2012

The impact of Black swan (Cygnus atratus) grazing on the seagrass Halophila ovalis in the Lower Swan River estuary

Gary Choney
Edith Cowan University

Recommended Citation

Choney, G. (2012). *The impact of Black swan (Cygnus atratus) grazing on the seagrass Halophila ovalis in the Lower Swan River estuary*. Edith Cowan University. Retrieved from https://ro.ecu.edu.au/theses/446

USE OF THESIS

The impact of Black swan (*Cygnus atratus*) grazing on the seagrass *Halophila ovalis* in the Lower Swan River estuary

Gary Choney

Bachelor of Environmental Science

This thesis is presented in fulfilment of the requirements for the degree of Master of Science (Environmental Science/Management)

Faculty of Computing, Health and Science
Edith Cowan University

March 2012

EDITH COWAN UNIVERSITY

Abstract

Grazing is an important ecosystem process, influencing community structure and rates of ecosystem processes. Although grazing on seagrasses is generally considered to be minor in many temperate regions of the world, waterfowl are often considered significant grazers in temperate lagoons and estuaries. This study examined spatial and temporal variation in swan abundance, grazing pressure and the impact grazing has on seagrass. Little is known on how grazing rates vary on larger water bodies in the southern hemisphere at different times of year and whether temporal changes in grazing rates affect the ability of seagrasses to tolerate grazing. The plant response to grazing may not be consistent seasonally, in light of recent terrestrial studies suggesting changes in environmental factors over a year such as light, temperature and nutrient supply can influence the ability of plants to cope with grazing. Furthermore, studies have suggested changes in sexual reproduction can be considered a trait to cope with grazing. However, very few studies have investigated this relationship, particularly in seagrasses.

With these three main knowledge gaps in mind, this study examined grazing interactions between the black swan (*Cygnus atratus*) and the seagrass *Halophila ovalis* in a temperate, estuarine seagrass ecosystem, the Lower Swan River estuary, Western Australia. Firstly, spatial and temporal variation in black swan abundance was documented across 45 sites in four seasons (spring, summer, autumn and winter) and at two times of day. Further investigations sought to determine whether there were changes in grazing pressure over a year. This was conducted at three high “swan use” sites in each season. Finally, the strategies seagrasses use to cope with grazing, and how these vary temporally were assessed using an observational approach across a natural grazing gradient and experimental manipulations (simulated grazing).

There was significant variation in black swan density among seasons, with the highest number of swans present during autumn (185 swans), intermediate numbers in summer (104 swans) and winter (80 swans) and the lowest in spring (53 swans). Swans may move to ephemeral wetlands during times of low swan abundance on the estuary. An analysis of the temporal variation in swan abundance on the surrounding wetlands on the Swan Coastal Plain does not show a consistent pattern of seasonal variation on the wetlands. Movement of black swans to ephemeral wetlands is likely to be due to a variety of factors including water height, food availability and the breeding needs of the black swan.

There were also significant spatial variations in swan abundance with three hot-spots identified. However, swans were not found in each hotspot at all times of the year. Swan abundance peaked in autumn at all hotspots, as well as summer and winter at Alfred Cove and Como Foreshore, and spring and summer at Point Walter. Factors that may influence swan abundance were collected in each season and were examined in a multiple regression analysis to determine which factors were most important. The key characteristics of sites with high swan abundance included: high cover of natural vegetation on the river bank and sub tidal seagrass vegetation (*Halophila ovalis* and *Ruppia megacarpa*) and a shallow sloping seabed. Conversely, sites with jetties and dogs had lower swan numbers. The results of this study suggest water bird distributions are affected by a suite of habitat characteristics, not just one in particular.

Swan grazing removed more seagrass biomass (g DW m^{-2} day^{-1}) in summer (3 g DW m^{-2} day^{-1}) and autumn (3 g DW m^{-2} day^{-1}), with intermediate amounts in spring (1 g DW m^{-2} day^{-1}) and the least in winter (0.4 g DW m^{-2} day^{-1}). However, despite this seasonal difference in biomass removal and a three-fold variation in swan abundance among seasons, there was no significant temporal difference in grazing pressure among the four seasons, with 6 - 25% of daily seagrass production consumed. This is explained by peak swan grazing occurring when seagrass production was at its peak. That is, when swan abundance was at its peak and the most biomass was removed, the seagrass was most productive. These results suggest seagrasses in the Lower Swan River estuary can cope with current levels of grazing.

Temporal variation in response to grazing across a natural gradient was observed. Long-term grazing reduced productivity in winter, reflected as reduced branching (23%) in naturally ungrazed meadows when grazing was simulated. In summer

the opposite was observed with a similar or slightly higher productivity across a natural grazing gradient and increased branching (58%) following simulated grazing in naturally ungrazed meadows. Across the natural grazing gradient, flowering and seed production were positively associated with grazing. This pattern was generally mirrored in the manipulative experiment with a 40% increase in flowering intensity.

Clearly, if changes in grazing are exerted on *Halophila ovalis*, then it can cope through traits of a tolerance strategy by increasing in growth and sexual reproduction. However, the expression of these growth traits was only observed during summer. The reproductive period for *Halophila ovalis* occurs between November and March, leaving a six month period during spring and winter where *Halophila ovalis* may be less resilient to grazing. Currently, this period coincides with low numbers of swans on the estuary, so *Halophila ovalis* can cope with current levels of grazing. If there were to be an increase in swan abundance during winter and spring, when other environmental conditions are limiting (temperature and light) and carbohydrate reserves are limited, grazing could reduce the capacity of seagrasses to respond, making them less resilient to grazing.

Plant-grazer interactions are dynamic and complex. This study revealed new findings about the seasonal nature of this relationship: the expression of traits associated with a tolerance strategy is dependent on the time of year grazing occurs. This study also identified that changes in the plants sexual reproduction may be another strategy plants use to cope with grazing. This has rarely been looked at and should be considered a trait of the tolerance strategy.

DECLARATION

I certify that this thesis does not, to the best of my knowledge and belief:

(i) incorporate without acknowledgment any material previously submitted for a degree or diploma in any institution of higher education.

(ii) contain any material previously published or written by another person except where due reference is made in the text; or

(iii) contain any defamatory material.

I also grant permission for the Library at Edith Cowan University to make duplicate copies of my thesis as required.

Signature:
Date: 8/3/2012

Acknowledgements

I am truly indebted and thankful to my supervisors: Kathryn McMahon and Paul Lavery for the support and guidance they showed me throughout this process. I would especially like to thank Kathryn McMahon for her patience, insight, guidance and involvement as well as her comprehensive knowledge, encouragement and her useful insights in to plant tolerance after disturbance. I am sure it would have not been possible without their help.

I am entirely indebted to those people who helped out with the mountain of field work involved in this study. This work could not have been done without you. This includes Kelly Sheldrick, Paul Lavery, Kathryn McMahon, Mark Waite and Jon To. I would like to make special mention of my parents Jacqui and Ron Choney who gave me the most help in the field and even came out with me during the early hours of the morning during winter.

Thank you to the School of Natural Sciences who provided much appreciated funding towards this work and the funding opportunities to attend conferences both nationally and inter-nationally. I would also like to thank the Centre for Marine and Ecosystem Management for their input and guidance during this process. I would also like to thank Dr Rob Davis for his insight into the sections dealing specifically with the black swan.

The support team at the School of Natural Sciences has been enormously helpful during this process. There has been no shortage of assistance from all the technical and administrative staff. My small editing team has been very much appreciated; thank-you to Kathryn McMahon, Paul Lavery, Greg Maguire, Mike Kenyon and Ron Choney.

I would also like to say a big thankyou to my amazing parents for being supportive and always encouraging me to pursue what I want, and have never giving up on me, even when other people in my life had. I would also like to thank my new family, especially Terri and Stuart Barnes for all their support,

especially during the writing phase of this dissertation. Finally and most importantly I would like to thank my fiancée Lisa for all her support during this process, whose support and patience on a daily basis, especially those nights I was in a grumpy mood, gave me the perspective needed to get through this challenge and emerge as a person.

Table of Contents

List of Tables

List of Figures

1. General Introduction

Grazing on seagrasses is considered to be minor in many temperate regions of the world (Powell et al. 1991). However, grazing by waterfowl in temperate estuaries can be an exception to this generalisation. This study investigated the significance of grazing by black swans in a temperate, estuarine seagrass ecosystem and the strategies seagrasses employ to cope with grazing.

1.1 Grazing

Grazing is an important ecological process, linking primary producers and grazers. Grazing can alter the growth dynamics of plants, in some cases increasing (Strauss & Agrawal 1999, Agrawal 2000) or decreasing (Kuiper-Linley et al. 2007, Alberti et al. 2011) growth, resulting in changes to plant productivity (Huntly 1991, Polis & Strong 1996). These changes in primary productivity can alter habitat and community structure. For example in areas with high productivity and grazing, plants more able to cope with grazing dominate, but when grazers are excluded, more competitive plant species may dominate (Chase et al. 2000).

Three key factors have been identified that influence the rates and magnitude of grazing: the amount and condition of the food source; the density of grazers and the presence of predators (Bailey et al. 1996, Leferve & Bellwood 2011). The quality and quantity of forage can influence grazing rates as grazers usually select high quality food sources (Owens et al. 1991, Bailey et al. 1996, Leferve & Bellwood 2011). Grazer abundance directly influences consumption rates (more grazers resulting in more consumption), but can vary due to movement of grazers from one region to another. Many species migrate or disperse to breed or to find a more suitable habitat, resulting in spatial and temporal variation in grazer density (Bailey et al. 1996, Marell et al. 2002, Leferve & Bellwood 2011). Finally, the presence of predators may reduce grazer biomass. This top down effect of predation can be transferred through trophic levels, affecting the consumption and distribution of plant communities (Boner et al. 2006, Leferve & Bellwood 2011).

One of the food sources for grazers in the marine environment is seagrass. Seagrasses are common in coastal waters along every continent except Antarctica. Until recently, few grazers were thought to feed directly on seagrasses, but is now known that seagrasses are an important link in the food chain, with large numbers of species feeding on them (Valentine & Duffy 2006).

1.2 Grazing on seagrasses

Seagrasses are flowering plants (angiosperms) which live in marine environments. Relative to other angiosperms, they are unique because they have the ability to live and complete a reproductive cycle submerged in saline environments (den Hartog & Kuo 2006). They have leaves suspended in the water column and a well developed rhizome and root system which anchor them in the substrate (den Hartog & Kuo 2006). Seagrasses play an important role in stabilizing sediment and providing habitat and food resources for a variety of animal species, including some of commercial value (Hemminga & Duarte 2000). Seagrasses are clonal plants that have the ability to reproduce sexually. Being clonal, seagrasses can translocate resources between connected individuals and store carbohydrates in their rhizomes (Liu et al. 2007). In addition, they have below-ground, and in some cases dormant meristems that produce new leaves after damage. These features may allow seagrasses, like other clonal plants to tolerate high levels of grazing (Kuiper-Linley et al. 2007, Eklof et al. 2009).

A range of grazers feed on seagrasses including fishes, turtles, waterfowl, dugongs, manatees and sea urchins. It is believed that seagrasses experience relatively low levels of grazing because of their low nutritional value (Valentine & Heck 1998). An alternative hypothesis suggests that grazing rates are lower in seagrass because of the past and current overharvesting of the large vertebrate grazers (green turtles, dugongs, manatees & fishes) that would otherwise graze them (Valentine & Duffy 2006). Despite this, some meadows and species of seagrass are regularly exposed to grazing. The amount of seagrass production entering near shore food webs ranges from 3 - 100% of net production, depending on the climatic regions and the number and species of grazers present. With respect to region, Valentine & Duffy (2006) hypothesised that grazing on seagrasses is greater in tropical areas compared to temperate regions, due to the higher abundances of large grazers, such as parrot fish, turtles, dugongs and manatees (Valentine & Duffy 2006). However, a recent meta-analysis argues that there is no difference in grazing on seagrass and macroalgae in marine systems across a latitudinal gradient (Moles et al. 2010).

1.3 Waterfowl grazers

Marine waterfowl include ducks, coots, geese and swans (Powell et al. 1991) and are often considered significant seagrass consumers in temperate coastal lagoons and estuaries (Powell et al. 1991). Yet, little work has been done on these grazers in temperate regions of the southern hemisphere. Waterfowl feed by removing the leaves of aquatic macrophytes (cropping) and also by digging into the sediment and removing below-ground material (Thayer et al. 1994, Eklof et al. 2009). In the northern hemisphere, there is a temporal component to waterfowl grazing, with most occurring during autumn and winter. These changes coincide with the southward migration of northern hemisphere waterfowl during winter, to seek a greater availability of food and a warmer climate (Warnock & Takeawa 1996, Petrie & Wilcox 2003). At these times they can consume up to 26% of daily seagrass production (Jacobs et al. 1981, Nienhuis & Groenendijk 1986). In the southern hemisphere the climate is generally milder and drier, so bird migrations are influenced more by river flooding patterns and filling of wetland habitats (Kingsford & Norman 2002, Dingle 2008). These movements may influence consumption rates of forage on larger water bodies, particularly during summer and autumn when smaller ephemeral wetlands dry out.

Two key factors have been identified that influence swan movements including the amount of food available for feeding (Marchant & Higgins 1990, Davis 2009) and habitat for breeding success (Birkhead et al. 1983, Storey et al. 1993). Movements appear to be influenced by changes in climate particularly during winter and summer in both the northern and southern hemispheres (Petrie & Wilcox 2003, Chambers & Loyn 2006). During summer, northern hemisphere swans are found swimming in swamps, marshes and shallow lakes, however, during the winter months swans follow food sources, as feeding through icy waters is impossible (Davis 2009). During these times, swans fly to slow moving rivers, flooded fields and coastal estuaries, creating the perfect winter habitat for swans (Davis 2009). There is a similar pattern in the southern hemisphere, however, in Australia aquatic macrophytes become more developed over an extended time after flooding when wetlands begin to fill, particularly during winter and spring. These provide a habitat for the aquatic macrophytes to grow, an important food source for the black swan (Kingsford et al. 1999, Kingsford & Norman 2002). There a number of significant habitat characteristics which have the potential to influence the breeding success and clutch size of swans (Birkhead et al. 1983, Storey et al. 1993). These include a range of geomorphic and biological characteristics, which are usually not found on estuaries.

Surveys on waterfowl abundance suggest seasonal variation in the abundance with peak abundances in summer and autumn (Chambers & Loyn 2006, Lane et al. 2007), which may coincide with peak grazing. Despite this potential for temporal variation, studies of seagrass consumption by grazers in the southern hemisphere have only been conducted in autumn, so it is not known if there are temporal changes in waterfowl grazing (Mitchell & Wass 1995, 1996, Eklof et al. 2009).

1.4 Plant strategies to cope with grazing

Over time and in the presence of grazers, plants have evolved traits that allow them to cope with grazing. These traits have been characterised into three key strategies: escape, resistance and tolerance (Agrawal 2000). Escape strategies allow plants to exist in different locations and/or time periods when grazers are not present. Resistance includes a group of chemical, nutritional and/or physical traits of plants that prevent grazers eating them. Tolerance traits reduce the effects of grazing by allowing plants to survive, regrow and reproduce after damage is sustained (Agrawal 2000). Seagrasses generally cope with grazing through tolerance (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009). Some of the traits of a tolerance strategy (Tiffin 2000) include:

- Changes in photosynthetic activity
- Activation of dormant meristems
- Utilisation of stored reserves; &
- Phenological changes.

Vegetative traits

Reproductive traits

1.4.1 Changes in photosynthetic activity

Partial leaf defoliation due to grazing may cause increased photosynthetic rates in the remaining plant tissue (Tiffin 2000). The removal of the leaf tissue by grazers decreases the leaf area available for photosynthesis. However, with a decreased leaf area it can also increase the light levels to previously shaded areas of the plant. This leads in turn to increased photosynthetic capacity in the remaining leaves (Trumble et al. 1993, Strauss & Agrawal 1999), allowing the plant to grow and tolerate grazing.

1.4.2 Activation of dormant meristems

Grazer damage can change the growth trajectories of plants through the activation of dormant meristems in order to replace the lost tissue (Liu et al. 2009, Bagchi & Ritchie 2011, Gruntman & Novoplansky 2011) with a correlation between grazing and an increase in growth and production of the remaining tissue (Nolet 2004, Kuiper-Linley et al. 2007, Eklof et al. 2009).

1.4.3 Utilisation of stored reserves

Some plants have the ability to utilise stored reserves after damage (Agrawal 2000). Terrestrial, freshwater and marine plants have the ability to utilise these reserves after damage to promote regrowth (De Iongh et al. 2007, Bagchi & Ritchie 2011, Quentin et al. 2011).

1.4.4 Reproductive biology changes

Delayed timing of flower and fruit production

The timing of growth, flowering and fruit production can allow plants to escape consumers after damage (Simms et al. 2000). Partial defoliation and meristem damage cause delayed growth and flower production and fruit production (Tiffin 2000). For example, in some cases plants live in seasonal environments where the end of the growing season limits reproduction. If grazing causes delays in seed maturation then genotypes that experience the shortest delay in seed maturation after damage may be the most tolerant. Alternatively, if herbivory causes equal delays for all genotypes, but genotypes differ in their development time, then faster developing genotypes may be the most tolerant. In both scenarios the length of the growing season will affect the tolerance level. During long growing seasons all genotypes may have time for seed maturation regardless of damage. In short growing seasons delays in seed production may result in damaged plants dying before seed production is complete (Pilson 2000, Tiffin 2000, Piippo et al. 2009).

Change in sex ratio after grazing

Not only can grazing affect sexual reproduction in plants but it may also affect the sex ratio of the grazed population. In some plant species females usually expend more resources into reproduction than males because additional energy is required to produce fruits and seeds (Delph 2011, Viejo et al. 2011), resulting in two potential and contrasting outcomes. First male-biased grazing occurs in some systems, resulting in more females relative to males (Cornelissen & Stiling 2005). The greater investment in reproduction by females, could potentially result in less investment in vegetative growth and therefore, they may have a lower nutritional quality than males, so the larger male plants become a more attractive food source for grazers (Cornelissen & Stiling 2005). The second hypothesis is that grazing results in male dominance (Quinn 1998). The greater investment in reproduction by females could result in less investment in vegetative growth than males, so overtime the proportion of male plants will increase and male plants may have the capacity to recover faster (Pickering & Hill 2002, Delph 2011, Viejo et al. 2011).

1.5 Other traits that might form part of a tolerance strategy

Although Tiffin (2000) noted that grazing can induce phenological changes in plants he did not address the role of sexual reproduction (intensity of flowering and fruiting and seed production) in the context of tolerance strategies. Theoretically, plants could increase in sexual reproduction after grazing damage to maintain a similar fitness to ungrazed plants, allowing them to pass on more or similar numbers of offspring to the next generation. Terrestrial plants have been observed to increase in sexual reproduction after grazing (Lazo et al. 1994, Quiroga et al. 2010) by increasing flowering intensity and fruit production (Whitman et al. 1991, Forbs et al. 1997). Other studies, however, have suggested a negative response to grazing with a decrease in sexual reproduction (Hickman & Hartnett 2002, Varga et al. 2009, Lal et al. 2010). However, little is known of sexual reproductive responses to grazing in seagrasses, although a few studies have suggested a positive relationship between flowering and dugong grazing (Conacher et al. 1994, Peterken & Conacher 1997, Heck & Valentine 2006) and some studies have shown an increase in flowering after physical disturbance (Phillips et al. 1983, Alexandre et al. 2005, Hammerstrom et al. 2006). From an evolutionary perspective seed production is a measure of a plant's fitness. Reproduction in a species will determine how successful the plant is to pass on its genes to future generations (Boalt et al. 2010). Few studies have focused on seed production as a measure of fitness following grazing, particularly in seagrasses.

1.6 Factors influencing the expression of traits

The plant's abiotic environment affects its ability to tolerate grazing. Some studies suggest that plants which are exposed to high levels of resources (light, temperature, water and nutrient availability), have the highest level of tolerance to grazing (Maschinski & Whitham 1989, Hawkes & Sullivan 2001, Bagchi & Ritchie 2011). In some studies nutrient availability has been found to be negatively associated with tolerance, especially when nutrient levels are high (Mutikainen & Walls 1995, Irwin & Aarssen 1996). One explanation for this may be that high nutrient availability reduces the below ground biomass of aquatic plants as they invest less in underground roots and rhizomes (Twilley et al. 1985) and hence the plants ability to tolerate grazing as they use below-ground stores to recover from grazing. The availability of light, water and suitable temperatures have been assumed to be positively associated with tolerance, as in optimum conditions, plants do not require high levels of resources for regrowth after grazing (Maschinski & Whitham 1989, Hawkes & Sullivan 2001, Bagchi & Ritchie 2011).

As discussed above, a number of abiotic factors (temperature, light levels, nutrient inputs) could mediate expression of tolerance traits. These factors are likely to vary temporally. Studies in the southern hemisphere suggest grazing should be greater in summer and autumn, so a shift in waterfowl abundance may not have an effect on the ability of plants to tolerate grazing, as this is also the time of peak production in aquatic plants, like seagrass (Hillman et al. 1995, Kirkman & Kirkman 2000). However, if there were to be increases in waterfowl abundance during winter and spring the seagrasses may not be as resilient to grazing.
As environmental conditions change over a year, the seagrass dynamics change. During spring and into summer, light conditions and water temperatures gradually increase, leading to increases in growth, production (Moncreiff et al. 1992, Perez & Romero 1992, Hillman et al. 1995) and increased carbohydrate stores (Alcoverro et al. 2001). During winter, low light conditions and water temperatures slow growth and production (Moncreiff et al. 1992, Perez & Romero 1992, Hillman et al. 1995) and there are often lower carbohydrate stores (Alcoverro et al. 2001). Therefore, when environmental conditions are limiting, growth and carbohydrates are lower and the plant may not be able to respond to grazing if the response depends on storage reserves. This is a key knowledge gap which this study sets out to examine.

1.7 Study species

This study focused on the seagrass *Halophila ovalis* (R. Brown) and the grazer *Cygnus atratus*, the black swan. *H. ovalis* is the dominant benthic plant of the Swan/ Canning Estuary, south-west, Western Australia (Hillman et al. 1995). *H.*

ovalis belongs to the family *Hydrocharitaceae* and can be found submerged in marine and estuarine systems throughout both tropical and temperate regions of the Indo-West Pacific (McMillan 1983). *H. ovalis* is a rhizomatous, dioecious seagrass species that is adapted to cope with high levels of disturbance through rapid growth rates, the presence of dormant meristems and its ability to quickly colonise areas (Hillman et al. 1995, Nakaoka & Aioi 1999, Eklof et al. 2009). In the Lower Swan River estuary *H. ovalis* is one of the preferred forage species for the black swan and is the dominant species in the regularly grazed habitats (Eklof et al. 2009).

Black swans are herbivorous waterfowl found in temperate terrestrial wetlands and in sheltered estuarine and marine habitats. They are found throughout Australia with the exception of Cape York Peninsula and are more common in the south (Marchant & Higgins 1990). In Western Australia the black swan has been observed to feed on seagrass in the Lower Swan River estuary (Brearley 2005). The abundance of black swans has changed since European settlement. In 1827 Charles Fraser noted large numbers of black swans, up to 500 in the Lower Swan River estuary (Brearley 2005). However, recent studies have only observed up to 78 black swans feeding in the estuary during summer with 69% of them feeding in the seagrass meadows (Eklof et al. 2009).

Black swans are usually found on large permanent water bodies and require abundant aquatic vegetation. It is possible that permanent water bodies, such as the Lower Swan River estuary, act as a refuge for swans during summer and autumn, when many surrounding wetlands dry. Given the seasonal nature of the rainfall and water levels in wetlands of the Swan Coastal Plain (SCP) and the known movements of black swans in relation to wetland characteristics, such as water levels and water quality (Marchant & Higgins 1990), it is possible that black swans move between aquatic habitats on the SCP on a seasonal basis. This may affects abundances at any given site and the interaction between swans and their forage species. Increases in swan abundance at smaller wetlands with variable water levels may be evident in winter and spring, coinciding with increasing water levels, increases in the availability of food or the specific breeding habitat characteristics of the wetlands. Alternatively swan abundance on permanent water bodies may be less in winter and spring when birds move to ephemeral lakes and wetlands.

There has been little work published on the ecology of the black swan in Western Australia and Australia. However, work has been conducted in New Zealand focusing specifically on grazing ecology and food choice of the swan (Mitchell & Wass 1995, 1996). These studies have found swan population density is closely correlated with plant biomass, with each swan consuming 104g DW per day. Studies on the Lower Swan River estuary indicated that the swans can consume up to 23% of seagrass production (Eklof et al. 2009). However, this study was only conducted during autumn, so little is known on how much seagrass the black swan consumes at other times of year, particularly during winter when there is minimal seagrass growth and production (Hillman et al. 1995).

Conservation of the black swan is considered important within Australia, though elsewhere, particularly in England and New Zealand the swan is considered an introduced species and its conservation status is not yet assessed (Kear 2005, Robertson & Barrie 2005). Its importance within Australia is reflected in its listing as secure under the Environmental Protection and Biodiversity Conservation Act of 1999, secure across state and territory biodiversity acts within Australia and is evaluated as least concern on the ICUN Red List of threatened species. Increasing urban and industrial development on the coast and increases in the number of people visiting the coast has led to the decline in coastal bird numbers worldwide (Green 1996). Habitat characteristics (shoreline configuration and prey density) and landscape characteristics (surrounding residential and industrial development, vegetated land and the extent of wetland edge) have been shown to influence the distribution of waterfowl (Burton et al. 2002, Bechet et al. 2004) as do human activities. For example, declines in waterbird species at Pelican Point and other areas of the Lower Swan River estuary have been attributed to a greater recreation use of the estuary with increases in boating, the presence of wind and kite-surfers and walkers with dogs (Creed & Bailey 2009). Therefore, as part of this study it was important to assess whether other factors may influence the abundances of black swans, to determine the effect of human use areas and disturbances on waterbirds, with emphasis on the black swan.

1.8 Focus of study and study questions

Although grazing in temperate seagrass systems is often considered minor from a global perspective (Valentine & Heck 1998), grazing by waterfowl observed in estuarine environments is a notable exception (Powell et al. 1991). This study will focus on grazing interactions between *Cygnus atratus* (black swan) and *Halophila ovalis*. The broad objective of this study was to improve our understanding of plant-grazer interactions in temperate seagrass ecosystems and provide information to resource managers on changes in black swan abundance and their habitat requirements (Figure 1.1).

