.

3. Black swans as potential patch creators in *Zostera* beds in western Golden Bay

Abstract

Seagrass beds are often patchy in nature and a number of possible causes for this patchiness have been proposed. This study investigates the potential for the foraging habits of black swans (*Cygnus atratus*) to cause and maintain patchiness in a tidal seagrass habitat in Golden Bay, north-west South Island, New Zealand. Seagrass is widespread but generally sparse with denser patches interspersed across the tidal flats at this site. Swan foraging activity was concentrated on denser seagrass at both the landscape scale and within individual patches. Experimental grubbings created to mimic the effect of swan foraging showed that their mode of feeding can be destructive to seagrass beds by converting intact seagrass to bare sand, and that these effects can last for at least two months. Paired benthos sampling showed that seagrass supports higher macro invertebrate diversity and abundance than adjacent bare areas. As swans are capable of converting seagrass to bare sand it is likely they also have a negative impact on the associated macro invertebrate fauna.

3.1 Introduction

Like seagrass beds in many parts of the world, *Zostera muelleri* beds in western Golden Bay, New Zealand, are patchily distributed across the tidal flats, at both large and small scales (Fig. 3.1). Patches can consist of isolated clumps or beds of seagrass in bare sand, or patches of bare sand set within larger seagrass beds. Generally fauna diversity and abundance is higher inside seagrass patches than adjacent bare substrate (Bell *et al.*, 2001; Boström & Bonsdorff, 1997; Cardoso *et al.*, 2007; Heck & Wetstone, 1977) but on a scale of centimetres to meters patch edges can have higher biodiversity than either within the patch or outside it (Bologna & Heck, 2002; Tanner, 2005). How patches such as these are created has been the focus of a number of studies looking at both biotic and abiotic agents.

Figure 3.1. *Zostera*/bare sand mosaic on the tidal flats at Puponga, Golden Bay.

In other seagrass systems, natural physical processes such as mobile underwater sand dunes (Marba & Duarte, 1995), seasonal wave action (Ramage & Schiel, 1999) and channel infilling (van der Laan & Wolff, 2006), or anthropogenic causes like boat anchors (Francour *et al.*, 1999) and, on a larger scale, pollution (Borum *et al.*, 2004), have been found to have contributed to the observed patchiness. Biogenic agents such as polychaete worms (Hughes *et al.*, 2000), fish (Verges *et al.*, 2008), crabs (Woods & Schiel, 1997) and dugongs (*Dugong dugon*) (Thyer *et al.*, 1984) have also variously been implicated in patch formation. Some of these possible causes of patchiness can easily be discounted on Farewell Spit and in western Golden Bay: dugongs are only found in tropical regions and public boat access is prohibited within the Farewell Spit Scientific Reserve and is uncommon over seagrass beds in the rest of western Golden Bay. Other patch creators could, and most probably do, play a role in the creation of the patchy landscape on the Farewell Spit and adjacent tide flats, although none of the causes found in other studies satisfactorily account for all of the patchiness present.

An unexplored possible agent of patchiness in New Zealand seagrass beds is the black swan (*Cygnus atratus*). This large waterfowl feeds extensively on intertidal seagrass beds, often destructively grubbing for sub-surface rhizomes (chapters 2 and 5), and may

be extremely numerous. On the tidal flats of Golden Bay, Northwest Nelson, New Zealand, up to 15,000 swans feed in shallow water above seagrass, or on exposed seagrass beds at low tide. While swan density is relatively low when taken across the total tidal area they were often observed congregating in localized areas. Formerly thought just to feed on above-ground leaves of *Zostera* (Sagar *et al.*, 1995), it is now evident that a substantial component of their foraging involves grubbing of rhizomes (chapter 2; Fig. 3.2). This has the potential to create numerous small holes in otherwise intact seagrass beds, or to expand existing holes.

In this chapter I investigate the potential of swans to influence the fine-scale patchiness across seagrass meadows in western Golden Bay. Seagrass cover was surveyed every 125 or 250 m across 255 ha at two sites, recording also the frequency and size of swan grubbings within a 5 m radius of each point. Using the size of 'natural' swan holes as a guide, I experimentally created large and small swan foraging holes to test the persistence of such holes.

Figure 3.2. Impact of black swan foraging on *Zostera* patch edges.

Finally, the benthic invertebrate fauna of vegetated and adjacent un-vegetated patches was compared to assess the impact on benthos that conversion from *Zostera* to sand would have. While the impact of waterfowl on tidal wetland vegetation has been well documented (Esselink *et al.*, 1997; Jacobs *et al.*, 1981; Mathers *et al.*, 1998; Tatu *et al.*, 2007b), to my knowledge this is the first study to look specifically at the role of swans in creating and maintaining patchiness in a tidal *Zostera* habitat.

3.2 Methods

Zostera cover survey and swan feeding activity

At two study sites (Puponga (40°31'20"S 172°44'32"E) and Te Rae (40°34'00"S 172°42'10"E)), a large-scale grid survey was undertaken to determine the surface *Zostera* patchiness and swan feeding activity. Using NZ grid lines (north-south and east-west), survey points were established every 250 m at Puponga and 125 m at Te Rae across the tidal flats with a handheld GPS (accuracy ± 5 meters). The surveys' grids covered approximately 175 ha (Puponga) and 80 ha (Te Rae), and contained 46 and 53 points respectively (Fig. 3.3). At each point a 5 m radius circle was scribed on the substrate using a stake driven into the sand at the centre and a sharp steel rod on a five meter long string (knotted every meter) giving a 78.5 m^2 circle (Fig. 3.4).

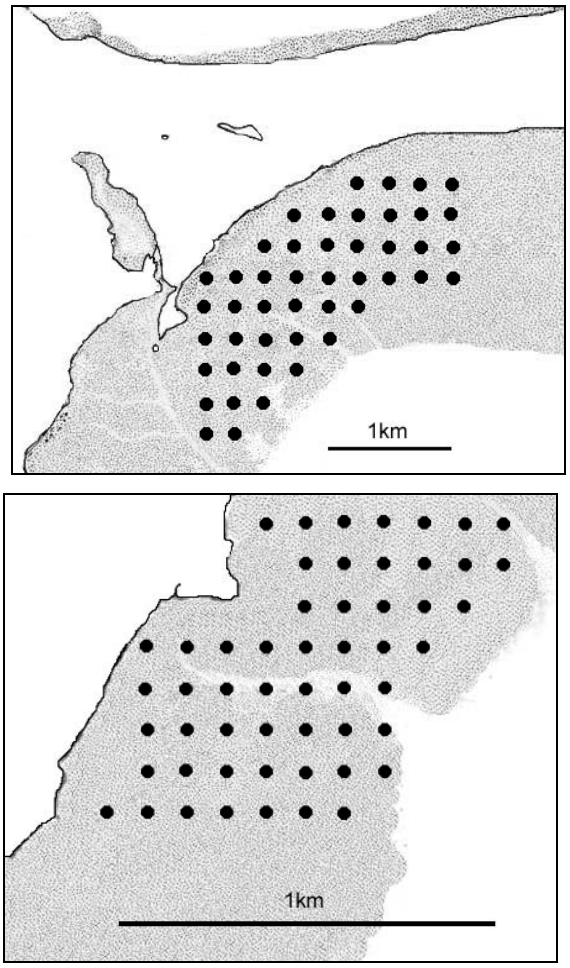


Figure 3.3. *Zostera* cover and swan feeding survey layout at Puponga (top) and Te Rae (bottom).

For the *Zostera* survey, at each site north was located using a compass then *Zostera* cover was scored across the 5-m radius at each knot along the string to give five cover scores from the centre to the edge of the sample area. Scores were based on a categorical 1-6 scale (Fig. 3.5). This was repeated for NW, W, SW, S, SE, E, and NE radiuses giving a total of 40 *Zostera* cover scores for each sample point. At each site, the number of points *Zostera* was found at and the average *Zostera* score cover was calculated. The coefficient of variation (CV) was calculated for each site to give an indication of heterogeneity of the 40 compass-point *Zostera* scores at each sample point.

Figure 3.4. An example of the *Zostera* surface cover and swan feeding survey point. The circle has a 5-m radius.

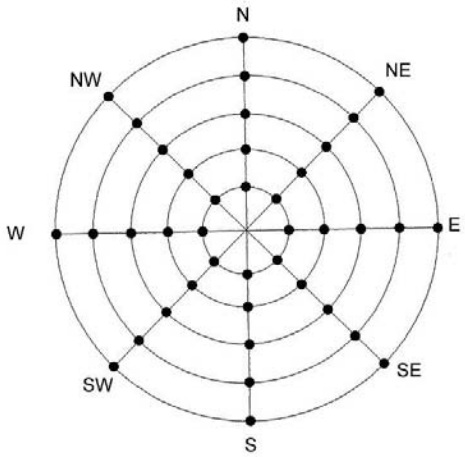


Figure 3.5. Layout of the 40 point *Zostera* cover score sampling used at each survey point.

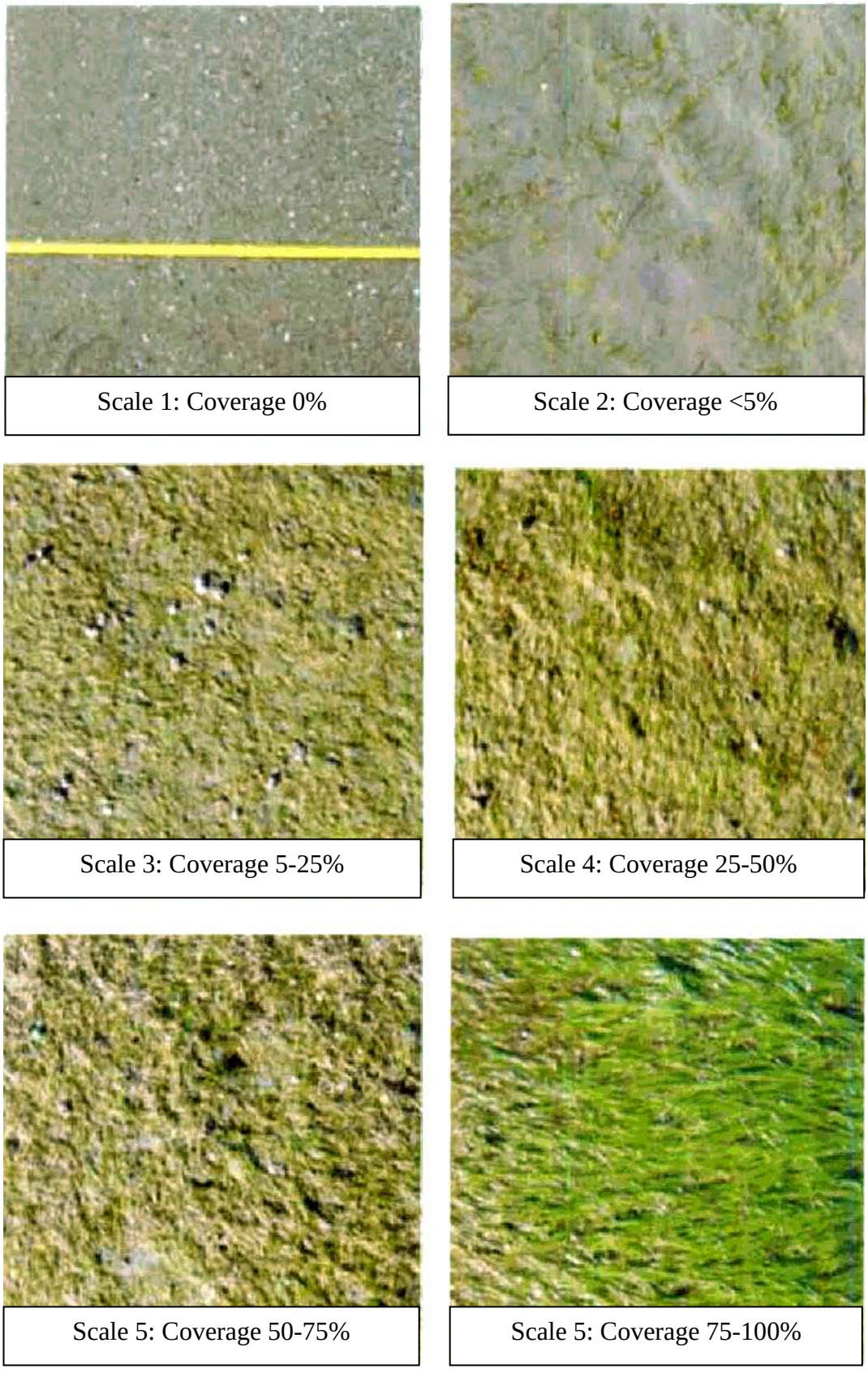


Figure 3.6. *Zostera* cover scoring schedule.

For the swan feeding activity survey the area within the circle was visually scanned for any evidence of feeding. Length and width of any swan holes or grubbings were measured to the nearest 10 cm. Other holes and disturbances were also measured and assigned a cause if identifiable. The percent of sample points with swan feeding, average number of feeding disturbances, average area of feeding disturbances per sample point and area of feeding disturbance were calculated for each site.

Experimental 'swan-holes'

Experimental holes were created at both Puponga and Te Rae to mimic the effect of swan grubbing for *Zostera* rhizomes. At each site four replicates were established, two near the low tide mark and two near high tide. Each replicate consisted of six large (40 cm long x 20 cm wide x 5 cm deep) and six small (10 cm round and 10 cm deep) holes, in areas of low *Zostera* and high *Zostera* cover (total of 24 holes per replicate, two replicates per elevation level, two elevation levels for a total of 96 holes per site; Figures 3.7 and 3.8. Hole sizes matched the most common hole type (small circular holes were 33% of the total) and the median hole sizes observed from the swan feeding survey. Photographs of each set of holes were taken when the holes were established and at every re-sampling period.

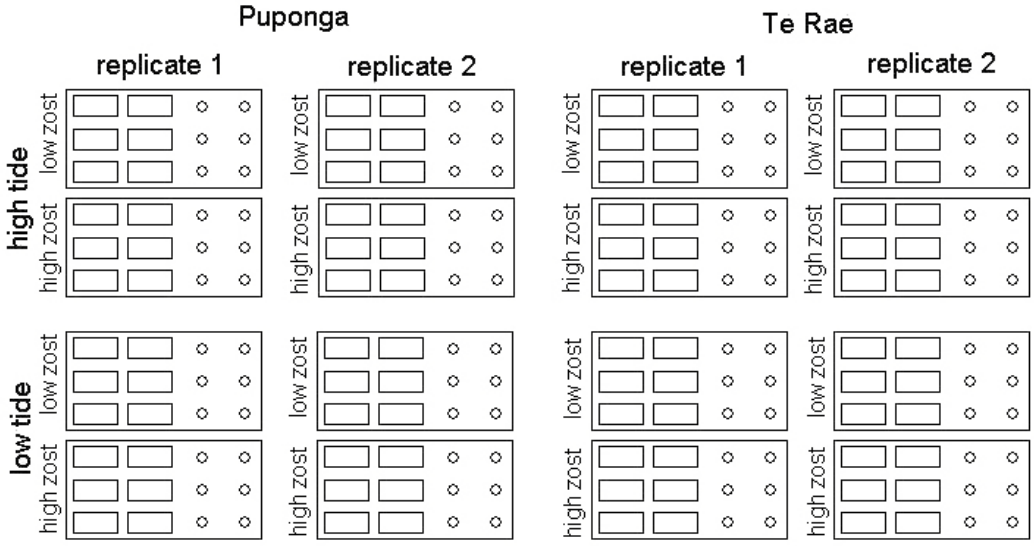


Figure 3.7. Layout of the experimental swan-holes.

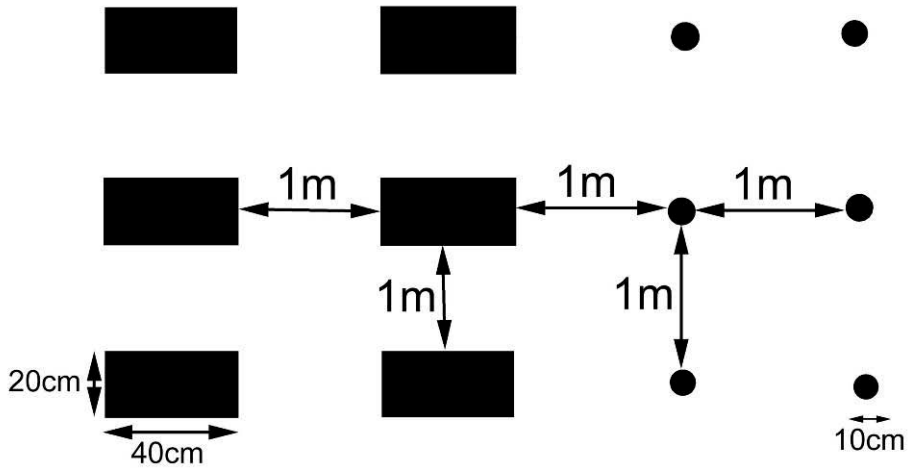


Figure 3.8. Detail of the layout of holes in one replicate of the experimental swan holes.

The holes were then monitored over a series of intervals: 1, 2, and 3 tides, and 5, 20, 40, and 60 days. At each interval the length, width and depth of holes were measured and any swan grubbing and other changes noted, including possible causes of enlargement and the amount of infilling. The 5, 20, 40 and 60 day sampling periods were converted to number of tide cycles using a tide table for analysis.

Sediment samples

Three sediment core samples 40 mm diameter by 50 mm deep were taken from each of the high and low *Zostera* plots in each replicate (at both tidal elevations), giving a total of 48 samples across both sites. The samples were dried at 80^{o}C for four hours then sieved through a ~2 mm^{2} mesh kitchen sieve to remove debris; all sediment particles were smaller than this. The remaining sediment was then passed through a five-tier stainless steel sediment sorter to separate out six sand particle size-classes using the Wentworth scale: >1 mm, >0.5 mm, >0.25 mm, >0.125 mm, >0.063 mm and <0.063 mm. Each portion was weighed to the nearest 0.01 g.

Paired benthos sampling

Paired benthos sampling consisted of taking 10 cm diameter x 25 cm deep core samples from approximately 1 m inside and outside the edge of a *Zostera* patch or where the bare sand or *Zostera* clearly ended. At Puponga, Te Rae and White Pine Creek five dense *Zostera* and five light *Zostera* cores were taken, each with an accompanying bare

sand core giving a total of 60 samples, thirty bare sand and fifteen each of high and low *Zostera*. These samples were collected within a 25 m radius of exclosure 1 at each of the study sites (see chapter 4). Cores were sieved using a 1 mm mesh sieve on site to remove sand and mud (Fig. 4.6), and the remaining material was placed in labelled plastic bags and stored in a refrigerator until sorting (within 48 hours of collection). Sample material was sorted and all invertebrates removed and stored for identification. Soft bodied invertebrates (worms, anemones) were stored in 90% ethanol; large molluscs and decapods were frozen.

Invertebrates were identified under a binocular microscope and measured on 2x2 mm graph paper or with callipers to the nearest mm. Identification was to the lowest practical taxonomic level, which varied considerably among groups. Most decapods and bivalves could be identified to species while ribbon worms, Nemertea, were not identified past phylum. Because of this the term ‘taxa’ is used to refer to the distinct taxonomic groups recognized in this study instead ‘species’, ‘genera’, etc.

Statistical analysis

ANOVA and linear regression were used to test for differences in *Zostera* cover and CV between sample points with and without swan feeding. A t-test and ANOVA were used to test for significant differences between paired macrobenthos samples.

3.3 Results

Zostera cover survey

Overall 73 of 99 (73.7%) points sampled had some *Zostera* present and 26 (26.3%) were bare sand (Table 3.1; Fig. 3.9). The average *Zostera* cover score across all 99 sample points from both sites was 2.2± standard deveation1.1, ranging from 1 (bare sand) to a point average score of 4.7. Of the points with *Zostera* present only one had a coefficient of variation of 0, i.e. a completely even cover of just one *Zostera* score. The overall coefficient of variance was 0.34.

At Puponga 39 of 46 or 84.7% of sample points had some *Zostera* present. The remaining seven points (15.3%) were entirely bare sand (Fig. 3.10). The average *Zostera* cover score was 2.41±1.1 with an average coefficient of variance of 0.32 (Table 3.1).

At Te Rae 34 of 53 or 64.2% of sample points had some *Zostera* present, while 35.8% or 19 sample points were bare sand (Fig. 3.10). The average *Zostera* cover across all sample points at Te Rae was 2.0±1.1 with a coefficient of variance of 0.35 (Table 3.1).

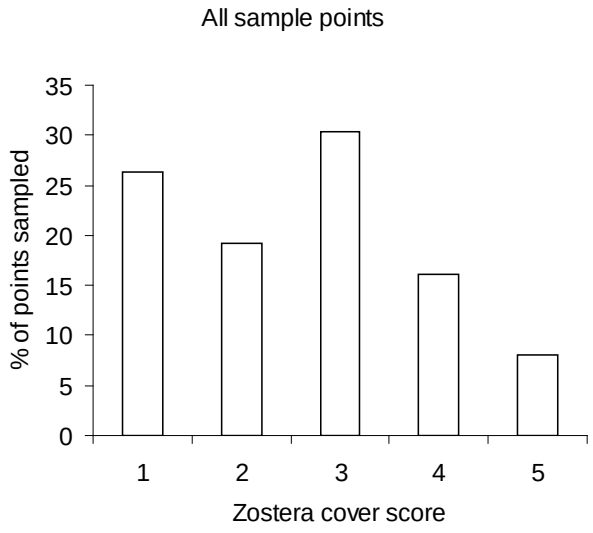


Figure 3.9. Percent of average *Zostera* cover scores across all sample points.

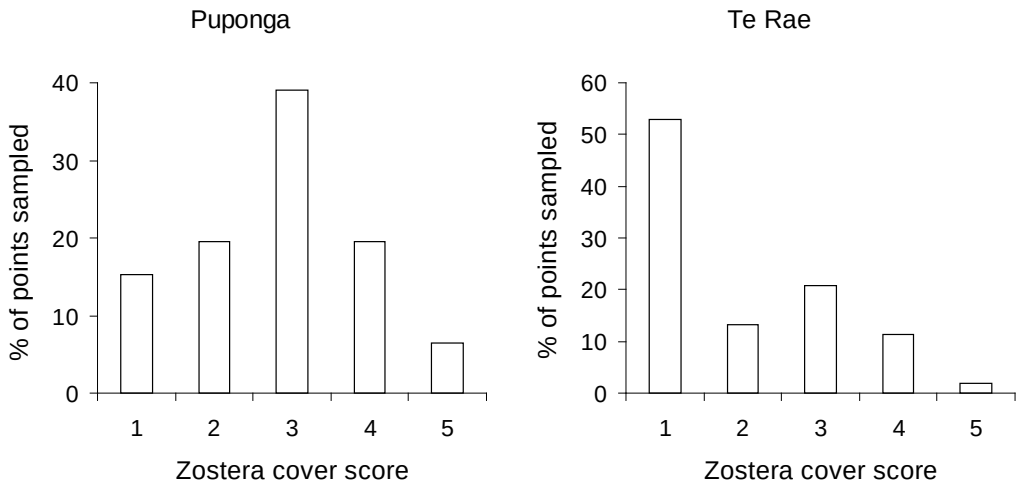


Figure 3.10. Average *Zostera* surface cover score at Puponga (46 sites) and Te Rae (53 sites).

Table 3.1. Summary of *Zostera* cover for Puponga and Te Rae.