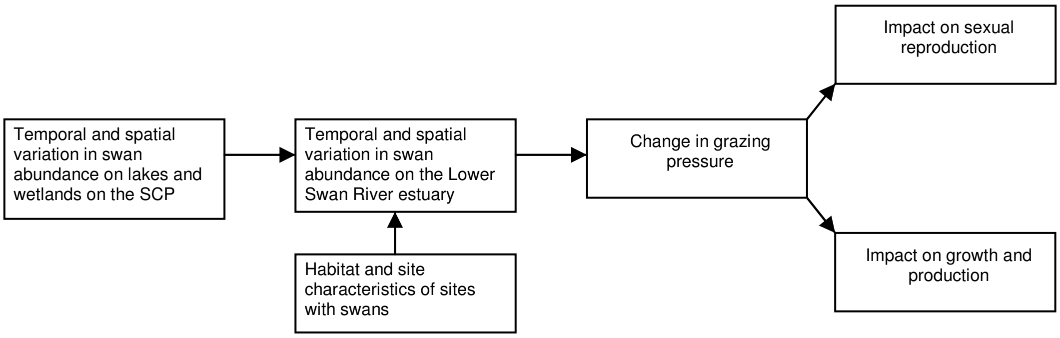


Figure 1.1 Conceptual model of how the topics in this masters project interrelate.

In the Lower Swan River estuary *H. ovalis*, is a keystone species (Hillman et al. 1995). The management agency for the Swan River estuary, the Swan River Trust, is attempting to improve the health of the estuary and increase swan numbers (Brearley 2005). If ephemeral and permanent wetlands on the SCP dry, swan abundance may increase on the Lower Swan River estuary during winter and spring. These are times swan abundance is expected to be low on the estuary. Understanding the habitat preferences and temporal variation in swan abundance will assist managers to highlight the best areas to target for swan conservation and whether there are particular habitat and disturbance factors that influence swan abundance. This study has improved our understanding of what, if any, impact increases of swans will have on the ecology of estuaries.

There has been one previous study examining black swan grazing on *H. ovalis* in the Lower Swan River estuary. That study (Eklof et al. 2009) focused on grazing during autumn at sites with high swan densities. This is the only study to assess whether *H. ovalis* has traits to support a tolerance strategy and found that *H. ovalis* was able to recover rapidly after being grazed, with a 70% higher branching frequency 21 days after grazing. They suggested that the plants utilised carbohydrates in below-ground tissues to produce new branches after grazing (Eklof et al. 2009). Eklof et al (2009) was restricted to a single season and thus did not examine temporal variation in grazing and plant responses. Furthermore, it did not examine reproductive strategies, leaving gaps in our knowledge on the effects of grazing over different seasons of the year.

This study addressed key information gaps on the effects of grazing on *H. ovalis*, specifically temporal variation in growth responses and also sexual reproductive responses (flowering, fruiting and seed production). From previous studies on *H. ovalis* in Lower Swan River estuary, flowering commences in late November, early December and fruiting begins in early January peaking in March (Hillman et al. 1995). Little is known about the impact of grazing on sexual reproduction in seagrasses, although recent studies have suggested a negative relationship (Lal et al. 2010) and others have suggested a positive relationship (Conacher et al. 1994, Peterken & Conacher 1997). This study provided the opportunity to investigate whether changes in the amount of flowering could be considered a mechanism of tolerance and whether plants exposed to grazing increase their fitness, through increasing seed production. No experimental studies to my knowledge have demonstrated this relationship, and this afforded an opportunity for important and original research.

1.8.1 Aims

The overall objective of this research was to enhance our knowledge of how seagrasses respond to grazing, especially focusing on the mechanisms of tolerance, such as the activation of dormant meristems which facilitate growth following grazing. In addition the impacts of grazing on sexual reproduction by seagrasses were also investigated to determine whether seagrasses increase their flowering after grazing, potentially another mechanism of tolerance. This study also determined whether seagrasses exposed to grazing have the same fitness as those not exposed by their ability to pass on their genes to future generations through the production of seeds. In order to meet these objectives, the study had the following specific aims:

1. Determine the number of wetlands used by black swans and if there are seasonal variations in swan abundance on a subset of lakes and wetlands on the Swan Coastal Plain and the reasons for these variations;

2. Determine if there are spatial and temporal variations in swan abundance and grazing on the Lower Swan River estuary and whether there is an association between specific site and habitat characteristics and swan abundance; and

3. Determine the vegetative and sexual reproductive response of *Halophila ovalis* to black swan grazing and how this varies at different times of year.

The thesis is divided into five main chapters:
Chapter 1. General Introduction;
Chapter 2. Seasonal variation in black swan abundance on a subset of lakes and wetlands on the Swan Coastal Plain;
Chapter 3. Spatial and temporal variation in swan abundance and grazing on the Lower Swan River estuary;
Chapter 4. Vegetative and sexual reproductive response of *Halophila ovalis* to black swan grazing; and
Chapter 5. Conclusions and management implications.

2. Seasonal variation in black swan abundance on a subset of lakes and wetlands on the Swan Coastal Plain

2.1 Introduction

Waterbirds are a large group of birds defined by their ecological dependence on aquatic habitats for at least some part of their lifecycle (Jaensch 2009). They are commonly found on lakes, rivers, dams, wetlands and estuaries and include many shore and seabirds such as ducks, geese, swans, grebes, pelicans, darters, cormorants, herons, ibises, spoonbills, storks, cranes, rails, moorhens, coots and waders. Many waterbirds migrate between different aquatic habitats to feed and/or breed, often on a seasonal basis (Kingsford & Norman 2002). These seasonal movements of waterbirds are usually caused by fluctuating water levels in wetlands and the breeding needs of the individual bird species (Musil & Fuchs 1994, Bancroft et al. 2002, Bolduc & Afton 2008).

In Australia the climate, including rainfall, is highly variable both temporally and spatially, influencing river flooding patterns and the filling of wetland habitats. This temporal and spatial variability has a strong influence on the ecology of Australian waterbirds. Many waterbirds respond to changes in water levels by moving to habitats when water levels are at a suitable height for feeding and breeding, and disperse from these areas once the wetlands dry (Roshier et al. 2009). Large migration movements are not common in most Australian species; however some waders migrate between the northern hemisphere breeding grounds and non-breeding habitats in Australia. In general, Australian waterbirds usually breed during winter and spring, coinciding with increases in food availability and water levels (Kingsford & Norman 2002).

One of the unique and important waterbirds within Australia, in coastal and southern regions, is the black swan (*Cygnus atratus*). The black swan is usually found in temperate terrestrial wetlands or in sheltered estuarine and marine habitats, as they can tolerate salinities ranging from freshwater to hypersaline. Most swans are found in large, permanent water bodies, with aquatic vegetation. As black swans require a large area (40m) for take-off before flight, they are usually not found in areas with large amounts of emergent vegetation (Marchant & Higgins 1990). They are almost entirely herbivorous, taking the leaves and shoots from aquatic plants and will occasionally graze on land, however, they are clumsy walkers making this difficult (Mitchell & Wass 1995, 1996). The aquatic food is usually taken while swimming, either from the surface or from submerged vegetation. When feeding on submerged vegetation, the swan can feed up to a depth of 1m by plunging its long neck into water. Occasionally it has been seen to stand in shallow water while feeding from the bottom or surface (Marchant & Higgins 1990).

Black swans breed in shallow wetlands where the eggs are placed in a nest made of reeds and grasses. The nest is placed either on small islands or floated in deeper water (Marchant & Higgins 1990). There are twenty-two significant habitat characteristics which have the potential to influence the breeding success and clutch size of black swans (Storey et al. 1993). These include geomorphologic characteristics of the wetland, vegetation type and vegetation cover as well as other factors that are likely to vary seasonally (Marchant & Higgins 1990), including area of water, depth, water quality and macrophyte cover.

Changes in food availability can impact on both the size of swan populations and their breeding success. However, black swans can move among wetlands to fulfil their requirements for food and breeding habitat (Roshier et al. 2009). Studies on the Port of Victoria, a permanent water body, showed a strong seasonal cycle in abundance, most occurring during autumn and winter, with local climate variables such as rainfall, having the greatest influence on abundance (Chambers & Loyn 2006), where lower rainfall resulted in less swans on the permanent water body. The black swan can also move from larger, permanent water bodies to smaller wetlands during winter and spring for breeding (Marchant & Higgins 1990).

The Swan Coastal Plain (SCP) has a Mediterranean climate, with mild wet winters and hot dry summers. In summer the average daily maximum temperature is 29°C and the minimum 17°C, with 40°C days common in January. In winter the temperature has an average high of 18°C during the day and 9°C at night. The average yearly rainfall is 880mm (Bureau of Meteorology 2011b), the majority occurring between June and September and, generally, wetland water levels peak during winter and spring.

Given the highly seasonal nature of the rainfall and water levels in wetlands on the SCP, and the known movements of black swans in relation to wetland characteristics such as water levels and water quality, it is possible that the black swan may move between aquatic habitats on the SCP on a seasonal basis. This may therefore affect the abundance at any given site and the interaction between swans and their forage species, such as macrophytes. Increases in swan abundance at smaller wetlands with variable water levels may be evident in winter and spring, coinciding with increasing water levels, increases in the availability of food or the specific breeding habitat characteristics of the wetlands. Alternatively, swan abundance on permanent water bodies may be less in winter and spring when birds move to ephemeral lakes and wetlands. Using historical data for a sub-set of SCP wetlands, three aims were addressed:

1. Determine the number of wetlands used by black swans and whether there is seasonal variation in swan abundance on a sub-set of ephemeral and permanent wetlands and lakes on the Swan Coastal Plain;
2. Identify if seasonal variation in swan abundance is related to the hydroperiod and/or water levels in the wetlands and lakes; and
3. Investigate if seasonal variation in swan abundance at any given wetland is related to breeding needs of swans.

2.2 Methods

2.2.1 Data selection & study area

Publicly available databases were used to assess the distribution of swans on the SCP between Guilderton & Gingin (~94km North of Perth) and Bunbury & Collie (~180km South of Perth) (Figure 2.1). Data were retrieved from the Birds

Australia National database (www.birdsaustralia.com.au) for all sites (280) containing the black swan (*Cygnus atratus*) over a ten years period (1999-2009). These sites consisted predominantly of lakes, wetlands and estuaries. An additional dataset was provided for Lake McLarty by Michael Craig (Murdoch University) from 1999-2009. This study only examined total swan abundance on the wetland, making the two data sets comparable. Additional data on the wetlands that may explain patterns in swan abundance were retrieved from the Department of Water (www.water.wa.gov.au) including water depth and length of hydroperiod and from Storey et al (1993); habitat characteristics significant for breeding swans.

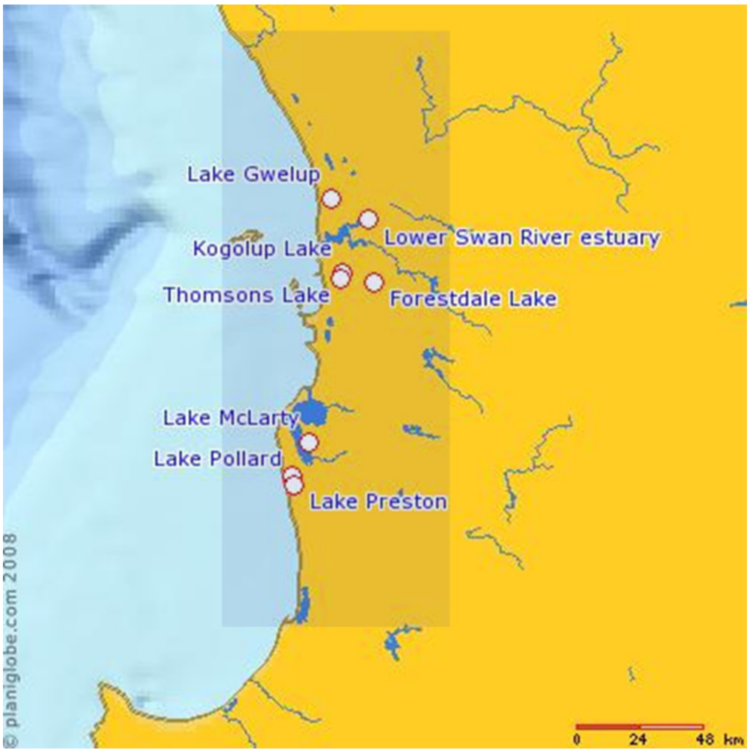


Figure 2.1 Locations of wetland sites used in the analysis of seasonal use of the Swan Coastal Plain by black swans and the location of the Lower Swan River estuary in relation to these sites. Blue shaded area = study area.

Presence and absence of swans on the Swan Coastal Plain

To determine the number of wetlands used by black swans on the SCP, data retrieved from the Birds Australia National Database was reduced by applying the following criterion to the full dataset: where more than one swan was observed on a wetland within the ten year period is was assumed that the wetland was suitable swan habitat. Data were then grouped into the number of times swans were observed on the wetland. To classify all wetlands on the SCP as either ephemeral or permanent and to define the total area of each wetland data were retrieved from the Department of Environment and Conservation (www.dec.wa.gov.au) database on wetlands of the SCP (Semeniuk & Semeniuk 1994). Wetlands classified as lakes or estuaries were assumed to be permanent wetlands and any other classifications ephemeral wetlands. In some cases, wetlands had previously been classed as permanent by other researchers when, in fact, they did dry out in some years, resulting in the apparent paradox of permanent wetlands that had dry period and, therefore, hydroperiods.

Seasonal variation in swan abundance and factors affecting variation

The data retrieved from the Birds Australia National Database was reduced by starting with the complete data set then applying the following criteria: any sites with less than four surveys over the entire time period were eliminated, as there was not enough data to ensure comparability and quality. Additionally, sites that did not have at least two seasons replicated and 4 surveys per season over the study period were also removed as there was insufficient data available for seasonal comparisons. This resulted in data for six wetlands being used from the Birds Australia National Database (Forestdale Lake, Thomsons Lake, Lake Gwleup, Kogolup Lake, Lake Pollard and Lake Preston) plus data for Lake McLarty (Figure 2.1). Three of these wetlands are seasonal, drying every year: Forestdale Lake, (247.5 ha), Thomsons Lake (253.7 ha) and Lake Preston (3150 ha). Lake Gwelup (18.5 ha), Lake McLarty (184.37 ha), Lake Pollard (120 ha) and Kogolup Lake (58 ha) are mostly permanent wetlands, but they can dry on some years. Limited site data was available including swan abundance, hydrological and breeding characteristic data, so the data for some variables were not available at each site or for every season (Table 2.1).

Table 2.1 List of available variables measured at each site. * Note seasonal range: spring = Sep-Nov, summer = Dec-Feb, autumn = March-May & winter = July-Aug. ✓ indicates available data for wetland & × indicates not available.

Location	**Seasons compared**	**Replicates for each season**	**Water depth & hydroperiod**	**Significant breeding characteristics**
Forestdale Lake	Spring & summer	7	✓	✓
Thomsons Lake	Spring & summer	4	×	✓
Lake Gwelup	All seasons	11	✓	✓
Kogolup Lake	Spring, summer & winter	4	×	✓
Lake Preston	Spring & summer	6	×	×
Lake Pollard	Spring & summer	4	×	×
Lake McLarty	All seasons	7	✓	×

2.2.2 Data analysis

Seasonal variation

To test for seasonal variation in swan abundance at each wetland, one-way ANOVA's were performed separately for each wetland, where the observations from all years were grouped into seasons (fixed factor). Total swan abundance data was log transformed to meet the assumptions of homogeneity of variance and normality as per, Quinn & Keough (2002). Statistical analyses were performed using GMAV (Underwood & Chapman. 1997). Due to missing data, not all four seasons could be included in the analyses at some locations. As the number of observations varied among seasons, the maximum number of replicates that could be used to ensure a balanced design was selected, with the minimum set at four.

Where there were more observations per season than the minimum number required for analysis, observations were randomly selected, ensuring that they covered all the years for which there were observations. If there was more than one observation in a month, only one was randomly selected.

Relationship with other variables

Hydroperiod & water levels

Three of the sites (Forestdale Lake, Lake Gwelup and Lake McLarty) were assessed to determine if there was a significant relationship between swan abundance and hydroperiod and between swan abundance and water height. Thomsons Lake, Kogolup Lake, Lake Preston and Lake Pollard were excluded as there was no water level data for these wetlands. The length of time or portion of the year the wetland holds ponded water (the length of time the water level in the wetland is > 0m) is referred to as the hydroperiod. Although wetlands were classed as permanent by others, this does not mean the wetland does not dry up during some years. A simple linear regression compared swan abundance versus hydroperiod and water levels as one or both of the characteristics may affect swan abundance. The linear regression was performed using SPSS (SPSS 2008). The R^2 value indicates the strength of the relationship.

Significant breeding characteristics

Four of the sites (Forestdale Lake, Lake Gwelup, Thomsons Lake and Kogolup Lake) were assessed to examine the relationship between swan abundance and the number of significant breeding characteristics based on, Storey et al. (1993), present at the lake. If more swans were present at the wetland during the breeding season than at other times of the year and if these wetlands had more than 10 relevant breeding habitat characteristics, it was assumed there was an association between swan abundance and the significant breeding habitat characteristics. Aquatic macrophytes are frequently identified as an important factor influencing waterbird usage of wetlands. Due to lack of data on aquatic macrophytes in these wetlands, this factor could not be assessed in this study.

2.3 Results

2.3.1 Presence and absence of swans on wetlands on the Swan Coastal Plain

Swans were observed at 61of 210 wetlands on the SCP, comprising of 39 ephemeral wetlands and 22 permanent wetlands (Table 2.2). However, at 51 of these wetlands, swans were observed less than ten times over ten years. Ephemeral wetlands accounted for 4804.1 ha while permanent wetlands accounted for 16975.77 ha (Table 2.2).

Table 2.2 Number of times swans are present on different wetlands in the past ten years on the SCP. This includes whether they are ephemeral or permanent wetlands and the area these wetlands cover.

Times Swans are present on different wetlands on the SCP	**Number of wetlands (#)**	**Number of ephemeral wetlands (#)**	**Area of Ephemeral Wetlands (ha)**	**Number of Permanent Wetlands (#)**	**Area of Permanent Wetlands (ha)**
1 Time	18	15	324.2	3	13240.1
2 Times	13	7	101.9	6	2903.8
3 Times	7	3	19.1	4	148.3
4 Times	2	1	5	1	25
5 Times	5	5	664.9	0	-
6-10 Times	6	5	37.8	1	5
11-20 Times	3	0	-	3	272.7
21-30 Times	4	3	3651.2	1	58
31 + Times	3	0	-	3	322.87
Total	61	39	4804.1	22	16975.77

2.3.2 Seasonal variation (1999-2009)

There was significant seasonal differences in swan abundance at six of the seven wetlands on the SCP between 1999-2009 (Figure 2.2, Table 2.3, $p<0.05$). The differences among seasons were not consistent among wetlands. Three wetlands had higher abundances during spring than summer (Forestdale Lake (154 ± 23 vs. 56 ± 11); Lake Preston (22 ± 11 vs. 3 ± 1) and Thomsons Lake (210 ± 29 vs. 72 ± 40, Table 2.3). Lake Pollard had a significantly higher abundance of swans during spring (219 ± 98) and summer (1090 ± 487) than in autumn (17 ± 8, Table 2.3). Lake Gwelup had significantly higher swan abundances during summer (11 ± 1) and winter (14 ± 13) than in autumn (8 ± 3) and spring (6 ± 1, Table 2.3). Swan abundance was significantly higher at Lake McLarty during summer (601 ± 112), however, there was no significant difference between the other three seasons, spring (188 ± 67), autumn (384 ± 136) and winter (40 ± 14, Table 2.3). There was no significant seasonal difference in swan abundance at Kogolup Lake during spring (6 ± 3), summer (3 ± 1) and winter (8 ± 3, Table 2.3, Figure 2.2). All data has been converted to km^2 for comparisons with swan abundance on the Lower Swan River estuary in the following chapters (Figure 2.3)

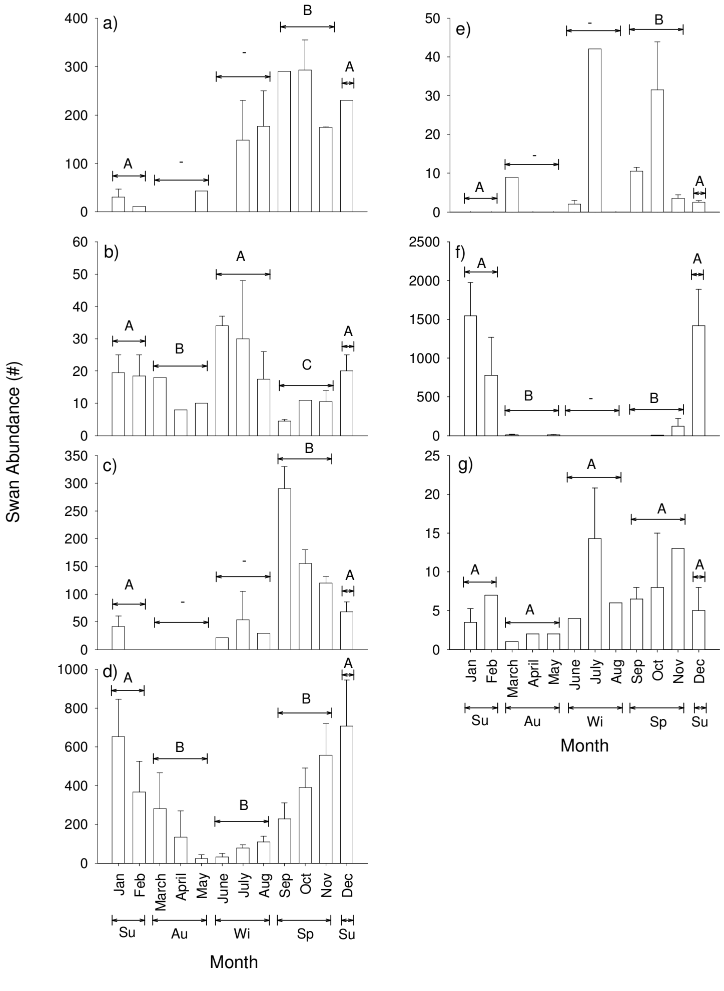


Figure 2.2 Average monthly swan abundance at: (a) Thomsons Lake (spring and summer), (b) Lake Gwelup (all seasons), (c) Forestdale Lake (spring and summer), (d) Lake McLarty (all seasons), (e) Lake Preston (spring and summer), (f) Lake Pollard (spring, summer and autumn) and (g) Kogolup Lake (spring, summer and winter). Letters above the columns indicate which seasons are different based on post-hoc comparisons. I--I indicates the four different seasons (spring, summer, autumn and winter). All data are means ± SE.

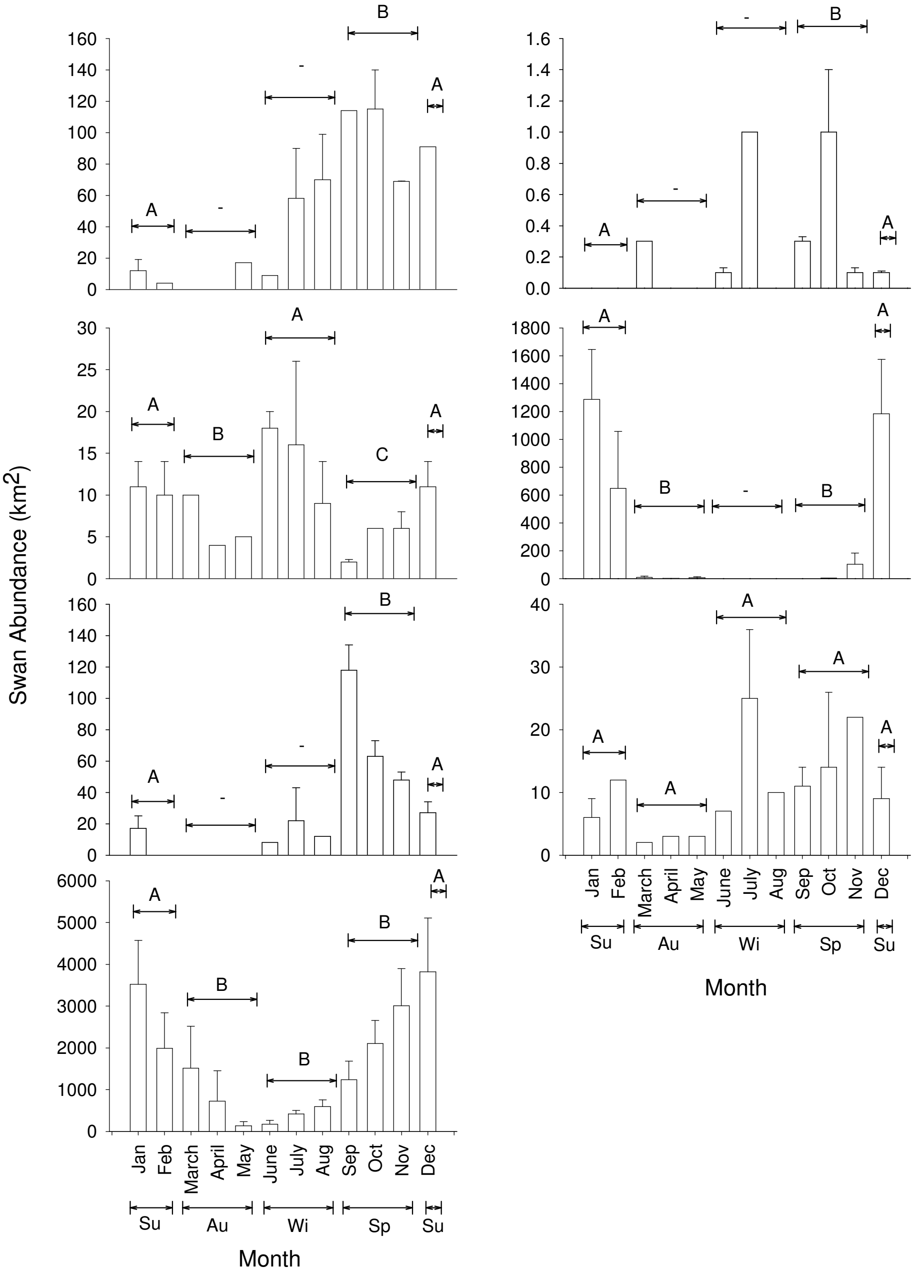


Figure 2.3 Average monthly swan abundance (km^2) at: (a) Thomsons Lake (spring and summer), (b) Lake Gwelup (all seasons), (c) Forestdale Lake (spring and summer), (d) Lake McLarty (all seasons), (e) Lake Preston (spring and summer), (f) Lake Pollard (spring, summer and autumn) and (g) Kogolup Lake (spring, summer and winter). Letters above the columns indicate which seasons are different based on post-hoc comparisons. I--I indicates the four different seasons (spring, summer, autumn and winter). All data are means ± SE.

Table 2.3 Summary of one-way ANOVA comparing swan abundance with season at Forestdale Lake (spring and summer), Lake Gwelup (all seasons), Thomsons Lake (spring and summer), Lake Kogolup (spring, summer and winter), Lake Pollard, (spring, summer and autumn), Lake Preston (spring and summer) and Lake McLarty (all seasons).

Location		**Sum of squares**	**Df**	**Mean Square**	**F**	**P**
Forestdale Lake	Season	11.79	1	11.79	6.35	0.02
	Residual	51.96	28	1.86		
	Total	63.74	29			
Lake Gwelup	Season	25.67	3	8.56	28.31	<0.01
	Residual	13.30	44	0.30		
	Total	38.96	47			
Thomsons Lake	Season	99201	1	99201	14.52	<0.01
	Residual	54658	8	6832		
	Total	153860	9			
Lake Kogolup	Season	105	2	52.87	1.61	0.24
	Residual	393	12	32.77		
	Total	498	14			
Lake Pollard	Season	62.27	2	31.14	8.45	<0.01
	Residual	66.37	18	3.68		
	Total	128	20			
Lake Preston	Season	25.63	1	25.63	178	<0.01
	Residual	1.15	8	0.14		
	Total	26.77	9			
Lake McLarty	Season	1654	3	551	7.43	<0.01
	Residual	2076	28	74.18		
	Total	3730	31			

2.3.3 Swan abundance vs. water level

There was a significant positive relationship between swan abundance and water level at two lakes, Forestdale Lake and Lake McLarty (Table 2.4, Figure 2.4). Water height explained 38% of the variation in swan abundance at Forrestdale Lake and 11% at Lake McLarty. There was no significant relationship between swan abundance and water height at Lake Gwelup, a permanent wetland (Figure 2.3).

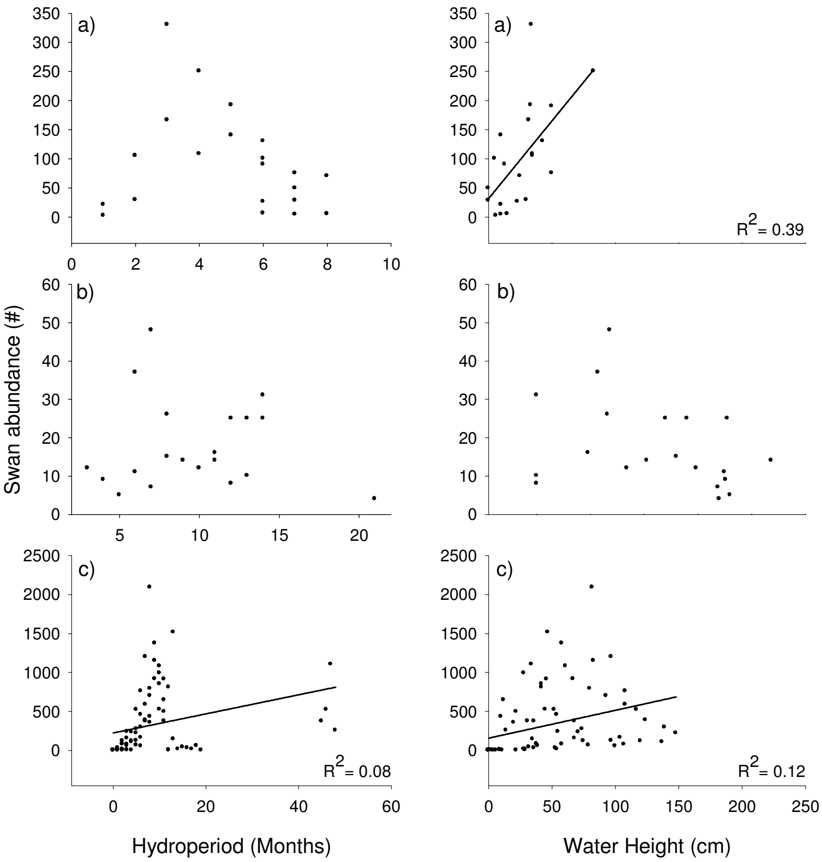


Figure 2.4 Swan abundance vs. hydroperiod (left) and water level (right) at (a) Forestdale Lake, (b) Lake Gwelup and (c) Lake McLarty.

Table 2.4 Simple linear regression comparing swan abundance and water level at three study lakes (Forestdale Lake, Lake Gwelup and Lake McLarty). *Note regression equations at bottom of table.

Location	Df	Beta	SE	R^2	P
Forestdale Lake	20	0.62	0.00	0.39	<0.01
Lake Gwelup	19	-0.35	3.77	0.12	1.33
Lake McLarty	77	0.34	113	0.12	<0.01

Regression equations
Forestdale Lake - Swan abundance predicted = 5.47 - 0.01 (hydroperiod).
Lake Gwelup - Swan abundance predicted = 9.99 - 0.16 (hydroperiod).
Lake McLarty - Swan abundance predicted = 5.91 - 0.01 (hydroperiod).

2.3.4 Swan abundance vs. hydroperiod

There was a significant positive relationship between swan abundance and the hydroperiod at one lake only, Lake McLarty (Table 2.5, Figure 2.4). At Forrestdale Lake, swan abundance initially increased with increasing hydroperiod up to 3 months and then declined with hydroperiod. A similar pattern occurred at Lake McLarty where peak abundance occurred at 13 months during the hydroperiod. There was no clear pattern at Lake Gwelup.

Table 2.5 Simple linear regression comparing swan abundance and hydroperiod at 3 study lakes (Forestdale Lake, Lake Gwelup and Lake McLarty). *Note regression equations at bottom of table.

Location	Df	Beta	SE	R^2	P
Forestdale Lake	21	-0.22	0.01	0.05	0.33
Lake Gwelup	19	-0.04	0.09	0.002	0.86
Lake McLarty	77	0.29	0.00	0.08	<0.01

Regression equations
Forestdale Lake - Swan abundance predicted = 31.48 + 267.07 (water height)
Lake Gwelup - Swan abundance predicted = 24.32 - 5.94 (water height)
Lake McLarty - Swan abundance predicted = 157.52 + 357.47 (water height).

2.3.5 Relationship between swan abundance and the significant breeding characteristics of wetlands

There was an association between swan abundance and the significant breeding characteristics of the wetlands at two sites, Forestdale Lake and Thompson Lake. These two sites had higher swan numbers during the breeding season (winter and/or spring) compared to the other seasons. Forestdale Lake had eleven of the significant habitat breeding characteristics and Thompsons Lake had ten (Table 2.6). The two other wetlands, Lake Gwelup and Kolgolup Lake did not have higher swan numbers during the breeding season, and both only had 5 of the significant breeding characteristics of the black swan (Table 2.6).

Table 2.6 Summary of the significant breeding characteristics at four study lakes (Forestdale Lake, Thomsons Lake, Lake Gwelup and Kogolup Lake), based on the criteria of Storey et al. (1993). Bold lettering indicates that the site has the preferred level for breeding.

Significant Breeding Characteristics	**Preferred Levels for Swan Breeding**	**Forestdale Lake**	**Thomsons Lake**	**Lake Gwelup**	**Kogolup Lake**
Area (ha)	>50	**248**	**250**	20	12
Shoreline (m)	>3000	**7000**	**6000**	2400	1200
Islands (P)	P	0	0	0	0
Drains	1	2	2	2	**1**
Buffer Pristine	0-50	**30**	90	0	**25**
Geometry Type	Ovoid	**Ovoid**	Round	Round	**Ovoid**
Distance to Coast (km)	1-5	15	**5**	**3.5**	6
Open Water (ha)	>10	**210.8**	**212.5**	**16**	7.2
Reed/ Rush cover (ha)	>5	**26.04**	**33.75**	3.6	4.32
Shrub/ Bush cover (ha)	>2	1.86	1.88	0.4	0.24
Tree Cover (ha)	>2	**11.16**	**3.75**	0.6	0.48
Dead Tree Cover (P/A)	P	A	A	**P**	A
Closed water area (ha)	>10	**37.20**	**37.5**	4	4.8
Vegetation Groups (UPGMA)	6	**6**	**6**	4	4
Tree Cover (%)	>25	0.05	0.02	0.03	0.04
Grass Cover (ha)	>5	1.86	0	0	0
Depth (m)	0.5-1	0.36	**0.81**	2.3	1.26
pH	>9.5	9.42	8.14	8.35	8.16
Temperature ($^{\circ}$)	15-20	22.28	20.06	**18.84**	**19.94**
Macrophyte cover (%)	>50	**50**	10	15	0
Macrophyte Biomass (DW m^2)	20-100	**56.99**	194.38	9.78	0
Zooplankton (DW m^2)	>0.1	0.0961	**0.2093**	**1.9**	**0.2063**
Total Significant breeding characteristics		**11**	**10**	**5**	**5**

2.4 Discussion

Despite the large Birds Australia database with 210 sites on the SCP only 61 had observations of swans recorded, and only a small subset (6 out of 210) contained counts of swans with seasonal replication. Therefore, conclusions drawn from this dataset are limited in that they only represent ~3% of the wetlands on the SCP and should not be considered representative of the entire area. Nonetheless, it was the most thorough analysis that could be carried out with the existing data, highlighting the need for a more concerted data collection to be able to document temporal and spatial patterns in swan habitat use. The majority of the observations in the database on swans were indicating the presence or absence of young swans. Within the limitations of this small dataset, there was seasonal variability in swan abundance at lakes and wetlands on the SCP. The variations were not consistent across wetlands.

Three main factors identified as influencing swan abundance were hydroperiod, water depth and the presence of features at the wetland that were favourable for black swan breeding. While no data were available on macrophyte biomass, the published literature suggests that this is also likely to be important in influencing swan abundance. Waterbirds have been seen to move to smaller lakes as macrophytes develop and graze until depletion when the lakes and wetlands dry out (Van Donk & Otte 1996, Perrow et al. 1997, Holm & Clausen 2006). In Australia aquatic macrophytes become more developed over an extended time after flooding when wetlands begin to fill, particularly during winter and spring. These provide a habitat for the aquatic macrophytes to grow, an important food source for the black swan (Kingsford et al. 1999, Kingsford & Norman 2002). Studies in Eastern Australia have shown increases in swan abundance may be related to increases in aquatic macrophytes after flooding (Kingsford et al. 1999, Roshier et al. 2009). The factors that were observed to influence swan abundance were not consistent across the wetlands, and they are likely to interact. Where there were >10 of the 22 identified breeding characteristics at a wetland, more swans were present during the breeding season (winter and spring). Generally the breeding success of many waterbirds is controlled by predation, food availability and weather (Martin & Wiebe 2004, Tulip & Schekkerman 2008). Some waterbirds also have specific habitat requirements for breeding, which vary between species. These specific requirements have the potential to influence the breeding success and clutch size of waterbirds, with some species having a greater number of requirements than others (Storey et al. 1993, Saab 1999, Norris et al. 2004). On the SCP there are a number of breeding waterbirds whose breeding activity can be associated with significant habitat characteristics, including the black swan with 22 habitat associations (Storey et al. 1993), the most of any other waterbird. Some of these vary seasonally including water depth, macrophyte cover, macrophyte biomass and zooplankton abundance, all of which are likely to increase during winter and spring with increasing water levels (Storey et al. 1993). The black swan could be moving to these wetlands for breeding.

Also in wetlands with annual fluctuations in water level, there was an increase in swans with increasing water level, but the relationship with hydroperiod varied. Maximum swan abundance was observed at a hydroperiod of 3 months at 1 site, and 10 at another. Globally, the length of the hydroperiod has commonly been found to be an important factor influencing waterbird abundances on lakes and wetlands (Van Donk & Otte 1996, Holm & Clausen 2006). Extended hydroperiods allow the growth of emergent macrophytes, an important food source for waterbirds (Van Donk & Otte 1996, Holm & Clausen 2006). Water levels can also influence the type and abundance of water birds found on wetlands around the world (Musil & Fuchs 1994, Bancroft et al. 2002, Bolduc & Afton 2008). For example, in the Northern Everglades of Florida water depth was the most important factor influencing bird abundance (Bancroft et al. 2002), while in the Czech Republic mutes swans were seen to increase with an increase in flooding (Musil & Fuchs 1994). This trend can be seen in Australia where a highly variable climate, both temporally and spatially, has significant impacts on wetland flooding patterns, influencing waterbird movements, including that of the black swan (Roshier et al. 2009).

Where the abundance of swans appears to vary among seasons, on ephemeral water bodies it was characterised by an increase during winter and spring. This could possibly be for breeding but also for forage as this is the time when water levels increase in the wetland. On permanent water bodies an increase in swan abundance was observed during summer and autumn when ephemeral water bodies were dry. During this time it is estimated 4804.1 ha are lost for swan habitat when ephemeral wetlands dry, 22% of all available wetland habitat. It is possible permanent water bodies act as a refuge for swans during summer and autumn, when many wetlands dry. If ephemeral and permanent wetlands on the SCP dry, swan abundance may increase on the Lower Swan River estuary during winter and spring as at these times swan abundance is expected to be low at the wetlands. The dominant food source for swans in the estuary, seagrass, is reduced in winter due to lower temperatures and salinity (Hillman et al. 1995); therefore increases in swan abundance may negatively impact on the seagrass.

This chapter has identified the need for more comprehensive investigations into spatial and temporal variations in the swan abundance on ephemeral and permanent lakes and wetlands on the SCP to gain a better understanding on swan movements and to determine if the Lower Swan River estuary has enough significant breeding characteristics to assist swan breeding if surrounding wetlands dry out. Seasonal changes in swan abundance on the Lower Swan River estuary will be investigated in Chapter 3.

3. Spatial and temporal variation in swan abundance and grazing on the Lower Swan River estuary

3.1 Introduction

Temporal variation in the abundance of waterfowl on larger lakes and estuaries in the southern hemisphere is often more complex than for their northern hemisphere counterparts (Chambers & Loyn 2006). In the latter case, waterfowl usually move south during winter to seek food and a warmer climate (Warnock & Takeawa 1996, Petrie & Wilcox 2003). In contrast, the southern hemisphere has a milder and drier climate and bird migration appears to be more influenced by aridity and rainfall (Kingsford & Norman 2002, Kingsford et al. 2010).

In Australia, the climate including rainfall is highly variable both temporally and spatially. This temporal and spatial variability has a strong influence on river flooding patterns and filling of wetland habitats and hence on the ecology of Australian waterbirds, especially for more nomadic species like the black swan (Dingle 2008). Black swan abundance is strongly seasonal on larger water bodies, increasing in summer and autumn with local climate variables such as rainfall having the greatest influence on abundance (Chambers & Loyn 2006, Kingsford et al. 2010). Increases in rainfall results in the movement of black swans away from larger water bodies to seek smaller ephemeral wetlands once they begin to fill (Chambers & Loyn 2006, Kingsford et al. 2010).

Food availability is an important factor that has been shown to influence waterbird abundance worldwide (Martin & Wiebe 2004, Tulip & Schekkerman 2008) and Australian waterbirds, including the black swan (Kingsford et al. 1999, Kingsford & Norman 2002). Aquatic macrophytes, including seagrasses, are an important food source on larger water bodies for black swans particularly during summer and autumn while surrounding wetlands are dry (Marchant & Higgins 1990, Mitchell & Wass 1995, 1996). It is important to determine whether black swans graze on the Lower Swan River estuary and if this varies both temporally and spatially, to asses if the Lower Swan River estuary is an important forage area for black swans.

Habitat loss, hunting and exotic introductions are the main threats to waterfowl world-wide and can significantly influence waterfowl abundance on water bodies (Green 1996). In the northern hemisphere, hunting of waterfowl is more common and increases in hunting activity depresses their abundance (Bechet et al. 2004, McKinney et al. 2006). Other habitat characteristics (shoreline configuration, increasing land-water interface, wind exposure and prey density) have also been found to influence waterfowl abundance. The boundary between the two habitat types (water and land) increases exposure of waterfowl to waves, winds and land-based predators (Burton et al. 2002, Bechet et al. 2004). Landscape characteristics (surrounding residential and industrial development, vegetated land and the extent of wetland edge) also influence the distribution of waterfowl (Burton et al. 2002, Bechet et al. 2004). Progressive residential and industrial development reduces waterfowl abundance around estuaries and wetlands as water bodies become less attractive to waterfowl (Paracuellos & Telleria 2004, McKinney et al. 2006). Other disturbances, such as human activities on larger lakes and estuaries have significantly reduced waterbird abundance. For example, declines in most bird species at Pelican Point and other areas of the Lower Swan River estuary have been attributed to greater recreational use of the estuary (Creed & Bailey 2009). Increases in boating produces wash that undermines the river beaches making them less available for waterfowl. Other human activities, such as the presence of wind and kite surfers and walkers with dogs may also have disturbed birdlife (Creed & Bailey 2009). There are some key habitat requirements for waterbirds as outlined in chapter 2, such as habitats providing sufficient amounts of available food at depths waterbirds can reach (Kingsford & Norman 2002, Roshier et al. 2009) and key habitat requirements required for breeding in some water birds (Musil & Fuchs 1994, Bancroft et al. 2002, Bolduc & Afton 2008). The presence of these factors is likely to influence the abundance of waterbirds at a particular site.

This study focused on the Lower Swan River estuary, a permanent water body with shallow waters to support swan feeding. The estuary has a variety of conservation values to protect estuarine habitats, fauna and migratory birds, as well as recreational, commercial, educational, historical and research values (Department of Environment and Conservation 1999). The aquatic and terrestrial environments on the estuary offer opportunities for a range of recreational activities, including bird watching, sightseeing, artistic pursuits, windsurfing, water sports, fishing and boating (Department of Environment and Conservation 1999). The estuary has three marine parks at Alfred Cove, Milyu and Pelican Point (Figure 3.1). In these areas no structures or development are allowed and there are restrictions on the type of watercraft allowed in the area (no jet skis and motorised watercraft have a speed limit of 8 knots/hour) and in addition special licences are required for recreational and commercial fishing.

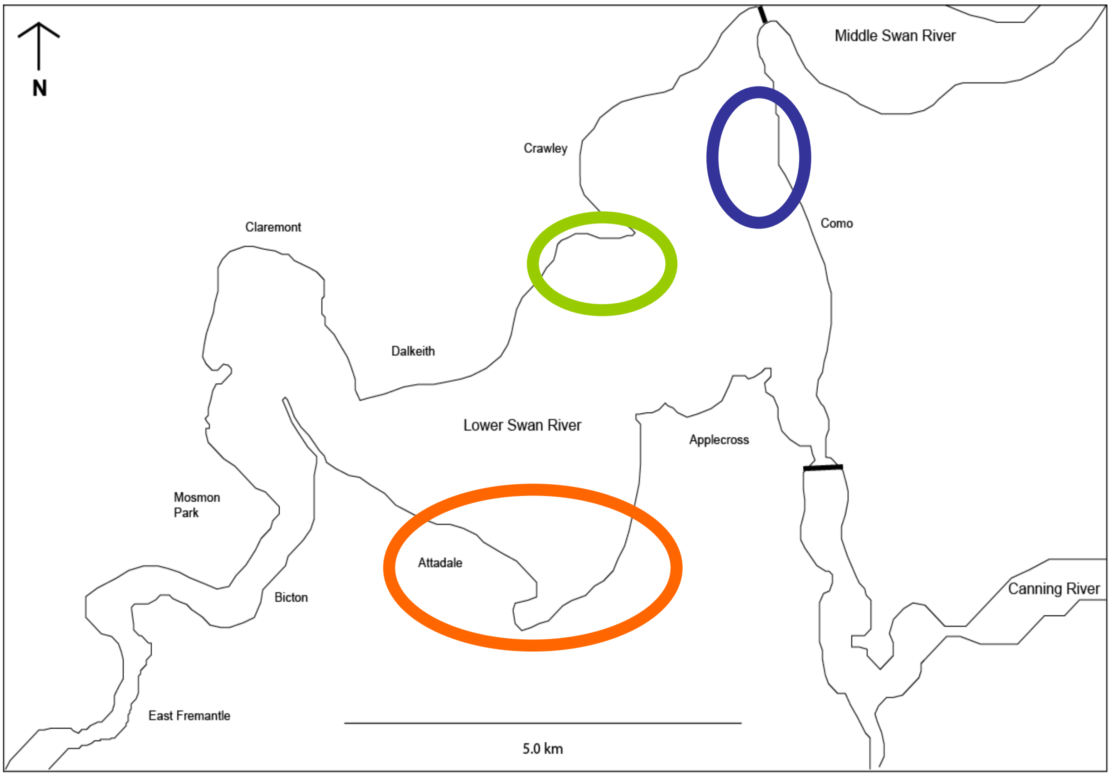


Figure 3.1 Locations of the marine parks on the Lower Swan River estuary. Alfred Cove (Orange), Milyu (Blue) and Pelican Point (Green).

On the estuary there have been some observations of swans recorded in the Birds Australia database. However, these were mostly documented as the presence of young swans. The abundance of adult birds was not recorded in this database.

From historic records, it is suggested the abundance of black swans has altered dramatically since European settlement. In 1827 Charles Fraser noted large quantities of black swans, up to 500 in the Swan River estuary (Brearley 2005). Recent surveys (2007/08) observed up to 78 black swans feeding in the Lower Swan River estuary during summer, with 69% of them feeding in the seagrass meadows (Eklof et al. 2009). In this study, spatial variation in swan abundance was observed on the Lower Swan River estuary. High numbers were seen at Point Walter, Alfred Cove marine park and Milyu marine park (Eklof et al. 2009). The latter study was conducted during summer, so little is known about seasonal variation in swan abundance. Other studies have suggested swans move to permanent water bodies during summer and autumn when ephemeral wetlands dry, then move back to these areas once they begin to fill (Chambers & Loyn 2006, Lane et al. 2007, Kingsford et al. 2010). Therefore the Lower Swan River estuary could act as a refuge when inland lakes and wetlands dry out between late spring and late autumn.

In the Lower Swan River estuary the most predominant species is the seagrass *Halophila ovalis*, a keystone species. However, the seagrasses *Ruppia megacarpa* (R. Mason) and *Zostera muelleri* (S.W.L Jacobs) also occur in the estuary and may be an important foods for the swan. The management agency for the Swan River estuary, the Swan River Trust, is attempting to improve the health of the estuary and increase swan numbers (Brearley 2005). This study assesses if there are key swan use areas and if they vary temporally, so management can be directed to these areas. This study also assesses if there are particular characteristics that can be used to predict where swans will be. This information can be used by managing agencies of the Swan River estuary to ensure features are maintained or enhanced to promote the return of the black swan to the estuary. Therefore, two aims will be addressed:

1. To determine if there is temporal and spatial variation in swan abundance and grazing on the Lower Swan River estuary; and
2. To determine whether there is an association between specific site and habitat characteristics and swan abundance.

3.2 Methods

3.2.1 Study area

This study was conducted in the Lower Swan River estuary which flows through Perth City centre in south-western Australia (Fig. 2.1). Three seagrass species are found in the Lower Swan River estuary with *H. ovalis* the dominant seagrass (Brearley 2005), covering 25% of the main basin from 0 to 2.5 m depth (Hillman et al. 1995). Other seagrasses in the estuary include *R. megacarpa* and *Z. muelleri* (Brearley 2005).

3.2.2 Surveys of swan abundance & behaviour

To determine if there were temporal (inter-annual and daily) and spatial variation in black swan abundance and behaviour on the Lower Swan River estuary, surveys were repeated throughout the year at 45 sites (Figure 3.2). The size of the sites varied as they were selected based on the ability to observe swans from a central observation point on the shoreline using binoculars. Surveys of all sites were conducted five times (i.e, separate days) in each season (spring, summer, autumn and winter) and twice during the day (morning and evening) on each sampling day. Surveys were conducted twice during the day as some studies have shown feeding by black swans increases through the day until dusk (Mitchell & Wass 1996, Hamilton et al. 2002). Morning surveys were conducted between 7am-10am in all seasons, while the evening surveys were conducted between 3pm-6pm in spring and autumn, 4pm-7pm in summer and 2:30 pm-5:30 pm in winter. The timing of the five surveys was organised so that at least one survey was conducted in each month so that the observations were spread across the three months in each season, to account for any seasonal movements of swans. Here the observations in each month were randomly allocated to one day (i.e. a total of 3 days, 1 per month). Then the remaining two surveys were randomly selected from two days in the three month period (Table 3.1).

Table 3.1 Dates surveys were conducted.

Season	**Date**
Spring	3/9/2009
	18/9/2009
	24/9/2009
	1/10/2009
	8/11/2009
Summer	10/12/2009
	24/12/2009
	7/1/2010
	12/1/2010
	25/2/2010
Autumn	18/3/2010
	9/4/2010
	23/4/2010
	7/5/2010
	25/5/2010
Winter	1/6/2010
	10/6/2010
	1/7/2010
	12/7/2010
	27/8/2010

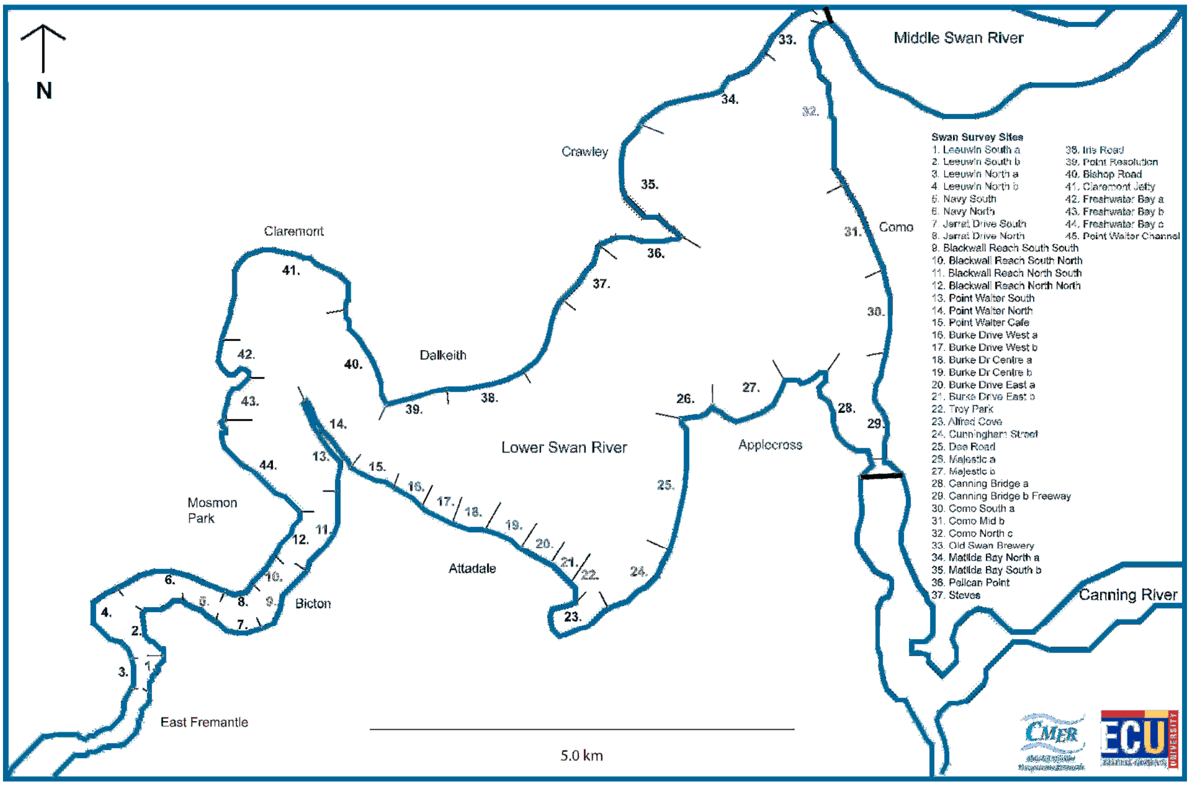


Figure 3.2 Map of the study area showing the 45 sites used in seasonal swan abundance surveys.