Measure	Both sites	Puponga	Te Rae
No. sample points	99	46	53
Points with feeding activity	73	39	34
%	73.7	84.8	64.2
Zostera cover score (±s.d.) for all points	2.2 (±0.86)	2.41 ±0.85)	2 (±0.88)
Coefficient of Variance for all points	0.34	0.32	0.35
Cover score (±s.d.) for points with *Zostera*	2.62 (±1.17)	2.67 ±1.00)	2.57 (±1.37)
Variance for points with *Zostera*	0.46	0.38	0.55

Swan feeding activity

Of all 99 points surveyed, 52 (52.5%) showed evidence of swan feeding activity (see Table 3.2). At those points, the average total area of disturbance was 0.47 m^2 (out of the 78.5 m^2 survey area). Across all points this equates to 31.94 m^2 of foraging disturbance per hectare. The average number of discrete grubbings or holes per sample point where there was feeding activity was 4.72; this equates to 321 grubbings or holes per hectare across all points.

At Puponga 14 of 46 (28.9%) of the points surveyed showed no sign of swan activity. At the 31 points where there was feeding activity the average area of grubbing ranged from 0.015 to 3.37 m^2 (average 0.55 m^2). The average *Zostera* cover score of discrete seagrass patches where swan feeding was found was 4.03. Overall there was an average of 47.21 m^2 grubbings per hectare and 404 grubbings or holes per hectare.

At Te Rae 22 of 53 or 41.5% of points surveyed showed no evidence of swan feeding activity. The average *Zostera* cover score of discrete seagrass patches where swan feeding was found was 4.77. At the sites with feeding activity the average area disturbed was 0.35m^2 (range 0.025 to 1.5 m^2). Overall there was an average disturbed area of 18.69 m^2 and 250 grubbings or holes per hectare. There were very few holes that were clearly identifiable as having been created by other species. Those of eagle rays (*Myliobatis tenuicaudatus*) were readily identified, but were always found in bare sand.

Table 3.2. Summary of swan feeding disturbances at Puponga and Te Rae.

Measure	Puponga	Te Rae	Both sites
No. sample points	46	53	99
Points with feeding activity	30	22	52
%	65.2	41.5	52.5
Average number of holes/grubbings per point	3.11 (0-15)	1.96 (0-23)	2.49 (0-23)
Average number of holes/grubbings per ha (range)	285	104	166
Average area of feeding activity per point (m^2)	0.35 (0-3.37)	0.15 (0-1.5)	0.24 (0-3.37)
Average area of feeding activity per ha (m^2) (range)	28.91	7.76	16.07
Average score of disturbed *Zostera* (±s.d.)	4.03 (±1.27)	4.78 (±0.99)	4.24 (±1.28)

A total of 219 individual swan feeding disturbances were recorded, 128 at Puponga and 91 at Te Rae. The median feeding hole area was 0.088 m^2. The most common type of hole was a small circular 'pock mark' type 10 cm in diameter, accounting for 33% of all holes identified. These often occurred in groups with 18 found together at one sample point. The largest individual hole was 1.35 m^2; this was the only hole with an area over 1 m^2 (Fig. 3.11).

Of the sample points where *Zostera* was present those with swan feeding activity had a significantly higher average *Zostera* cover ($F_{1,72}$=13.88, P=0.0004) than those without evidence of swan feeding; when all sites were considered this was even more pronounced ($F_{1,98}$=69.83, P<0.0001) (Fig. 3.12).

Within the sample points, swans appeared to concentrate their foraging in high-cover *Zostera*. The *Zostera* score of the discrete patches that grubbings were present in was higher ($F_{1,50}$=13.70, P=0.0005, r^2=0.2150) than the overall *Zostera* score for the sample point (Fig. 3.13, left). Sample points where swans fed in the densest *Zostera* had more variable cover (a higher CV: $F_{1,50}$=24.27, P=<0.0001, r^2=0.3268) than those where feeding took place in sparser *Zostera* (Fig. 3.13, right). Of the sample points where *Zostera* was present the CV did not differ significantly between sample points with and without feeding activity (Fig. 3.14).

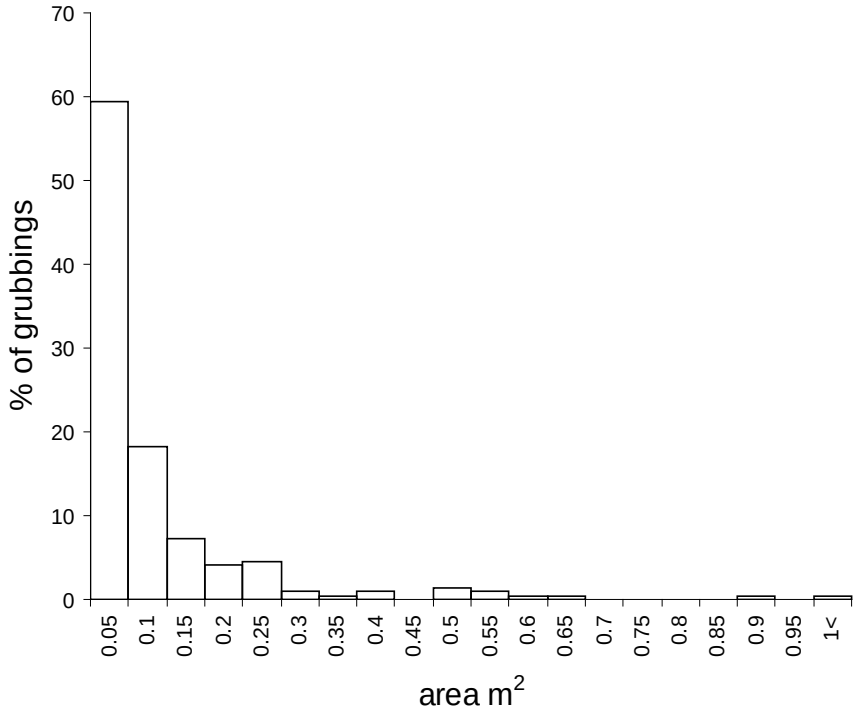


Figure 3.11. Frequency distribution of sizes of swan feeding holes across all sample points.

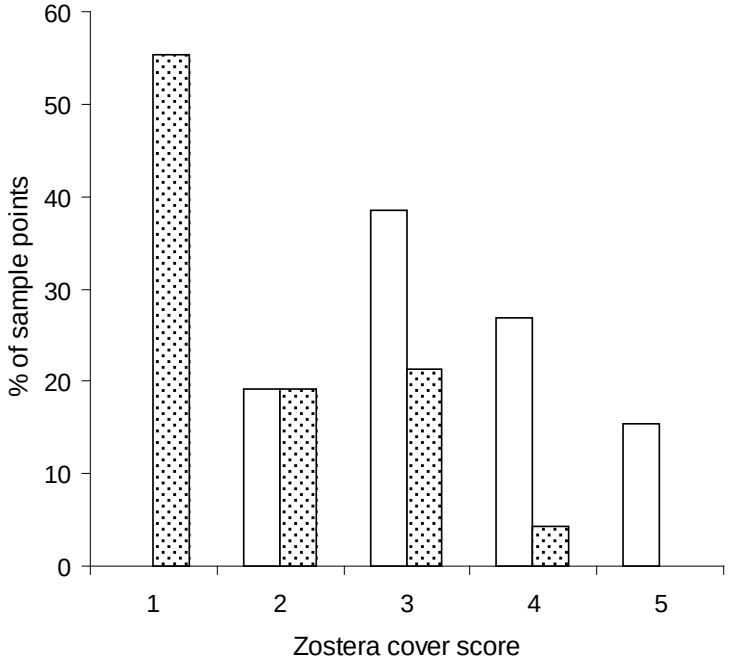


Figure 3.12. Percent of sample points with and without swan feeding activity by *Zostera* cover score. Open bars, points with swan feeding; filled bars, points with no swan feeding.

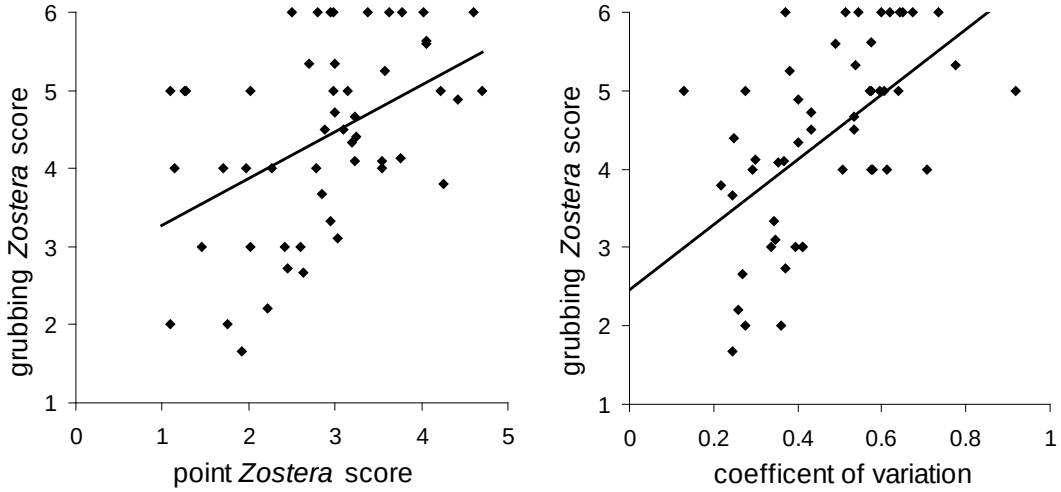


Figure 3.13. Regression plots of the relationship between the *Zostera* score for the discrete patch where individual grubbings occurred and sample point *Zostera* score (left) and CV (right).

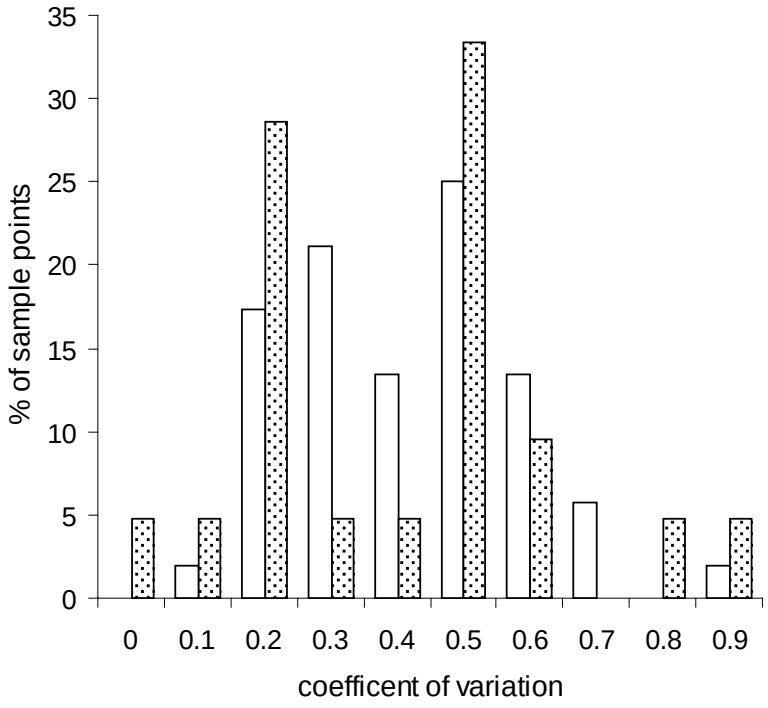


Figure 3.14. Percent of sample points with and without swan feeding activity in relation to the coefficient of variation in *Zostera* cover at each point. Open bars – points with swan feeding; filled bars – points with no swan feeding.

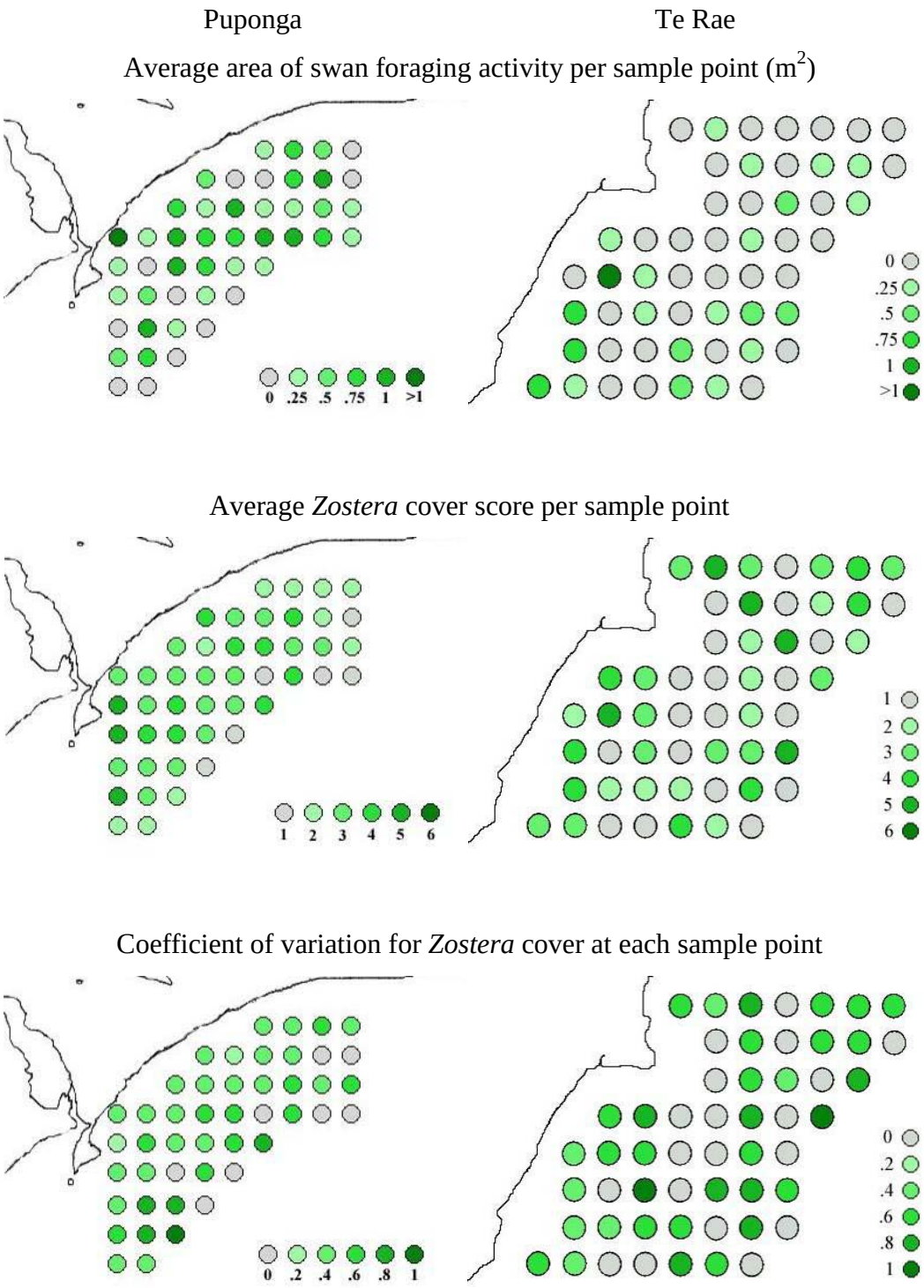


Figure 3.15. Visual representation of area of foraging activity (m^2), *Zostera* cover and coefficient of variation at Puponga (left) and Te Rae (right). Each circle represents one sample point (not shown to scale).

Although there was a significant relationship between the presence of swan feeding sign and *Zostera* cover there was no significant correlation between the total area or number of grubbings and *Zostera* cover. Total area grubbed and the number of grubbings were not related to the CV of the point (Fig. 3.16).

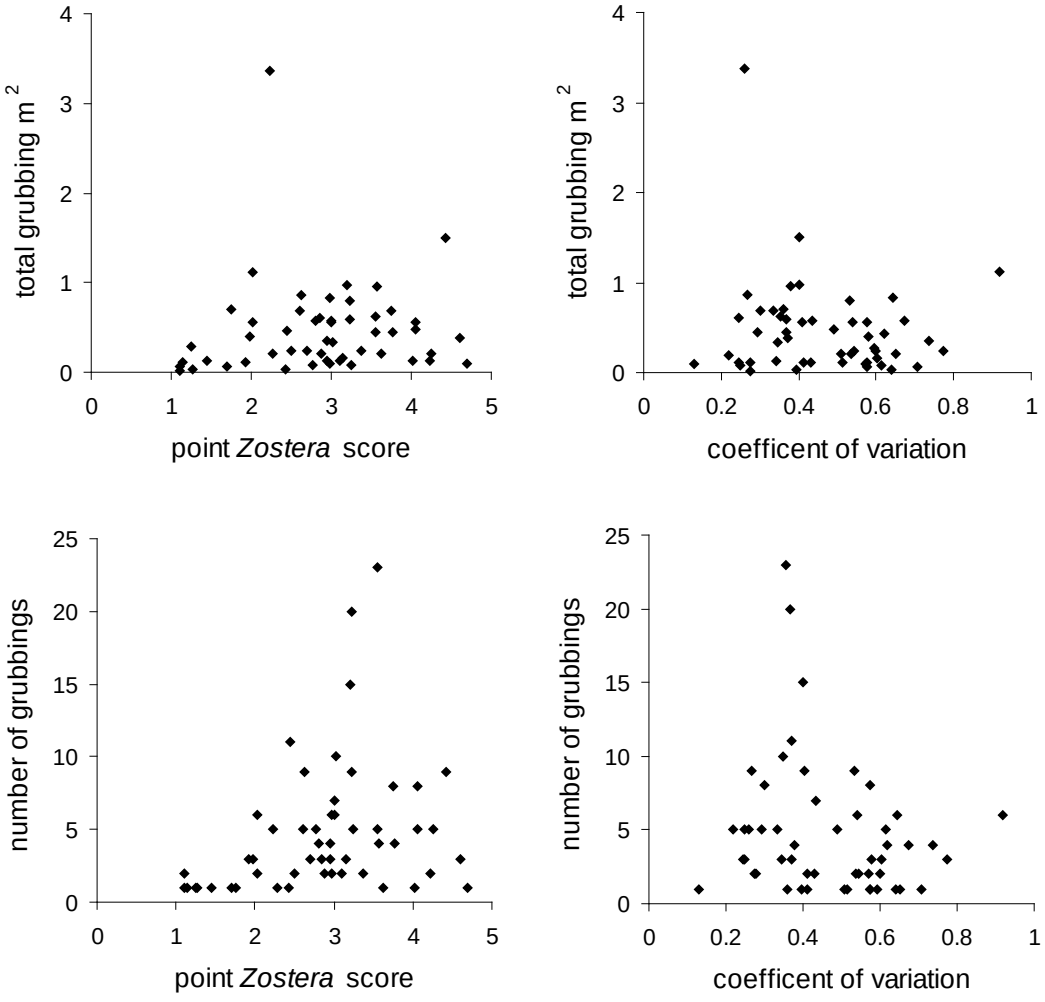


Figure 3.16. Scatter plots showing the relationships between total hole area (m^2, upper plots) and number of holes (lower plots), and sample point *Zostera* score and CV.

Experimental grubbing

The number of small holes that were detectable declined rapidly over even just two tides (Table 3.3) and after 40 tides none remained apart from one that became dramatically enlarged by swan feeding activity (Fig. 3.17). Except for this hole, which was in a low tide/high *Zostera* plot, the average area of holes in all tide position/*Zostera* cover

combinations steadily declined over 1, 2, 3 and 10 tides with the low tide plots shrinking fastest (Fig. 3.18 A).

The apparent persistence and expansion of small holes in low tide/high *Zostera* conditions is due entirely to the presence of one hole that was greatly enlarged by swans (Fig. 3.17). With this hole removed from the analysis small holes in low tide/high *Zostera* conditions follow the pattern of other variable combinations and were undetectable by 40 tides.

There were substantial differences in the persistence and size of the large holes under the various combinations of variables. *Zostera* cover was the most important factor in hole persistence: those in dense patches lasted longer and grew more than those in sparse *Zostera* patches (Fig. 3.18 B). Position on the tide flats was not an important factor in the stability of large holes in dense *Zostera*.

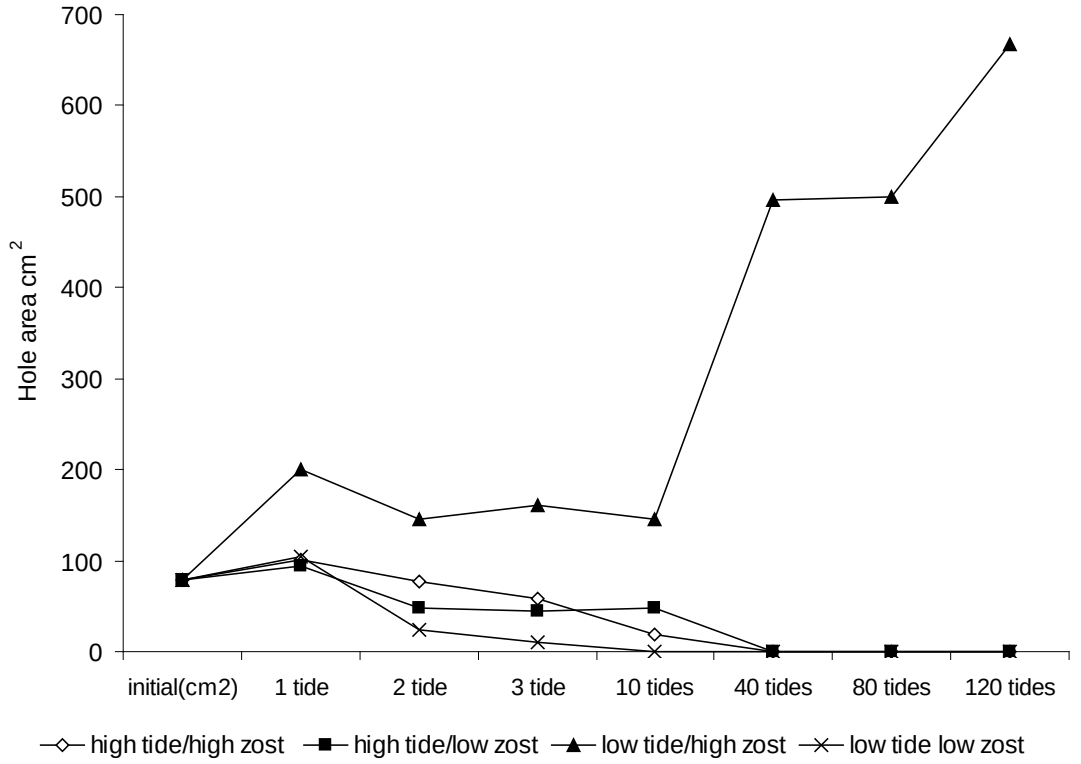
Several of the artificial holes were obviously enlarged by swans. In two replicates swans enlarged holes to the extent that two or three holes joined to form one larger hole. At 60 days some recolonisation of *Zostera* into the bare sand patches left by in filled holes appeared to be occurring. Whether this was from vegetative growth from surrounding *Zostera* or new seedlings was not ascertained.

Table 3.3. Percent of small and large holes remaining over time.

	Initial area	Number of tides						
	(cm^2)	1	2	3	10	40	80	120
small holes	100	92.7	42.7	33.3	17.7	1.0	1.0	1.0
large holes	100	100.0	79.2	67.7	60.4	55.2	45.8	62.5
all holes	100	96.4	60.9	50.5	39.1	28.7	23.4	31.8

Figure 3.17. Low tide/High *Zostera* replicate 1 at Puponga; left to right top to bottom after 1 tide, 2 tides, 10 tides, 40 tides, 80 tides and 120 tides. The development of a small hole expanded by swan foraging over time is shown by the ovals.

A.



B.