At each site, the total number of swans and their behaviour was recorded by consistent left to right tracking with binoculars which was repeated five times with the average taken. Abundances were normalised to one square kilometre to account for the variation in site size. Site size was calculated from Figure 3.2 using Image J™. Behaviours were classified as feeding, loafing, sleeping, transiting across site, grooming or 'other' (i.e. any behaviours that did not fit the other classifications, including vocalising, social displays or other behaviours). Feeding was the only behaviour addressed in this chapter as this was the focus of the study, however, analyses were run for all 6 behaviours and are presented in the appendixes.

Data Analysis

To determine if swan abundance and the proportion of swans observed feeding in the Lower Swan River estuary varied among seasons and between times of day, a two-way ANOVA was performed. Observations were grouped into seasons and time of day (fixed factors) and all data were pooled across sites. Total swan abundance data was log transformed to meet assumptions of homogeneity of variance and normality and the proportion data was arc-sin transformed as per, Quinn & Keough (2002). Statistical analyses were performed using GMAV (Underwood & Chapman. 1997).

To determine if there were temporal (inter-annual and daily) and spatial variations in swan abundance and the proportion of swans observed feeding at each of the 45 sites on the Lower Swan River estuary, a PERMANOVA was performed. A PERMANOVA was used for the analysis because the data was not normally distributed. The PERMANOVA does not assume normal distribution of data. Observations were grouped into site, season and time of day. Sites with no observations of black swans during the entire study period were excluded (n=15). Post-hoc tests were performed by pair wise comparisons using PRIMER™ (Clarke & Gorley 2006).

3.2.3 Associations between swan abundance and site characteristics

To determine whether there was an association between site characteristics and the abundance of black swans on the Lower Swan River estuary, specific site characteristics were recorded in the morning and afternoon of each survey day at all 45 sites (Table 3.2). Most site characteristics were noted during the visual observations of swans, including; number of boats, jetties, boat moorings, people, dogs, jets skis, people feeding swans, café's and length of the limestone wall at each site. However, the remaining characteristics required additional equipment and calculations. These are discussed below.

Site characteristics

Noise level

Noise level was measured using a DSE Digital Sound Level Meter. Four replicates were taken at a minimum of approximately ten metres apart, at random locations at each site. Measurements were averaged in the analysis.

Natural vegetation cover along shoreline

Natural vegetation cover along the shoreline was estimated by placing a 0.04 m^2 quadrat every 10 m on a transect along the shoreline and the percentage cover of natural vegetation was recorded. Each quadrat value was averaged across each transect, so one replicate was taken at each site.

Natural vegetation condition

The condition of the vegetation was assessed according to the system described in the Bush Forever guides (Government of Western Australia 2000). The Bush Forever condition rating scale ranges from pristine (where the vegetation exhibits no visible signs of disturbance) to completely degraded (where the vegetation structure is no longer intact and without native plant species).

Cloud cover

To estimate the cloud cover at each site the sky was divided up into quadrants, after which an estimate of cloud cover was taken in each quadrant based on methods described in (Globe 2003). Estimates were averaged at each site, so one replicate was taken at each site.

Tide height

Tide height data was obtained from the Australian Bureau of Meteorology (2011) on each of the sampling days during the morning and afternoon, as tide height changes throughout the day. One replicate was taken in the morning and afternoon at each site.

Relative Exposure Indexes (REI)

Multiple REIs were generated in each month both in the morning and afternoon at each of the 45 sites during the course of the study period (September 2009 to August 2010). The calculation for the REIs required climatic information and the effective fetch at each site. Climatic information for the 45 sites was obtained from the Australian Bureau of Meteorology (2011). The climatic variables used for the calculations were as follows:

1. Mean wind velocity (V), the average monthly wind speed (ms^{-1}) was based on two daily readings, at 9am and 3pm, from September 2009 to August 2010.
2. Directional percentage frequency (Pi), the frequency (%) at which wind occurs from the compass direction. Data was based on two daily readings, at 9am and 3pm, from September 2009 to August 2010.

Effective Fetch is defined as the distance between a site and the nearest wave-blocking obstacle (shoreline) along a given compass direction (Valesini et al. 2010). The effective fetch data used to calculate the relative exposure index were sourced from Valesini et al. (2010). Five effective fetches were calculated in this study N, E, S, W and the fetch perpendicular to the beach. Each fetch was used to calculate the REI at each site.

REI was calculated for each site using the equation derived in (Garcon et al. 2010). The sum of the five fetch directions (N, E, S, W and perpendicular fetch) were multiplied by the average wind velocity and directional percentage frequency, so one replicate was taken in the morning and afternoon at each site.

Table 3.2 Site characteristics recorded during each swan survey.

Additional site factors	**Measurement**
Number of other birds	(#)
Natural vegetation condition	Bush Forever scale (1 degraded – 5 Pristine) (Government of Western Australia 2000)
Natural vegetation cover along shoreline	(%)
Beach width	(m)
Number of jetties	(#)
Number of cafes	(#)
Number of people feeding swans	(#)
Number of boat moorings	(#)
Length of limestone wall	(#)
Number of boats	(#)
Number of jet skis	(#)
Number of people	(#)
Number of dogs	(#)
Noise level	(db)
Tide height	(m) (Bureau of Meteorology 2011a)
Cloud cover	(%) (Globe 2003)
Relative exposure index (Garcon et al. 2010) Fetch data used to calculate the relative exposure index was sourced from (Valesini et al. 2010)	REI

Physical and biological habitat characteristics

An additional fifteen physical and habitat characteristics were collected once in each season (spring, summer, autumn and winter) at a subset of 9 sites (Table 3.3). The sites were arranged in a gradient from high to low swan use and then subsets of sites were selected across the gradient. This information was added to the previous site characteristics to asses if there were associations between swan abundance and site/ habitat characteristics. These could not be collected on each sampling occasion due to time constraints. These are as follows:

Seagrass

1. *Zostera* % cover
2. *Zostera* biomass
3. *Halophila* % cover
4. *Halophila* biomass
5. *Ruppia* % cover
6. *Ruppia* biomass

Macroalgae

7. Green algae biomass
8. Red algae biomass
9. Brown algae biomass

Water Quality

10. Water temperature
11. Salinity
12. pH
13. Turbidity

Landscape

14. Width of vegetative area available for feeding
15. Slope of area

Table 3.3 Table of nine sites used for the habitat characterisation study during the four seasons (spring, summer, autumn and winter).

	Season			
	Spring	**Summer**	**Autumn**	**Winter**
Site	Point Walter Café	Point Walter Café	Point Walter Café	Como South A
	Point Walter South	Point Walter South	Point Walter South	Dee Road
	Freshwater Bay A	Freshwater Bay A	Freshwater Bay A	Troy Park
	Blackwell Reach South South	Bishop Road	Bishop Road	Bishop Road
	Matilda Bay B	Matilda Bay B	Cunningham Street	Burke Drive West B
	Majestic A	Majestic A	Majestic A	Majestic A
	Claremont Jetty	Claremont Jetty	Claremont Jetty	Leeuwin South B
	Como Mid B	Como Mid B	Leeuwin South B	Como Mid B
	Burke Drive East B	Burke Drive East B	Burke Drive East B	Burke Drive East B

The methods of collection for each of these physical and habitat characteristics are descried in more detail below:

Seagrass cover

Seagrass cover was estimated in a 40×40m area within the site where swans were most regularly observed. Within the area, four 20 m transects were randomly located within a depth of less than 1m, which is approximately the maximum depth of black swans feed. A 0.04 m^2 quadrat was positioned every 2 m on each transect and the species of seagrass (*H. ovalis, R. megacarpa* or *Z. muelleri*) was recorded giving a total of 40 points within each site. Seagrass cover was estimated from a photograph of each 0.04 m^2 quadrat. The photos were later analysed on the computer by placing a clear cover with ten random dots over the screen and the species present under each dot recorded. Only one species was recorded per point. Species cover in each quadrat was reported as the (%) of points containing the species of interest. Each quadrat value was averaged across each transect, so four replicates were taken for each site.

Seagrass biomass

To determine the seagrass biomass at each site, four cores (i.d. 10.5cm, depth=10cm) were collected from randomly located points on each of the four transects described in the previous section. The core samples were sieved though a

2 mm sieve to remove sediment, placed in plastic bags, stored on ice during transport and then frozen until processing. Later, the different seagrass and algae were separated, washed to remove salt and dried at 60˚C for 24 hours before weighing.

Water quality

Water quality was measured using a WTW meter (pH, salinity, water temperature and turbidity). Four replicates were taken at a minimum of approximately ten metres apart and randomly located at each site. They were taken in 1m depth of water, the same depth in which the seagrass measurements were taken. Measurements were taken at the top and bottom of the water column. To prevent mixing of the water column, slow movements were made through the water and measurements were taken a few minutes after a sampling point was reached. Top and bottom measurements were averaged in the analysis.

Site bathymetry

The slope of the site (m) and width of vegetative area available for feeding (m) was determined using an automatic level instrument (Bear) and staff, measuring the height relative to the ground level from the water's edge, every five metres until the point 1m depth of water was reached (or exceeded) or the point where the horizontal distance exceeded 300m. In this investigation, the only interest was in the slope of the area, therefore it is a relative measure and the absolute height was not important; only how the depth changes with distance. Therefore, only the slope was recorded (m). In addition, the horizontal distance at which seagrass started and ended was recorded to determine the width of vegetative area available for feeding (m).

Data analysis

To determine whether specific site characteristics were associated with swan density, a forward step multiple linear regression was performed. However, as there were many variables (n=32) these were reduced using a principal component analysis (PCA) to determine which variables were co-correlated (Jongman et al. 1995) and then removing all but one of the co-correlated variables. This analysis was performed using PRIMER (Underwood & Chapman. 1997) and all data were range standardised. If any variables were co-correlated, the factor showing the most variation, indicated by the longest line on the PCA, was selected to use in the multiple linear regression. The multiple linear regression examined swan density against the site characteristics to determine which characteristics were associated with swan density. The multiple linear regression was performed using SPSS (SPSS 2008). The R^2 value indicates the strength of the relationship while the B value indicated which characteristics were most important. Due to the different frequency of data collection for specific site characteristics (every survey, 40 sampling days x 2 times a day x 45 sites: n=1800, 17 predictor variables) and physical and biological characteristics (once every season at a subset of sites, 4 sampling days x 2 times a day x 9 sites: n=72, 32 predictor variables) two different analyses were run. In the first multiple regression, swan abundance data was the abundance observed at the particular site, day and time. For the second multiple regression, the data used were the average abundance at the site in that season (average of 5 days x 2 times of day: n=10).

3.3 Results

3.3.1 Temporal (season and daily) variation in the total abundance of swans on the Lower Swan River estuary

There were significant seasonal differences in the number of swans observed on the Lower Swan River estuary ($p<0.05$), but no significant differences between time of day ($p>0.05$, Table 3.4, Figure 3.3). The greatest abundance of swans was observed in autumn (185 ± 15 equating to a density of 20 ± 2 km^{-2}), while the lowest was observed during spring (53 ± 4 equating to a density of 6 ± 0 km^{-2}). There was no significant difference in swans observed during summer and winter (104 ± 11 & 80 ± 9 equating to densities of 11 ± 1 & 9 ± 1 km^{-2}, Figure 3.2).

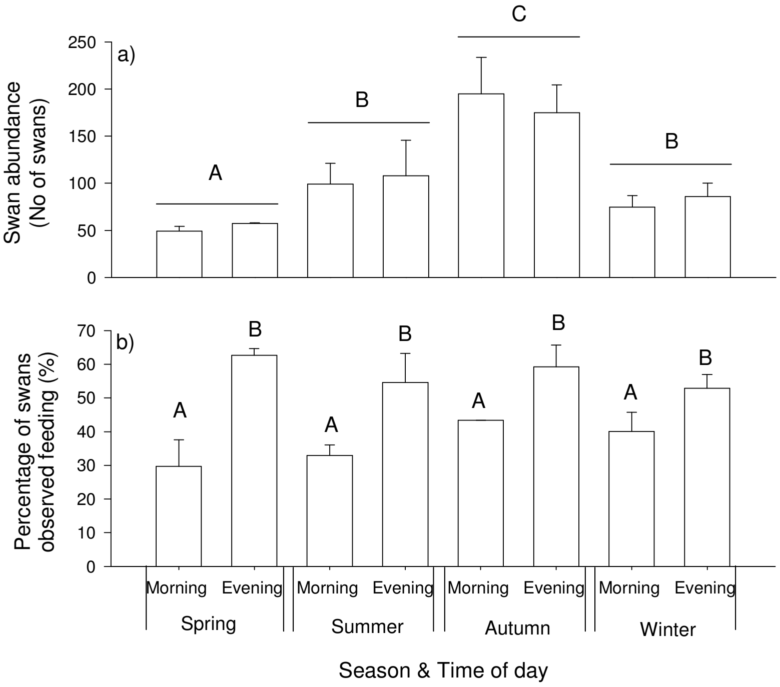


Figure 3.3 Swan abundance and percentage of swans observed feeding during different seasons (spring, summer, autumn and winter) and times of day (morning and evening) on the Lower Swan River estuary: (a) Total counts across all sites on the 5 sampling occasions within each season and (b) Percentage observed feeding. Letters above the columns indicate which seasons are different based on post-hoc comparisons. All data are means ± SE.

Table 3.4 Summary of two-way ANOVA testing for differences in the total number of swans among times of year (spring, summer, autumn and winter) and between times of day (morning and afternoon).

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Season	8.01	3	2.74	25.30	<0.01
Time of Day	0.03	1	0.04	0.33	0.57
Season X Time of Day	0.08	3	0.03	0.27	0.85
Residual	3.38	32	0.11		
Total	11.51	39			

3.3.2 Temporal (season and daily) variation in the percentage of feeding swans

There was no significant seasonal difference in the percentage of swans observed feeding in seagrass meadows on the Lower Swan River estuary (Table 3.5, p>0.05). A significantly greater percentage of swans were observed feeding in the seagrass meadows during the afternoon than in the morning (Figure 3.3). Averaged across all seasons, 57 ± 4% were feeding in afternoons compared with 37 ± 2% in mornings.

Table 3.5 Summary of the two-way ANOVA testing for differences in the percentage of swans observed feeding among times of year (spring, summer, autumn and winter) and between times of day (morning and afternoon).

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Season	110.35	3	36.78	0.55	0.65
Time of Day	1552.59	1	1552.59	23.26	<0.01
Season X Time of Day	205.73	3	68.58	1.03	0.39
Residual	2136.19	32	66.76		
Total	4004.87	39			

3.3.3 Spatial and temporal variation in swan density

There was significant spatial variation in swan density on the Lower Swan River estuary. However, these differences were dependent on the time of year (Table 3.6, Site x Season interaction: p<0.05, Figure 3.4). Fifteen sites had no swans present during the study period (sites 2, 3, 5, 6, 10, 12, 26, 33, 34, 37, 38, 39, 40, 44, 45) and were not included in this analysis. Based on the post-hoc tests, of the 30 sites that had swans present, 16 of those showed significant seasonal variation (sites 7, 8, 9, 11, 13, 14, 15, 18, 19, 21, 22, 23, 24, 25, 27, 31). Blackwell Reach South South and Jarrat Drive South (sites 7, 9) showed significant seasonal variation with higher swan abundance during autumn (16 ± 6 & 11 ± 5) compared to spring (1 ± 1 & 0 ± 0), summer (0 ± 0 & 3 ± 3) and winter (0 ± 0 & 0 ± 0). Burke Drive Centre A and Burke Drive Centre B (sites 18, 19) showed significant seasonal variation with higher swan abundance during summer and autumn (24 ±

12 & 17 ± 7 and 69 ± 26 & 28 ± 12) compared to spring (0 ± 0 & 2 ± 2) and winter (2 ± 2 & 3 ± 3). The other sites showing seasonal variation had low densities of swans present. Fourteen sites showed no significant seasonal variation (sites 1, 4, 16, 17, 20, 28, 29, 30, 32, 35, 36, 41, 42, 43).

Examining these patterns across the whole estuary, three high-use areas were identified; Point Walter, Milyu (Como) and Alfred Cove. The time of year these high-use areas were utilised also varied. During spring the greatest density of swans on the river were at Point Walter (sites 13, 14, 15) (76 ± 18; 57 ± 14 & 46 ± 12), while during winter the greatest density was seen at Alfred Cove (sites 21, 22, 23, 24) (74 ± 23; 134 ± 32; 42 ± 18 & 11 ± 6) and Como (site 31) (56 ± 9). During summer most of the swans on the river were observed at Point Walter (70 ± 15; 96 ± 26 & 20 ± 7) and Alfred Cove (116 ± 24; 100 ± 13; 1 ± 1 & 20 ± 20), while during autumn most swans were observed at Point Walter (61 ± 20; 122 ± 30 & 27 ± 7), Alfred Cove (237 ± 39; 184 ± 24; 37 ± 18 & 55 ± 16) and Como (54 ± 4) (Figure 3.4).

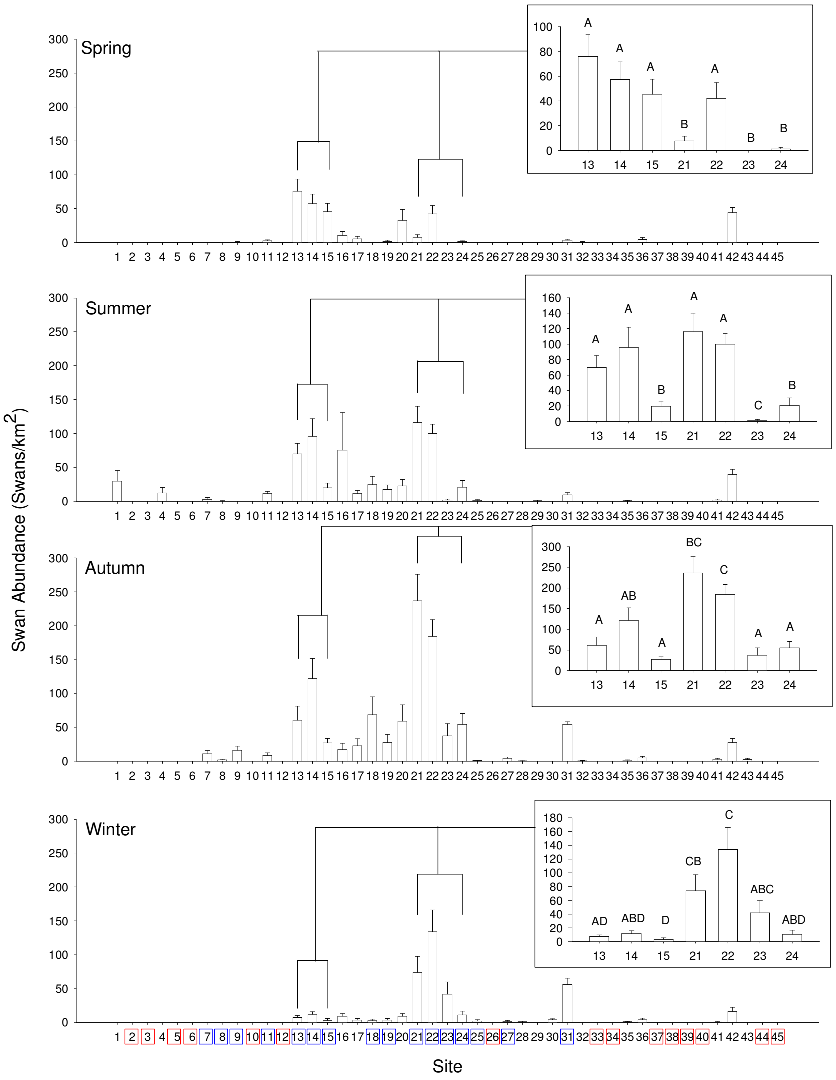


Figure 3.4 Swan density at forty five sites during four seasons (spring, summer, autumn and winter) on the Lower Swan River estuary. Sites in red boxes were excluded from the analysis. Sites in blue boxes indicate significant difference among seasons (Pair wise comparisons) and sites without boxes had no significant seasonal variation. Inserted graphs show differences in swan density at the areas with most swan activity throughout all four seasons. Letters above the columns on these graphs indicate which sites are different based on post-hoc comparisons. All data are means ± SE.

Table 3.6 Summary of the PERMANOVA testing for differences in spatial (45 sites), temporal (inter-annual) (spring, summer, autumn and winter) and daily (morning and afternoon) variations in swan abundance.

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Site	5.73	29	19767	29.47	<0.01
Season	49118	3	16373	24.41	<0.01
Time of day	592.71	1	592.71	0.88	0.34
Site X Season	2109	87	2109	3.14	<0.01
Site X Time of day	679.15	29	679.15	1.01	0.45
Season X Time of day	971.06	3	971.06	1.45	0.22
Site X Season X Time of day	673.22	87	673.22	1.0	0.47
Residual	670.82	960	670.82		
Total	1.53	1199			

3.3.4 Association between site characteristics and the density of swans

There was a significant relationship between swan density and a sub-set of site characteristics (number of other birds, length of limestone wall, tide height, natural vegetation condition, number of boat moorings and number of boats) on the Lower Swan River estuary. Some site characteristics (4) were co-correlated and removed from the analysis (Table 3.7). However, these six variables explained only 14% of the variation in swan density (Table 3.7). Most of the variation in swan density was explained by a positive relationship with other birds (B = 13.53). Vegetation condition along the shoreline (B = 3.09) and tide height (B = 2.88) were also positively correlated with swan density. The number of boats in the area (B = -2.26) was negatively correlated with swan density, as were the length of the limestone wall (B = -3.67) at a site and the number of boat moorings (B = -2.72) (Table 3.8).

Table 3.7 Co-correlated variables in the multiple regression analysis as determined by a PCA analysis.

Variables included in the multiple-linear regression	**Co – correlated variables removed from the multiple linear regression**
Number of other birds	-
Length of limestone wall	-
Tide height	-
Natural vegetation condition along the shoreline	-
Number of boat moorings	Number of jetties
Number of boats	-
Relative exposure index	-
Beach width	Cloud cover
Noise level	-
Number of jet skis	-
Number of people	-
Number of dogs	# people feeding swans & # café's
Natural vegetation cover along shoreline	-

Table 3.8 Multiple linear regression comparing swan abundance and site characteristics on the Lower Swan River estuary. R^2= 0.14. *Note regression equations at bottom of table.

Variable	**Std. error**	**B**	**Sig**
Number of other Birds	0.95	13.53	<0.01
Length of limestone wall	0.97	-3.67	<0.01
Tide height	0.93	2.88	<0.01
Natural vegetation condition	0.94	3.09	<0.01
Number of boat moorings	0.97	-2.72	<0.01
Number of boats	0.93	-2.26	0.02

Regression equation

Swan abundance predicted = 13.71 + 13.53 (number of other birds) - 3.67 (length of limestone wall) + 2.88 (tide height) + 3.09 (natural vegetation condition) - 2.72 (number of boat moorings) - 2.26 (number of boats).

3.3.5 Association between physical, biological and site characteristics and the density of swans

Using a smaller subset of data (only 9 sites per season) but additional physical and biological descriptors of the sites, there was a significant relationship between swan density and a sub-set of the physical, biological and site characteristics (number of other birds, natural vegetation cover along shoreline, number of jetties, slope of area, *Zostera %* cover and salinity) on the Lower Swan River estuary. Once again some site and habitat characteristics were co-correlated and removed from the analysis (Table 3.9). These eight significant variables explained 34% of the variation in swan density (Table 3.10). Most of the variation was explained by a positive relationship with other birds (B = 20.63). Swan abundances were positively correlated with a high cover of natural vegetation along the shoreline (B = 11.64), higher salinity (B = 15.14) and healthier vegetation condition along the shoreline (B = 17.65). A large amount of variation was also explained by a negative relationship between swan density and the number of jetties (B = -22.78), slope of the area (B = -24.02), *Zostera %* cover (B = -12.27) and brown algae biomass (B = -7.73) (Table 3.9).

Table 3.9 Co-correlated variables in the multiple regression analysis as determined by a PCA analysis.

Variables included in the multiple-linear regression	**Co – correlated variables removed from the multiple linear regression**
Number of other birds	-
Natural vegetation cover along shoreline	-
Relative exposure index	Temperature
Slope of area	-
Number of jetties	Number of dogs
Natural vegetation condition along the shoreline	*Ruppia* & *Halophila* biomass & % cover
Salinity	Red algae biomass & tide height
Green algae biomass	Cloud cover
Length of limestone wall	-
Noise level	-
pH	-
Brown algae biomass	-
Water colour	Number of boats
Number of boat moorings	-
Number of people feeding swans	Beach width, # jet skis & # café’s
Number of people	-
Length of vegetative area available for feeding	-
Zostera % cover	*Zostera* biomass

Table 3.10 Multiple linear regression comparing swan abundance and specific site and habitat characteristics on the Lower Swan River estuary. $R^2 = 0.34$. *Note regression equations at bottom of table.

Variable	Std. error	Beta	Sig
Number of other birds	2.78	20.63	<0.01
Natural vegetation cover along shoreline	4.68	11.64	0.01
Number of jetties	3.71	-22.78	<0.01
Slope of area	3.44	-24.02	<0.01
Natural vegetation condition along the shoreline	4.03	17.65	<0.01
Salinity	3.38	15.14	<0.01
Zostera % cover	3.07	-12.27	<0.01
Brown algae biomass	3.11	-7.73	0.01

Regression equation

Swan abundance predicted = 31.09 + 20.63 (number of other birds) + 11.64 (natural vegetation cover along shoreline) + 22.78 (number of jetties) - 24.02 (slope of area) + 17.65 (natural vegetation condition along the shoreline) + 15.14 (salinity) - 12.27 (zostera % cover) - 7.73 (brown algae biomass).

3.3.6 Spatial and temporal variation in the proportion of swans observed feeding

There was significant spatial variation in the proportion of swans observed feeding in the Lower Swan River estuary, however, these were dependent on the time of year and time of day (Table 3.11, Site x Season & Site x Time of Day interaction: $p<0.05$, Figure 3.5). Burke Drive West A, Troy Park and Freshwater Bay B (sites 16, 22, 43) were the only sites to have variation in the proportion of swans observed feeding with more feeding observed in the afternoon (0.25 ± 0.1; 0.5 ± 0.1 & 0.4 ± 0.1) compared to the morning (0 ± 0 ; 0.3 ± 0.1 & 0.2 ± 0.1).