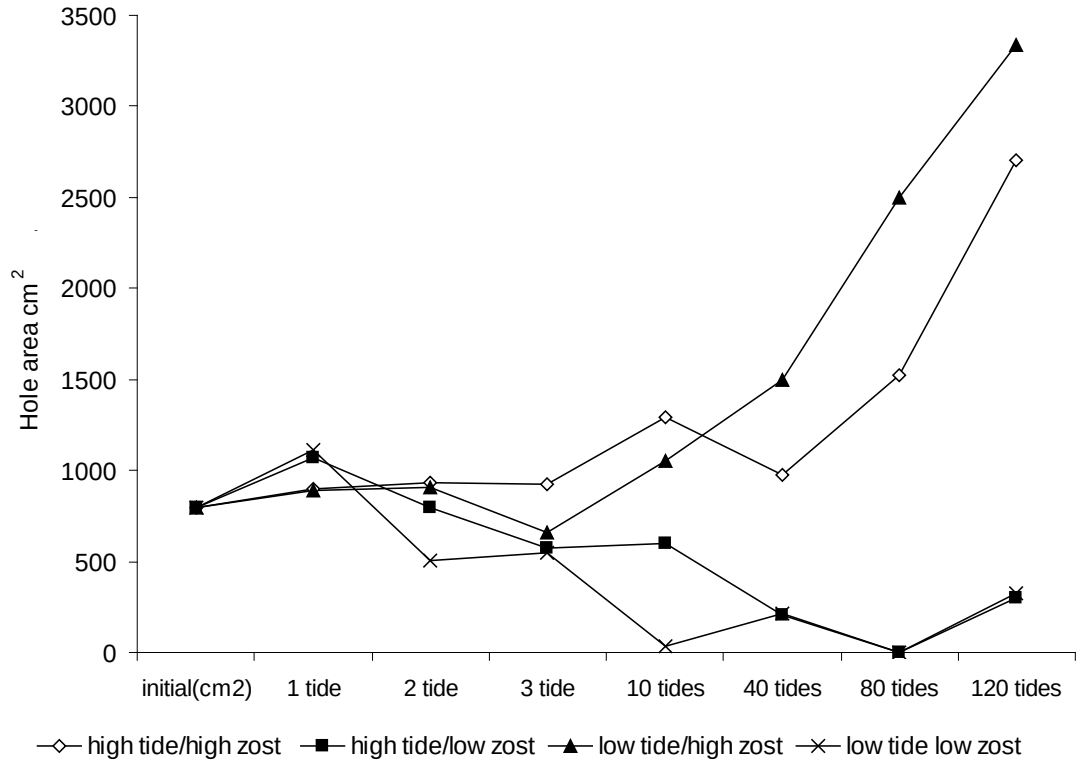


Figure 3.18. Persistence of small (A) and large (B) artificial swan grubbings over 120 tide cycles. See text for discussion of the low tide/high *Zostera* holes.

Sediment analysis

Sediment samples from Te Rae show that the distribution of sediment grain size depended more on position on the tide range than on high or low *Zostera* cover (Fig. 3.19). The predominant grain size class at high tide sites is >0.125 mm while at low tide sites grain size distribution peaks around the >0.25 mm class. Grain size was more evenly distributed high on the tide range than at low sites (Fig. 3.20).

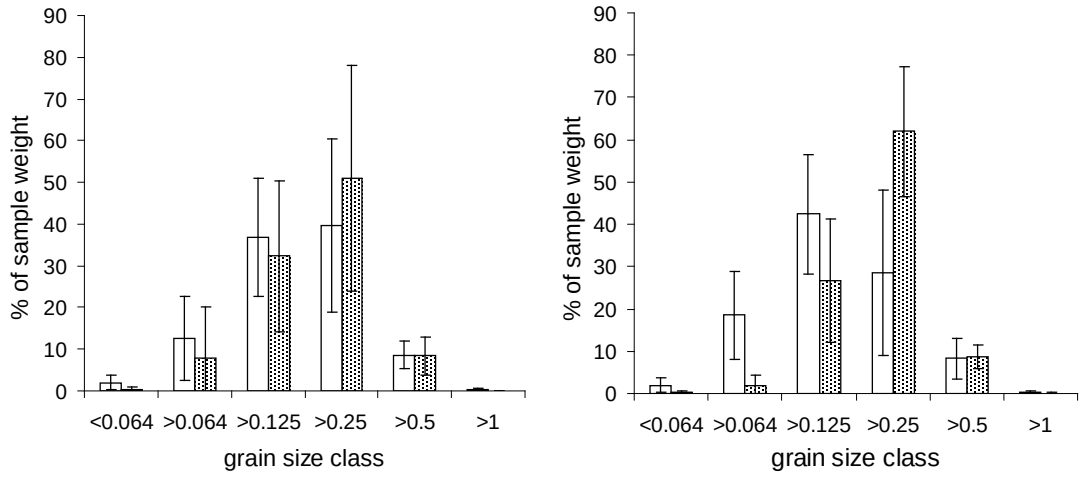


Figure 3.19. Sediment grain size distribution (±s.d.) by *Zostera* cover and tidal elevation. Left plot – *Zostera* cover (open bars = high cover, filled bars = low cover). Right plot – position on the tide range (open bars = high elevation, filled bars = low elevation). N = 24 for both.

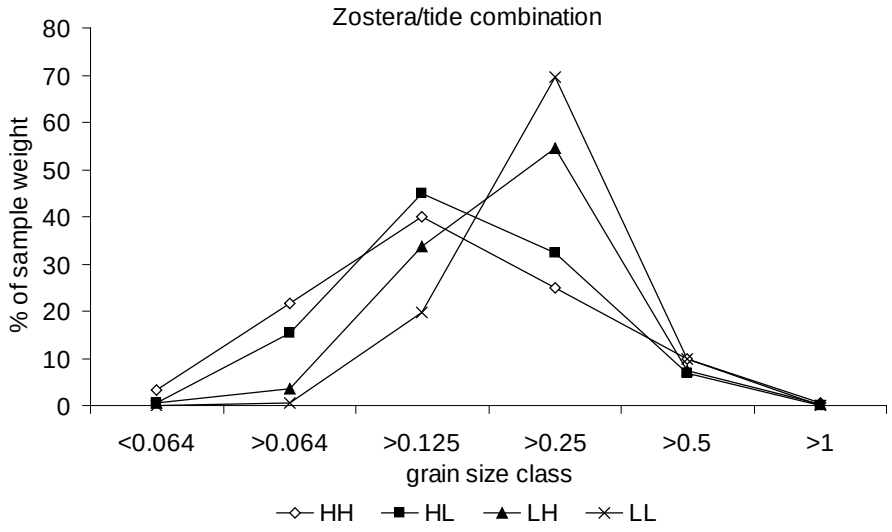


Figure 3.20. Sediment grain size distribution for each variable combination (first letter gives tide position, second letter gives *Zostera* cover: H – high, L – low).

Paired benthos samples

Overall, *Zostera* patches had higher invertebrate abundance (t_{58} = -2.85, P = 0.0061) and diversity (t_{58} = -3.85, P = 0.0007) than did bare sand across the three sites (Fig. 3.21).

At the site level, differences in the relationships of invertebrates to substrate were evident (Table 3.4). The two Golden Bay sites, Puponga and Te Rae, had significant or near-significant differences in invertebrate abundance and diversity in *Zostera* and bare sand, with *Zostera* being higher in both measures (Table 3.4). White Pine Creek, in contrast, showed very little difference overall in invertebrate abundance, and a smaller reduction in the number of taxa present at the sandy sites.

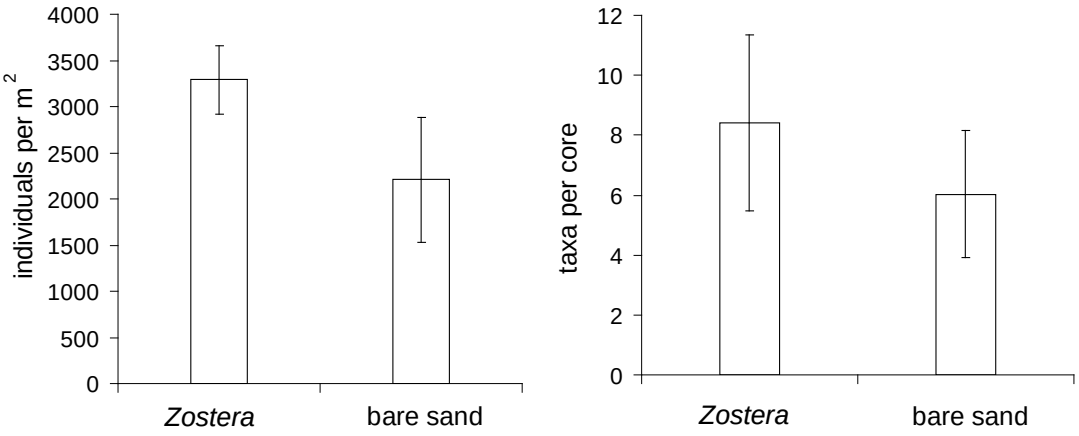


Figure 3.21. Average density (number m^{-2}) (left) and taxa per core (right) in *Zostera* and bare sand.

Table 3.4. Mean invertebrate abundance per m^2 and number of taxa in *Zostera* and bare sand patches at Puponga, Te Rae and White Pine Creek. F and *P* values are from an ANOVA, with significant values marked by an asterisk.

	Zostera		Bare sand			
	mean	std dev	mean	std dev	F-value	*P*
Invertebrate abundance (# m^2)						
Puponga	3157.6	1430.2	1387.8	577.1	$F_{1,19}$=13.17	0.0019*
Te Rae	2852.1	1242.0	1808.0	1103.2	$F_{1,19}$=3.95	0.0623
White Pine Creek	3857.9	1544.4	3425.0	1808.1	$F_{1,19}$=0.33	0.5719
Number of taxa						
Puponga	8.5	2.3	5.6	1.6	$F_{1,19}$=10.68	0.0043*
Te Rae	8.6	3.9	5.7	2.3	$F_{1,19}$=4.15	0.0567
White Pine Creek	8.1	2.6	6.8	2.4	$F_{1,19}$=1.31	0.2682

When high and low density *Zostera* cover and the associated bare sand samples were considered separately the only significant difference in invertebrate abundance ($F_{3,19}$ = 5.72, P = 0.0074) was found between dense *Zostera* and bare sand associated with sparse *Zostera* at Puponga. While not significant at the 95% confidence level ($F_{3,19}$ = 2.94, P = 0.0651) invertebrate abundance at Te Rae followed the same pattern with high *Zostera* having the highest individual abundance and diversity. However at both Puponga and Te Rae a consistent trend was apparent in all sample pairs with *Zostera* having higher invertebrate abundance than the accompanying bare sand samples for both dense and sparse cover. White Pine Creek showed the least amount of variation between high and low *Zostera* and accompanying sand samples with a slightly higher abundance found only in the dense *Zostera* sample pairs (Fig. 3.22).

Invertebrate diversity followed a similar pattern to that of density, with bare sand having lower average diversity than the adjacent *Zostera* samples (Fig. 3.23). The substantial overlap in values, however, meant that a significant difference was detected only between dense *Zostera* and bare sand associated with sparse *Zostera* at Puponga ($F_{3,19}$ = 3.53, P = 0.0392), with marginal significance found for the same comparison at Te Rae ($F_{3,19}$ = 3.2, P = 0.0519). Again White Pine Creek showed no clear patterns between the four different surface types (Fig. 3.23).

The response of the relative abundance of invertebrate species to *Zostera* and bare sand varied at the three sample sites (Fig. 3.24). At Puponga the *Zostera* and bare sand communities were similar in composition but with generally lower numbers in bare sand.

The most marked community differences at Te Rae was that while abundance was mostly higher in *Zostera* there was a high number of *Paphies* in bare sand compared to *Zostera*. An unidentified polychaete worm was also much more abundant in bare sand.
The *Zostera* and bare sand communities at White Pine Creek showed a similar pattern of abundance though spionid polychaetes were more abundant in bare sand. *Eatoniella* snails were restricted to *Zostera* while *Maldanidae* tubeworms were more common in bare sand.

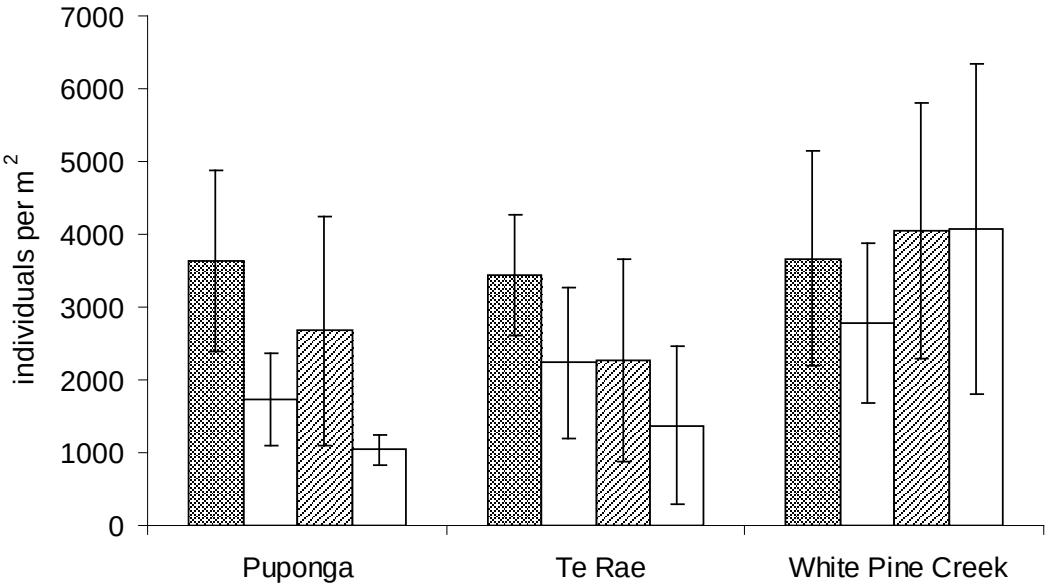


Figure 3.22. Macrobenthos density in high and low *Zostera* cover and associated bare sand core samples at each study site. Bars from left: cross hatch – high *Zostera*, open – high *Zostera* sand, right hatch – low *Zostera*, open – low *Zostera* sand.

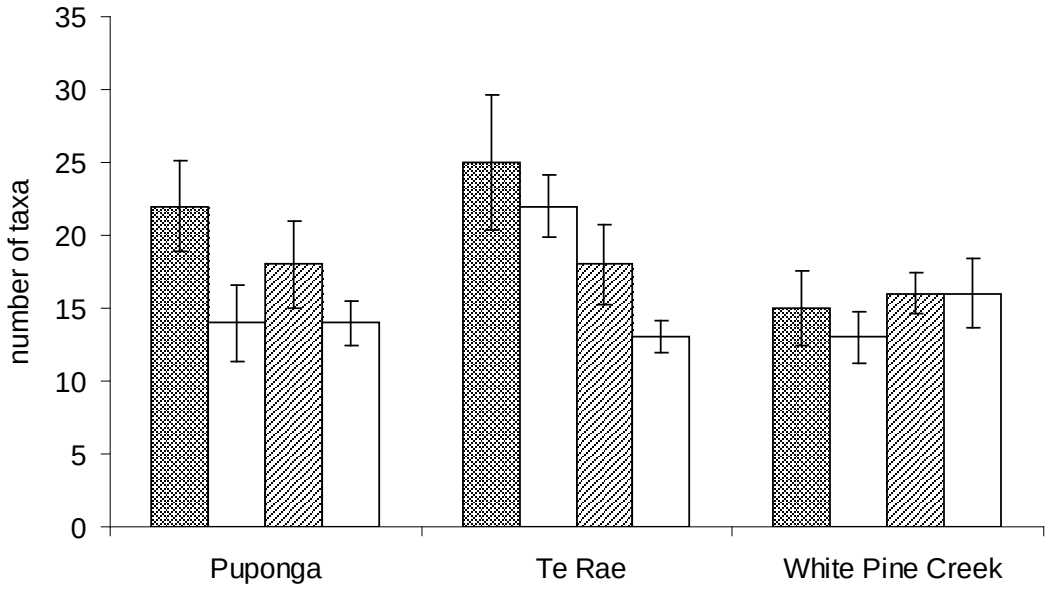


Figure 3.23. Number of taxa in high and low *Zostera* cover and associated bare sand core samples at each study site. Bars from left: cross hatch – high *Zostera*, open – high *Zostera* sand, right hatch – low *Zostera*, open – low *Zostera* sand.

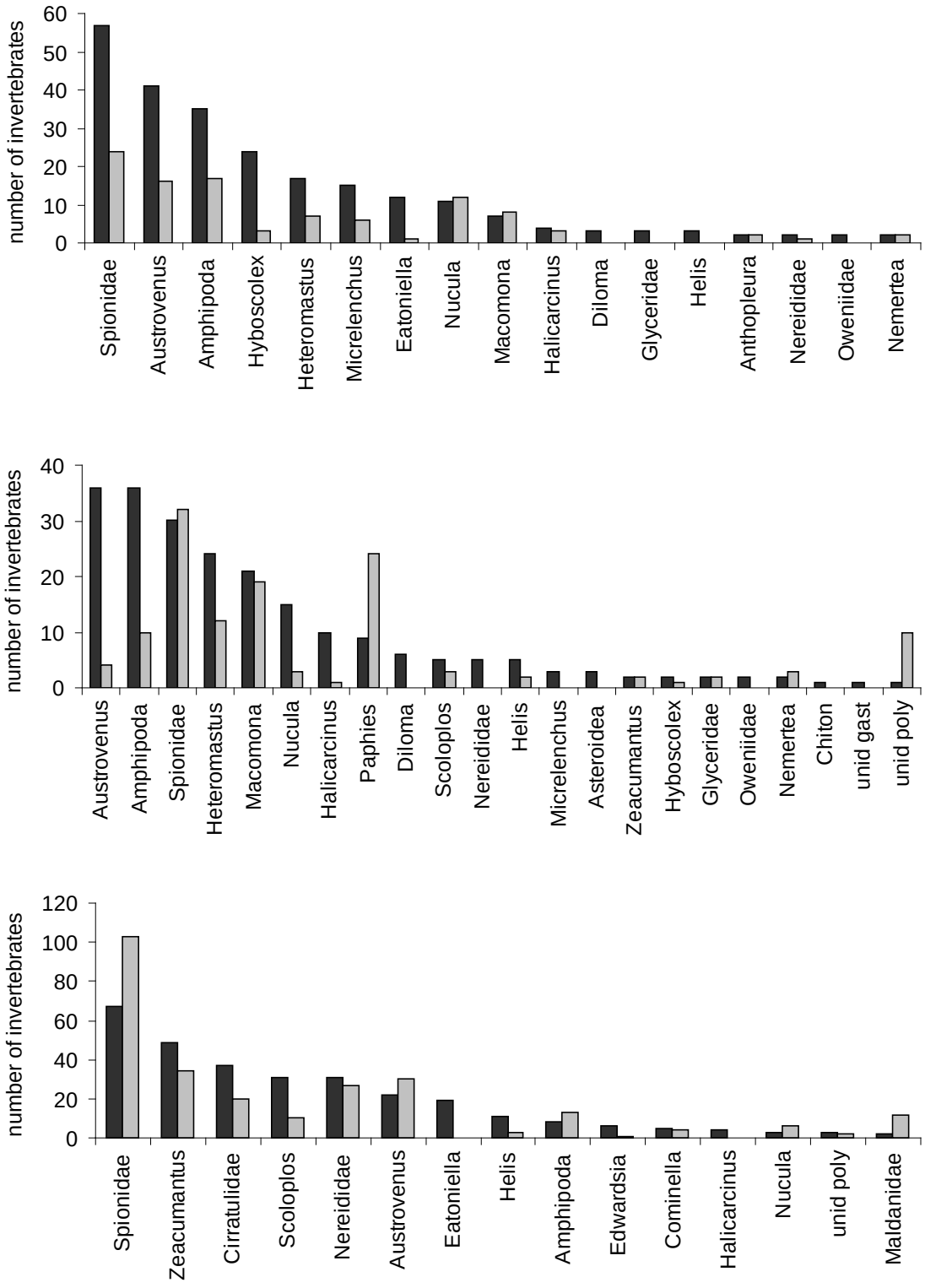


Figure 3.24. Total number of invertebrates found in *Zostera* (dark grey bars), and bare sand (light grey bars) at Puponga (top), Te Rae (middle) and White Pine Creek (bottom). Unid poly = unidentified polychaete, unid gast = unidentified gastropod. Taxa with l individual or less than 5% of total for both *Zostera* and sand are not shown.

3.4 Discussion

Zostera cover survey

Zostera seagrass is widespread but patchily distributed across the tidal flats of western Golden Bay. This patchiness is observed at multiple scales, from meters to hectares. Where found, *Zostera* cover is mostly sparse with smaller areas of dense cover. Puponga had higher cover than Te Rae and a lower CV indicating denser, more homogenous *Zostera* beds. This difference between the sites is likely to be due to environmental factors; if swan feeding were the principle cause the opposite result would be expected, as Puponga has a higher swan density and more feeding activity. The coefficient of variation only captures part of the patchiness as it does not differentiate between a few large patches or many small patches with the same area and cover scores (Figure 3.22). This means that it is not overly effective in separating characteristic swan foraging from other agents that may be operating in forming the patchiness of the landscape.

The pattern of patchiness observed at the scales used in this study, characterized by widespread but sparse *Zostera* interspersed by smaller denser patches, mirrors the larger scale patchiness found across the whole of the Farewell Spit tidal flats in the benthic survey carried out in 2003 (Battley *et al.*, 2005).

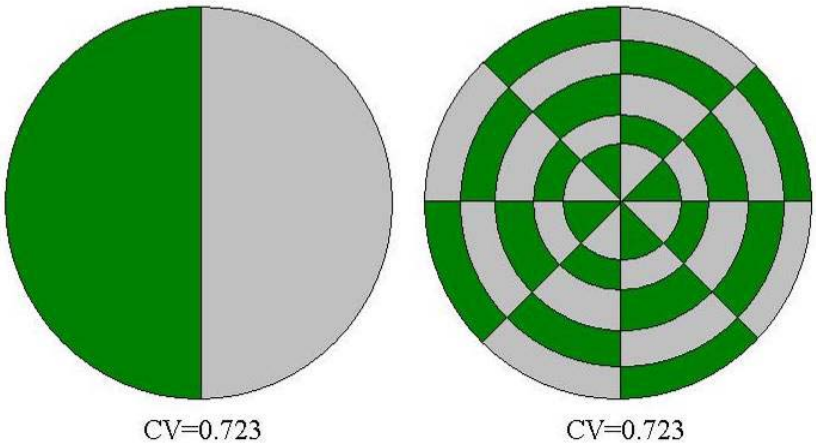


Figure 3.22. Example of two distributions that have the same *Zostera* cover, area and CV, but in very different arrangements.

Swan foraging activity survey

Swan foraging activity is widespread at the study sites but concentrated in areas with higher *Zostera* cover than the average. At the patch level swans select denser than average *Zostera* to feed on, so they are selecting foraging sites both on large (hectares) and small (meters) scales. It is also possible that the apparent increased evidence of swan activity in dense patches is a result of an accumulation of feeding evidence that would disappear in sparse *Zostera*, rather than an actual preference for dense *Zostera* patches.

Areas where swan feeding was found did not have a higher degree of patchiness, as measured by the CV, than areas where no feeding activity was present. This may be because other agents contribute to the patchiness at these points but the CV cannot differentiate these from those caused by swans, for example a dense *Zostera* patch next to a bare sand channel. Alternatively because swan holes can still be present long after they are identifiable as such, points with high a CV and no swan feeding may be the result of historic feeding activity.