Fifteen sites had no swans present during the study period (sites 2, 3, 5, 6, 10, 12, 26, 33, 34, 37, 38, 39, 40, 44, 45) and were not included in this analysis. Of the sites included in the analysis, two had no swans feeding (7, 30). The remaining 28 sites had feeding swans, eight of these with significant seasonal variation (sites 14, 16, 19, 20, 22, 24, 25, 43). The nature of this seasonal variation varied with site. For example, Point Walter North and Freshwater Bay B (sites 14, 43) had a significantly higher proportion of swans observed feeding during spring (0.4 ± 0.1 & 0.4 ± 0.1), summer (0.6 ± 0.1 & 0.4 ± 0.1) and autumn (0.5 ± 0.1 & 0.4 ± 0.1) compared to winter (0.1 ± 0.1 & 0 ± 0). Burke Drive Centre A, Burke Drive East A and Dee Road (sites 19, 20, 25) had a significantly higher proportion of swans observed feeding during autumn (0.25 ± 0.11; 0.43 ± 0.16 & 0.56 ± 0.14) than spring (0.00 ± 0.00; 0.03 ± 0.03 & 0.05 ± 0.05). Troy Park had a significantly higher proportion of swans observed feeding during summer and autumn (0.42 ± 0.11; 0.54 ± 0.1) compared to spring (0.15 ± 0.11). The other sites, Cunningham Street and Burke Drive West A (Sites 16, 24), had relatively low proportions of swans observed feeding. Twenty sites showed no significant seasonal variation (sites 1, 4, 8, 9, 11, 13, 15, 17, 18, 21, 23, 27, 28, 29, 32, 33, 35, 36, 41, 42).

Three high swan feeding sites were identified, however, the proportion of swans feeding at these sites varied seasonally. The highest proportion of swans observed feeding on the river were seen at areas with the highest swan abundance (Point Walter (13, 14, 15), Alfred Cove (21, 22, 23, 24) and Como (32). During spring, the highest proportion of swans observed feeding were seen at Point Walter (0.1 ± 0.1; 0.41 ± 0.09 & 0.45 ± 0.10) and Como (0.40 ± 0.16), while during winter the highest proportion of swans observed feeding on the river were seen at Alfred Cove (0.13 ± 0.1; 0.52 ± 0.15; 0.41 ± 0.09 & 0.21 ± 0.09) and Como Mid B (0.27 ± 0.11). During summer and autumn, the highest proportions of swans observed feeding on the river were spread between the three areas (Figure 3.5). These results are similar to those observed in the spatial variations in the density of swans in the Lower Swan River estuary section.

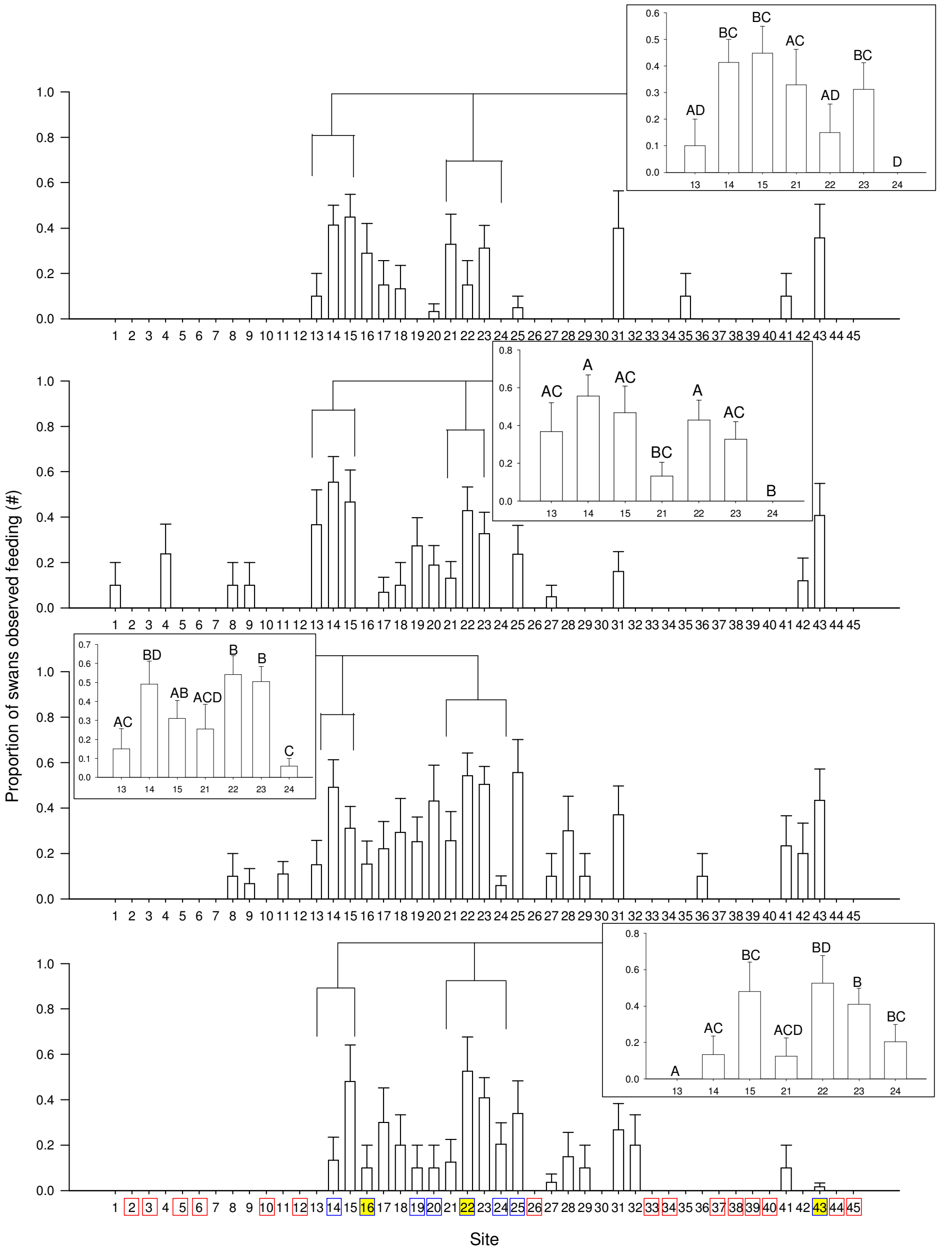


Figure 3.5 Proportion of swan observed feeding at forty-five sites during four seasons (spring, summer, autumn and winter) on the Lower Swan estuary. Sites in red boxes were excluded from the analysis. Sites in blue boxes indicate significant differences among seasons and those shaded in yellow indicate significant differences among times of day (morning and afternoon) (Pair wise comparisons). Inserted graphs show differences in the proportion of swans observed feeding in each season. Letters above the columns on these graphs indicate which sites are different based on post-hoc comparisons. All data are means ± SE.

Table 3.11 Summary of PERMANOVA testing for differences in spatial (45 sites), temporal (inter-annual) (spring, summer, autumn and winter), and daily (morning and afternoon) variations in the proportion of swans observed feeding.

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Site	42637	29	1470.2	14.62	<0.01
Season	3230.20	3	1076.7	10.71	<0.01
Time of day	899.34	1	899.34	8.94	<0.01
Site X Season	14565	87	167.41	1.66	<0.01
Site X Time of day	4913	29	169.41	1.68	0.01
Season X Time of day	351.13	3	117.04	1.16	0.32
Site X Season X Time of day	8286.40	87	95.25	0.95	0.62
Residual	95.25	960	100.55		
Total	100.55	1199			

3.4 Discussion

Inter-annual variation in black swan abundance was observed on the Lower Swan River estuary, with triple the number of swans observed on the river during autumn compared to spring and intermediate numbers in summer and winter. The variability in swan abundance on the Lower Swan River estuary may be explained by movements of waterbirds to wetlands during spring and winter when they fill and away from these areas during summer and autumn when they begin to dry, as outlined in Chapter 2. After the main rainfall season in winter, wetlands that dry up over summer and autumn are likely to fill and more habitats become available for the black swan. So the minimum number of swans was observed on the river in spring, coinciding with the period of maximum water height in wetlands.

These wetlands also provide suitable feeding and breeding habitats for the black swan which breeds generally in spring. These two factors result in the movement of birds from the river in winter and spring to surrounding wetlands (Storey et al. 1993, Scott 1997, Chambers & Loyn 2006). The Lower Swan River estuary appears to provide a refuge and suitable foraging habitat for black swans during autumn when surrounding wetlands are dry. However, based on the habitat characteristics of the river and observations of the absence of cygnets during spring, this area is not a suitable breeding habitat for the black swan, which accounts for the low numbers on the river at this time.

Particular areas on the Lower Swan River estuary had high numbers of swans and high proportions of swans feeding, however, the particular time that peak abundance and grazing occurred varied, depending on the time of year (Table 3.12). These areas will be referred to as swan hotspots hereafter. In autumn all hotspots had high numbers of swans. However in spring high numbers of swans occurred at Point Walter, while during summer, high numbers of swans only occurred at Point Walter and Alfred Cove. During winter only Alfred Cove and Como foreshore had high numbers of swans (Figure 3.6).

Table 3.12 Hotspots for swan abundance and grazing on the Lower Swan River estuary during the four seasons (spring, summer, autumn and winter). ✓ indicates a swan hotspot for the season & × indicates a non swan hotspot for the season.

	Season	**Point Walter**		**Alfred Cove**		**Como**	
		Swan hotspot	Number of swans (km^2)	Swan hotspot	Number of swans (km^2)	Swan hotspot	Number of swans (km^2)
Peak abundance	Spring	✓	59 ± 9	×	13 ± 4	×	3 ± 1
	Summer	✓	62 ± 12	✓	59 ± 11	×	9 ± 3
	Autumn	✓	70 ± 14	✓	128 ± 18	✓	54 ± 4
	Winter	×	8 ± 2	✓	65 ± 13	✓	56 ± 9
Peak feeding	Spring	✓	26 ± 6	×	4 ± 1	✓	3 ± 1
	Summer	✓	29 ± 7	✓	23 ± 6	✓	4 ± 2
	Autumn	✓	33 ± 10	✓	63 ± 10	✓	17 ± 8
	Winter	×	4 ± 2	✓	36 ±	✓	16 ± 8

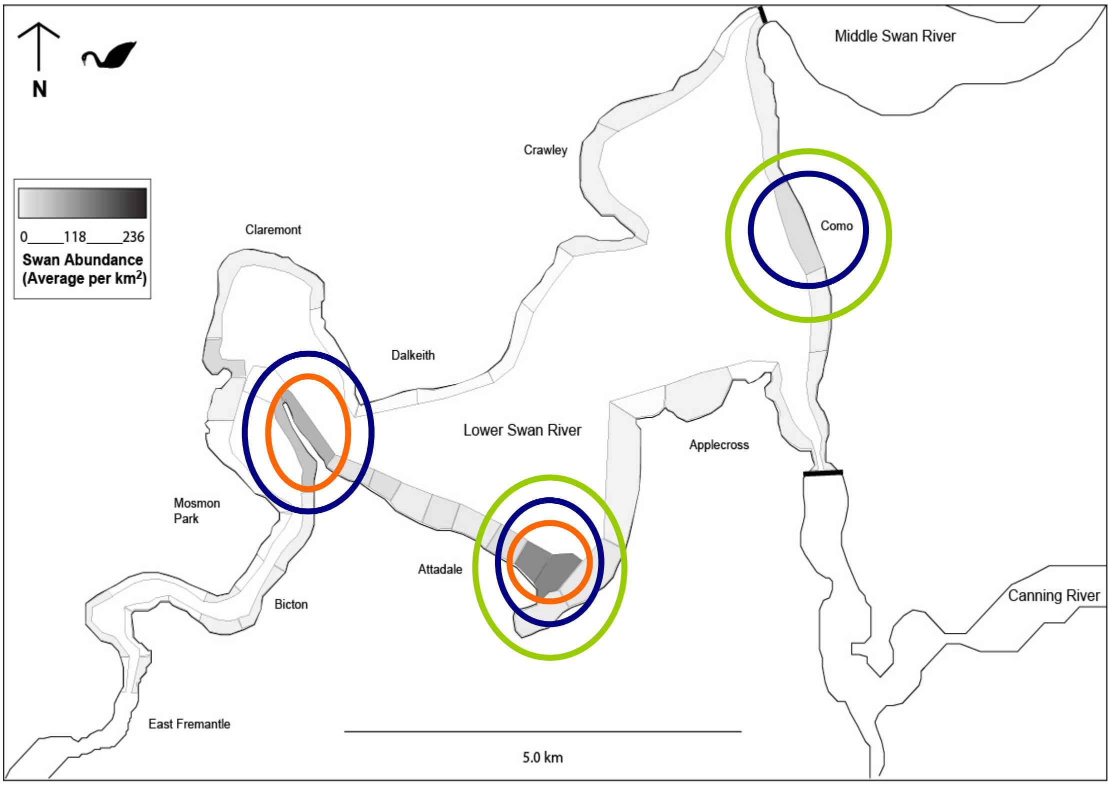


Figure 3.6 Swan hotspots on the Lower Swan River estuary during spring and summer (orange), autumn (blue) and winter (green).

Two of these areas, Alfred Cove and Como Foreshore are Marine Parks (Alfred Cove Marine Park & Milyu Marine Park) and have particular characteristics that could promote swan abundance. Based on the findings of this study, there are some key site and habitat characteristics that predict swan abundance. These include human disturbances (jetties and dogs), shoreline and submerged vegetation cover and condition and the slope of the area.

These predictors are similar to findings of other studies including habitat, landscape and human disturbance characteristics (Burton et al. 2002, Bechet et al. 2004, McKinney et al. 2006) that positively and negatively influence swan abundance. High numbers of swans were associated with sites that generally had good vegetation condition and a larger area of natural vegetation along the shoreline. These have been shown to be important factors influencing the distribution of waterfowl world-wide, as it protects them from predators and other human disturbances when feeding and also breeding (Paracuellos & Telleria 2004, McKinney et al. 2006).

Not only does the shoreline vegetation influence swan numbers but the submerged vegetation and structure of the bottom may influence them also. This is most likely related to the swans' foraging behaviour and preference. Previous studies have shown that black swan abundance is affected by the amount and type of food present (Williams 1979, Congdon & McComb 1981, Mitchell & Wass 1996) and this study has shown that the amount, type and its distribution along a depth gradient is also important. The highest abundance of black swans were in areas with a gentle slope and a large cover of the seagrasses *R. megacarpa* and *H. ovalis*. The gentle slope may provide a larger shallow area for the black swan to feed (Marchant & Higgins 1990), as it can only feed in water depths less than 1m (Marchant & Higgins 1990, Mitchell & Wass 1995, 1996). In other studies, *R. megacarpa* has been documented as the preferred food source of the black swan (Williams 1979, Congdon & McComb 1981, Mitchell & Wass 1996), while on the Lower Swan River estuary Eklof et al. (2009) found the black swan consumed a significant amount of *H. ovalis* which had a higher nutritional value relative to *R. megacarpa*.

Other human disturbances such as the presence of jetties and dogs negatively affected black swan abundance. Constructions on rivers and estuaries, such as jetties have been shown to reduce the local habitat quality for water birds and the carrying capacity of estuaries (Van den Bergh et al. 2005), by reducing the area available for feeding and breeding (Burton et al. 2002). In these areas there are also high levels of human activity such as the presence of dogs, which were also shown to negatively impact the abundance of black swans on the river. Previous studies have found increases in human disturbances such as ferries, boats, the presences of kite & wind surfers and increases in the number of walkers with dogs were significant factors reducing waterfowl abundance on the river (Creed & Bailey 2009).

The black swan appears to have large inter-annual variation in abundance that corresponds with rainfall timing and breeding season. Fewer birds were seen on the river during spring; times when smaller surrounding wetlands are most likely to be filled and when swans breed. At this time birds are likely to use the permanent water body of the Lower Swan River estuary as a refuge, during the drier months particularly autumn. This chapter has shown that the abundance of the study species, the black swan, and the amount of grazing varies over a year within the Lower Swan River estuary, and also at locations within the estuary. The next chapter will examine the grazing interaction between black swans and seagrass, particularly how the plant responds to grazing at different times of year.

4. Vegetative and sexual reproductive response of *Halophila ovalis* to black swan grazing.

4.1 Introduction

Waterfowl, including ducks, coots, geese and swans are often considered significant seagrass grazers in coastal lagoons and estuaries (Powell et al. 1991). In the northern hemisphere, temporal variation in grazing pressure on estuaries and larger water bodies often corresponds with changes in waterfowl abundance; consumption is typically greater in autumn and winter, during their migration south (Jacobs et al. 1981, Nienhuis & Groenendijk 1986, Baldwin & Lovvorn 1994). These studies conducted in the northern hemisphere suggested waterfowl can consume between 7.5-26% of daily seagrass production during autumn and winter (Jacobs et al. 1981, Nienhuis & Groenendijk 1986). However, in the southern hemisphere there have been very few studies focusing on waterbird grazing. Of those studies most have focused on one of the larger waterfowl, the black swan. It has been observed to consume 104g DW swan^{-1} d^{-1} in New Zealand (Mitchell & Wass 1995), while in the Lower Swan River estuary10-15 black swans were shown to consume around 23% of daily seagrass production (Eklof et al. 2009). This study was conducted during autumn, so little is known whether swan grazing pressure varies temporally and whether seagrasses have traits, allowing them to cope with grazing. Based on the findings in chapter 3 it is likely the grazing pressure (removal of seagrass material) will vary temporally as the number of swans feeding varies through the year.

Similar to other angiosperms, seagrasses have evolved a number of traits allowing them to cope with natural levels of grazing (Hauxwell et al. 2004). These traits have been characterised into a number of strategies, including escape, defence and tolerance (Agrawal 2000). As discussed in the introduction, the tolerance strategy is the focus of this study as *H. ovalis*, the dominant seagrass in the Lower Swan River estuary, is known to show responses to grazing that correspond with this strategy (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009). A tolerance strategy allows plants to survive, regrow and reproduce after damage is sustained (Agrawal 2000). Seagrasses do this through a number of key traits, including the activation of dormant meristems, utilisation of stored reserves (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009) and possibly, changes in the sexual reproduction after grazing (Conacher et al. 1994, Peterken & Conacher 1997). The expression of these traits results in re-growth, so grazed plants return to a similar biomass as non-grazed plants, or have increased growth and production following grazing.

Based on a literature review of studies on seagrasses that examined responses to grazing, only five out of thirteen demonstrated the expression of traits associated with the tolerance strategy (Table 4.1). None of these studies was conducted at different times of year. Although four studies measured seagrass response to grazing at different times of year and two showed contrasting patterns in productivity, these did not directly asses tolerance traits (Table 4.1). This highlights the lack of knowledge of whether tolerance traits in seagrasses vary at different times of year.

Table 4.1 Studies looking at seagrass response to grazing. Bold lettering represents studies measuring seagrass response at different times of year. Italic lettering represent studies measuring tolerance traits in seagrasses.

Location	Seagrass type	Findings	Season study was conducted	Reference
Indonesia	*Halodule univervis*	Increase in below ground biomass	-	(De Iongh et al. 2007)
Australia	*Halophila ovalis*	*Increase branching frequency & initiated apices*	Summer	(Eklof et al. 2009)
Bermuda	*Thalassia testudinum*	*Decrease in primary production & soluble carbohydrates*	Autumn	(Fourqurean et al. 2010)
Australia	*Halophila ovalis* *Zostera capricorni* *Cymodocea serrulata.*	*H. ovalis* – increase leaf regrowth rate *Z. capricorni* and *C. serrulata* - leaf biomass decreased *C. serrulata* – reduced leaf size	Summer	(Kuiper-Linley et al. 2007)
USA	*Thalassia testudinum*	Winter – decrease shoot density and productivity Summer - increases in productivity	**Summer & winter**	(Macia 2000)
Bahamas	*Thalassia testudinum*	Summer & winter – increase linear growth	**Summer & winter**	(Moran & Bjorndal 2005)
Thailand	*Halophila ovalis*	*Increased branching & rhizome elongation*	Autumn	(Nakaoka & Aioi 1999)
USA	*Thalassia testudinum*	Increase in short shoots	**Spring & summer**	(Valentine et al. 1997)
USA	*Thalassia testudinum*	Spring – decrease in productivity Summer - increase in productivity	**Spring & summer**	(Valentine et al. 2000)
USA	*Zostera marina L.*	*Decrease in Growth rates, carbon reserves, root proliferation and net photosynthesis*	Winter	(Zimmerman et al. 1996)
Zanzibar, Tanzania	*Thalassia hemprichii*	*Decrease in growth rate and sugar and starch content*	Spring	(Eklof et al. 2008)
India	*Cynodocea rotundata* *Thalassia hemprichii*	Increase in the number of leaves per shoot	Summer	(Lal et al. 2010)
Puerto Rico	*Thalassia testudinum*	Decreased biomass and shoot density	Spring	(Olsen & Valiela 2010)

In *H. ovalis,* dormant meristems are activated by grazing, changing the growth trajectories of the plant and stimulating replacement of some or all of the tissue removed by grazing (Kuiper-Linley et al. 2007, Eklof et al. 2009). These growth changes may be the result of the utilisation of stored reserves, where seagrasses typically use carbohydrate stores in the underground rhizome to promote new growth and in some cases, to promote regrowth after damage (Cebrian et al. 1998, De Iongh et al. 2007, Fourqurean et al. 2010).

Recently a number of terrestrial studies have shown environmental factors can mediate the response of plants to grazing (temperature, light and nutrient levels) by influencing the carbohydrate supplies and the expression of tolerance traits (Whitman et al. 1991, Hawkes & Sullivan 2001, Bagchi & Ritchie 2011). There is good reason to hypothesise that the capacity of seagrasses to tolerate grazing will vary throughout the year. Two studies have shown that productivity declines following grazing in spring or winter but increases following grazing in summer (Macia 2000, Valentine et al. 2000). As environmental conditions change over a year, the seagrass dynamics change. During spring and into summer, light conditions and water temperatures gradually increase, leading to increases in growth and production (Moncreiff et al. 1992, Perez & Romero 1992, Hillman et al. 1995) and increased carbohydrate stores (Alcoverro et al. 2001). During winter, low light conditions and water temperatures slow growth and production (Moncreiff et al. 1992, Perez & Romero 1992, Hillman et al. 1995) and there are often lower carbohydrate stores (Alcoverro et al. 2001). Therefore, when environmental conditions are limiting, growth and carbohydrates are lower and the plants may not be able to respond to grazing if that response depends on storage reserves.

Plants cannot only respond to grazing through vegetative growth responses but also through changes in sexual reproduction. These changes can be considered a strategy of tolerance. These traits were not included in the Tiffin (2000) summary paper, but other studies in terrestrial plants have observed an increase in sexual reproduction after grazing (Whitman et al. 1991, Lazo et al. 1994, Quiroga et al. 2010) by increasing flowering intensity and fruit production (Whitman et al. 1991, Forbs et al. 1997). Other studies, however, have suggested a decrease in sexual reproduction after grazing (Hickman & Hartnett 2002, Varga et al. 2009, Lal et al. 2010). Little is known of these responses in seagrasses. A few studies have suggested a positive relationship between seagrass flowering and dugong grazing (Conacher et al. 1994, Peterken & Conacher 1997) and others have suggested an increase in flowering after physical disturbance (Phillips et al. 1983, Alexandre et al. 2005, Hammerstrom et al. 2006). In some cases there is a negative effect of grazing on flower production (Lal et al. 2010).

Not only can grazing affect sexual reproduction but it can also affect the sex ratio of populations. There are several hypotheses for why sex ratios can change as a result of grazing. In some plant species, females usually expend more resources into reproduction than males because additional energy is required to produce fruits and seeds (Delph 2011, Viejo et al. 2011), resulting in two separate outcomes. The greater investment in reproduction by females could potentially result in less investment in vegetative growth. Therefore, they may have a lower nutritional quality than males, so the larger male plants become a more attractive food source for grazers (Cornelissen & Stiling 2005). This results in male-biased grazing, resulting in more females relative to males (Cornelissen & Stiling 2005). The second hypothesis is that grazing results in male dominance (Quinn 1998). The greater investment in reproduction by females could result in less investment in vegetative growth than males, so overtime the proportion of male plants will increase as plants lose biomass and energy when grazed and males may have the capacity to recover faster (Pickering & Hill 2002, Delph 2011, Viejo et al. 2011).

Three important knowledge gaps will be assessed in this chapter. Surveys showed seasonal variation in the abundance of feeding swans, with peak abundance in autumn (Chapter 3). However, it is not clear if this results in any difference in grazing pressure on seagrasses. Secondly, the study species *H. ovalis* has a number of traits that allow it to tolerate grazing. However, it is not known if the response to grazing is dependant on the time of year, particularly during winter, when light limitation, low water temperatures and potentially lower carbohydrate concentrations could limit the capacity of seagrasses to tolerate grazing.
Thirdly, sexual reproduction could also respond to grazing, but this has rarely been tested in seagrasses. Therefore, the three aims are:

1. Determine whether there are temporal variations in black swan grazing pressure on the Lower Swan River estuary;
2. Identify detectable growth responses in *H. ovalis* after grazing and determine whether this varies temporally; and
3. Investigate the impact of grazing on the reproductive capacity of *H. ovalis*, specifically flowering, fruit production, seed production, and sex ratios.

4.2 Methods

4.2.1 Temporal variation in swan grazing pressure

Site selection

To determine if there was temporal (inter-annual) variation in swan grazing pressure on the Lower Swan River estuary, a 14 day experiment was conducted to determine how much seagrass was consumed by black swans. The experiment was conducted at three sites with a high abundance of swans in each season (spring, summer, autumn and winter). These sites were a subset of those sampled for the 'associations between swan abundance and site characteristics' study (see section 3.3.3). As the aim of the study was to determine the maximum grazing pressure exerted by swans and whether this varied seasonally, only the high abundance sites were selected (Table 4.2). Therefore, different sites were used in each season.

Table 4.2 Table of three sites used for habitat characterisation study during the four seasons (spring, summer, autumn and winter).

	Season			
	Spring	**Summer**	**Autumn**	**Winter**
Site	Point Walter South	Point Walter South	Point Walter South	Troy Park
	Freshwater Bay A	Freshwater Bay A	Freshwater Bay A	Como Mid B
	Burke Drive East B	Burke Drive East B	Burke Drive East B	Burke Drive East B

Observational study

The ‘grazing pressure’ experiment was conducted over 14 days in each season (spring – November, summer – February, autumn – May & winter - August). At each site, grazing pressure was measured using five 2×2m plots which were randomly located in a 40×40m patch of seagrass meadow where swans actively graze, following the methods of Eklof et al. (2009). All plots were in water depths of up to 1m. The quadrat location was marked with four marker pegs so that it could be re-located at the same position on the repeat survey. To map the initial grazing scars, the plot was divided into four 1 x1 m quadrants and each quadrant sub-divided into 10 x 10 cm squares. A diver then mapped the location and size of the grazing scars in each square to provide an estimate of total area grazed (to the nearest 0.1% of the plot). A grazing scar was classified as an empty patch of seagrass with torn pieces of rhizome and leaves in the patch (Figure 4.1).

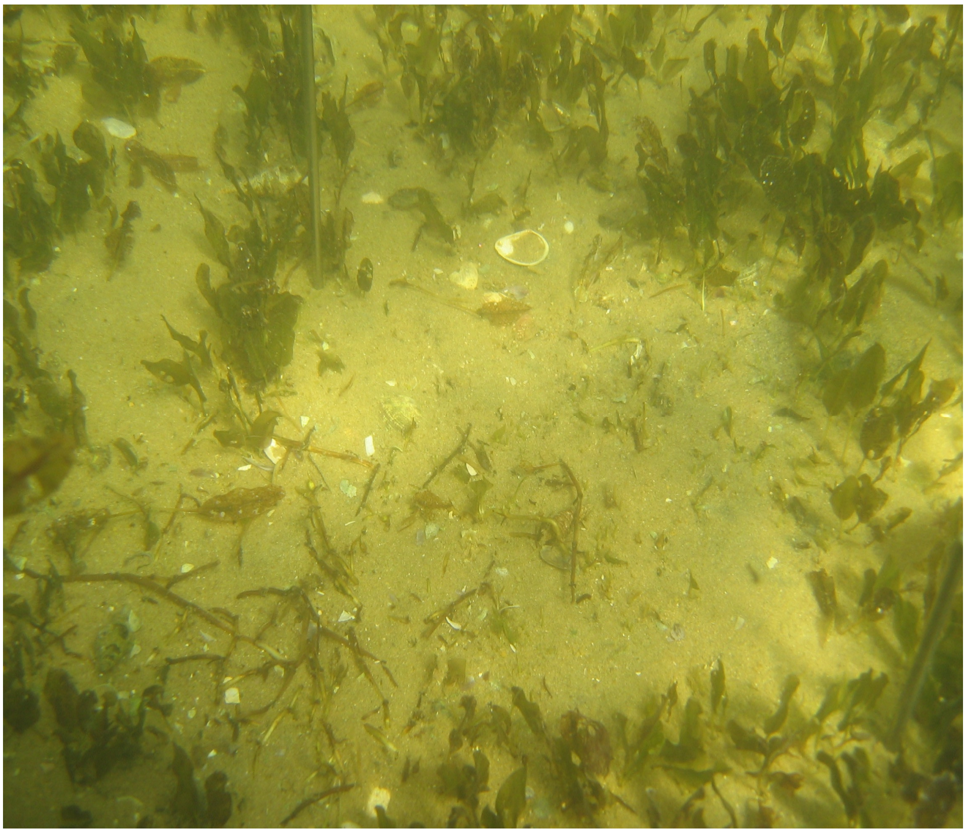


Figure 4.1 Image of a swan grazing scar showing an empty patch of seagrass with torn pieces of rhizome and leaves.

After 14 days the plots were revisited and the area of all new grazing scars were measured. Seagrass biomass was sampled inside and outside the grazing scars in each plot using a corer (i.d.10.5cm, depth=10cm). Core samples were processed to count the number of apice m^{-2}, providing an indication of the potential for growth in the plot. After, all plant material was dried for 24 hours at a temperature of 60°C. After drying the plant material was weighed to determine the difference in seagrass biomass outside and inside grazing scars, indicating how much biomass was removed by grazing.

Seagrass production was estimated by tagging 20 apices of *H. ovalis* (using plastic coated garden wire) at each site (Dennison 1985) at the beginning of the 14 day period. After 14 days, the marked apices with new production were collected and returned to the laboratory for processing. The new tissue produced from the tagged plants was dried for 24 hours at a temperature of 60°C and weighed. Areal seagrass production (g DW m^{-2} d^{-1}) was then calculated by multiplying the weight of new tissue per apex (g DW apice^{-1} d^{-1}) by the density of the apices (apices m^{-2}). The total biomass removed by grazing (g DW m^{-2} d^{-1}) was estimated by the difference in biomass (g DW m^{-2}) between ungrazed and newly grazed areas in each plot, multiplied by the total area grazed (m^{2}) in each plot, then divided by the number of days. Finally the proportion of daily production removed (% of growth day^{-1}) removed by grazing was calculated by dividing the biomass removed (g DW m^{-2} d^{-1}) by total production (g DW m^{-2} d^{-1}).

Data analysis

To test for temporal (inter-annual) variations in swan grazing pressure on the Lower Swan River estuary, surface area grazed (% day^{-1}), biomass of *H. ovalis* removed (g DW m^{-2} day^{-1}), total seagrass production (g DW m^{-2} day^{-1}) and production removed (% of daily production) were compared using one-way nested ANOVA's, with temporal variation treated as a fixed factor nested in site. Statistical analyses were performed using GMAV (Underwood & Chapman. 1997).

4.2.2 Temporal variation in the vegetative response of *H. ovalis* to black swan grazing

In order to investigate the response of *H. ovalis* to black swan grazing, both observational and manipulative studies were undertaken, measuring both vegetative growth and sexual reproduction. The timescales were different for vegetative response vs sexual reproductive response due to the sexual reproductive patterns of *H. ovalis*. Vegetative growth was measured four times during the year to investigate temporal variation, while sexual reproduction was only measured during and summer and autumn, the period of flowering and fruiting in *H. ovalis* in the Lower Swan River estuary (Hillman et al. 1995).

Approach

Two approaches were used to test for any effect of grazing intensity on growth characteristics of *H. ovalis*: an observational study of growth characteristics at sites of differing natural grazing intensity and a simulated grazing experiment. These two approaches are described separately below.

Observational (correlative) study

An observational study was undertaken to determine if there was an association between growth characteristics of the seagrass *H .ovalis* and grazing intensity, and whether this differed inter-annually. The study was repeated four times: spring (10/11/2009-24/11/2009), summer (4/2/2010-18/2/2010), autumn (1/4/2010-14/4/2010) and winter (8/7/2010-22/7/2010) at nine sites across a natural grazing intensity gradient. These nine sites were the same sites used for the 'associations between swan abundance and site characteristics' study (see section 3.3.3) and captured the range of grazing pressures occurring in the Lower Swan River estuary.

Growth measures

At each site and time, vegetative growth was measured using rhizome tagging as described above, with 20 individuals tagged at each site. The tags were left for 13-16 days after which all tagged plants were collected. The tagged plants were traced forward to find the new apical meristem and all new growth was collected, including, roots, rhizome and leaves. All material was brought back to the laboratory and stored in a freezer until processing. Based on the new growth over the tagging period, the number of nodes, initiated apices (no internodes produced) and newly produced branches (containing at least one and a maximum of three internodes) were counted from the rhizome, the number of new leaf pairs formed and the rhizome length was measured. From these measurements, five variables were calculated: rhizome extension rate (cm day^{-1}); leaf production rate (leaf pair day^{-1}); branching frequency (number of branches/ nodes); initiated apices (initiated apices/nodes); and apice productivity (g DW apice^{-1} d^{-1}). Apice productivity was estimated by first removing all algae on the seagrass then drying it for 24 hours at a temperature of 60° C and the dried material was weighed. Production was estimated from the dry weight of new production (g DW apice^{-1}) divided by the number of days the experiment took place.

Data analysis

To assess if there was a relationship between swan grazing (density of swans observed grazing (km^{-2}) at each site) and *H. ovalis* vegetative growth, each growth variable was correlated (simple linear regression) against density of grazing swans for each time, using SPSS (SPSS 2008). The variable 'density of swans observed grazing' was an average of all observations at the site within each season (i.e. n=10), as described in section 3.3.1.

Simulated grazing experiment

Changes in growth measured in the correlative study may be due to a variety of factors, not just grazing. The experimental study manipulated just one factor to test the effect of grazing on growth patterns.

In order to detect any growth responses in *H. ovalis* after grazing and to test if this response varied temporally (inter-annually), a simulated grazing experiment was undertaken over 21 days in summer (January) and in winter (June). These times were chosen as peak growth of the seagrass *H. ovalis* occurs in summer in the Lower Swan River estuary and minimal growth in winter (Hillman et al. 1995). At these times, light limitation, low water temperatures and potentially lower carbohydrate concentrations could limit the capacity of seagrasses to tolerate grazing. One type of grazing was simulated - repeated rhizome grazing. While black swans are known to perform two types of grazing ('rhizome' and 'mowing') (Eklof et al. 2009), rhizome grazing is the most common and was the only grazing type to induce a response from *H. ovalis* in earlier studies (Eklof et al. 2009). The experiment was conducted at Bishop Road (Figure 4.2, 32○00'12.73, 115○47'28.32), an area where little swan grazing or human activity has been observed. Therefore, the findings give an indication of how ungrazed *H. ovalis* meadows respond to grazing and not how pre-grazed meadows, which may have adapted to this selective pressure, respond to additional grazing.

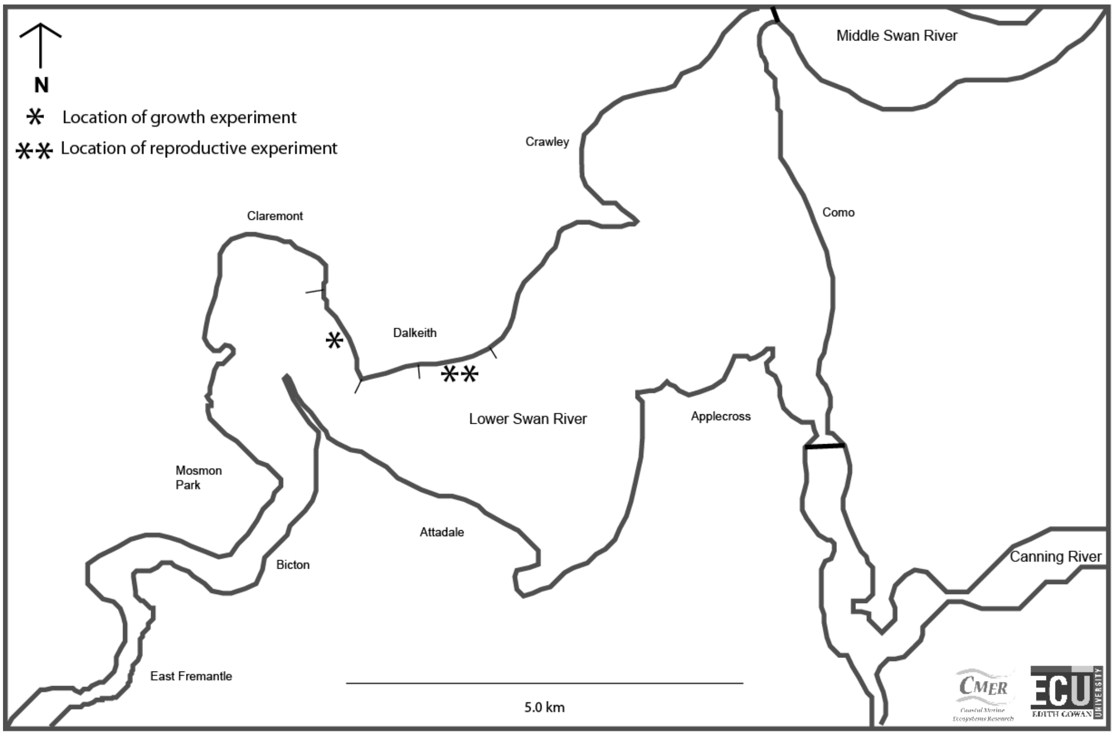


Figure 4.2 Location of the sites used for growth and reproductive experiment.

The grazing treatment (repeated rhizome grazing) was applied to six replicate plots. An additional six plots were established as controls and were similar to the treatment plots in all respects but were not subjected to simulated grazing. Each plot was 1x1m and the treatments were randomly assigned. Plots were located at depths ranging between 0.5-1m to ensure factors such as light were consistent, and that it is ecologically relevant as this is the depth in which swans can graze. Furthermore, Hillman et al. (1995) showed that most *H. ovalis* in the Swan River estuary lies in the depth range of 0-1m. Since seagrasses have the potential to translocate energy stores through their rhizomes, it was important to ensure the plots were physiologically independent. Consequently, plots were placed 1m apart as previous studies have shown this is an adequate distance to ensure there is no translocation of resources between grazing treatments (Marba et al. 2002). Grazing was simulated at the start of the experiment by cutting rhizomes with a corer (i.d. 4.0cm, depth=10cm), four times in each 1x1m plot, on three separate occasions within the first week. This simulated repeated rhizome grazing and removed approximately 12 % of the surface area, as previous studies have indicated this grazing pressure can induce a vegetative response (Eklof et al. 2009). Once the simulated rhizome grazing was completed, 4 randomly selected apices within the plot were tagged using plastic coated garden wire for growth measures as described above. The plots were left for 21days and were not exposed to any more grazing, then the tagged plants were traced forward to find the new apical meristem and the entire new growth, including roots, rhizome and leaves were collected. All material was treated as described in the observational study and the same variables calculated.

Data analysis

A two-way ANOVA was used to test for significant effects of simulated grazing and time of year (fixed factors) on each of the five growth variables using GMAV (Underwood & Chapman. 1997). All data was tested for conformity with the assumptions of homogeneity of variance and normality; data failing to meet these assumptions were log transformed and all proportion data were arc-sin transformed (Quinn & Keough 2002). Post-hoc tests were performed by the Student-Newman Keuls (SNK) test.

4.2.3 Sexual reproductive response of *H. ovalis* to black swan grazing

Approach

Two approaches were used to test for any effect of grazing intensity on sexual reproductive characteristics of *H. ovalis*: an observational study of sexual reproductive characteristics at sites of differing natural grazing intensity and a simulated grazing experiment. These two approaches are described separately below.

Observational (correlative) study

In order to assess if there was a relationship between grazing intensity and sexual reproductive characteristics of the seagrass *H. ovalis*, an observational study was undertaken similar to that undertaken for 'associations between vegetative growth and grazing' (Section 4.3.2). The reproductive study was only carried out at one time of year, as flowering and fruiting has only been observed initiating in spring and continuing through summer. At each site (Table 3.3) twenty (i.d.10.5cm, depth=10cm) cores were collected in summer (January) for flowering intensity and sex ratio measures and autumn (March) for fruiting intensity and seed production. These times were chosen as January is the peak flowering period for *H. ovalis* in the Lower Swan River estuary, while March is the time of peak fruiting and seed production (Hillman et al. 1995). The material was frozen until processing in the laboratory where the number of flowers (male and female), fruits, nodes and seeds per fruit were counted in each sample. Male flowers were counted if they were at any stage from the initiation phase through to a flower with a stalk and empty pollen sacs. Female flowers were counted through their development from the initiation phase through to the mature stage with extended styles. Once the styles were broken and blackened at the tips, it was no longer defined as a female flower, but a fruit.

Flowering intensity was calculated as:

$$F_I = \frac{TM + TF}{TotalNodes} x100$$

Where F_1 = flowering intensity, TM = total number of male flowers and TF = total number of female flowers.

Fruiting intensity was calculated as:

$$F_2 = \frac{TFr}{TotalNodes} x100$$

Where F_2 = fruiting intensity and TFr = total number of fruits.

Seed production was calculated as:

$$S_I = \frac{TotalSeeds}{TFr}$$

Where S_1 = seed production and TFr = total number of fruits.

Sex Ratio was calculated as:

$$S_I = \frac{TM}{(TM + TF)}$$

Where S_1 = Sex ratio, TM = total number of male flowers and TF = total number of female flowers.

Sex ratios are commonly calculated based on the proportion of males to females in offspring or have also been calculated based on the number of male to female individuals in an adult population (de Jong & Klinkhamer 2002).

Data analysis

To determine whether there was a relationship between swan grazing intensity and sexual reproductive characteristics of *H. ovalis* simple linear regressions were performed for each reproductive characteristic (flowering intensity, sex ratio, fruiting intensity and seed production) against the density of swans observed grazing (km^2), as described in section 3.3.1, using SPSS (SPSS 2008). Flowering intensity and sex ratio results were taken from the January collection while seed production and fruiting intensity were taken from the March collection. For flowering intensity and sex ratio calculations, the density of swans observed grazing was averaged from the start of the survey period 13/9/2009 through to the point of sample collection in January (12/1/2010). For the fruiting intensity and seed production calculations, swan grazing densities were averaged from the start of the survey period through to the point of collection in March (18/3/2010). Irrespective of the time period, 'density of swans observed grazing' was an average of all observations at the site in each season (i.e. average of the 5 morning and 5 evening observations), as described in section 3.3.1.

Simulated grazing experiment

To determine if sexual reproduction is affected by grazing, a simulated grazing experiment was carried out between October 2009 and March 2010. The flowering period of *H. ovalis* in the Lower Swan River estuary starts in November/ December (Hillman et al. 1995), therefore simulated grazing needed to be initiated before flowering started in November (Hillman et al. 1995). Plants were collected during January, as this is the time of peak flowering and also March, as this is the time of peak seed production (Hillman et al. 1995). Due to the rapid growth rates and turnover of plants, grazing was repeated through-out the experiment every two weeks to ensure a continual grazing pressure was exerted on the plants.

This experiment was conducted at Iris Road on the Lower Swan River estuary (Figure 4.2, 32○00'12.26, 115○47'59.63). This site was chosen for the reasons described in the growth response manipulation study. Seagrass plots were located randomly at depths ranging between 0-1m to ensure factors such as light were as similar as possible. The depth of 0-1m was chosen as previous studies have shown swans usually graze up to a depth of 1m (Marchant & Higgins 1990).

Six replicate plots (2 x 2 m) were randomly assigned to the simulated grazing treatment and six to controls. Treatment plots received repeated, simulated rhizome grazing. The rhizomes were cut using a corer (i.d. 4.0 cm, depth=10cm) and coring areas of seagrass in each 2 x 2m plot 27 times, approximately 6 % of the surface area, every two weeks for the duration of the experiment. Control plots were treated identically to treatment plots but were not subjected to the simulated grazing. During January and March five cores (i.d. 10.5 cm, depth=10cm) were taken in each plot and the samples sieved, frozen and brought back to the laboratory to be stored until being analysed. In each of the treatments 4 variables were measured: the flowering intensity, sex ratio, fruiting intensity and seed production.

Data analysis

An independent sample T-test was used to test for significant effects of simulated grazing on each of the four reproduction variables. All data were tested for conformity with the assumptions of homogeneity of variance and normality, data failing to meet these assumptions were log transformed and proportion data were arc-sin transformed as per, Quinn & Keough (2002). Data were analysed using SPSS (SPSS 2008).

4.3 Results

4.3.1 Swan grazing pressure

Surface area grazed (% day^{-1})

There were significant differences in the surface area grazed (% day^{-1}) between different times of year and sites nested within times of year (Table 4.3, p.0<0.05). Autumn had a significantly higher percentage of surface area grazed (0.81 ± 0.08 % day^{-1}) compared to summer, spring and winter (0.64 ± 0.07; 0.28 ± 0.03 & 0.28 ± 0.03 %, day^{-1} respectively). There were significant differences among sites in spring, summer and autumn but not in winter. Cunningham Street had the highest surface area grazed during autumn (1.06 ± .05 % day^{-1}), while Freshwater Bay A had the least during spring (0.14 ± 0.02 % day^{-1}) (Figure 4.3, Table 7.2).

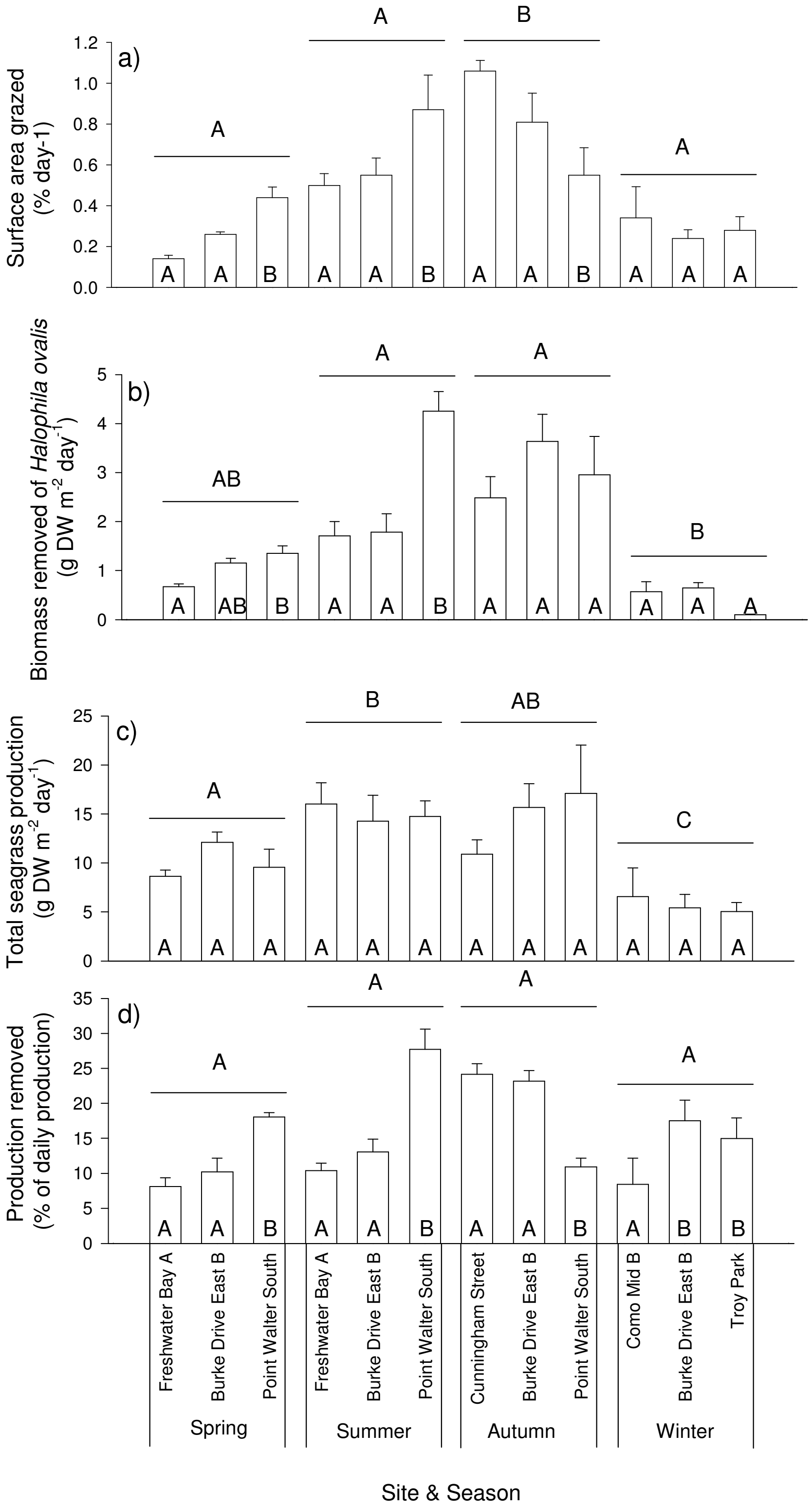


Figure 4.3 Seasonal (spring, summer, autumn and winter) seagrass (*H. ovalis*) production and swan grazing parameters for the Lower Swan River estuary: (a) surface area grazed, (b) biomass removed by swan grazing, (c) total seagrass production, (d) percentage of production removed by swans. Two-way nested ANOVA comparing site (letters in columns) and season (letters on top of columns). All data are means ± SE.

Table 4.3 Summary of nested ANOVA results for the surface area grazed (% day^{-1}) of *H.ovalis* by swans during different seasons (spring, summer, autumn and winter) and sites (three per season) on the Lower Swan River estuary.

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Season	50.21	3	16.74	6.63	0.01
Site within season	20.20	8	2.52	4.15	<0.01
Residual	29.23	48	0.61		
Total	99,63	59			

Biomass of H. ovalis removed (g DW m^{-2} day^{-1})

There were significant differences in the biomass removed of *H. ovalis* (g DW m^{-2} day^{-1}) among seasons and sites within seasons (Table 4.4, p.0<0.05). Autumn and summer (3.02 ± 0.33 & 2.58 ± 0.84 g DW m^{-2} day^{-1}) had significantly more biomass removed than winter (0.44 ± 0.17g DW m^{-2} day^{-1}). The biomass removed during spring (1.05 ± 0.20 g DW m^{-2} day^{-1}) was not significantly different to that in the other seasons. There were also significant differences among sites in spring and summer; however, there were no significant differences between sites in autumn or winter. Point Walter South had the greatest biomass removed (4.25 ± 0.40 g DW m^{-2} day^{-1}) during summer. Como Mid B had the lowest biomass removed (0.57 ± 0.21 g DW m^{-2} day^{-1}) during winter (Figure 4.3, Table 7.2).

Table 4.4 Summary of nested ANOVA results for the biomass removed of *H. ovalis* (g DW m^{-2} day^{-1}) by swans during different seasons (spring, summer, autumn and winter) and sites (three per season) on the Lower Swan River estuary.

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Season	25.23	3	8.42	9.83	<0.01
Site within season	6.85	8	0.86	2.92	0.01
Residual	14.06	48	0.29		
Total	46.15	59			

Total seagrass production (g DW m^{-2} day^{-1})

There were significant differences in the total seagrass production (g DW m^{-2} day^{-1}) between different times of year (p.0<0.05). However, there was no significant differences at sites within seasons (Table 4.5, p>0.05). Peak production was observed across all sites in summer and autumn (15 ± 1.18 & 14.56 ± 1.89 g DW m^{-2} day^{-1}), while the minimum production was observed across all sites in winter (5.68 ± 0.55 g DW m^{-2} day^{-1}). There was no difference between sites in any season (Figure 4.3, Table 7.2).

Table 4.5 Summary of nested ANOVA results for the total seagrass production of *H. ovalis* (g DW m^{-2} day^{-1}) during different seasons (spring, summer, autumn and winter) and sites (three per season) on the Lower Swan River estuary.

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Season	8.44	3	2.81	21.37	<0.01
Site within season	1.05	8	0.13	0.55	0.81
Residual	11.49	48	0.24		
Total	20.99	59			

Production removed (% of daily production)

There was no significant effect of time of year on the proportion of *H. ovalis* production removed by grazing (% of daily production). However there were significant differences among sites within seasons (Table 4.6, p>0.05), in all four seasons. The highest estimated removal of production was at Point Walter South (27.71 ± 2.91%) during summer while, Freshwater Bay A had the lowest production removed (8.1 ± 1.28%), during spring (Figure 4.3, Table 7.2).

Table 4.6 Summary of nested ANOVA results for the production removed (% of daily production) of *H.ovalis* by swans during different seasons (spring, summer, autumn and winter) and sites (three per season) on the Lower Swan River estuary.