The differences in feeding sign intensity between Te Rae and Puponga are most likely because of the difference in swan density (see Chapter 2) but as the *Zostera* cover is also denser at Puponga, feeding activity may remain detectable for longer and so contribute to the higher feeding intensity observed there.

Experimental grubbing

Small grubbings declined in both number and size over a relatively short period of time and became undetectable. This is probably due to the holes' small size – little subsurface damage was done to the rhizome structure and any sediment that collapsed from the edge rapidly filled them in. Large experimental grubbings lasted for an extended period and in some situations got larger over time. Grubbings in high *Zostera* patches were enlarged while those in low *Zostera* patches tended to fill in. The substrate in areas with dense *Zostera* is more stable than that in sparse *Zostera* because the rhizome and root mass binds the sediment and the leaves reduces water flow speeds. Given this, it might be expected that grubbings in less stable sparse *Zostera* patches would be more prone to expansion. However, due to the substrate stability, dense

Zostera holes maintained a distinct edge for longer than those in sparse *Zostera*. This favours the swans' mode of feeding by grubbing along patch edges and, coupled with the swans' preference for feeding in dense *Zostera*, may explain the observed pattern.

In localized sites black swans are capable of facilitating the creation and expansion of large bare sand patches. However, because most of the *Zostera* patches are sparse and a large portion of swan grubbing consists of small holes, much of the evidence of swan feeding activity would rapidly disappear.

Sediment analysis

Seagrass can facilitate fine particle settlement by slowing water currents and allowing particles to settle out of the water column. At Te Rae the sediment profile varied across the tide range with sediment high on the tide range having a higher percentage of finer particle sizes than that lower on the tide range. This is to be expected as low tide areas of the flats are subject to greater water flow than high on the tidal range.

Zostera cover was less important than elevation on the tide range in determining the sediment particle size profile but finer particle sizes were more common in dense *Zostera* patches than areas with sparse *Zostera* cover. This follows the findings of other studies that have examined the effect of seagrass on current movement and particle settlement (Bradley & Stolt, 2006; Heiss *et al.*, 2000). By causing sediment to settle out of the water column seagrass creates a positive feedback: as more sediment is removed from the water column, turbidity is reduced allowing greater light penetration and photosynthesis so the seagrass grow and capture more sediment. This feedback loop can also operate in reverse where increased turbidity reduces seagrass growth which allows more sediment to be re-suspended (de Boer, 2007). In addition to the direct impacts of feeding, swans could potentially be causing indirect damage to *Zostera* by stirring up sediment, increasing the turbidity of the water and reducing the ability of *Zostera* to photosynthesise.

Paired benthos sampling

As found in a number of studies in other countries (Cardoso *et al.*, 2007; Connolly, 1997; Gambi *et al.*, 1998), macrobenthos abundance and taxonomic diversity found in

Zostera patches was significantly higher than in adjacent bare sand. If swans are causing the conversion from *Zostera* cover to bare sand then they may be reducing the abundance and diversity of associated macrobenthos.

There was higher macrobenthos diversity and abundance in dense seagrass than bare sand at the Puponga study site and a similar pattern was seen at Te Rae but there was no difference between seagrass and bare substrate at White Pine Creek. This difference between the sites within Golden Bay and White Pine Creek in Whanganui inlet is most likely to be because the sediment at White Pine Creek is a fine mud which is found both inside and outside seagrass patches, and is very stable compared to the sandy sediment at the other sites.

The classification of *Zostera* and bare sand patches only took into consideration the surface cover. Often bare sand patches had extensive mats of live or dead *Zostera* rhizome beneath the surface while some apparently dense *Zostera* patches had very little subsurface material. The presence of seagrass rhizome supports certain invertebrate species while excluding others (van Houte-Howes *et al.*, 2004) so this may reduce differences observed between the two habitat types as classified by surface cover (Tanner, 2005).

In some studies the highest macrobenthos biodiversity in seagrass beds is associated with the patch edges (Bologna & Heck, 2002; Tanner, 2005); this may be because it has the greatest range of microhabitats. Patch edges can act as a 'net' as planktonic invertebrate larvae settle when encountering the stiller water provided by the seagrass (Bologna & Heck, 2000). There may be an edge effect operating at Puponga and Te Rae as the bare sand patches next to dense *Zostera* patches had higher diversity and abundance than those next to sparse *Zostera* patches. Benthos samples would need to be taken at varying distances within and out from *Zostera* patches to confirm this.

Conclusions

In western Golden Bay *Zostera* is variable spatially over large and small scales from meters to kilometres. Swan foraging is concentrated in areas of denser *Zostera* than are available randomly, indicating they focus their feeding on these dense patches. Swan

forage on all parts of the *Zostera* plant, which results in discernible damage to the *Zostera* beds by creating and/or expanding holes and converting intact *Zostera* to bare sand. Such holes may remain for long periods and have the potential to increase in size depending on the characteristics of the *Zostera* bed. Rhizome and root structure combined with finer sediment makes the substrate more stable so swan holes in dense *Zostera* beds persisted longer that those in sparse beds.

The bare sand patches created by swans are likely to harbour lower abundance and diversity of invertebrates than the *Zostera* beds in which they are made. This is probably primarily because the removal of *Zostera* reduces habitat structure and the range of micro-habitats available to invertebrates.

Swans are likely to be an important agent of patchiness on these tidal flats, and have the potential to indirectly affect invertebrate communities. However as the effects of swans foraging are concentrated on denser *Zostera* the scale of impact on invertebrates would vary considerably across the tidal flats as a whole.

4. Impacts of swans on *Zostera* biomass and associated invertebrate communities

Abstract

Seagrass beds have been shown to support higher invertebrate diversity and abundance than adjacent bare substrate. Waterfowl can significantly reduce seagrass coverage and biomass through foraging so can potentially have a negative impact on the invertebrate fauna associated with the seagrass-dominated ecosystem. This study investigates if this process is occurring in tidal seagrass beds that black swans forage on. Exclosures to eliminate avian grazing were used between summer and autumn 2008 to compare the response of *Zostera* shoot number and biomass and invertebrate diversity and abundance in grazed and ungrazed plots at three study sites. Differences between the exclosures and control plots showed that at sites in Golden Bay black swan foraging can significantly reduce both *Zostera* biomass and the associated invertebrate faunal abundance and diversity within two months.

4.1 Introduction

A number of studies have established that there is commonly a positive relationship between seagrass cover and the abundance and diversity of the associated invertebrate fauna (Arrivillaga & Baltz, 1999; Connolly, 1997; Heck & Wetstone, 1977; Orth *et al.*, 1984). Seagrass provides a complex and stable environment which benefits invertebrates in a number of ways. The seagrass plant itself creates a three-dimensional structure that creates habitat and encourages epiphyte growth providing food for grazing invertebrates (Heck & Valentine, 2006). This structure also provides refugee from predators and environmental risks like dislodgement by water movement (Cardoso *et al.*, 2007). For some invertebrates with planktonic larvae, particularly bivalves, seagrass increases settlement rates of juveniles (Bologna & Heck, 2000). As a result of these factors, density and diversity of invertebrate species is typically higher in areas covered with seagrass than areas of bare sand.

Waterfowl have been shown to be capable of reducing biomass of seagrass beds in tidal wetland areas (Baldwin & Lovvorn, 1994; Ganter, 2000; Jacobs *et al.*, 1981). Brent

geese over-wintering in Strangford Lough, Ireland reduced *Zostera* spp. shoot biomass to 7% and rhizome to 23% of the autumn biomass values (Portig *et al.*, 1994). The impact of waterfowl foraging does not necessarily affect all parts of the seagrass plant in the same way. Bortolus *et al.* (1998) found that while above-ground biomass was higher when protected from waterfowl foraging, below-ground biomass was higher when exposed to foraging.

As the black swans in western Golden Bay forage in a manner that disturbs all parts of the *Zostera* plant and are present in high numbers (see Chapter 2) it is possible that they could have a measurable impact on *Zostera* and reduce the abundance and diversity of the associated invertebrate fauna. This chapter tests this hypothesis by comparing *Zostera* shoot number, above- and below-ground biomass and invertebrate abundance and diversity in swan exclusion plots and open controls at three different sites. This sampling also allowed for a characterization and comparison of the invertebrate communities at each of these sites.

Figure 4.1. Left – close-up of swan feeding activity showing discarded *Zostera* leaves and disturbed sand. Right – black swans feeding on *Zostera* at Pakawau at dawn.

4.2 Methods

Study sites

Exclosures that prevented swans from foraging in an area but admitted fish and invertebrates were established at three sites: White Pine Creek near Rakopi in Whanganui Inlet, Puponga on the tide flats immediately to the right of the Farewell Spit

access gate, and at Te Rae adjacent to the mouth of Billy King Creek (Fig. 4.2). The exclosures were situated at approximately the mid-tide water level in areas of dense *Zostera*.

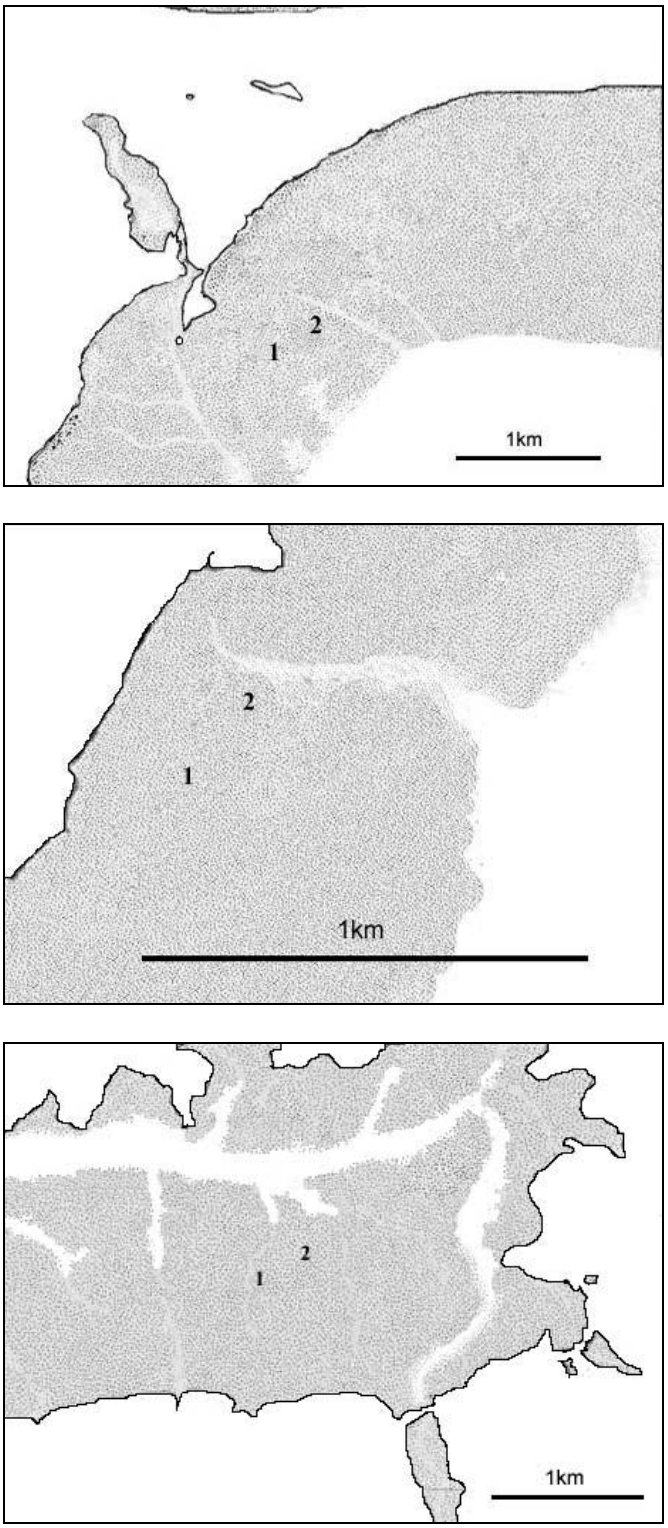


Figure 4.2. Top to bottom – Puponga, Te Rae, and White Pine Creek study sites, showing location of exclosure replicates 1 and 2.

Exclosure design and construction

Two replicates were established at each of the three sites, with each replicate consisting of an exclosure and a control plot. Exclosures were 3 x 3 m and 1 m high. They were constructed of bamboo poles or steel waratahs driven into the substrate, and a barrier fence was created with baling twine (Fig. 4.3 and Fig. 4.4, left). The exclosures were erected in patches of *Zostera* with an uniformly high cover score (i.e. 5 or 6, see *Zostera* cover score schedule Ch.3 Fig. 3.6). A control area was demarcated with short stakes in a patch adjacent to the exclosure with the same *Zostera* cover.

Figure 4.3. Exclosure in position at Puponga.

The internal area of the squares was divided into half meter square quadrats to give 36 smaller squares. A 0.5 m buffer zone was left around the perimeter and sampling was carried out in the middle 16 quadrats (Fig. 4.4, right). Which particular quadrats were to be sampled on each occasion was predetermined and all replicates were sampled following the same pattern.

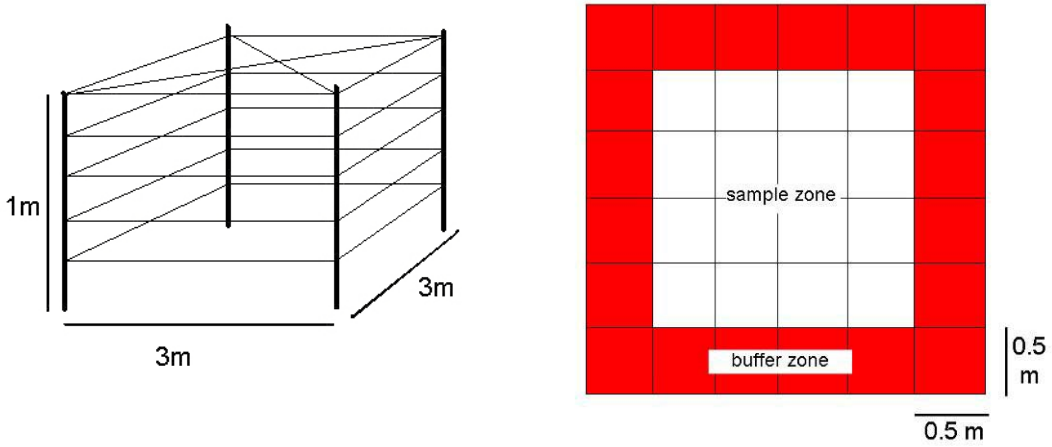


Figure 4.4. Left – exclosure design showing dimensions (some strings not shown for clarity). Right – exclosure grid layout used for core sampling.

Core sampling and sorting

Three samples were taken from each exclosure and control every two months either once, twice or three times depending on the site. The incomplete sampling was due to the collapse of the initial bamboo exclosures established at Puponga and Te Rae which then had to be rebuilt with waratahs and thus sampling was delayed at these sites. This meant that White Pine Creek had the initial sampling plus three re-sampling events, Te Rae had the initial plus two re-samplings and Puponga had only the initial and one follow up sampling event (Table 4.1).

Table 4.1. Sampling dates at each study sites.

	2007			2008				
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Puponga					initial			final
Te Rae			initial			2nd		final
White Pine Creek	initial		2nd		3rd			final

Three 10 cm diameter x 25 cm deep core samples were taken from each exclosure and control during each sample period from the pre-determined quadrates. Cores were sieved using a 1 mm mesh sieve on site to remove sand and mud (Fig. 4.5), and the remaining material was placed in labelled plastic bags and stored in a refrigerator until sorting (within 48 hours of collection). Sample material was sorted and all invertebrates

and live *Zostera* material were removed and stored for identification. Soft-bodied invertebrates (e.g. worms and anemones) were stored in 90% ethanol; large molluscs and decapods were frozen, as was *Zostera*.

Figure 4.5. Left – core sampling, right – material retained after sieving.

Invertebrates were identified under a binocular microscope and measured with 2 mm^2 graph paper placed beneath the examination dish or with callipers to the nearest mm. Identification was to the lowest practical taxonomic level, this varied considerably among groups, most decapods and bivalves could be identified to species while ribbon worms (Nemertea) were not identified past phylum. Because of this the term 'taxa' is used to refer to the distinct taxonomic groups recognized in this study instead of 'species', 'genera', etc. The *Zostera* rhizomes and shoots were separated, but root material was only retained if attached to rhizome. Shoot number was recorded then shoot and rhizome material was dried to constant weight at 70ºC and weighed to 0.0001 g.

Statistical analysis

Linear regression was used to detect significant relationships between *Zostera* shoot number and biomass and invertebrate diversity and abundance using data from all sites. ANOVAs were used to detect significant differences in shoot number, shoot and rhizome biomass and invertebrate abundance and number of taxa between exclosures and controls after 2 months at Puponga, 4 months at Te Rae and 6 months at White Pine

Creek. Analysis of all sites combined was not considered meaningful as they were sampled over different time frames and at different times of year meaning any results would be confounded by seasonal variation. Non-metric multidimensional scaling analysis of the invertebrate communities was used to detect possible groupings in the invertebrate community composition. This was carried out on abundance data from all sites to show any location groupings, and on abundance data from Puponga, Te Rae and White Pine Creek separately to detect divergence in the exclosure and control communities over time.

4.3 Results

Zostera response to exclosures

Zostera shoot number and shoot and rhizome biomass showed a variable response depending on site. At the two sites within Golden Bay there was a significant difference between all three variables in the exclosures and control plots by the last sampling period with Te Rae showing the most significant difference. The treatments at White Pine Creek in Whanganui Inlet showed no clear difference between any of the variables (Table 4.2).

Table 4.2. Mean values of shoot number per m^2, shoot biomass g per m^2 and rhizome biomass g per m^2 after 2 months at Puponga, 4 months at Te Rae and 6 months at White Pine Creek.

		mean			
		exclosure	control	*F*	*P*
Puponga	shoot number/m²	11417	4923	$F_{1,11}$=15.18	0.0030
	shoot biomass g/m²	86.2	27.4	$F_{1,11}$=29.20	0.0003
	rhizome biomass g/m²	136.3	51.1	$F_{1,11}$=19.90	0.0012
Te Rae	shoot number/m²	8722	212	$F_{1,11}$=163.25	<.0001
	shoot biomass g/m²	108.2	1.9	$F_{1,11}$=100.92	<.0001
	rhizome biomass g/m²	108.8	5.3	$F_{1,11}$=70.75	<.0001
White Pine Creek	shoot number/m²	8212	8085	$F_{1,11}$=0.01	0.9235
	shoot biomass g/m²	102.8	98.2	$F_{1,11}$=0.13	0.7246
	rhizome biomass g/m²	79.7	71.9	$F_{1,11}$=0.52	0.4891

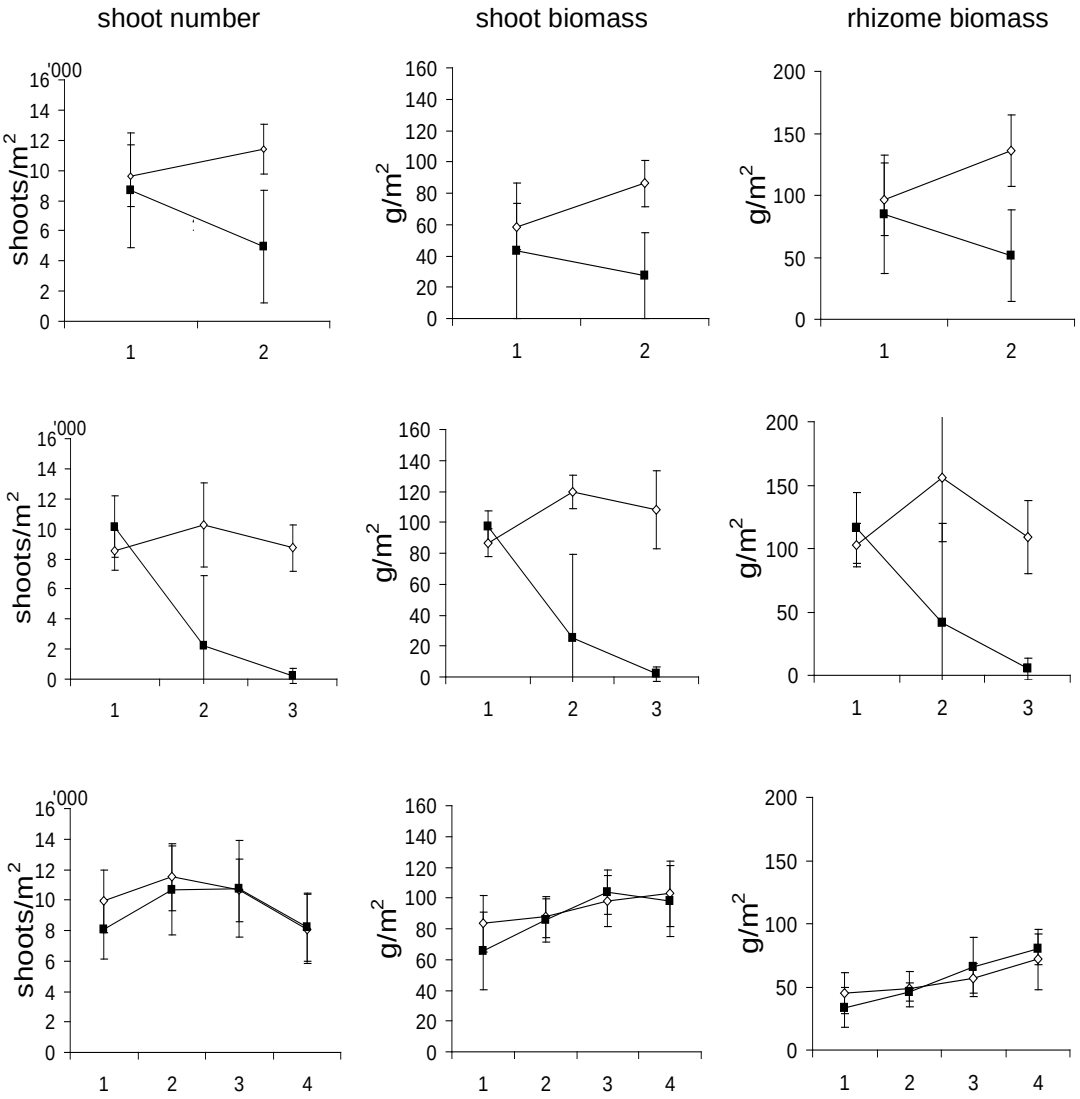


Figure 4.7. *Zostera* shoot number, shoot biomass and rhizome biomass change (± standard deviation) over time. Top – Puponga, middle – Te Rae, bottom – White Pine Creek. Open diamonds are exclosures; filled squares are controls. X-axis = sample periods.

Figure 4.8. Left – exclosure set over intact *Zostera*, Right – control (marked by pegs) of the same replicate, in which much of the *Zostera* has been removed. Both photos were taken during the last re-sampling event.

General invertebrate community structure

A total of 3547 individuals from 53 distinct taxa were recorded from the exclosure and control core samples. Taxa per core sample ranged from 3 to 16 with an average of 9 (Fig. 4.9). The number of individual organisms found per core ranged from 6 to 77, with an average of 33 (Fig. 4.10).