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Season	335.25	3	111.75	0.72	0.57
Site within season	1237.39	8	154.68	9.32	<0.01
Residual	796.63	48	16.60		
Total	2369.27	59			

4.3.2 Temporal variation in growth characteristics across a natural gradient of grazing

There were significant linear relationships between the density of grazing swans and three growth characteristics of *H. ovalis* (seagrass productivity, leaf production rate and number of initiated apices). However, the nature of these associations was dependent on the time of year (Table 4.7, Figure 4.4). In summer, seagrass productivity was higher at sites with greater densities of grazing swans, but in winter the pattern was reversed with productivity being lower at sites with greater densities of grazing swans. However, although statistically significant the relationship was weak in summer (4%) and moderate in winter (33%). Therefore there are likely to be other factors affecting seagrass production, not just grazing. In spring and autumn there was no significant relationship between grazing swan density and productivity.

Leaf production rate had a positive linear relationship with the density of grazing swans, but only occurred in spring. During this time there was also a decrease in initiated apices with greater densities of grazing swans. However, although statistically significant these were weak relationships (7 & 8%). Therefore there are likely to be other factors affecting leaf production and initiated apices, not just grazing. No other variables had any significant linear relationships with swan grazing density.

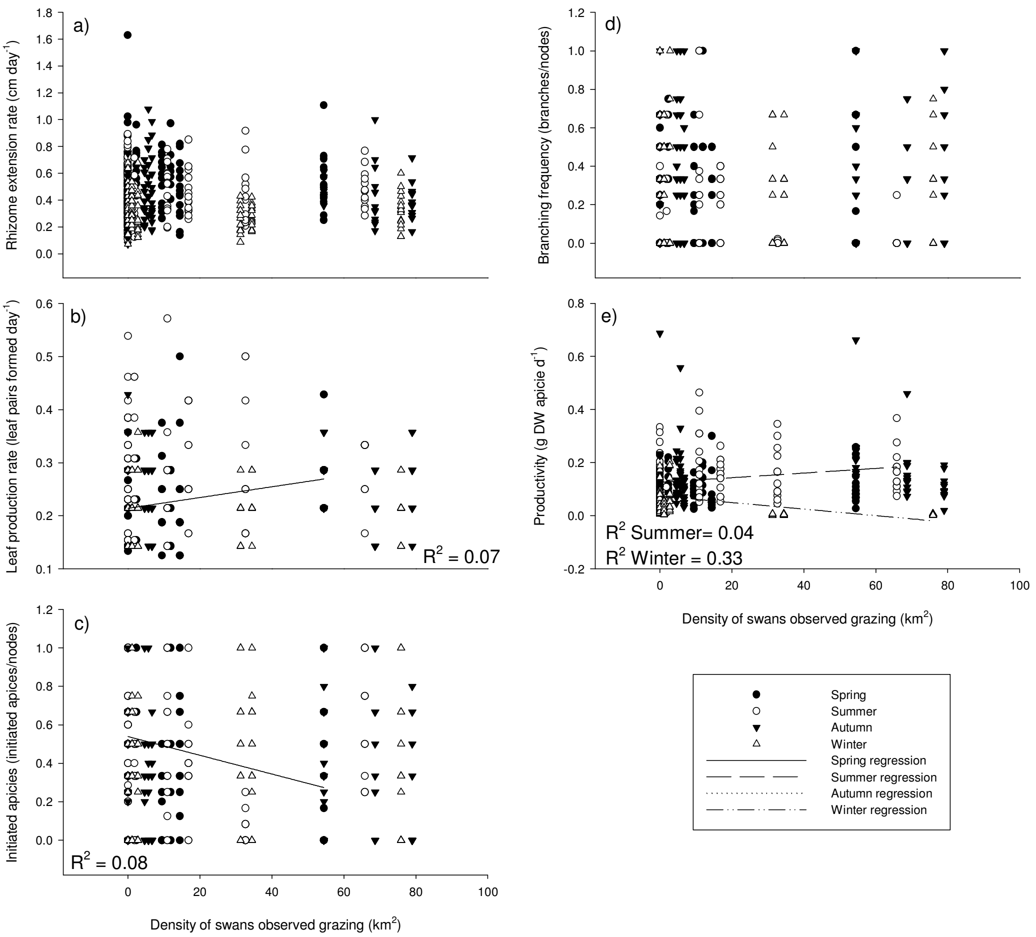


Figure 4.4 Simple linear regressions comparing grazing swan density (km^2) with five different growth characteristics: (a) rhizome extension rate, (b) leaf production rate, (c) initiated apices, (d) branching frequency and (e) apical productivity of *H. ovalis* on the Lower Swan River estuary in four different seasons (spring, summer, autumn and winter).

Table 4.7 Simple linear regression results comparing swan grazing density and five different growth characteristics (rhizome extension rate, leaf production rate, initiated apices, branching frequency and apical productivity) of *H. ovalis* on the Lower Swan River estuary in four different seasons (spring, summer, autumn and winter). *Note regression equations at bottom of table.

Season & variable	**Df**	**B**	**SE**	**R^2**	**P**
Spring					
Rhizome extension rate	105	-0.00	0.00	0.01	0.46
Leaf production rate	105	66.36	24.24	0.07	**0.01**
Initiated apices	105	-15.32	5.29	0.08	**0.01**
Branching frequency	105	4.13	6.72	0.00	0.54
Productivity	105	48.61	30.79	0.02	0.12
Summer					
Rhizome extension rate	126	2.26	10.27	0.00	0.83
Leaf production rate	126	13.83	20.14	0.00	0.49
Initiated apices	126	-2.56	6.40	0.00	0.69
Branching frequency	126	2.37	1.50	0.02	0.12
Productivity	126	48.55	20.65	0.04	**0.02**
Autumn					
Rhizome extension rate	122	-0.40	14.66	0.00	0.98
Leaf production rate	122	1.75	45.02	0.00	0.97
Initiated apices	122	14.05	9.16	0.01	0.13
Branching frequency	122	15.14	8.94	0.02	0.09
Productivity	122	36.94	27.06	0.02	0.18
Winter					
Rhizome extension rate	128	-22.57	18.34	0.01	0.22
Leaf production rate	128	-23.87	50.22	0.00	0.64
Initiated apices	128	10.83	7.98	0.01	0.18
Branching frequency	128	4.37	8.77	0.00	0.62
Productivity	128	5.12	0.64	0.33	**<0.01**

Regression equations

Spring

Rhizome extension rate - Swan abundance predicted = 0.56 - 0.001 (rhizome extension rate).
Leaf production rate - Swan abundance predicted = -0.31 + 66.36 (leaf production rate).
Initiated apices - Swan abundance predicted = 19.23 - 15.32 (initiated apices).
Branching frequency - Swan abundance predicted = 10.78 + 4.14 (branching frequency).
Productivity - Swan abundance predicted = 7.55 + 48.61 (productivity).

Summer

Rhizome extension rate - Swan abundance predicted = 12.47 + 2.26 (rhizome extension rate).
Leaf production rate - Swan abundance predicted = 9.60 + 13.83 (leaf production rate).
Initiated apices - Swan abundance predicted = 14.64 - 2.56 (initiated apices).
Branching frequency - Swan abundance predicted = 12.69 + 2.37 (branching frequency).
Productivity - Swan abundance predicted = 6.84 + 48.55 (productivity).

Autumn
Rhizome extension rate - Swan abundance predicted = 23.88 - 0.40 (rhizome extension rate).
Leaf production rate - Swan abundance predicted = 23.28 + 1.75 (leaf production rate).
Initiated apices - Swan abundance predicted = 19.27 + 14.05 (initiated apices).
Branching frequency - Swan abundance predicted = 18.89 + 15.14 (branching frequency).
Productivity - Swan abundance predicted = 18.43 + 36.94 (productivity).

Winter
Rhizome extension rate - Swan abundance predicted = 24.65 - 22.57 (rhizome extension rate).
Leaf production rate - Swan abundance predicted = 22.50 - 23.87 (leaf production rate).
Initiated apices - Swan abundance predicted = 13.90 + 10.83 (initiated apices).
Branching frequency - Swan abundance predicted = 16.52 + 4.37 (branching frequency).
Productivity - Swan abundance predicted = 5.66 + 5.12 (productivity).

4.3.3 Growth response to simulated grazing

There was a significant effect of simulated grazing on the branching frequency of *H. ovalis,* but this was dependent on the time of year (S x G: $p<0.05$). It resulted in more branching (branches/nodes) during summer (0.58 ± 0.02 vs 0.18 ± 0.05) but significantly lower branching (0.08 ± 0.04 vs 0.34 ± 0.06) in winter (Table 4.8, Figure 4.5).

Grazing had no significant effect on any of the other growth parameters measured in the experiment, though there was a significant effect of time of year on some variables. During summer, the rhizome extension rate (cm day^{-1}, 0.62 ± 0.06 vs 0.34 ± 0.03), leaf production rate (leaf pairs formed day^{-1}, 0.28 ± 0.02 vs 0.21 ± 0.01) and productivity (g DW apex day^{-1}, 0.16 ± 0.02 vs 0.07 ± 0.01) were significantly higher compared to winter (Table 4.8, S: $p<0.05$, Figure 4.5).

There was no significant difference in the number of initiated apices (initiated apices/nodes) of *H. ovalis* when subjected to simulated grazing or at different times of the year (Table 4.8, Figure 4.5).

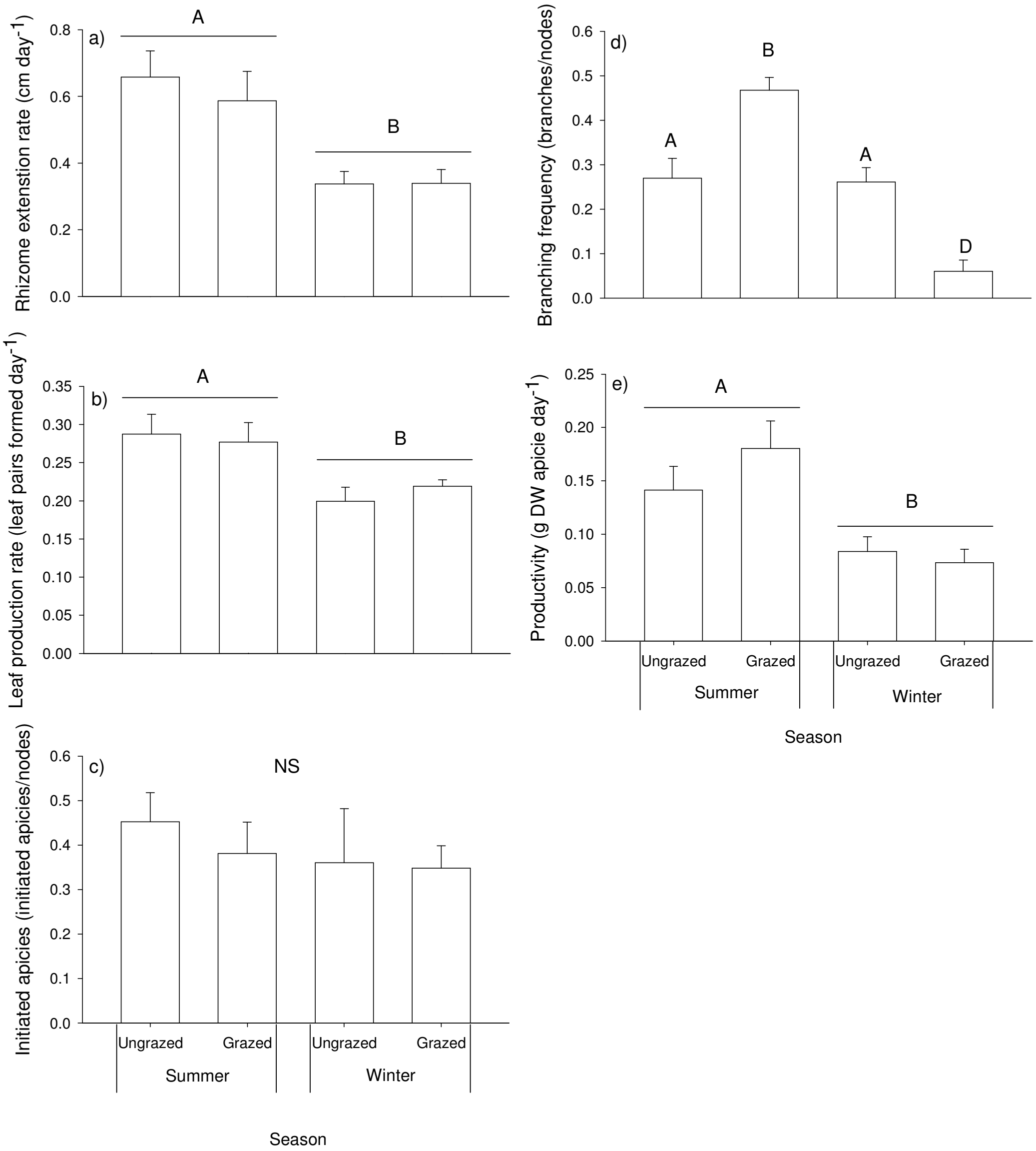


Figure 4.5 Growth characteristics: (a) rhizome extension rate, (b) leaf production rate, (c) initiated apices, (d) branching frequency and (e) apical productivity of *H. ovalis* with and without exposure to simulated grazing at two times of year (summer and winter) on the Lower Swan River estuary. Letters above columns indicate which treatments are different based on post-hoc comparisons. All data are means ± SE.

Table 4.8 Summary of two-way ANOVA results comparing growth characteristics (rhizome extension rate, leaf production rate, initiated apices, branching frequency and apical productivity) of *H. ovalis* to simulated grazing and ungrazed plots during summer and winter.

Variable	**Source**	**Sum of squares**	**Df**	**Mean Square**	**F**	**P**
Rhizome extension	Season	2.19	1	2.19	19.66	<0.01
	Grazing type	0.03	1	0.03	0.23	0.65
	S*G	0.02	1	0.02	0.21	0.65
	Residual	2.23	20	0.11		
	Total	4.45	23			
Leaf production rate	Season	0.51	1	0.51	13.86	<0.01
	Grazing type	0.01	1	0.01	0.21	0.65
	S*G	0.03	1	0.03	0.91	0.35
	Residual	0.73	20	0.04		
	Total	1.28	23			
Initiated apices	Season	147.36	1	147.36	0.79	0.39
	Grazing type	8.73	1	8.73	0.05	0.83
	S*G	57.83	1	57.83	0.31	0.58
	Residual	3737.32	20	186.86		
	Total	3951.25	23			
Branching frequency	Season	1627.90	1	1627.90	13.28	<0.01
	Grazing type	110.81	1	110.81	0.90	0.35
	S*G	2522.61	1	2522.61	20.58	<0.01
	Residual	2451.21	20	122.46		
	Total	6712.52	23			
Productivity	Season	3.28	1	3.28	17.28	<0.01
	Grazing type	0.01	1	0.01	0.07	0.79
	S*G	0.24	1	0.24	1.27	0.27
	Residual	3.79	20	0.18		
	Total	7.32	23			

4.3.4 Variation in sexual reproduction across a natural grazing gradient

There were significant linear relationships between the density of grazing swans and some reproductive characteristics of *H. ovalis* (Table 4.9, Figure 4.6). Flowering intensity, sex ratio and seed production were higher at sites with greater densities of grazing swans (more flowers per node, more males and more seeds per fruit (and per m^2) were observed where there were more grazing swans)

(Table 4.10). However, although statistically significant, sex ratio and seed production were weak relationships (8 & 6%) and flowering intensity was a moderate relationship (19%). Therefore there are likely to be other factors affecting flowering intensity, sex ratio and seed production, not just grazing. There was no significant relationship with fruiting intensity.

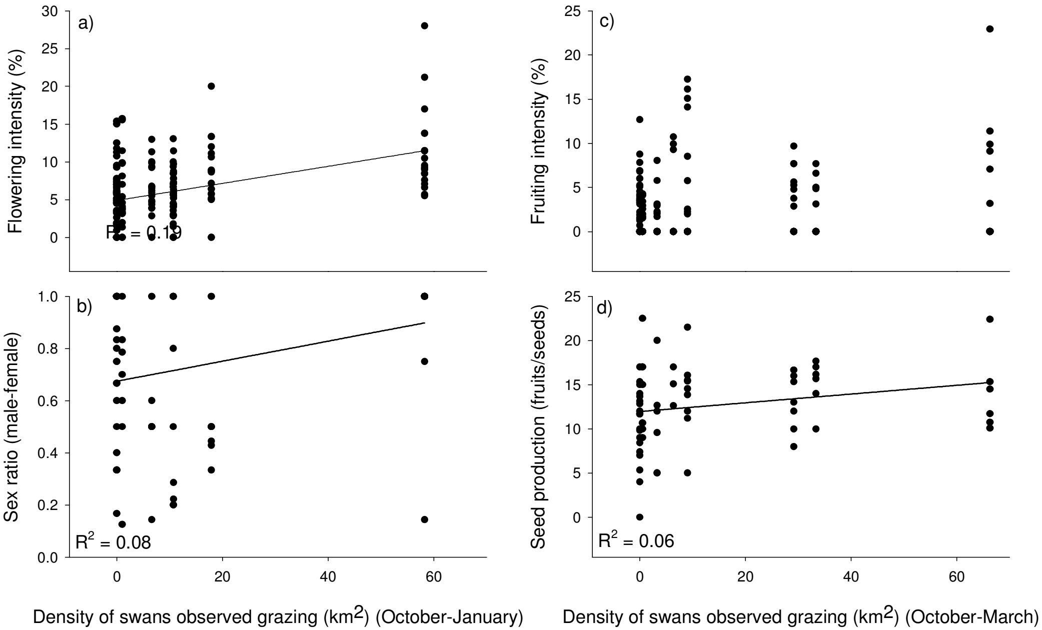


Figure 4.6 Simple linear regressions comparing swan abundance (km^2) with four reproductive characteristics: (a) fruiting intensity, (b) sex ratio, (c) fruiting intensity and (d) seed production of *H. ovalis* on the Lower Swan River estuary.

Table 4.9 Simple linear regression comparing swan abundance and four different reproductive characteristics (flowering intensity, sex ratio, fruiting intensity and seed production) of *H. ovalis* on the Lower Swan River estuary. *Note regression equations at bottom of table.

Variable	**Df**	**B**	**SE**	**R^2**	**P**
Flowering intensity	179	1.65	0.26	0.19	<0.01
Sex ratio	88	22.37	7.82	0.08	0.01
Fruiting intensity	179	0.22	0.41	0.00	0.59
Seed production	66	1.08	0.56	0.06	0.05

Regression equations
Flowering intensity - Swan abundance predicted = 1.43 + 1.65 (fruiting intensity).
Sex ratio - Swan abundance predicted = 0.25 + 22.37 (sex ratio).
Fruiting intensity - Swan abundance predicted = 2.22 + 0.001 (fruiting intensity).
Seed production - Swan abundance predicted = 0.98 + 1.06 (seed production).

Table 4.10 Summary of reproductive characteristic variables for *H.ovalis* on the Lower Swan River estuary at nine sites.

Site	**Variable**	**Averages** ± SE
Bishop Road	Male flowers (m^2)	393 ± 68
	Female flowers (m^2)	63 ± 23
	Nodes (January) (m^2)	10033 ± 635
	Fruits (m^2)	355 ± 70
	Seeds (m^2)	3822 ± 834
	Nodes (March) (m^2)	11322 ± 820
Majestic A	Male flowers (m^2)	31 ± 18
	Female flowers (m^2)	215 ± 42
	Nodes (January) (m^2)	5867 ± 500
	Fruits (m^2)	285 ± 76
	Seeds (m^2)	1530 ± 674
	Nodes (March) (m^2)	9055 ± 629
Matilda Bay B	Male flowers (m^2)	203 ± 61
	Female flowers (m^2)	165 ± 67
	Nodes (January) (m^2)	8978 ± 608
	Fruits (m^2)	101 ± 30
	Seeds (m^2)	1276 ± 409
	Nodes (March) (m^2)	8801 ± 755
Claremont Jetty	Male flowers (m^2)	247 ± 86
	Female flowers (m^2)	584 ± 143
	Nodes (January) (m^2)	15335 ± 1112
	Fruits (m^2)	114 ± 49
	Seeds (m^2)	1009 ± 491
	Nodes (March) (m^2)	9258 ± 770
Point Walter Café	Male flowers (m^2)	165 ± 44
	Female flowers (m^2)	304 ± 57
	Nodes (January) (m^2)	7537 ± 441
	Fruits (m^2)	165 ± 93
	Seeds (m^2)	2343 ± 1324
	Nodes (March) (m^2)	9734 ± 726
Como Mid B	Male flowers (m^2)	234 ± 80
	Female flowers (m^2)	222 ± 70
	Nodes (January) (m^2)	10274 ± 1184
	Fruits (m^2)	146 ± 58
	Seeds (m^2)	2057 ± 800
	Nodes (March) (m^2)	8528 ± 657

Table 4.10 (con't).

Site	**Variable**	**Averages ± SE**
Freshwater Bay A	Male flowers (m^2)	50 ± 20
	Female flowers (m^2)	660 ± 65
	Nodes (January) (m^2)	10725 ± 903
	Fruits (m^2)	361 ± 127
	Seeds (m^2)	4908 ± 1688
	Nodes (March) (m^2)	9194 ± 660
Burke Drive East B	Male flowers (m^2)	158 ± 43
	Female flowers (m^2)	412 ± 65
	Nodes (January) (m^2)	7023 ± 767
	Fruits (m^2)	222 ± 73
	Seeds (m^2)	2616 ± 850
	Nodes (March) (m^2)	7842 ± 570
Point Walter South	Male flowers (m^2)	1060 ± 151
	Female flowers (m^2)	120 ± 81
	Nodes (January) (m^2)	10864 ± 742
	Fruits (m^2)	260 ± 98
	Seeds (m^2)	3435 ± 1329
	Nodes (March) (m^2)	10325 ± 957

4.3.5 Response of sexual reproduction to simulated grazing

H. ovalis flowering intensity was greater in grazed treatments than control plots (25 ± 2 % vs. 12 ± 2 %) (Table 4.11, $p<0.05$, Figure 4.7). There was no significant difference in the other reproductive characteristics, sex ratio (0.38 ± 0.19 vs. 0.19 ± 0.14), fruiting intensity (7 ± 2.7 vs. 4 ± 1.4) and seed production (16 ± 0.6 vs. 14 ± 0.9) (Table 4.12, $p>0.05$, Figure 4.7), despite a trend of increasing mean values in the grazed treatments (Table 4.11 & 4.12).

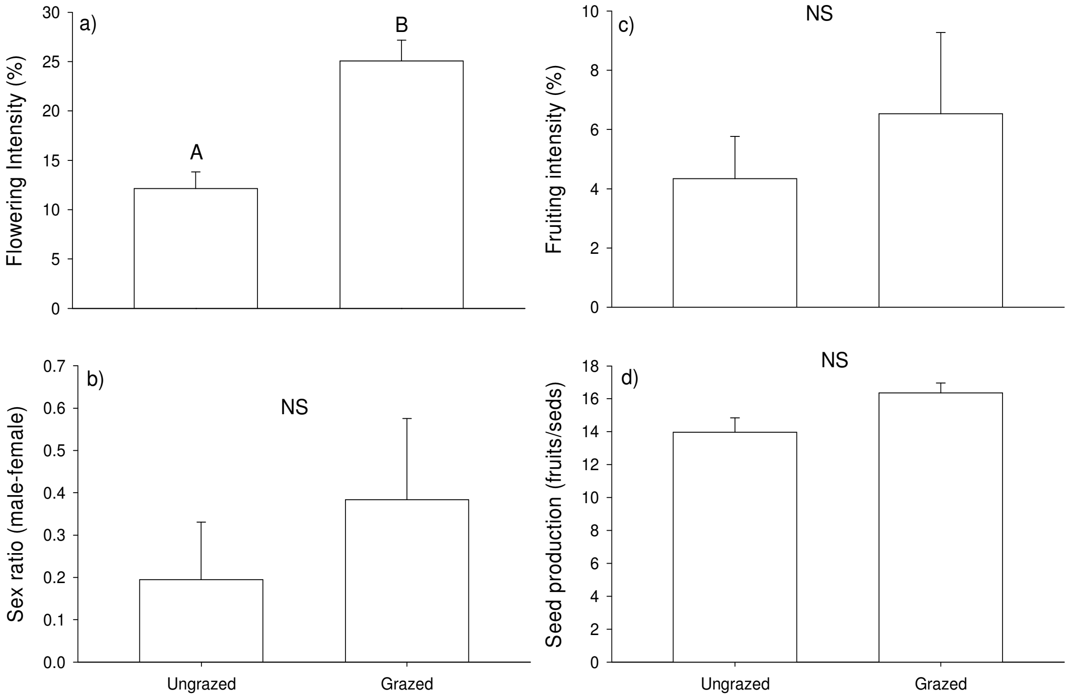


Figure 4.7 Four reproductive characteristics: (a) fruiting intensity, (b) sex ratio, (c) fruiting intensity and (d) seed production of *H. ovalis* with and without exposure to simulated grazing. Letters above columns indicate which treatments are different based on post-hoc comparisons. *Note flowering intensity and sex ratio samples collected in January 2010 and fruiting intensity and seed production samples collected in March 2010. All data are means ± SE.

Table 4.11 Summary of independent samples T-tests comparing rhizome grazing treatment and control treatment for four reproductive characteristics (fruiting intensity, sex ratio, fruiting intensity and seed production) of *H.ovalis*.

Variable	Df	T	P
Flowering intensity	-4.81	10	0.01
Sex ratio	-0.90	10	0.39
Fruiting Intensity	0.71	10	0.49
Seed production	-2.27	10	0.06
Seeds (m^2)	-1.98	10	0.08
Fruits (m^2)	0.28	10	0.79
Nodes (January) (m^2)	-0.09	10	0.93
Nodes (March) (m^2)	1.18	10	0.26
Fruits (m^2)	0.28	10	0.79
Male flowers (m^2)	-0.92	10	0.38
Female flowers (m^2)	-0.12	10	0.90

Table 4.12 Summary of reproductive characteristic variables on the Lower Swan River estuary.

Variable	Control	Rhizome Grazing
Male flowers (m^2)	325 ± 249	1250 ± 682
Female flowers (m^2)	1216 ± 242	2087 ± 748
Nodes (January) (m^2)	13391 ± 1300	13279 ± 684
Fruits (m^2)	616 ± 206	758 ± 315
Seeds (m^2)	6656 ± 819	15162 ± 4279
Nodes (March) (m^2)	13608 ± 1663	11370 ± 726

4.4 Discussion

4.4.1 Temporal variation in grazing pressure

The black swan was a significant seagrass consumer on the Lower Swan River estuary. Maximum consumption occurred during summer and autumn, periods of maximum swan abundance (Chapter 3). Despite the seasonal variation in the mass of seagrass consumed, there was no seasonal difference in the total proportion of seagrass production consumed, 5-25%, approximately 6% of the standing crop. This was similar to that observed by Eklof et al. (2009). The lack of variation in total production removed over the year is due to the concurrent change in seagrass production, which was observed in this study and by Hillman et al. (1995), to be greatest in summer and autumn. Generally, the amount of net seagrass primary production removed by grazers is 2-40% (Valentine & Duffy 2006), indicating despite the low numbers of black swans on the Lower Swan River estuary they are significant grazers in this temperate system.