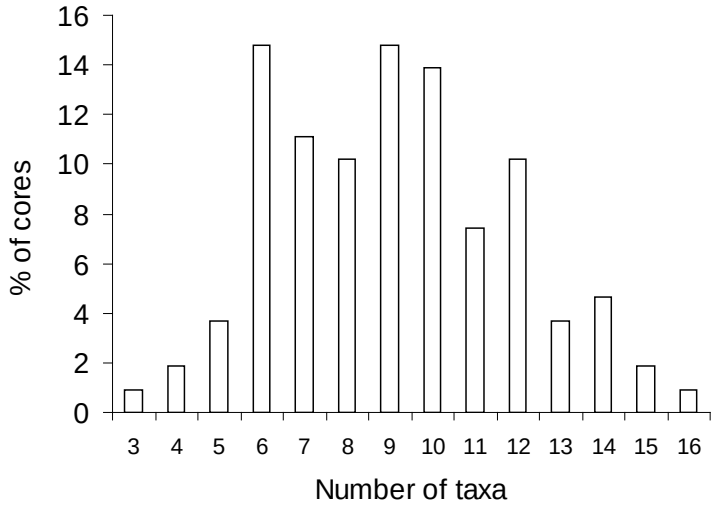


Figure 4.9. Number of taxa per core across all samples. N = 108 cores.

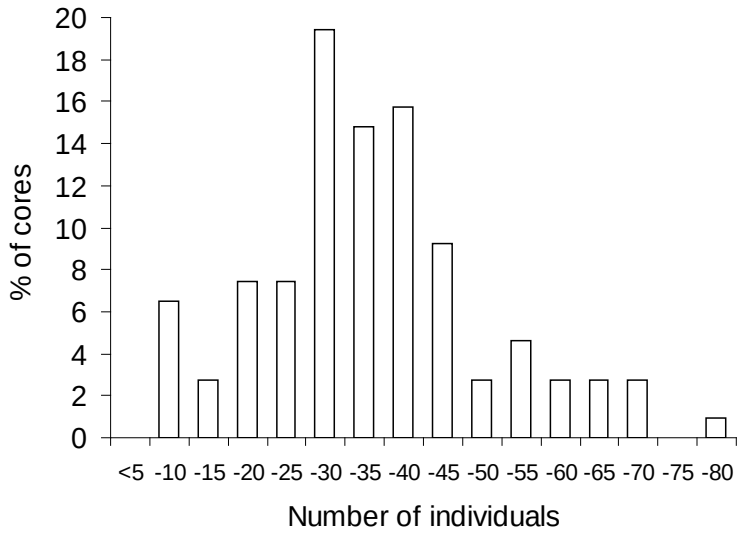


Figure 4.10. Number of individuals per core across all samples. N = 108 cores.

Cirratulid worms were the most abundant taxon overall but were only found at White Pine Creek. *Austrovenus stutchburyi* was the second-most abundant taxon and was the most common species at the Puponga and Te Rae sites, followed by Nereid and Spionid polychaetes and *Zeacamantus* gastropods. These five groups constituted 52.3% of all individuals present. The invertebrate communities of Puponga and Te Rae were the most similar sharing 9 of the 10 most abundant taxa at each site. Four of the most abundant taxa at White Pine Creek were among the 10 most abundant at one or both of the other sites (Fig. 4.11).

There were significant relationships between *Zostera* shoot number and biomass and invertebrate fauna abundance and diversity. The strongest relationships were between shoot biomass and invertebrate abundance and rhizome biomass and invertebrate diversity (Table 4.3, Fig. 4.12). This pattern was similar whether sites were considered separately or combined.

Table 4.3. Linear regressions of invertebrate diversity and abundance against *Zostera* shoot number, shoot biomass and rhizome biomass at all sites.

Zostera	invertebrate community	F value	P	r^2
shoot number	diversity	$F_{1,107}$=7.74	0.0064	0.068
	abundance	$F_{1,107}$=11.97	0.0008	0.102
shoot biomass	diversity	$F_{1,107}$=11.84	0.0008	0.101
	abundance	$F_{1,107}$=22.34	<.0001	0.174
rhizome biomass	diversity	$F_{1,107}$=42.04	<.0001	0.284
	abundance	$F_{1,107}$=14.51	0.0002	0.120

Invertebrate response to exclosures

At Puponga, when re-sampled after two months there were significantly more taxa ($F_{1,11}$=13.24, P=0.0046) found in exclosures than control plots. There was no significant difference in the number of invertebrates per m^2 in exclosures and control plots.

Te Rae showed clear divergence between the exclosure and control treatments for both invertebrate abundance and diversity over time. By the third sample period taxa per core ($F_{1,11}$=76.92, P=<0.0001) and individuals per m^2 ($F_{1,11}$=15.71, P=0.0027) were both significantly lower in the control plots than the exclosures. At White Pine Creek the number of taxa per core and invertebrates per m^2 both trended upwards over the duration of the experiment and exclosure and control numbers were similar except for the last sample period where the number of invertebrates was significantly higher ($F_{1,11}$=7.9, P=<0.0185) in the exclosures than the controls (Fig. 4.13).

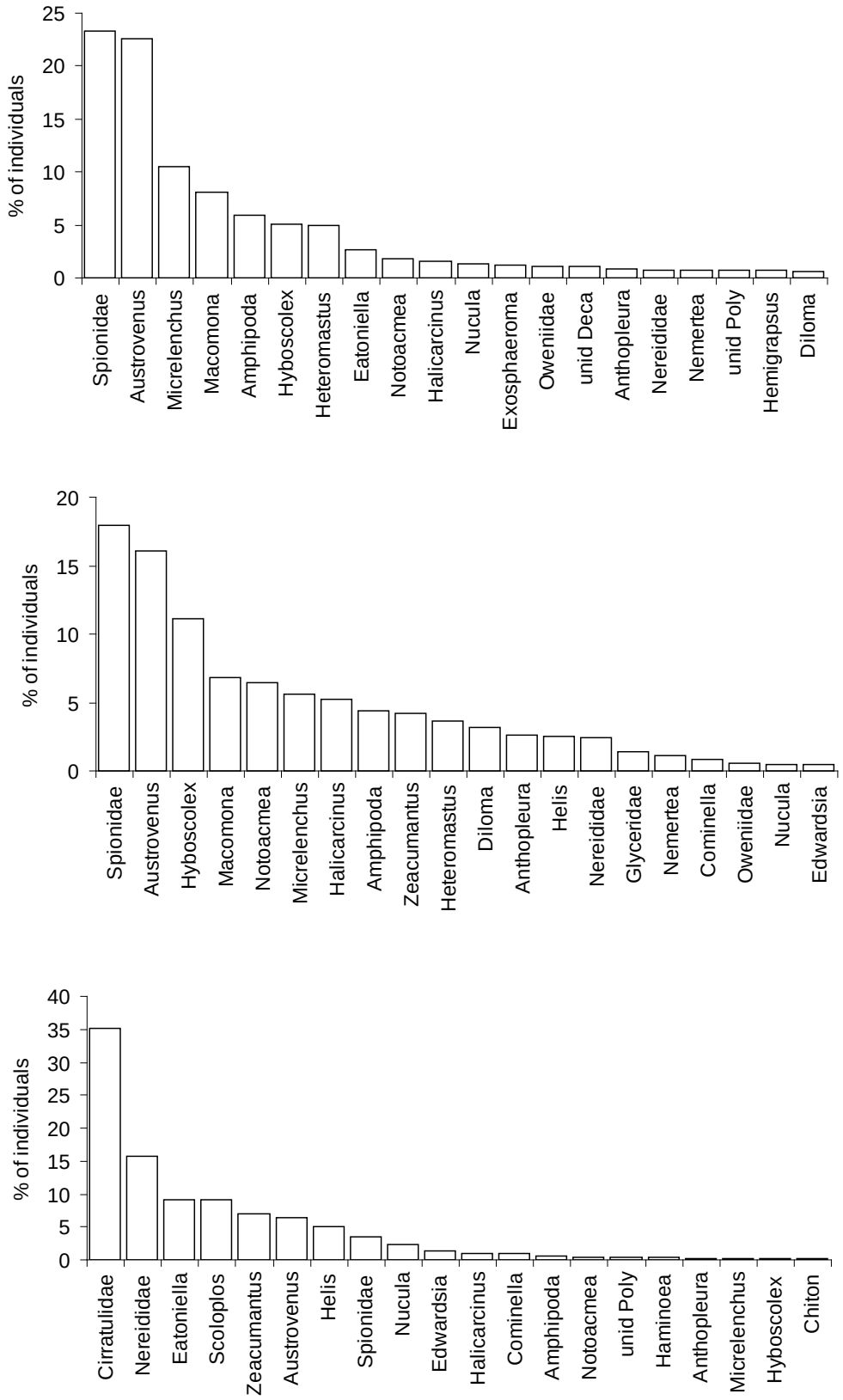


Figure 4.11. Ranked abundance of the 20 most abundant taxa found at each site. Top – Puponga, middle – Te Rae, bottom – White Pine Creek. Unid deca = unidentified decapod, unid poly = unidentified polychaete.

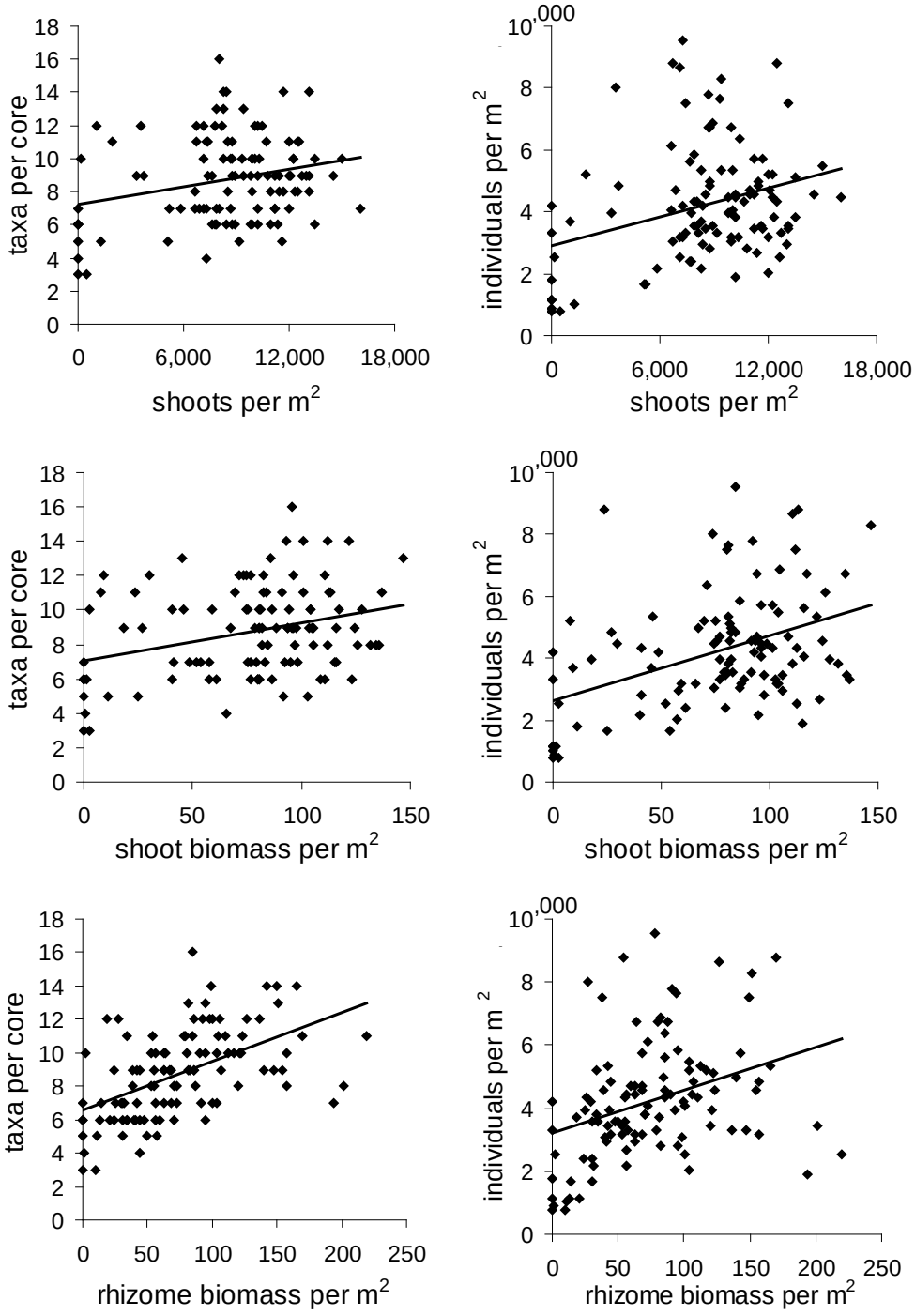


Figure 4.12. Relationships between invertebrate diversity and density, and *Zostera* variables, across all sites. Lines are linear regressions.

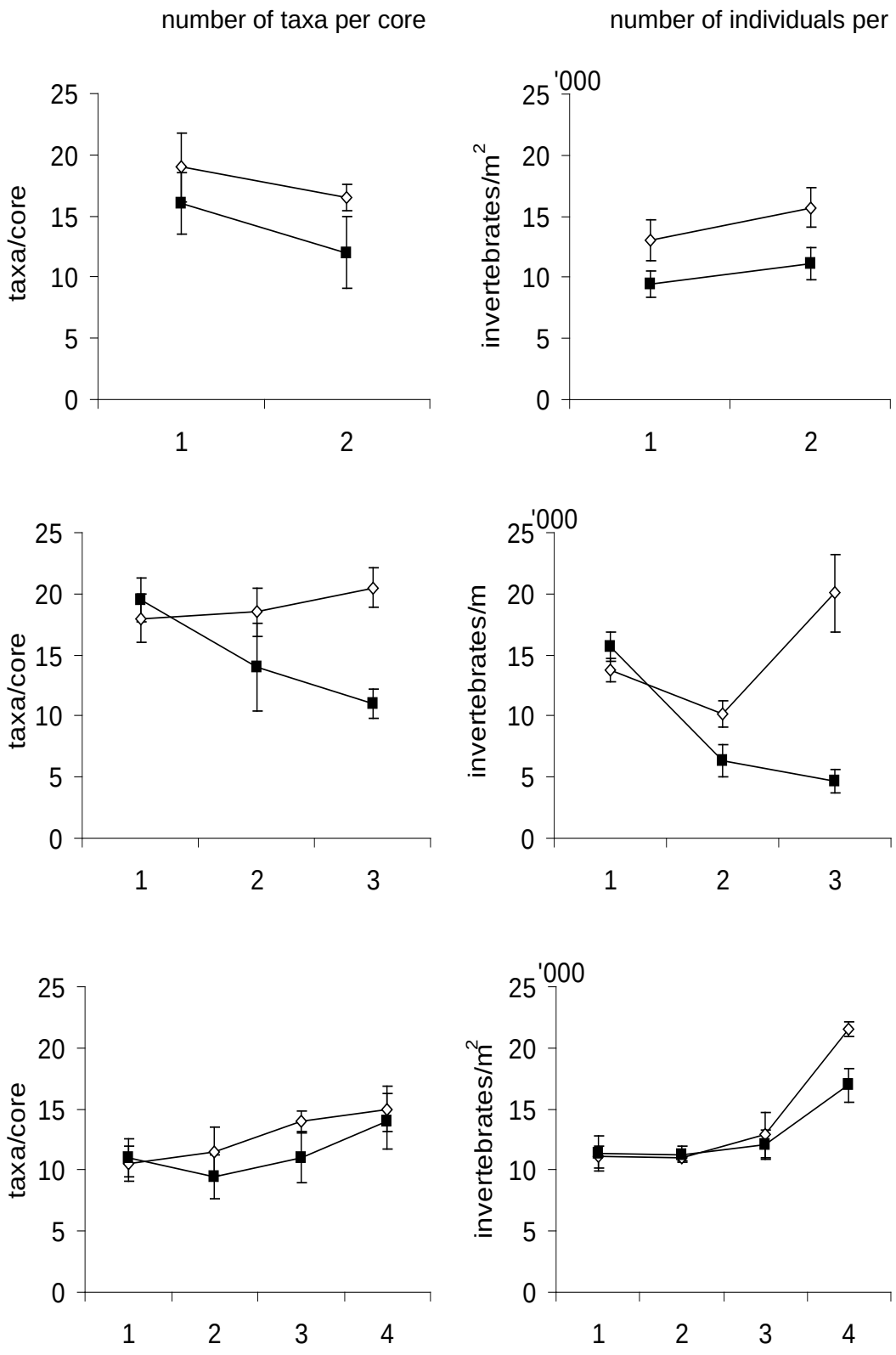


Figure 4.13. Changes in taxa number and invertebrate number at each site over the duration of the experiment ± standard deviation. Top – Puponga, middle – Te Rae, bottom – White Pine Creek. Open diamonds are exclosures; filled squares are controls. X-axis = sample periods.

Non-metric multidimensional scaling (NMS) analysis of the invertebrate communities at all sites combined placed samples from White Pine Creek in a distinct grouping apart from Puponga and Te Rae (Fig. 4.14). NMS analysis of the invertebrate community at Puponga did not show any clear pattern of change over time between the exclosures and controls but both treatments shifted from their original composition (Fig 4.15). At Te Rae the invertebrate communities of both the exclosures and controls diverged from composition found during the initial sampling. By the third sample period the exclosures and controls were separated and trending apart from each other (Fig 4.16). There was no clear pattern in the changes observed in the invertebrate community composition over time at White Pine Creek (Fig 4.17).

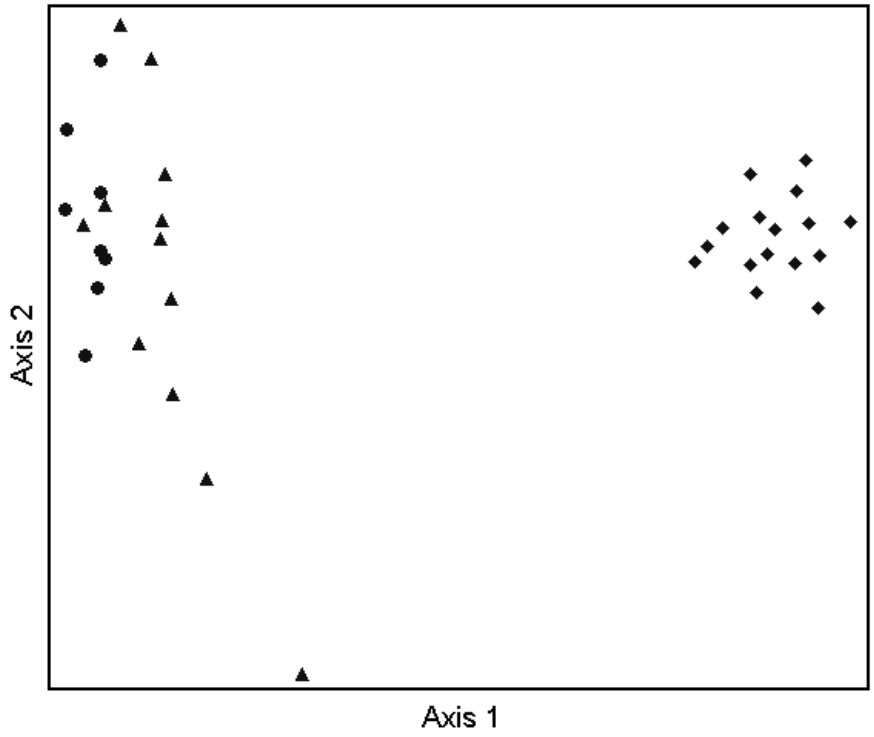


Figure 4.14. Ordination plot of a non-metric multidimensional scaling analysis of species data showing sample location groupings. Circles = Puponga, triangles = Te Rae, diamonds = White Pine Creek.

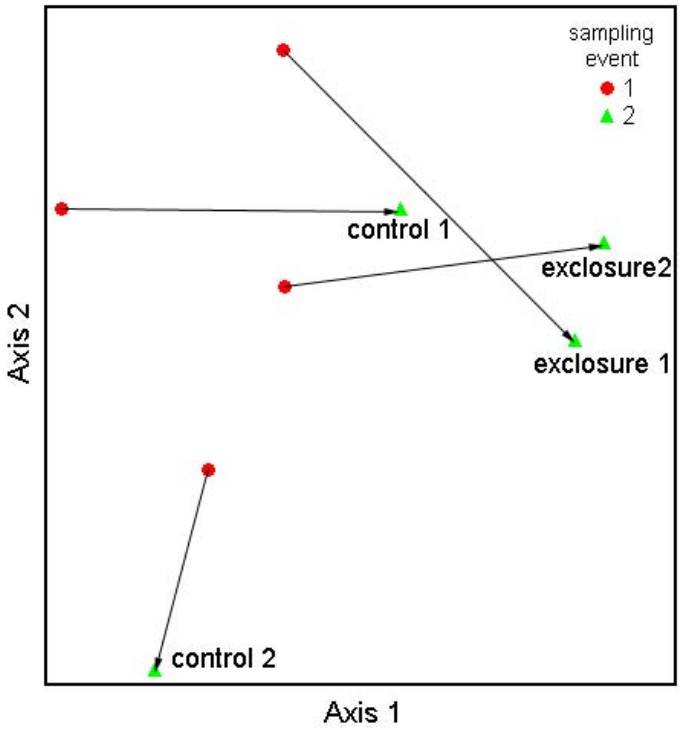


Figure 4.15. Ordination plot of a non-metric multidimensional scaling analysis of species data from Puponga showing shifts in community composition over time.

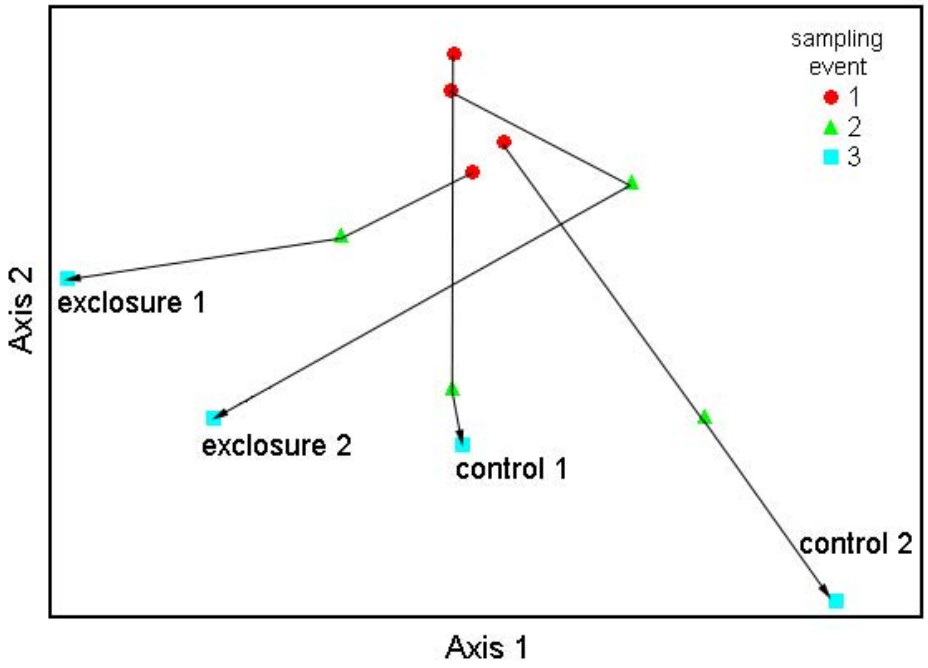


Figure 4.16. Ordination plot of a non-metric multidimensional scaling analysis of species data from Te Rae showing shifts in community composition over time.

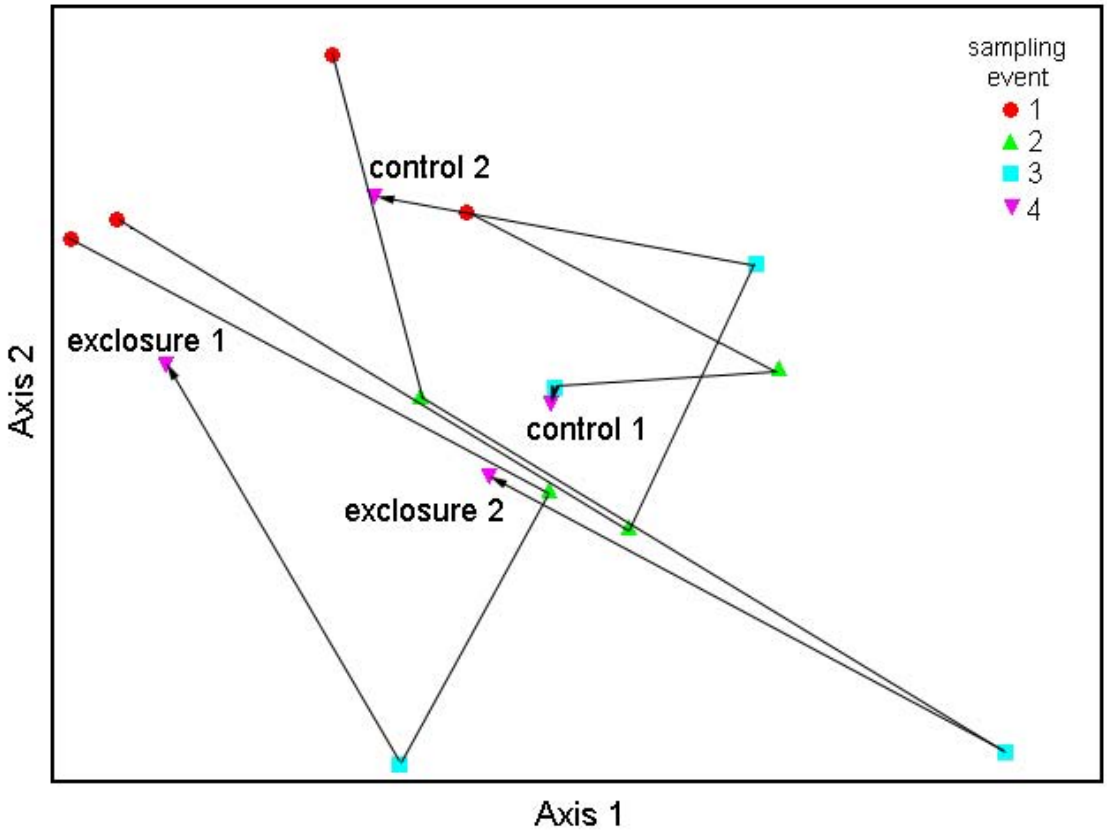


Figure 4.17. Ordination plot of a non-metric multidimensional scaling analysis of species data from White Pine Creek showing shifts in community composition over time.

4.4 Discussion

Effect of swan foraging on Zostera shoot number and biomass

Black swan foraging had demonstrable effects on *Zostera* morphology (shoot number and biomass, and rhizome biomass) within two months, with ungrazed *Zostera* having two to five times higher values for all measures than grazed *Zostera* at Golden Bay sites. This decline in *Zostera* shoot number and biomass caused by black swan foraging is consistent with findings in other studies examining waterfowl herbivory on seagrass over similar time frames e.g. (Portig *et al.*, 1994). However because sampling was carried out at these two sites for only two to four months of one year it only captures short-term changes. Longer term studies (years to decades) better capture wider trends in seagrass habitats that are probably more relevant to the overall health of the seagrass ecosystem. For example, migratory duck herbivory caused shoalgrass in a Texas lagoon

to decline by 60% over a 30-year period. The ducks removed up to 75% of the biomass annually, which the plants were unable to fully regenerate by the following year when the ducks returned (Mitchell *et al.*, 1994). An exotic *Zostera* species on the west coast of America continued to expand its range over 50 years even with more than 50% of biomass removed by geese and ducks annually (Baldwin & Lovvorn, 1994). These studies illustrate both negative and positive changes in seagrass habitat that would not be apparent if trends within one year only were observed.

No differences in *Zostera* measures were evident in control and exclosure plots at White Pine Creek in Whanganui Inlet. Whether this is due to some feature of the *Zostera* or habitat itself (e.g. the sediment surrounding the plants) or to lower foraging pressure from swans (densities over the course of the experiments varied from roughly 1-3 swans ha^{-1} at Puponga, 0.5-1.5 at Te Rae but were only c. 0.5 ha^{-1} in Whanganui Inlet) is unknown.

The growth and biomass of seagrass in temperate zones can be highly seasonal with growth and biomass increasing toward summer and declining toward winter (Kerr & Strother, 1990; Lee *et al.*, 2005); correspondingly, associated invertebrate abundance and diversity can change seasonally too (Gambi *et al.*, 1998). These background changes may influence the impact swan foraging has. As this study was carried out from summer to winter it is probable that *Zostera* growth rates were relatively low so the impacts of swan foraging on the plant would greater than at other times of year due to the inability of the *Zostera* plant to replace lost biomass. Had this study been conducted from winter to summer the decline resulting from swan foraging may not have been as marked as this is the maximum growth period for *Zostera* (Turner & Schwarz, 2006b).

A pattern of increasing then declining *Zostera* shoot number and biomass in the control plots was evident at Te Rae and also in shoot number at White Pine Creek. This pattern was not seen at Puponga where all *Zostera* measures increased in the control plots from autumn to winter. This may be because there are higher swan densities here than at the other two sites so the drop in swan density towards winter from outward migration may have outweighed the seasonal reduction in growth rate and allowed a net gain in shoot number and biomass.

Characteristics of the invertebrate community in western Golden Bay

The invertebrate communities of Puponga and Te Rae are similar, which is not unexpected as sites are contiguous and have similar physical attributes. The invertebrate communities at these two sites were a subset of those taxa identified in the wider scale benthic survey carried out on Farewell Spit in 2003 (Battley *et al.*, 2005), with spionid polychaetes and the cockle *Austrovenus* being the most abundant taxa in both studies. Some of the taxa e.g. pipi *Amphidesma* and barnacles *Eliminius*, that were most abundant in the 2003 survey, did not feature prominently in this study because the sampling was restricted to *Zostera* patches at mid-tide level.

The markedly different invertebrate community found at White Pine Creek in Whanganui Inlet was most probably because of the different substrate type. At White Pine Creek samples were taken in a dense clayey mud whereas at Puponga and Te Rae the sample sites were on coarser sand. These different habitats are known to support different benthic invertebrate fauna (Morton & Miller, 1968). This was most evident in the dominance at White Pine Creek of polychaetes of the family Cirratulidae, which were not recorded at all at the Golden Bay sites.

Effects of swan foraging on invertebrate abundance and biomass

The impact of waterfowl foraging on the invertebrate fauna is probably largely indirect, through disturbing seagrass and the associated substrate. The response can be less pronounced or more variable than the impact on the seagrass itself. The main effect that a reduction of seagrass has for invertebrates is the loss of habitat and increased exposure to predation (Heck & Wetstone, 1977). Species that live intimately associated with the plant are likely to be affected more than motile species or those that live deeper in the substrate (Bortolus *et al.*, 1998).

The invertebrate fauna in exclosures and control plots at Puponga followed the same trends with diversity decreasing and abundance increasing over the study period, though exclosures remained higher. This variable result may be because although the *Zostera* in the control plots was significantly lower than the exclosures it may still have provided sufficient habitat for the invertebrate fauna. This was observed by Bologna and Heck

(2002) in Florida where medium density seagrass on the edge of patches had higher density of invertebrates than denser patches.

The decline in invertebrate diversity and abundance at Te Rae closely followed the pattern seen in *Zostera* except that invertebrate abundance and diversity in the exclosures trended up instead of down by the last sample period. This could be because with the removal of surrounding *Zostera* the intact patches within the exclosures served as refuges for displaced invertebrates.

The invertebrate response to exclosures at White Pine Creek showed no clear trends except for the final sample period when there was significantly higher invertebrate abundance in exclosures than the control plots. This coincided with an increase in the control plots, despite there having been no change in *Zostera* shoot number or biomass that explained these increases. It may be that the increased numbers represent a cohort of juvenile invertebrates that reached >1 mm by the final sample period and so were detected when they would have been missed earlier.

There were significant changes in the abundance and taxonomic diversity in the invertebrate fauna in exclosures and controls at Puponga and Te Rae and this was supported by non-metric multidimensional scaling that also showed shifts in the communities over the course of the experiment. However whether these shifts were due to changes in the taxa present or changes in the relative proportions of taxa found in the initial sampling event is not clear.

Conclusions

Within Golden Bay black swans can significantly reduce *Zostera* shoot number and biomass through their foraging within two months. However the impact of swan foraging varies from one location to another so without looking at the dynamic relationship between *Zostera* growth and swan foraging intensity and longer term trends in *Zostera* bed expansion or contraction, whether these impacts are having a lasting detrimental effect on the seagrass at these sites remains unclear.

The macroinvertebrate communities of Puponga and Te Rae are very similar while that found in at White Pine Creek in Whanganui Inlet is quite different from the other two sites. This is most likely due to the difference in the physical environment in western Golden Bay and Whanganui inlet.

Following the pattern seen in *Zostera*, within Golden Bay black swans can cause a significant decline in the abundance and diversity of macroinvertebrate as a result of their foraging activity in the seagrass beds. Again, while there was a clear pattern of decline in the controls exposed to swan foraging at Te Rae and, to a lesser degree, Puponga there are undoubtedly natural seasonal variations in the invertebrate fauna that would need further exploration before the extent of long term impacts of swan foraging could be known.

Black swan foraging does not appear to influence the abundance of either *Zostera* or the associated macroinvertebrate fauna at White Pine Creek. Investigation of the invertebrate faunal changes over a year may shed light on the apparent increased invertebrate abundance in winter at this site.

5. The diet of black swans and their role in nutrient cycling

Abstract

Through their foraging, herbivorous waterfowl can turn over significant quantities of vegetation biomass and facilitate nutrient cycling in aquatic ecosystems. This speeds up a cycle that would otherwise take much longer and makes nutrients available to other trophic levels in the ecosystem. This chapter uses faecal analysis to investigate the diet of black swans and shows that *Zostera* is the sole food source. The *Zostera* biomass turned over by black swans is estimated from a faecal deposition survey. The nutritional value and fibre content of *Zostera* and swan faeces is characterized and shows that *Zostera* rhizome has lower fibre and higher carbohydrates while shoots have a higher N, P and Ca content. This differential nutritive value may explain why black swans expend extra effort to secure rhizomes. Nutrient turnover facilitated by swans is likely to be important at peak rates but is probably only a minor contributor of available nutrients in this tidal ecosystem on an annual basis.

5.1. Introduction

Waterfowl are a conspicuous component of most wetland ecosystems around the world. A range of waterfowl have been shown to have measurable effects on wetlands not only through the direct impacts of foraging on vegetation (Ganter, 2000; O'Hare *et al.*, 2007) but also by altering the balance of nutrients held in the vegetation, substrate and water column (Hahn *et al.*, 2008; Manny *et al.*, 1994). Being comparatively large and having high food intake requirements, swans and geese in particular are capable of dramatically altering the ecology of a wetland (Cargill & Jefferies, 1984; Tatu *et al.*, 2007b).

Figure 5.1. Swans foraging on the water at Puponga. Photo: Alistair Robertson.

Until quite recently the prevailing paradigm has been that large herbivores play a relatively minor role in cycling nutrients in seagrass systems with the majority of nutrients being made available through detritus that results from natural senescence. This paradigm has been strongly questioned by recent studies that show the effects that large herbivores can have constitute an important pathway for nutrient flow (Heck & Valentine, 2006). Because seagrass is of relatively low nutritional value swans and geese feeding solely on vegetation must consume a large volume of plant matter to compensate. The high fibre content of seagrass makes it difficult to fully digest so in order to meet their nutritional requirements black swans compensate by having a high through-put rate resulting in large amounts of bulky fibrous droppings (Valentine & Heck, 1999) (Fig. 5.2). These droppings make particles of seagrass and the nutrients within that would otherwise have remained part of the living plant available to other species living in this environment (Heck & Valentine, 2006). Therefore it is possible that the high numbers of swans in western Golden Bay are important as agents to release the nutrients held in seagrass into other trophic levels of the ecosystem through their droppings (Fig 5.3).

Figure 5.2. Swan droppings amongst *Zostera* disturbed by feeding. Photos: Alastair Robertson.

In many aquatic ecosystems there is more than one species of macrophyte present in significant amounts. This can allow preferential targeting by herbivores of species that have high nutritional value or require the least effort to gather (Aragones *et al.*, 2006; Zacheis *et al.*, 2001). In western Golden Bay however the seagrass *Zostera muelleri* is the dominant plant species in the ecosystem. A smaller amount of epiphyte present on

the *Zostera* leaves and macroalgae on the tide flats and a few species of salt marsh plants found at the upper tide limit represent the only other vegetation present in this environment (see Chapter 1).

While this ecosystem is dominated by just one plant species the overall nutritional content of *Zostera* and how nutrients are partitioned within an individual plant varies between seasons (Pergent-Matini *et al.*, 2005) and with the background nutrient availability (Lee *et al.*, 2005; Morris *et al.*, 2007). There are other external sources of nutrient input and loss (e.g. river outflow and marine currents) that also have an important influence on the overall nutrient budget of seagrass habitats (Nienhuis, 1993). Quantifying the ecosystem nutrient budget of the western Golden Bay wetland area in this study and the contribution of external processes was beyond the scope of this study, which focused only on the seagrass swan pathway (see Fig. 5.2 for a flow diagram of potential nutrient pathways involving *Zostera* and swans).

This chapter aims to quantify the role black swans play in biomass turnover and nutrient cycling in western Golden Bay. This is investigated using a number of approaches. The first part of this involved examining the components of the black swan diet to confirm whether *Zostera* is the principal food source and what the proportion of above- and belowground matter is being consumed. Secondly a faecal deposition survey was conducted which allowed the swans food intake, assimilation and faecal deposition rates to be calculated. The third aspect of this study looked at the content of several biologically important nutrients and fibre in swan faeces and *Zostera* shoot and rhizome by carrying out nutrient analysis. This allowed annual nutrient turnover to be estimated and provided evidence for why swans may target different sections of the *Zostera* plant.

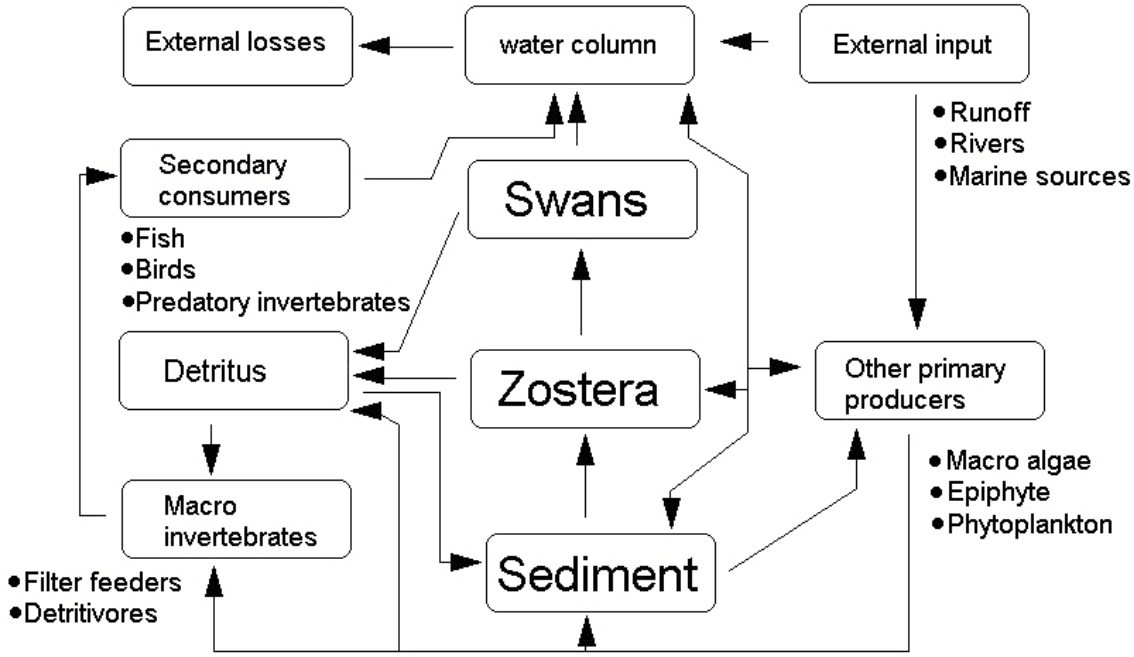


Figure 5.2. Schematic diagram of potential nutrient flow pathways in the western Golden Bay tidal flats.

5.2 Methods

Faecal analysis

Swan faeces were examined under a dissecting microscope to determine the main dietary components. The relative proportions of *Zostera* shoots and rhizome in swan faeces were calculated by placing faecal matter along a 1 mm x 18 mm grove and scoring the number of mm^2 containing mostly shoot or mostly rhizome matter. Eighteen droppings collected on four occasions from two sites were sampled. Seven subsamples of faecal matter from each dropping were examined.

Faecal survey

For faecal deposition rates three transects were marked from high to low tide spaced 500 m apart at Puponga (Fig. 5.4). Along each transect at 100 m intervals 20 m diameter circles were scribed on the substrate surface and all swan droppings within the area were collected. Droppings were collected from the same points at every second low tide over a four day period. There were 32 sample points in total, each with an area of 314.2

m^2 and 10,054 m^2 when combined. Swan numbers across the study site were recorded each day faecal samples were collected. Droppings were dried at 75ºC to constant weight and weighed to the nearest 0.05 g to give a dry weight (DW). The daily combined totals were divided by 10,054 then multiplied by 10,000 to give a per hectare deposition rate. To get a per swan deposition rate the per-hectare rate was multiplied by the total area and divided by the number of swans present at the site during the survey. As these calculations were for consumption and deposition over one tidal cycle they were doubled to give daily rates.

The food intake rate of swans can be calculated by comparing the fibre content of the faeces deposited and the fibre content of the food source if it is assumed that no fibre is digested i.e. fibre consumed equals fibre in faeces.

To determine the persistence of whole droppings on the tidal flats, several droppings were placed under small plastic netting cages anchored in the sand then checked after a tide had passed over them.

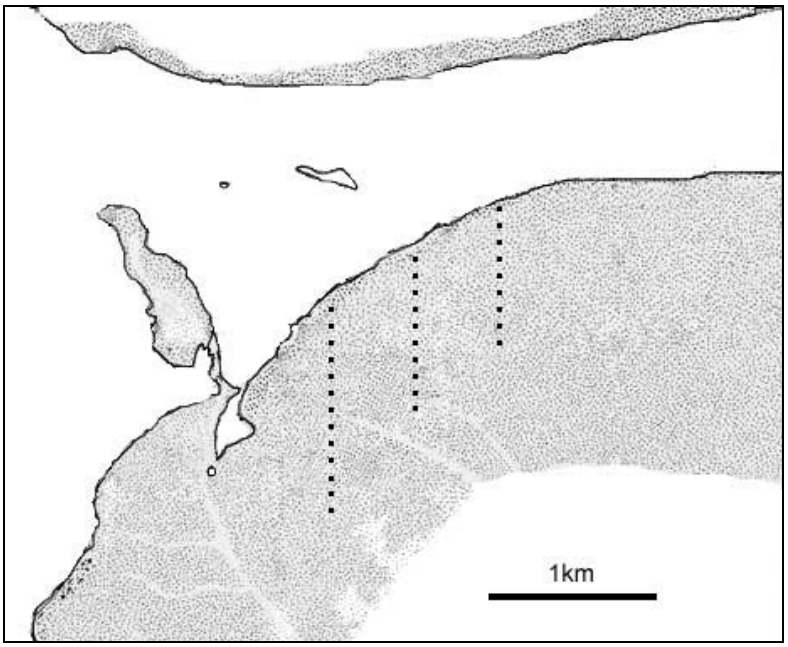


Figure 5.4. Layout of faecal survey transects and sample points at Puponga.

In this study neutral detergent fibre (NDF) was the fibre marker used for this calculation. NDF is a combination of several fibre components and was one of the elements measured during nutrient analysis (see Figure 5.5 for more detail).

The following equation was used to calculate food intake rate (adapted from Mitchell and Wass (1995)):

$$\text{intake rate(g)} = \frac{\text{faeces produced(g)} \times \text{neutral detergent fibre in faeces(\%)}}{\text{neutral detergent fibre in food(\%)}}$$

Assimilation efficiency was calculated by:

$$\text{assimilation efficiency(\%)} = 100 \times \frac{\text{(intake rate - faeces produced)}}{\text{intake rate}}$$

Using the DW intake rate from the equations above to calculate the amount of fresh *Zostera* consumed required the fresh weight (FW) to DW ratio. To determine this, six *Zostera* samples (three each from Puponga and Te Rae) were separated into rhizomes and shoots and patted dry with paper towels to remove excess water then weighed. The samples were dried at 75°C to a constant weight and weighed again. From this the dry weight to fresh weight ratio for rhizomes and shoots could be calculated. Using rhizome and shoot biomass figures from samples taken as part of the exclosure experiment (Chapter 4, Table 4.2) the FW:DW ratio for the whole plant could be calculated.

The ratio of rhizome to shoot in the droppings was used to estimate the intake rate of each plant component using the equation above. Because the relative contribution of rhizome and shoot NDF to the total NDF in faeces was based on the frequency of particles of each material in fresh droppings, the percentage of each material was adjusted to match the percentages found in dry *Zostera* when calculating the NDF in the rhizome and shoot. As the accuracy of the faeces particle identification was uncertain and whether the dry weight of shoot and rhizome in the faeces is the same as that in the plant was not tested, these figures are estimates only.

Adapting published seagrass biomass values (Battley *et al.*, 2005; Duarte, 1999; Long *et al.*, 1994), an approximation of the standing crop of *Zostera* at Puponga was calculated. This allowed an estimate of the relative significance of the swan consumption.

Nutrient analysis

Three fresh *Zostera* samples and three faecal samples were collected from both Puponga and Te Rae. In the lab the *Zostera* samples were separated into rhizomes and shoots. Root matter was only included if it was attached to a rhizome. This gave a total of eighteen samples, six each of rhizome, shoot and faeces. These eighteen samples were analyzed for nitrogen, calcium, phosphorus and fibre content. Hot water soluble carbohydrates are an easily digestible component of *Zostera* (Mathers *et al.*, 1998) and were analyzed in the *Zostera* rhizome and shoot samples to give an indication of the relative quantity in each of these plant parts. The three samples of rhizome and shoot from Puponga were used for this analysis. At least 35 g FW of each was collected to provide enough material for analysis after drying. Samples were dried to constant weight and ground to <1 mm particle powder then submitted to the Nutrition Laboratory at Massey University's Institute of Food, Nutrition and Human Health for nutrient analysis.

Fibre components analyzed were neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin, cellulose, and hemicelluloses (Fig. 5.5). Calcium and phosphorus were analysed via preparation AOAC 968.08D followed by colorimetric analysis; nitrogen content was measured by a Leco analyser, total combustion method (AOAC 968.06). NDF, ADF and Lignin were measured using a Tecator Fibretec System (Robertson & Van Soest, 1981). Nelson's determination of reducing sugars was used for analyzing hot water soluble carbohydrates.

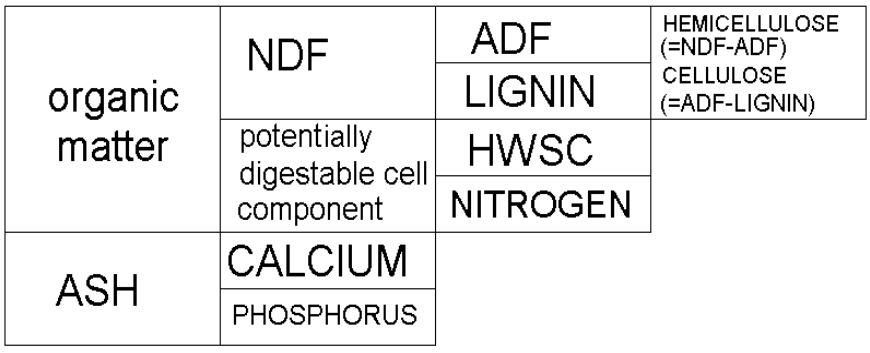


Figure 5.5. Visual representation of the breakdown of plant component nutrient analyses. Components to the right are part of that to the left. NDF = neutral detergent fibre, ADF = acid detergent fibre, HWSC = hot water soluble carbohydrates. Adapted from Prop and Vulink (Prop & Vulink, 1992).

Nutrient turnover rates

The nutrient turnover rate was calculated using the *Zostera* deposition rates from the faecal survey and the nutrient content percentages provided from the nutrient analysis. The deposition rates were calculated from turnover $swan^{-1}$ day^{-1} and swans ha^{-1} day^{-1} and estimated for m^{-2} $year^{-1}$ and total yearly input.

Statistical analysis

ANOVA was used to test the differences between the nutrient and fibre content of faeces, shoot and rhizome. A Tukey's post hoc test was used to detect significant differences among the three materials.

5.3 Results

Faecal analysis

From the dropping analyses 42.23% ± standard error 2.3% of *Zostera* particles were identifiable as shoot and 57.77% ± standard error 2.3% was identified as rhizome (Fig. 5.6, Table 5.1). The range of both was 0-100% with some samples consisting entirely of either shoot or rhizome.

No evidence of other food sources was identifiable in the droppings used for the shoot/rhizome counts, e.g. invertebrates or algae. In earlier preliminary investigation remnants of a polychaete worm and several cumaceans (hooded shrimps) were identified.

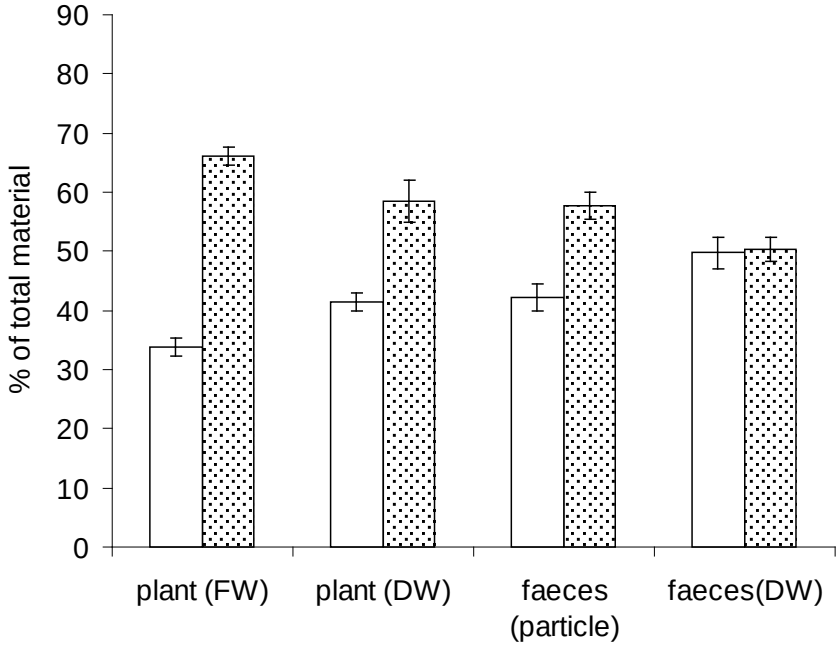


Figure 5.6. Percentages of shoot (open bars) and rhizome (filled bars) in *Zostera* plant and black swan faeces ± standard error.

Faecal survey deposition rate

The average faecal deposition rate was 11.70 g (±s.d. 9.78) DW ha^{-1} $tide^{-1}$ or 23.40 g DW ha^{-1} day^{-1}. The average intake rate was 27.25 g DW ha^{-1} day^{-1}. On the days samples were collected there was an average of 77 (±5.7) swans present at the study site. For this number of swans to turn over this volume of *Zostera*, each swan would need to consume 175.53 g DW and deposit 150.71 g DW per day. The swans' assimilation efficiency for the total quantity of *Zostera* consumed was 14.14 % (Table 5.1). The average DW for the whole *Zostera* plant was 14.61% of the FW. Rhizome DW was 12.30% and shoot DW was 17.30% of the respective components FW. Calculated from these plant averages the intake rate of fresh *Zostera* was estimated to be 96.22 g FW ha^{-1} day^{-1} or 1239.60 g FW $swan^{-1}$ day^{-1}.

Using the ratio of rhizome and shoot DW biomass in the *Zostera* plant (determined using data from exclosure core samples in chapter 4 as a guide) the DW % and intake/deposition rate of each component in faeces were estimated (Table 5.1). Shoot made up 49.74% ± s.d.26.02% of the faeces DW with an intake rate of 13.00 g DW ha^{-1} day^{-1}, a deposition rate of 11.64 g DW ha^{-1} day^{-1} and an assimilation rate of 10.47%.

The remaining 50.26% ± s.d.19.13% of faeces DW was rhizome with an intake rate of 14.30 g DW ha^{-1} day^{-1} and a deposition rate of 11.76 g DW ha^{-1} day^{-1} giving an assimilation rate of 17.78%.

Table 5.1. Shoot and rhizome percentages in *Zostera*, and faeces production, intake, deposition and assimilation rates.

Measure	Shoot	Rhizome	Total
plant (% FW)	33.93	66.07	100
plant (% DW)	41.43	58.57	100
NDF (% DW total plant)	18.24	16.93	35.16
faeces (% particle)	42.23	57.77	100
faeces (% DW)	49.74	50.26	100
NDF (% DW total faeces)	20.37	20.59	40.96
intake rate (g DW ha -1 day-1)	13	14.3	27.3
deposition rate (g DW ha -1 day-1)	11.64	11.76	23.4
assimilation rate (%)	10.47	17.78	14.3

The estimated total *Zostera* biomass DW at Puponga was 496 tons based on an average of 100 g DW m^{-2} of live *Zostera* biomass. Annual swan consumption would account for 12.6% or 62.3 tons of this figure (Fig 5.7).

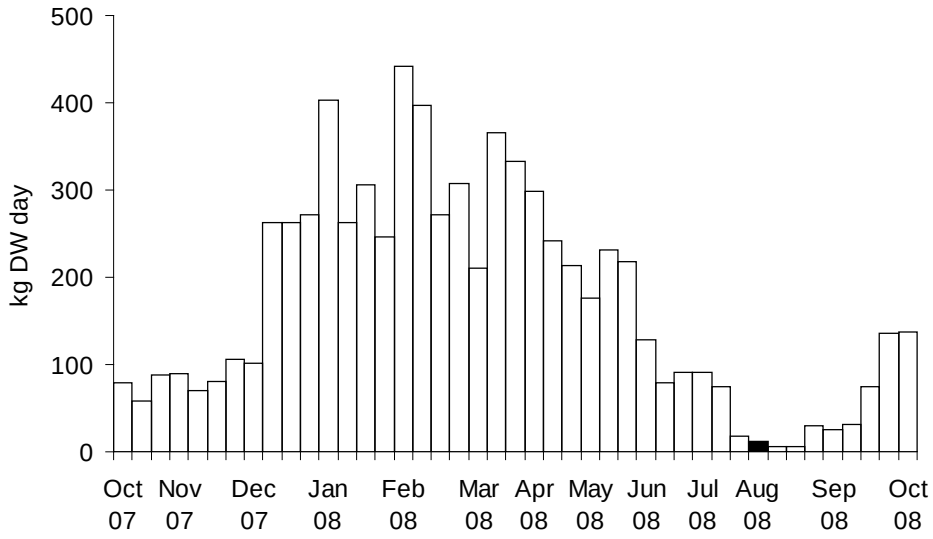


Figure 5.7. Estimated total daily fresh *Zostera* consumed by swans at Puponga over a year based on swan consumption rates in August (filled bar) and weekly swan count numbers (Chapter 2).

Nutrient analysis

Full nutrient analysis results of faeces, shoots and rhizomes are given in table 5.2. There were significant differences amongst the three material types in all measures. Between shoots and rhizomes, the minerals N and Ca were at significantly higher levels in shoots. P content, while not significant, was also higher in shoots (Fig. 5.8). All fibre components were markedly higher in shoot than rhizome, NDF, ADF, lignin and hemicellulose significantly so. The HWSC content on the other hand was much higher in rhizome than shoots (Fig. 5.9).

When comparing the nutrient and fibre content of faeces with that of the *Zostera* plant all three mineral levels were higher in the faeces than either plant component. The content of fibre components in faeces were all between the levels found in shoots and rhizome except for cellulose, which was significantly higher in the faeces than shoot or rhizome.

Table 5.2. Mean values of the nutrient and fibre components of *Zostera* as percentages of DW in faeces, shoot and rhizome material. Shared small letters within rows denote means that are not significantly different (Tukey tests). The highest means (or pair of means where the two highest values are not significantly different) are in bold.

	Faeces		Shoot		Rhizome			
	mean	s.d.	mean	s.d.	mean	s.d.	*F* value	*P* value
N	**2.56** ^{A}	0.56	**2.39** ^{A}	0. 18	0.63 ^{B}	0.11	$F_{2,17}=56.55$	<.0001
P	**0.33** ^{A}	0.07	0.31 ^{B}	0.02	0.21 ^{B}	0.04	$F_{2,17}=11.1$	0.0011
Ca	**1.07** ^{A}	0.09	**0.59** ^{A}	0.04	0.51 ^{B}	0.06	$F_{2,17}=129.12$	<.0001
HWSC	.	.	5.92 ^{B}	0.92	**18.29** ^{A}	3.18	$F_{1,5}=42.02$	0.0029
NDF	**40.96** ^{A}	1.86	**44.02** ^{A}	2.70	28.90 ^{B}	2.53	$F_{2,17}=67.02$	<.0001
ADF	**27.17** ^{A}	1.67	**27.74** ^{A}	1.99	15.86 ^{B}	1.87	$F_{2,17}=78.69$	<.0001
Lignin	3.64 ^{B}	0.96	**8.32** ^{A}	2.13	3.13 ^{B}	0.44	$F_{2,17}=26.03$	<.0001
Cellulose	**23.53** ^{A}	1.85	19.42 ^{B}	3.87	12.73 ^{C}	1.69	$F_{2,17}=25.21$	<.0001
Hemi Cellulose	**13.78** ^{BA}	1.38	**16.29** ^{A}	1.68	13.04 ^{B}	2.21	$F_{2,17}=5.42$	0.0169
DM	**96.68** ^{A}	0.23	94.62 ^{B}	0.20	94.23 ^{B}	0.39	$F_{2,17}=128.56$	<.0001
Ash	**31.04** ^{A}	5.08	25.45 ^{B}	1.88	**31.40** ^{A}	1.59	$F_{2,17}=6.29$	0.0104

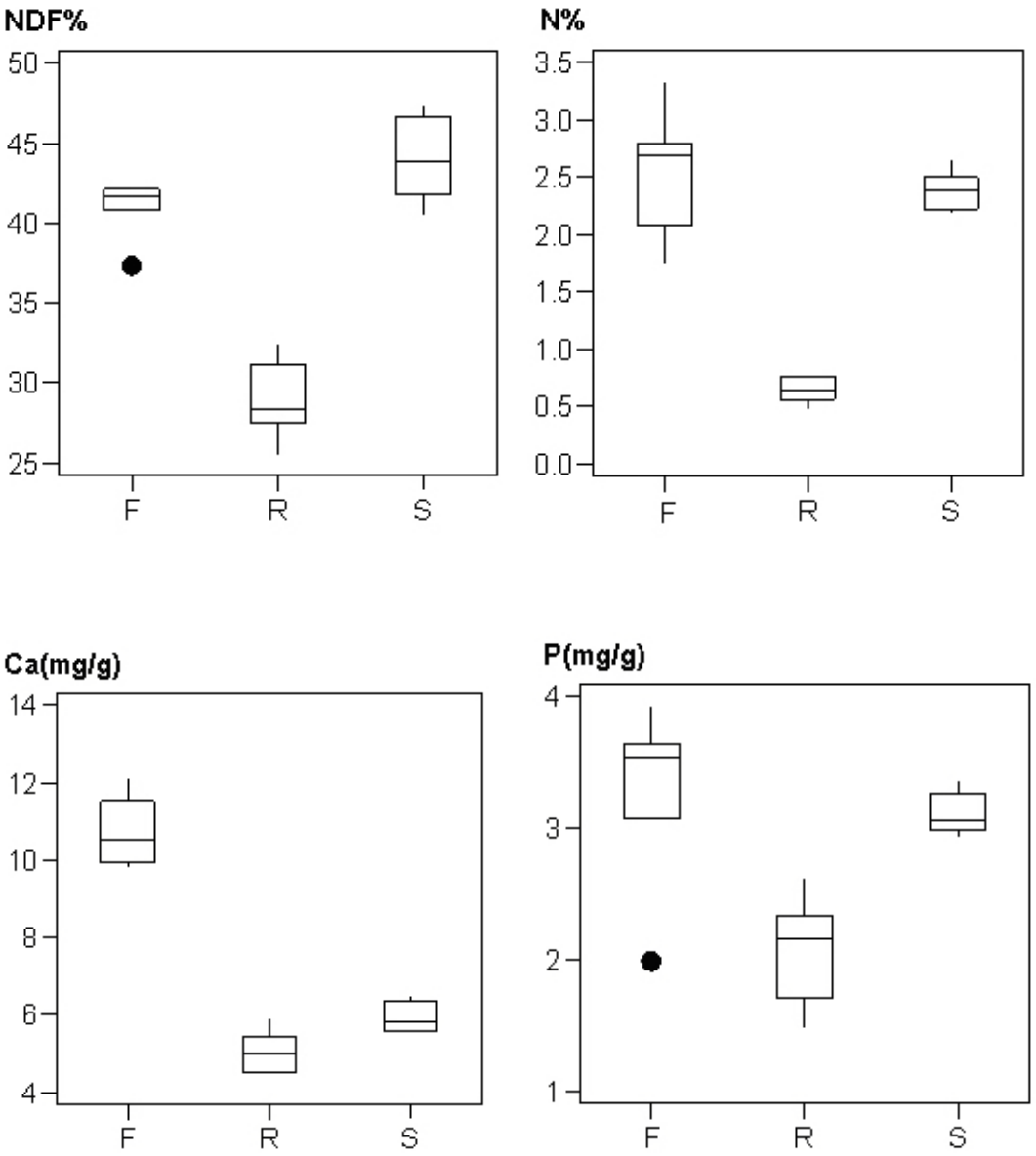


Figure 5.8. Box plots of NDF, N, Ca and P in faeces (F), rhizome (R) and shoot (S) as a percent of DW (NDF, N) and mg/g (Ca, P). Boxes enclose 25-75% (with median), whiskers cover 5-95% with outliers shown as dots.

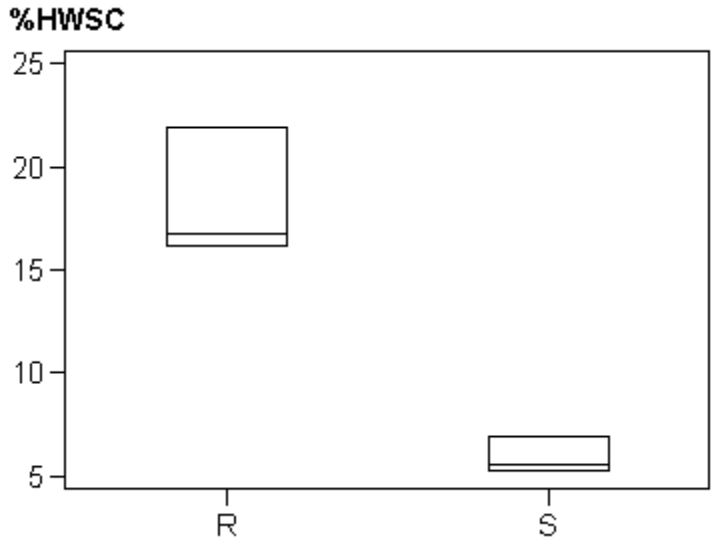


Figure 5.9 HWSC percent expressed as glucose in rhizome (R) and shoot (S) as a percent of DW.

Nutrient turnover

Of the total 23.40 g DW ha^{-1} day^{-1} estimated to be deposited at Puponga, N, Ca and P is estimated at 0.60 g, 0.25 g and 0.08g respectively (Table 5.3). Using these values converted to g $swan^{-1}$ day^{-1} and the average number of swans at this site from weekly swan counts (Chapter 2) the average annual turnover was estimated. From the average annual deposition rate a hypothetical total was calculated at 0.23 g m^{-2} $year^{-1}$ for N, 0.10 g m^{-2} $year^{-1}$ for Ca and 0.03 g m^{-2} $year^{-1}$ of P (Table 5.3). The total yearly nutrient input for Puponga based on the $swan^{-1}$ deposition rate at the time of this study was estimated to be 1368 kg of N, 575 kg of Ca and 177 kg of P with a maximum daily deposition of 9.72 kg, 4.08 kg and 1.26 kg respectively (Fig. 5.10).

Table 5.3. Nutrient deposition rates per hectare per day, per swan per day and per meter per year expressed in grams.

	N	Ca	P
g ha^{-1} day^{-1} (during study)	0.60	0.25	0.08
g ha^{-1} day^{-1} (annual average)	6.32	2.66	0.81
g $swan^{-1}$ day^{-1}	3.86	1.62	0.50
g m^{-2} $year^{-1}$	0.23	0.10	0.03

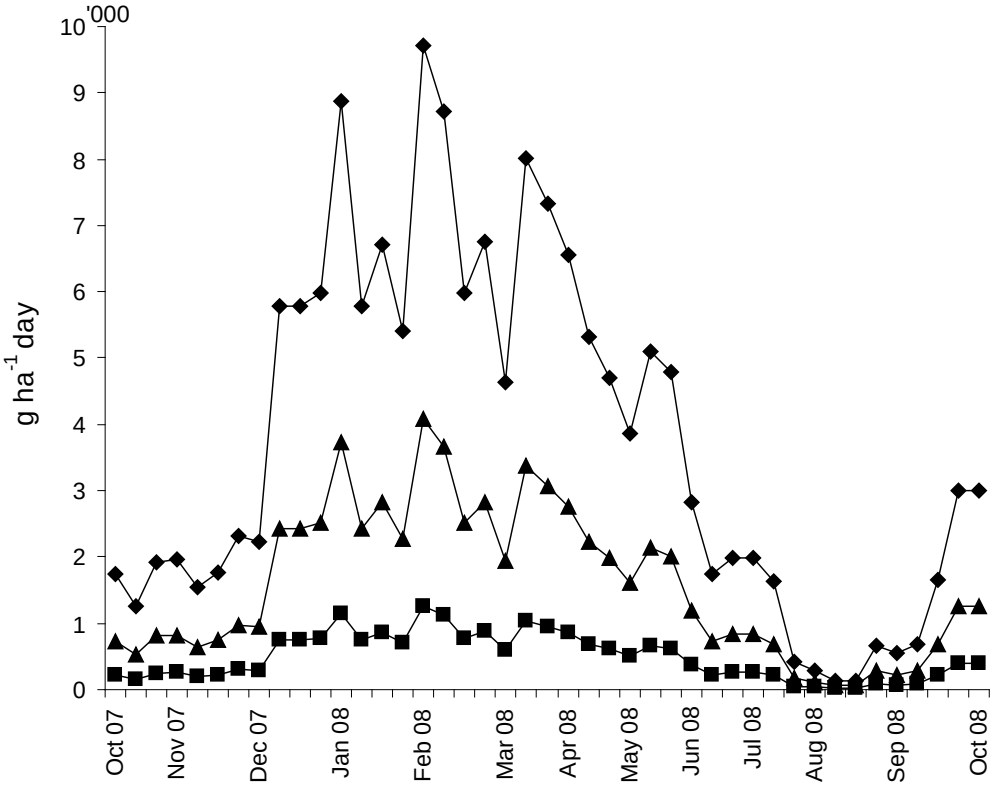


Figure 5.10. Estimated daily ha^{-1} deposition rates of N - diamonds, Ca - triangles and P - squares, based on deposition rates found in faecal survey and weekly swan count numbers (Chapter 2).

5.4. Discussion

Faecal analysis

While in some locations identifying dietary components of waterfowl diets from faeces requires identification of plant epidermal material (Owen, 1975), in black swan faeces on in western Golden Bay this was not necessary. *Zostera* was the overwhelmingly dominant plant food source available and as it is relatively poorly digested, fragments in faeces were readily identified under a binocular microscope. A portion of the faecal matter consisted of tiny particles that were not possible to identify with the equipment used. Fine particles were present in every sample but only made up a small fraction of the total. This may skew the proportion of each component slightly as rhizome has less fibre and may be easier to digest.

In any case it was clear that the swans exclusively feed on *Zostera* and appeared to eat slightly more rhizome than shoot (Table 5.1). That the swans are entirely herbivores is in agreement with the findings of other studies of black swan diet. The presence of rhizome in the faeces negates the assertion by Byrom and Davidson (1992) that black swan feed exclusively on the shoots of *Zostera*. However waterfowl feeding on *Zostera* rhizome has been noted in other studies (Jacobs *et al.*, 1981; Mathers *et al.*, 1998) so it is obviously a resource they are capable of utilizing and the swans in western Golden Bay clearly do.

Other food sources

While *Zostera* was the only food source for the swans identified in the faeces a number of macroalgae species are also present in smaller quantities across the tidal flats. These may form an important part of the swan diet at times. Swans were twice observed eating floating *Enteromorpha* at high tide, and macroalgae have been noted elsewhere as a food source for waterfowl (Byrom & Davidson, 1992; Perry *et al.*, 2004). The absence of macroalgae in the faeces may be because it is digested more completely; black swans have been shown to assimilate algae much more effectively than the assimilation rates for *Zostera* reported in this study (Mitchell & Wass, 1995). No attempt was made to formally quantify the extent or species composition, but from incidental observation the most conspicuous macroalgae on the shore were *Ulva*, *Enteromorpha* and *Codium* species along with a number of smaller red seaweeds.

As summer progressed the amount of epiphyte on *Zostera* fronds increased and in some places completely covered every *Zostera* shoot. In some cases epiphyte has been shown to have higher primary production than the seagrass itself and provide an important nutrient source for some grazers (Bologna & Heck Jr, 1999). The swans at Puponga presumably consume this epiphyte along with *Zostera* incidentally though it is not known if it is preferentially targeted.

In other parts of New Zealand black swans have been known to feed on farm pasture (Byrom & Davidson, 1992), sometimes to damaging levels. This activity has been recorded mostly when aquatic vegetation is in short supply. At the sites in this study,

both of which were adjacent to farm land, swans were not observed on pasture foraging, indicating this does not form part of their diet at these locations.

Faecal survey deposition rate

Forage intake rates were calculated using the fibre portion of the faeces on the assumption that none is digested. This assumption was not tested in this study but others have shown by comparing fibre content in faeces with actual intake and output that faeces fibre content is an accurate means of estimating actual intake (Cargill & Jefferies, 1984; Summers & Grieve, 1982).

The intake rate and faecal deposition rate (175.5 and 150.7 g DW swan^{-1} day^{-1} respectively) of swans at Puponga is higher than that observed in black swans feeding on a freshwater lake (104 and 52 g DW swan^{-1} day^{-1}) but the assimilation rate was markedly lower (14.3% in this study vs. 50% observed by Mitchell & Wass, 1995). The diet of the swans feeding on the lake consisted mainly of algae so it is possible that there is a difference in the digestibility of the two food sources. This difference may also have been because the nutrient requirement of the swans was different at the time of these studies; increased assimilation during moulting has been observed in greylag geese (*Anser anser*) (Fox & Kahlert, 1999). However the N and P levels in the food plant (1.51 vs. 1.16 for N and 0.26 vs. 0.33 for P) and faeces (2.56 vs. 2.3 for N and 0.33 vs. 0.44 for P) in this study and that of Mitchell and Wass (1995) were very similar so it would not appear that the difference in assimilation rate is due to differing nutrient requirements. The black swan intake rate (175.5 g DW swan^{-1} day^{-1}) in this study is very similar to that seen in Brent geese feeding on *Zostera* (175.5 g DW goose^{-1} day^{-1}) (Mathers *et al.*, 1998) suggesting that that the higher consumption is due to lower digestibility of *Zostera* compared to algae (Table 5.3). However, the assimilation rate of the swans was still less than half (14.3% vs. 32.78%) that of Brent geese feeding on a similar diet.

The swans' daily intake rate in this study was calculated by doubling the intake rate over one tide on the assumption that these remain consistent throughout the entire day; if the swans reduce their intake at night then these values would be overestimates. Conversely, as the faeces are prone to disintegrate when submersed any faeces defecated while the swan is foraging on water may go undetected which would cause

the intake rate to be (possibly considerably) underestimated. This may explain why the assimilation rate appears so low.

The annual consumption of 62.3 tons DW represents 12.6% of the biomass standing *Zostera* crop. The annual *Zostera* biomass production is likely to be many times higher than this (Nienhuis & Groenendijk, 1986) meaning the proportion of total biomass production consumed by swans would be reduced.

Table 5.3. Food intake rates per bird^{-1} day^{-1} compared to other studies.

species	black swan[1]	black swan[2]	Brent goose[3]	Brent goose[4]
principle food	*Z. muelleri*	algae	*Z. noltii*	*Z. spp.*
intake rate DW (g)	175.53	104	175.7	121.6
N (%DW)	1.51	1.16		
P (%DW)	0.26	0.33		
daily faecal output DW (g)	150.71	52	118.1	
N (%DW)	2.56	2.3		
P (%DW)	0.33	0.44		
assimilation rate (%)	14.3	50	32.78	
habitat	tidal flat	lake	tidal flat	tidal flat
country	New Zealand	New Zealand	Ireland	England

[1]This study, [2]Mitchell and Wass (1995), [3]Mathers et al. (1998), [4]Charman (1977).

Nutrient analysis

Analysis showed there were significant differences in the nutrient content of shoot and rhizome and faeces. Seagrasses are capable of shifting nutrients from one part of the plant to another depending on the plant's needs (Erftemeijer & Middelburg, 1995). This means that the relative nutrient values for shoot and rhizome can vary seasonally (Lee *et al.*, 2005). The nutrient value of seagrass is influenced by the nutrient availability in the surrounding environment (Oshima *et al.*, 1999; Tomasko & Lapointe, 1991) so would vary between locations and over time, however the average N and P content for *Zostera* shoot and rhizome in this study were similar to the nutrient values of *Zostera marina* (Pedersen & Borum, 1993) and other seagrass (Duarte, 1990) so this is not likely to bias the results significantly.

The rhizome had more of the easily digested carbohydrates than shoots did, a pattern that has also been found in other studies (Burke *et al.*, 1996; Mathers *et al.*, 1998). This, coupled with the lower fibre content of the rhizome, make it a potentially richer and more readily assimilated source of energy than shoot material. This provides a likely

explanation for the grubbing behaviour observed (Chapter 2) – it is highly likely that the energy expended grubbing for the rhizome is outweighed by the energy gain. In situations where the substrate is less penetrable it may take more energy to obtain the rhizome than is gained from it (Mathers *et al.*, 1998). This may be the case in Whanganui Inlet, where the low swan density observed there compared to Puponga and Te Rae seems unexpected considering the extensive luxuriant *Zostera* beds present there (Chapter 1). However, because the substrate consisted of thick mud and the proportion of rhizome to shoot is much lower, it may that the *Zostera* does not provide a sufficient energy return on the effort used to obtain it at this site.

It is possible that swans can differentiate between high and low nutrient food sources both between and within plants. Such selective foraging has been observed in a number of other species. For example, moulting greylag geese preferentially remain feeding on high nutritional food patches even when other food sources are more plentiful (Fox *et al.*, 1998), and Takahe select nutrient rich flowering tussock tillers over those not flowering (Mills *et al.*, 1991). The *Zostera* nutrient values in this study are from randomly selected patches – whether this accurately reflects the nutrient content of the *Zostera* the swans actually choose to consume would require further testing.

While N, Ca, P, soluble carbohydrates and fibre were the only components investigated in this analysis other constituents of seagrass, for example lipids, are also an important source of nutrition for grazers (Klump and Nichols, 1983) and the relative concentrations of these in different parts of the plant may influence swan foraging behaviour.

Nutrient turnover

The total nutrient deposition by swans at Puponga varies greatly across the year and reaches considerable levels (19.6, 8.2 and 2.5 g ha^{-1} day^{-1} for N, Ca and P respectively) when the maximum swan population is present. However because this site covers a large area and as it is open to the wider marine environment the contribution of nutrient input through this pathway to the total nutrient availability in this ecosystem is probably modest. Mitchell and Wass (1995) showed the nutrient input from black swans at a

density of 9.7 swans ha^{-1} on an enclosed lake was a minor (<5%) component of the available nutrients in that environment.

As spring and summer is when most growth and reproduction in *Zostera* occurs this is when the plants' maximum nutrient requirement is. This period of spring growth is probably critically important for survival throughout the rest of the year (Burke *et al.*, 1996) and is when nutrient limitation most likely to occur (Alcoverro *et al.*, 1997). This coincides with the period when swan numbers are increasing and many swans are moulting so are likely to have elevated nutrient requirements for new feather growth (Fox & Kahlert, 1999). Given this, the level of swan foraging during this period could potentially negatively affect the nutrient balance of the *Zostera* beds for the rest of the year. However the impact of swan grazing on *Zostera* during spring is probably less important than in late autumn and winter because *Zostera* growth outpaces loss to swans, allowing sufficient biomass development and nutrient assimilation to sustain the plant through autumn and winter (Mitchell & Wass, 1996; Oshima *et al.*, 1999) whereas losses during winter can not be readily replaced due to poorer growing conditions (Lee *et al.*, 2005).

External inputs and losses

Waterfowl can, in some instances, contribute significant quantities of new nutrients into aquatic habitats through moving to and from terrestrial feeding grounds (Hahn *et al.*, 2008; Manny *et al.*, 1994). The input of new nutrients into the tidal ecosystem by swans at Puponga would be limited to that which is brought in during spring from overwintering site as they do not feed on shore at this site. Furthermore, unlike lakes and reservoirs (which have been investigated in other studies) the tidal environment in this study is a part of the wider marine environment so this input would be unlikely to contribute substantially to the total nutrient pool.

Weather conditions are likely to play a role in the persistence of nutrients in the environment with strong wave action and currents removing faeces more rapidly than calm conditions. Agricultural activity along the coast adjacent to the tidal flats could be a significant source of extra nutrient input via streams and run-off, particularly during heavy rainfall. Nutrients originating from agricultural land have not been quantified in

Golden Bay but are potentially significant (Duarte, 2002). The large Takaka and Aorere Rivers that drain into Golden Bay undoubtedly contribute significantly to the nutrient budget of the surrounding coastal waters, especially during periods of high rainfall as has been observed at other sites in the wider Tasman Bay environment (Mackenzie & Gillespie, 1986). Extensive areas of Golden Bay are occupied by aquacultural activity; the role of these in nutrient cycling in the wider marine ecosystem is unknown but mussel farms have been shown to act a nitrogen sinks (Kaspar *et al.*, 1985).

Conclusions

Black swans in western Golden Bay feed almost exclusively on *Zostera* and consume slightly more (14.3 vs. 13 g DW ha -1 day-1) rhizome than shoot material. This is probably because the nutritive value of *Zostera* varies significantly between the shoots and rhizome. Rhizome has a high soluble carbohydrate content making it a rich energy source while the shoot material provides higher nitrogen, phosphorus and calcium for cellular function and growth.

Black swans had high intake and defecation rates and a low assimilation rate at this location during the study period. This is may be due to the high fibre content of *Zostera* making digestion difficult. It could also be an artefact of the sampling method which involved a considerable degree of extrapolation and combinations of different parameters each prone to sampling error. The per-hectare consumption is likely to change following the changing number of swans present across the year. This seasonal variation matches the annual growth pattern of *Zostera* meaning the impact of high swan grazing pressure in summer is likely to be compensated for by high seagrass growth rates. The *Zostera* consumed by swans is likely to constitute a small percentage of the total annual *Zostera* biomass production at Puponga.

Similarly the nutrient turnover facilitated by swans at this site is highly seasonal with summer having the highest levels and winter the lowest. At peak numbers the nutrient input from swans is probably important. However, over a year, the total nutrient contribution of swans is likely to be minor in comparison to other sources.

6. Summary

6.1 The influence of black swans on the tidal ecosystem of western Golden Bay

The black swans in north western Golden Bay form a large and dynamic population that follows a strong seasonal pattern with numbers peaking in late summer at 4193 and dropping to a minimum of 147 in winter. On a shorter time scale (i.e. daily) their activity closely follows the tide cycle as this dictates the availability of their major food resource, the seagrass *Zostera muelleri*. This study showed that the way the swans utilize this resource has direct and indirect effects on the seagrass itself and the wider ecosystem.

The *Zostera* cover survey showed that on a scale of meters to hectares *Zostera* in western Golden Bay is widespread, being present at nearly 75% of survey points. The cover is mostly sparse with only small patches (around 8% of survey points) having greater than 50% surface cover. This is in keeping with the pattern observed on a broader scale (kilometres) by Battley *et. al.* (2005).

What this study addressed for the first time was the ability for swans to create and maintain patchiness in the seagrass landscape. Observations and faecal analysis showed that swans feed almost exclusively on *Zostera* at this site, as has been recorded previously (Byrom & Davidson, 1992). However the suggestion by Byrom and Davidson that the swans feed only on the *Zostera* shoots and do not dig for rhizome proved incorrect with the swans consuming about equal quantities of above-ground (leaves, which they cropped) and below-ground (rhizomes, which they grubbed for) material. It is through this grubbing that swans affect the tidal landscape and the patchiness of *Zostera* distribution.

The swan foraging activity survey showed that, like the *Zostera* distribution, foraging is widespread but is concentrated on the denser seagrass patches both on a scale of meters (within survey points) and hectares (between sample points). The foraging activity observed mostly consisted of small disturbances with occasional larger areas affected, and as the experimental grubbings showed these small (78.5 cm^2) disturbances tended to

fill in and disappear relatively rapidly (within 20 days). The larger (800 cm^2) experimental grubbings, however, showed that swan disturbances in dense *Zostera* have the potential to persist for at least two months (and probably much longer) and in some instances may be expanded by swans to form large areas of bare sand within the seagrass beds. In a few cases the holes were expanded to such an extent that they were no longer identifiable as having been created by swans. This means that many of the bare sand areas recorded in the *Zostera* cover survey and swan foraging activity survey could well have been initiated and expanded by swans but were not recognised as such. Swans are probably responsible for a lot more of the overall patchiness of the landscape than the results of this study suggest. As paired benthos sampling showed, bare sand patches support lower invertebrate abundance than *Zostera* beds so this transition from seagrass to bare sand caused by black swans is likely to markedly reduce the abundance of invertebrates on the tide flats as a whole.

To explore this further it would be of interest to track swan-created patches over a longer time frame and record the rate at which *Zostera* and invertebrates recolonise bare sand. This would show how long such patches last before recovering, and would mean that bare sand patches that are not obviously swan created could be more confidently assigned as such.

Larger scale mapping of *Zostera* distribution over a longer time frame (e.g. decades) could be used in conjunction with the annual swan count data collected by Fish and Game to show whether the two are linked in any way. Trends in large-scale long term seagrass distribution have been effectively tracked elsewhere using aerial photography (Frederiksen *et al.*, 2004; Kendrick *et al.*, 1999). This approach in north western Golden Bay could provide valuable additional information to help quantify the role of swans in this environment

In addition to directly impacting on invertebrate numbers through removal of seagrass, swans can have indirect impacts on invertebrates through changing the characteristics of the seagrass itself. When swans were excluded from foraging on seagrass at two sites in Golden Bay, there was a measurable reduction in *Zostera* biomass (above- and below-ground) and invertebrate biodiversity in the control plots where swans could feed compared with the exclosure plots.

These findings demonstrate that black swans can have significant direct and/or indirect negative effects on the seagrass and the associated invertebrates as a result of their foraging activity. This agrees with other similar research on waterfowl in tidal situations (Ganter, 2000; Jacobs *et al.*, 1981) and more broadly in a variety of wetland types and locations around the world (Allin & Husband, 2003; O'Hare *et al.*, 2007; Sherfy & Kirkpatrick, 2003) that show waterfowl are capable of reducing aquatic vegetation biomass and as a result the associated invertebrate biodiversity.

The impacts of swans in this study were not consistently apparent at all sites, suggesting that other factors also affect seagrass biomass and invertebrate biodiversity. Sediment type can influence seagrass growth (Matheson & Schwarz, 2007) and is most probably an important reason for some of the difference observed between the sites. This is particularly so for White Pine Creek (Whanganui Inlet) that has fine muddy sediment compared to the other two sites that generally have coarser sandy sediment.

Related to this is how exposed the sites were to water currents and wave action, which have been shown to significantly influence seagrass distribution (Frederiksen *et al.*, 2004). The most exposed site, Te Rae (Golden Bay), saw dramatic declines in both seagrass biomass and invertebrate biodiversity over time in the control plots. Environmental effects may work in combination with or compound the destructive foraging of swans.

The food intake rate of black swans at this site was high (176 g swan^{-1} day^{-1} vs. 104 g swan^{-1} day^{-1}) and the assimilation rate low (14.3% vs. 50%) compared to intake rates recorded on a freshwater lake by Mitchell and Wass (1995) where swans feed on algae. This supports the notion that *Zostera* constitutes a relatively poor food source and that the swans consume larger quantities in order to meet their nutritional requirements (Heck & Valentine, 2006). It also means that swans turn over large quantities of plant material and release it into the tidal ecosystem as particulate matter that other detritivores can consume. The volume of *Zostera* being turned over is obviously directly related to the number of swans present so would mirror the fluctuations in swan numbers over the year. In summer when seagrass growth is rapid (Lee *et al.*, 2005) and swans are most numerous their input into the environment would be highest and is

probably an important pathway for biomass and nutrient flow. In winter when swan numbers are at a minimum and seagrass is declining naturally (Ramage & Schiel, 1999), the contribution of swans probably only contributes a minor portion of the biomass and nutrients available.

By separating *Zostera* into shoot and rhizome for nutrient analysis it became clear why swans consume both portions of the plant. The nutritional value of the shoots is higher than rhizome for the essential nutrients nitrogen, phosphorus and calcium. On the other hand rhizome has more soluble carbohydrates and less fibre so is presumably a richer, more easily digested source of energy than shoots and helps to explain why the swans engage in the seemingly laborious and destructive grubbing behaviour to obtain it.

The effect black swans have on the intertidal landscape in north western Golden Bay creates and maintains changes in the physical habitat that affect other species in the ecosystem. Because of this they could be considered an ecosystem engineer species (Jones *et al.*, 1997). In this concept, physical ecosystem engineers are *"organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials"* (Jones *et al.*, 1997). Swans operate as an ecosystem engineer species both through the direct effect of their foraging on *Zostera* biomass and indirectly through the creation and maintenance of bare sand patches across the tide flats that influences invertebrate biodiversity.

The cycling of nutrients facilitated by swans is a less direct but potentially important form of ecosystem engineering. Swans make nutrients available to other species that would otherwise have remained locked within the living *Zostera*. Their potential indirect impacts on wading birds are less clear (see below).

6.2 Linking swan foraging with wader food availability

Swan foraging can cause dramatic reductions locally to the seagrass cover and invertebrate fauna. They are also likely to be responsible for much of the habitat patchiness present in the landscape at this location. These effects mean that swans could

potentially reduce the food supply for waders. However for several reasons this conclusion can not be drawn from the findings of this study.

Swans may raise overall invertebrate diversity through increasing habitat heterogeneity thus creating a wider range of microhabitats for the invertebrate fauna to utilize. If this meant more or better prey species were able to exist on the tidal flats the patchiness created by swans could be beneficial for waders. While the invertebrate species that are the preferred prey of the knots are known (Battley *et al.*, 2005) without further study of the utilisation by waders of different habitat types (e.g. bare sand and *Zostera*) it is not possible to say whether the swan foraging is having a detrimental effect on their food supply. Similarly it is not clear that *Zostera* is optimum foraging habitat for all waders – it may be that they feed in this habitat simply because it is the most widespread. Even if *Zostera* is the best foraging habitat for waders it is not known whether the availability of *Zostera* is the limiting the wader population – there may be more than enough foraging habitat even with any reductions caused by swans.

To shed more light on the possibility that swans are indirectly influencing wader numbers more investigation of the interaction between waders and invertebrates is needed. This could include prey and foraging habitat preferences of waders.

6.3 Further study

Extending the time frame of investigation

All the aspects of swan and tidal flat ecology investigated in this project were carried out over a short time frame (<1 year). Many of the findings would be more robust if the sampling period was extended beyond a year. This would begin to capture the annual change that is undoubtedly present in many of the processes. This would be particularly useful for monitoring longer-term swan-hole development, the swans' *Zostera* intake and deposition rates and the nutrient content of *Zostera* over a seasonal cycle.

Increasing study sites

This study focused on only three sites and while extrapolation of some findings is justified, including study sites on Farewell Spit proper would confirm whether the observed patterns at Puponga and Te Rae are representative of the wider environment. Swan counts across the wider Farewell Spit would give a firmer picture of how swan numbers fluctuate across the year.

Ecosystem nutrient balance

The nutrient analysis in this project was focused solely on the nutrient content of *Zostera* and swan droppings. To gain an understanding of the significance of this as a proportion of total nutrient availability, analysis of the nutrient content of the water column and sediment, and measurement of nutrient input from external sources such as runoff and rivers, would be needed. Monitoring *Zostera* growth rates would allow accurate calculation of biomass production and thus give an idea of the proportion of total biomass production that is channelled through swans.

Captive feeding trials

Inferring consumption rates from faecal deposition in the field has a degree of error resulting from potential misidentification and from possible digestion of some fibre components. A feeding trial using captive swans would allow direct measurement of their consumption rate, dietary preferences, assimilation efficiency, and defecation rates.

Further investigation of swan activity in Whanganui Inlet

The tidal environment in Whanganui Inlet clearly differs from that inside Golden Bay. *Zostera* and swan feeding activity and faecal deposition surveys and nutrient analysis of *Zostera* in carried out in Whanganui Inlet would be of interest for comparison with the findings from the inside of Golden Bay and as an investigation of the ecology of this unique environment.

Further investigation of the swan population in western Golden Bay

Tracking of individual swans behaviour would help to show whether there are got example behavioural differences in the foraging of females and male or adults and

juveniles. If present, these differences could be important if the demographics of the swan population changes seasonally. More investigation of the link between numbers at this site and breeding and migration habits in the rest of New Zealand would be of interest as would the possible effects of swan culling both in western Golden Bay and in breeding areas on the swan population.

Acknowledgements

It would have been impossible for me to carry out this project without the guidance and support of many others.

I would like to thank Phil Battley for taking me on as a student and providing the foundation for this project. Thanks also to Alastair Robertson, my co-supervisor, for going beyond the call of duty and accommodating me during my intermittent appearances on campus. And to both for their guidance, advice, discussion and reassurance throughout.

Massey University provided much appreciated funding for this project in the form of a Masters scholarship.

Thank you to Paul Barrett and Tracy Harris for their technical advice and expertise.

Many thanks also to the New Zealand Department of Conservation (DOC) for permission to carry out this project, and in particular to Hans Stoffregen and Greg Knapp at the Takaka area office for providing access to DOC information and giving this project their blessing.

Rod Asher at the Cawthron Institute provided invaluable help with invertebrate identification and taxonomy.

Lawson Davey at Fish and Game made available for my use their swan count data and invited me to participate in the annual aerial swan count which was very much appreciated despite all appearances!

I would like to thank David Melville, Rob Schuckard, Derek Macleod, Chris Petyt and the other ornithologists from the Nelson region who have shared their enthusiasm and expertise about Farewell Spit and its avian inhabitants with me.

Thanks to Tane, Bertie, Guy, James, Jessie, Mark, Chris, Todd, Lea, and Kate for their willing assistance in field despite sometimes trying conditions of which, we discovered, are many and varied in this environment.

A big thank you to my parents, Jane and Andrew, for their support both financially and logistically without which this project would have not been possible.

And finally to Emi, my wife, who has put up with so much to see this project to completion and whose encouragement and whip cracking ensured it got there - I dedicate this project to you.

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Appendix 1

Invertebrate taxa list

A total of 4843 individuals from 55 distinct groups were found in the exclosure and paired sampling. All of these groups were present in the large scale 2003 (Battley *et al.*, 2005) survey except Turbellaria, *Diloma subrostruta*, *and Exosphaeroma chilensis*.

Phylum	**Class**	**Order/Family**	**Genus/species**
Cnidaria	Anthozoa		*Edwardsia sp.*
			Anthopleura aureoradiatus
Turbellaria			
Nemertea			
Annelida	Polychaeta	*Unidentified Polychaete*	
		Arenicolidae	
		Capitellidae	*Heteromastus filiformis*
		Cirratulidae	
		Glyceridae	*Hemipodus sp.*
		Maldanidae	
		Nephtyidae	
		Nereididae	
		Orbiniidae	*Orbinia papillosa*
			Scoloplos cylindrifer
		Oweniidae	
		Scalibregmatidae	*Hyboscolex sp.*
		Spionidae	*Aonides sp.*
			Prionospio sp.
		Terebellidae	
Mollusca	Bivalvia		*Austrovenus stutchburyi*
			Macomona liliana
			Nucula hartvigiana
			Paphies australis
	Gastropoda		*unidentified gastropod*
			Amphibola crenata
			Cominella glandiformis

Phylum	Class	Order/Family	Genus/species
			Micrelenchus tenebrosus
			Notoacmea helmsi
			Diloma subrostrata
			Diloma bicanalliculata
			Zeacumantus spp.
			Eatoniella sp.
			Haminoea zelandiae
	Polyplacophora		*Chiton glaucus*
			Acanthochiton zelandicus
Arthropoda	Maxillopoda	Cirripedia	*Eliminius modestus*
	Malacostraca	Amphipoda	
		Cumacea	
		Isopoda	*Exosphaeroma chilensis*
			Isocladus spiculatus
		Stomatopoda	*Squilla armata*
		Decapoda	*unidentified crustacean*
			Halicarcinus cooki
			Halicarcinus whitei
			Hemigrapsus crenulatus
			Macrophtalmus hirtipes
			Helis crassa
			Callianassa filholi
			Pantophlus australis
	Insecta		*unidentified insect*
			caddis larva
Echinodermata	Holothuroidea	Apodida	*Trochodota dendyi*
	Stelleroidea	Asteroidea	*Patiriella regularis*