4.4.2 Vegetative and reproductive responses to grazing

In this study *H. ovalis* was observed to show traits of a tolerance strategy by its growth and sexual reproductive responses to grazing. Many seagrass species are tolerant of grazing, through increasing growth and production after grazing (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009). They do this by regrowing plant tissue removed by grazing, through the activation of dormant meristems and the utilisation of stored reserves, two key traits of the tolerance strategy (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009). However, in this study the variables that responded were not always consistent between the observational and manipulated studies, and varied with time of year.

Based on a tolerance strategy, it is expected that plants would increase initiation of apices and branching following grazing, resulting in a similar or faster growth and productivity, compared to ungrazed plants (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009). In addition, if conditions are limiting for growth (i.e. low light, temperature, nutrients or carbohydrate reserves) at different times of year, this could limit the ability of the plant to respond using a tolerance strategy and may reduce initiation of apices, branching and productivity following grazing. For example, when plants were shaded and carbohydrate reserves reduced prior to grazing, initiation of apices was negatively affected (Eklof et al. 2009). Increased seagrass productivity after grazing during summer and reduced productivity during winter has been observed in other studies (Macia 2000, Valentine et al. 2000).

In this study, there was no effect of grazing on the branching frequency across a natural swan grazing gradient, but a negative and weak relationship with initiation of apices in spring only. This does not support the tolerance strategy. However, the manipulated experiment showed that branching frequency was higher following grazing in summer; supporting the tolerance strategy. However, during winter branching frequency was reduced in grazed areas. This indicates that other environmental factors (temperature, light or nutrients) or conditions of the plant (carbohydrate supplies) affect how the plant responds to grazing. Growth (productivity) was positively affected by grazing across the swan grazing gradient in summer, although this was a very weak relationship. This indicates that with increased grazing *H. ovalis* plants can maintain their growth. However, in winter there was a negative and moderate effect of grazing on productivity.

This pattern was not supported by the manipulated experiment, although there was a trend of decreased branching in winter. The experiment shows that *H. ovalis* plants can cope with grazing by maintaining a similar productivity to ungrazed plants.

The trends revealed in the observational study reflect a population adapted to grazing over a long period of time (decades, centuries or possibly millennia). The observational study was carried out in an area that has repeated swan grazing of different densities, and although conditions were kept as similar as possible, except for the density of grazing swans, many other site specific differences may be affecting the growth response of the seagrass. The manipulated experiment clearly shows that *H. ovalis* seagrasses rarely grazed by swans have the potential to cope with grazing using the initiation of meristems and branching. This supports other studies that suggest *H. ovalis* can cope with grazing as it is a fast growing and highly resilient species (Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009). However, their ability to respond is reduced in winter, potentially due to other limiting factors. Despite this reduced ability to respond, there were no negative effects on the growth of *H. ovalis* in the manipulated experiment, but there was across the grazing gradient. This may be due to the fact that in the natural setting plants are repeatedly grazed which may result in declines in productivity over time.

This study has shown changes in sexual reproduction of *H. ovalis* after grazing. This allows the plants to maintain a similar or slightly higher fitness to ungrazed plants. In some terrestrial plants, grazing has been observed to increase sexual reproduction (Whitman et al. 1991, Lazo et al. 1994, Quiroga et al. 2010), by increasing flowering intensity and fruit production (Whitman et al. 1991, Forbs et al. 1997). This has also been observed in seagrasses but this is the first study to experimentally demonstrate it (Conacher et al. 1994, Peterken & Conacher 1997). Physical disturbance, somewhat similar to grazing has also caused increased flowering in seagrasses (Phillips et al. 1983, Alexandre et al. 2005, Hammerstrom et al. 2006).

The responses of some of the sexual reproductive characteristics were consistent between the observational and manipulated studies, but others varied. Flowering intensity responded consistently, increasing following grazing in the manipulated experiment and increasing across a grazing pressure gradient. While not statistically significant, there was a trend of increased seed production in the manipulated experiment and a corresponding significant positive relationship of seed production across a grazing pressure gradient, although it was a weak relationship. These results suggest grazed plants maintain a similar or slightly higher fitness to ungrazed plants (e.g. 15000 seeds m^2 in grazed plots vs 6600 seeds m^2 in ungrazed plots). The fitness of the plant from an evolutionary sense refers to an individual organism's contribution of offspring to the next generation, in this case through the amount of seeds the plant can produce (Campbell & Reece 2005). In some terrestrial studies populations of plants exposed to high levels of grazing had a higher fitness (measured as seed production) than populations with low levels of grazing (Boalt et al. 2010).

A weak relationship was also observed between grazing pressure (abundance of grazing swans) and sex ratio (increase in the proportion of male flowers with grazing pressure). Again, this trend has previously been observed in some terrestrial plants (Quinn 1998). In some dioecious plant species there is no bias in grazing on males or females but the costs of sexual reproduction are more in females, than males because additional energy is required to produce seeds (Delph 2011). Thus, the proportion of males will increase as plants lose biomass and energy when grazed, since males are suggested to recover more quickly (Pickering & Hill 2002, Delph 2011, Viejo et al. 2011).

These changes in sex ratio, together with flowering intensity in response to grazing may together be an advantage allowing the plant to cope with grazing. An evolutionary explanation is that some individuals may suffer pollen limitation and lower reproductive success, through a reduced quality and amount of pollen available to fertilise female flowers (Aschero & Zquez 2009). Following the removal of plants by grazing an increase in males, as observed in the observational study, may be a mechanism to reduce pollen limitation as more male flowers could produce more pollen, resulting in more pollen reaching the stigma of female flowers and therefore more ovules may be fertilised, producing more seeds (Zimmerman 1988, Stephenson et al. 1992, de Jong & Klinkhamer 2002).

Interestingly, the manipulated experiment did not show the same response as the observational study, although there was a trend of increasing males. This may be due to the time scale of the study. The plants measured in the observational study have been repeatedly grazed over time and are likely to have adapted to grazing, resulting in a shift in the sex ratio. However, the plants in the manipulated study are from an area rarely grazed, and were exposed to grazing for four months. Perhaps with repeated grazing for a longer period of time, the trend in increased males may become significant.

4.4.3 Management implications

From a local perspective, if swan abundance was to increase on the Lower Swan River estuary it could result in greater pressure being exerted on *H. ovalis* meadows. An increase in swan abundance is a strong possibility if wetlands on the SCP continue to dry and stay dry all year with the changing climate. Hydrological changes on the SCP is one of the main causes of wetland degradation and is driven by a number of processes including climate variability, land-use change and patterns of groundwater extraction (Horwitz et al. 2009). If these changes continue to occur, this study has shown *H .ovalis* can cope with increases in grazing during summer through an increase of growth, production and sexual reproduction. However, during winter the seagrass may not be as resilient to grazing and the limited carbohydrate reserves could reduce its capacity to respond to repeated grazing. Swan grazing should not be considered in isolation of other stresses. Other stresses on the seagrass, such as light limitation from algal mats, human disturbances and other potential grazers, may compound any effect of swan grazing on the potential for the seagrass to persist.

5. Conclusions and management implications

5.1 Temporal variation in waterbird abundance

In Australia, waterbird distributions are mostly influenced by episodic events, where movements are the result of rainfall and river flooding patterns creating a new habitat for waterbirds to use when ephemeral lakes and wetlands fill (Chambers & Loyn 2006, Dingle 2008, Roshier et al. 2009). In this study, black swan abundance tripled on the Lower Swan River estuary during autumn, compared to spring and doubled in summer and winter compared to spring. Winter and spring are periods when ephemeral lakes and wetlands on the surrounding SCP begin to fill and also coincides with the breeding cycle of the black swan. These changes in habitat availability and breeding behaviour may cause movements of waterbirds away from the Lower Swan River estuary, to ephemeral lakes and wetlands (Chambers & Loyn 2006, Lane et al. 2007, Kingsford et al. 2010). Waterbirds have been shown to make small scale movements, moving between wetlands, estuaries and lakes in the same region seeking water bodies to provide them with a suitable habitat for feeding and breeding (Bancroft et al. 2002, Bolduc & Afton 2008).

Permanent water bodies act as an important refuge for black swans while surrounding ephemeral water bodies are dry (Chambers & Loyn 2006, Lane et al. 2007, Kingsford et al. 2010). Although the Lower Swan River estuary showed increases in swan abundance during times that ephemeral water bodies were dry, swan linkages and connections between water bodies appear to be complex. It is estimated at times 4804.1 ha of seasonal wetlands are lost for swan habitat. Therefore, they are likely to seek permanent water bodies for refuge. Therefore, they are likely to seek permanent water bodies for refuge. For example, permanent wetlands on the SCP, such as Lake McLarty and Lake Pollard were also important for black swan habitat during these times, supporting even higher numbers than the Lower Swan River estuary (3112 ± 1064 & 1039 ± 386 vs 11 ± 1) (Table 5.1). Furthermore, some wetlands on the Birds Australia database showed seasonal variation, with increases in swan abundance during winter and spring on ephemeral wetlands and increase on permanent water bodies during summer and autumn, however, these patterns were not consistent across wetland types.

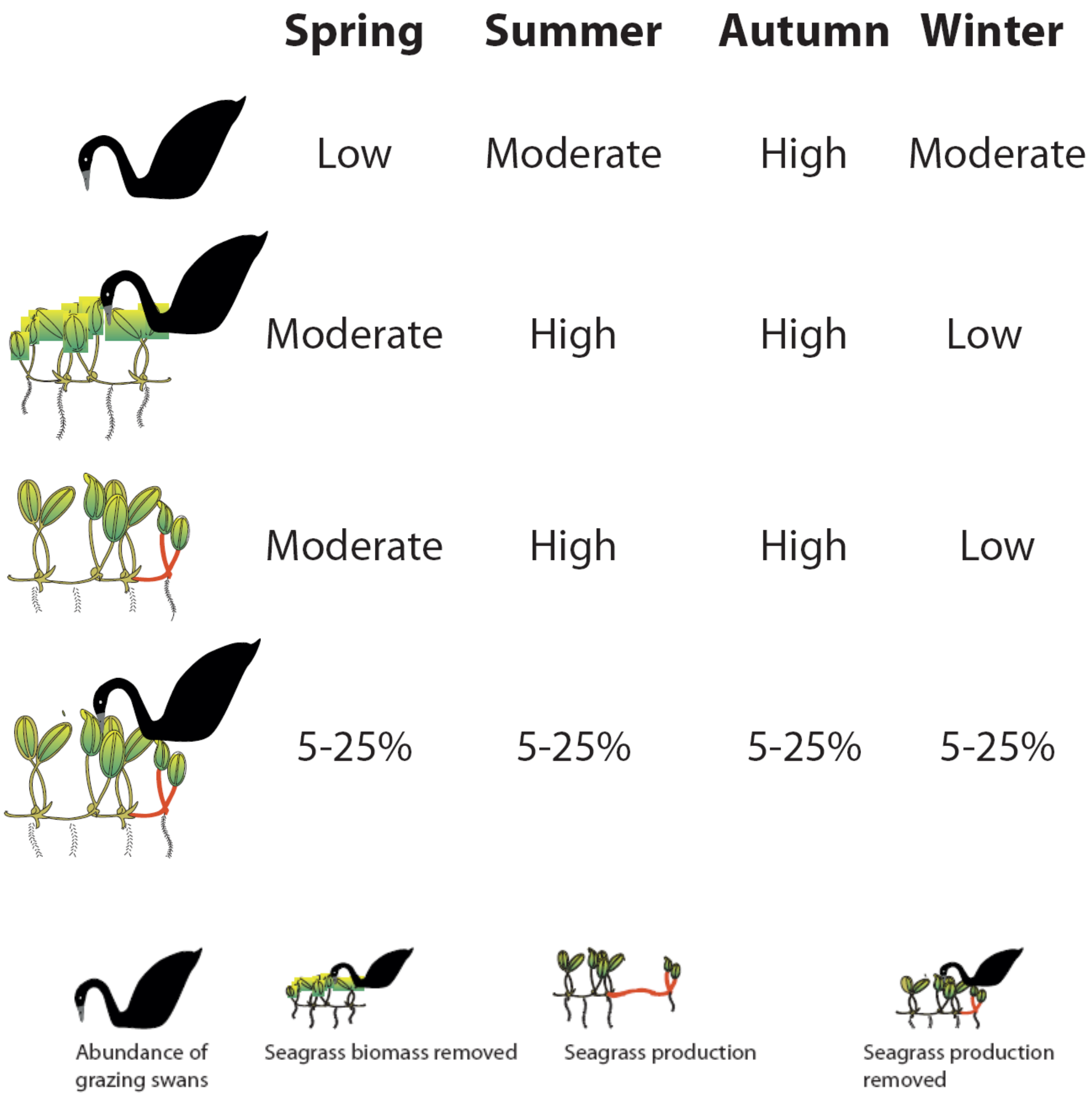
Table 5.1 Seasonal comparison of swan abundance (km^{-2}) at seven different wetlands and the Lower Swan River estuary

Site	Season	Swan abundance (km^{-2})
Swan River	Spring	6 ± 0
	Summer	11 ± 1
	Autumn	20 ± 2
	Winter	9 ± 1
Lake Kogolup	Spring	16 ± 0
	Summer	9 ± 3
	Autumn	3 ± 0
	Winter	14 ± 4
Lake Pollard	Spring	36 ± 27
	Summer	1039 ± 386
	Autumn	7 ± 5
	Winter	0 ± 0
Lake Preston	Spring	1 ± 0
	Summer	0 ± 0
	Autumn	0 ± 0
	Winter	1 ± 0
Thomsons Lake	Spring	99 ± 10
	Summer	36 ± 2
	Autumn	6 ± 0
	Winter	46 ± 20
Lake Gwelup	Spring	5 ± 1
	Summer	11 ± 3
	Autumn	6 ± 0
	Winter	14 ± 6
Forestdale Lake	Spring	76 ± 10
	Summer	15 ± 5
	Autumn	0 ± 0
	Winter	14 ± 7
Lake McLarty	Spring	2118 ± 626
	Summer	3112 ± 1064
	Autumn	794 ± 610
	Winter	398 ± 114

This complexity may indicate that these patterns are due to multiple factors (e.g. water height, food availability and breeding). These changes may be the result of increasing water levels in ephemeral habitats, where the swans move to smaller wetlands once they fill, then move to larger permanent water bodies, such as the Lower Swan River estuary, once the smaller wetlands dry. The black swan may also move to smaller wetlands for breeding as increasing water levels coincides with the breeding period of the black swan. However, only 3% of the data on the Birds Australia database contained counts of swans across different seasons. Therefore, conclusions about seasonal variation in this study were limited and cannot be considered representative of the entire area.

5.2 Temporal variation in swan grazing pressure

This study has shown that *H. ovalis* is an important food source for the black swan on the Lower Swan River estuary over the entire year. This extends the work of Eklof et al. (2009), who found seagrass was an important food source in autumn. In this study the majority of seagrass biomass removed across a year occurred during summer and autumn (Chapter 4**).** This corresponded with an increase in swan abundance on the river during summer and autumn (Chapter 3). At these times, swans move to the estuary as it provides a permanent habitat when ephemeral wetlands dry out (Chapter 2). This caused the number of feeding swans to increase on the river (Chapter 3). However, during this time seagrass production was at its peak (Chapter 4). So, although swan numbers changed with season, there was no significant difference in the amount of seagrass consumed, between 5-25% of total seagrass production all year round (Chapter 4, Figure 5.1). The production removed by grazing falls between the known percentages of net seagrass primary production consumed by marine grazers (2-40%), indicating the black swan is a significant seagrass consumer on this temperate estuary (Valentine & Duffy 2006).



	Spring	Summer	Autumn	Winter
Abundance of grazing swans	Low	Moderate	High	Moderate
Seagrass biomass removed	Moderate	High	High	Low
Seagrass production	Moderate	High	High	Low
Seagrass production removed	5-25%	5-25%	5-25%	5-25%

Figure 5.1 Summary of results from observational studies of swan abundance and the grazing pressure experiment on the Lower Swan River estuary.

Little is known on the variation in waterfowl grazing over a year in the southern hemisphere. However, from northern hemisphere studies we know a lack of variation in grazing pressure across a year is unusual: more grazing occurs during autumn and winter, due to an increase in bird abundance, coinciding with annual migrations (Jacobs et al. 1981, Nienhuis & Groenendijk 1986, Baldwin & Lovvorn 1994). However, in the southern hemisphere bird migration patterns appear to be more strongly influenced by aridity and rainfall frequency, with a milder and drier climate (Kingsford & Norman 2002). Therefore, birds move to larger permanent water bodies when smaller ephemeral wetlands dry out. This suggests that grazing in these permanent water bodies should be greater in summer and autumn. However, summer and autumn are also times of peak production in aquatic plants, like seagrass (Hillman et al. 1995, Kirkman & Kirkman 2000) so a shift in waterfowl abundance is unlikely to have an effect on macrophyte productivity removed by grazing, as this study demonstrated.

If there were to be a shift in the number of grazing waterbirds to permanent wetlands such as the Lower Swan River estuary during winter and spring, plants will be more susceptible to grazing because other environmental conditions limit there growth. Therefore any changes to the production removed by grazing can have implications for the plant's response, leading to a decline in total seagrass biomass. This has been observed in other wetlands in New Zealand and North America (Baldwin & Lovvorn 1994, Mitchell & Wass 1996) under high numbers of waterfowl grazers. However, swan grazing should not be considered in isolation of other stresses. Light limitation from algal mats, human disturbances and other potential grazers may compound any effect of swan grazing on the potential for the seagrass to persist.

5.3 Evidence for traits of a tolerance strategy and increased fitness

In this study *H. ovalis* was identified as a fast growing species with the ability to tolerate sustained levels of grazing. This was observed through the strategy of tolerance to grazing; the ability to survive regrow and reproduce after damage is sustained (Agrawal 2000). In this study *H. ovalis* expressed a number of traits of this strategy, including the activation of dormant meristems. Although it was not measured, it is also likely that stored reserves were utilised to support the activation of dormant meristems, as demonstrated by Eklof et al. (2009); both traits promote regrowth after damage is sustained. *H. ovalis* also showed changes in sexual reproduction, altering its flowering intensity and seed production following grazing. Other studies on seagrasses have observed these traits (Conacher et al. 1994, Peterken & Conacher 1997, Nakaoka & Aioi 1999, Kuiper-Linley et al. 2007, Eklof et al. 2009), however, past studies have only focused on the response at one time of year and few have looked at changes to sexual reproduction. This study showed the seagrass response to grazing varied at different times of the year, though the results were not consistent across the observational studies and experimental manipulations:

- Productivity was similar or slightly higher in the grazed areas during summer compared to winter in the observational study, but no difference was observed in the manipulative experiment;
- Branching frequency was higher in the experimental manipulation experiment in summer compared to winter, but no difference was observed in the observational study;
- Flowering intensity was higher in the experimental manipulation experiment and was slightly higher in grazed areas in the observational study; and
- Seed production was similar or slightly higher in grazed areas in the observational study, but no difference was observed in the manipulative experiment (Figure 5.2).

The different results between the observational studies and experimental manipulations may be due to the times scales of response. The trends revealed in the observational study reflect a population adapted to grazing over a long period of time (decades, centuries or possibly millennia), with the study observing the end result instead of the expression of the traits. On the other hand, the short-term experiments may not present a sufficient period of exposure to grazing to result in detectable effects. Therefore, the length of the experiment may only show a change in one particular trait and not a change in the longer term response of the plant. These traits may include changes in stored reserves, the number of activated meristems or changes to the plants sexual reproduction.

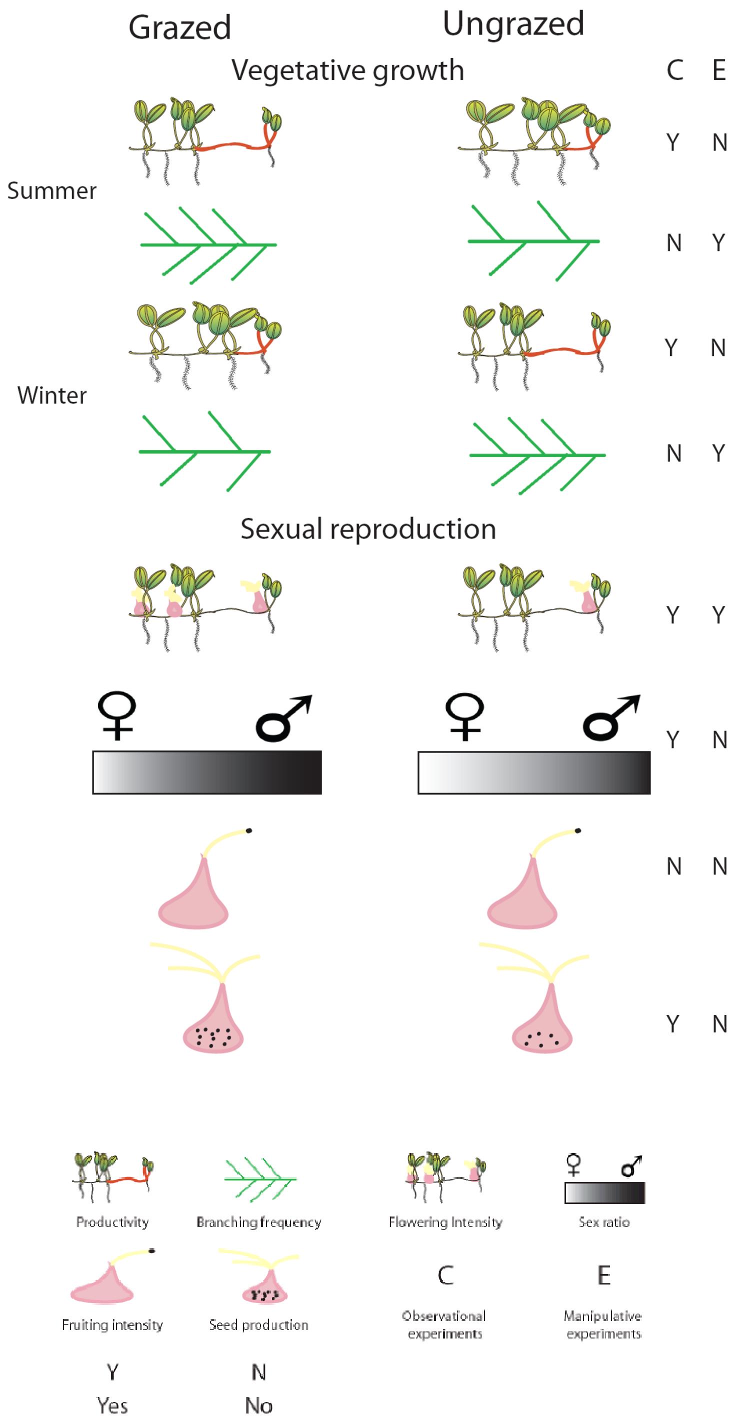


Figure 5.2 Conceptual model of results from observational and manipulative experiments. Y & N indicate whether a difference was detected in the observational and manipulative experiments.

This study has shown *H. ovalis* can cope with grazing through traits of a tolerance strategy. *Halophila* is one of the smaller seagrass species and is the preferred food source for many seagrass herbivores (green turtles, dugongs, manatees and fishes) (Valentine & Duffy 2006), so it is expected that *Halophila* would have evolved mechanisms to cope with grazing. Other larger species of seagrass are also able to cope with grazing, such as *Posidonia oceanica* (Verges et al. 2008) or *Thalassia testudinum* (Moran & Bjorndal 2005), but may be less resilient to grazing (Fourqurean et al. 2010, Olsen & Valiela 2010), particularly under high grazing pressures or when whole plants are removed. Despite these differences, across the range of seagrass species, from small to large, similar resource allocation and growth responses allow the plants to cope with grazing.

Due to the limited number of studies and contrasting results, there are no clear patterns at this stage as to how different species of seagrass vary in their response to grazing at different times of year. All studies carried out on *Thalassia testudinum* showed increased growth and productivity in summer following grazing. However, contrasting patterns occurred in winter and spring, either increasing or decreasing growth (Valentine et al. 1997, Macia 2000, Valentine et al. 2000, Moran & Bjorndal 2005, Fourqurean et al. 2010, Olsen & Valiela 2010). There are indications from my research on *Halophila* and those cited above that during winter seagrasses may be less resilient to grazing, possibly due to limited carbohydrate reserves, reducing their capacity to respond to repeated grazing. More work is needed to improve our understanding of the effect of time of year on plant response to grazing.

Sexual reproductive responses to grazing have rarely been studied. Of those species that have been studied, the smaller, faster growing ones such as *Halophila* (this research) and *Zostera* (Conacher et al. 1994) have been associated with increased flowering following grazing, whereas in larger species flowering is reduced (Lal et al. 2010). Potentially, the smaller faster growing seagrasses such as *Halophila,* which are more R-selected, will increase investment in sexual reproduction to cope with grazing, whereas the larger, slower growing, k-selected species will invest less under a grazing regime as they allocate resources to growth and prolonging life (Gadgil & Solbrig 1972). More work is needed to test this hypothesis.

5.4 Management of water birds and water bird habitat

Sustaining healthy populations of waterbirds on water bodies is a challenge for resource managers worldwide (Zhijun et al. 2010). Usually, there are a suite of characteristics that influence water birds including water depth, water level fluctuation, vegetation, salinity, topography, food type, food accessibility, wetland size, and wetland connectivity (Zhijun et al. 2010). In order to manage waterbirds there are two key questions managers have to ask;

1. How important is a site for waterbird use?
2. How do you co-ordinate actions across the landscape so waterbirds have the right amount of quality habitat available, at the right time in the right places?

In this study, temporal variation in swan abundance was observed on the Lower Swan River estuary and it is proposed that this reflects a movement of swans to ephemeral wetlands. This builds on our understanding of swan linkages and suggests ephemeral wetlands are important water bodies during winter and spring providing habitat for feeding and breeding. However, once these areas dry waterbirds move to larger permanent water bodies during summer and autumn. In terms of management, if swans are more common in certain areas at different times of year on larger water bodies, such as the Lower Swan River estuary, to maximise the abundance and survival of swans, management actions could be applied in different locations restricting activities that negatively impact on swans (e.g. number of dogs, number of jet skis & number of boats).

In this study three swan hotspots were identified on the Lower Swan River estuary and there were particular characteristics of these sites that were associated with swan abundance (Figure 5.3). These hotspots included Point Walter (spring, summer and autumn), Alfred Cove (spring, summer, autumn and winter) and Como Foreshore (autumn and winter). Previous studies have also shown these were key swan hotspots during summer (Eklof et al. 2009).

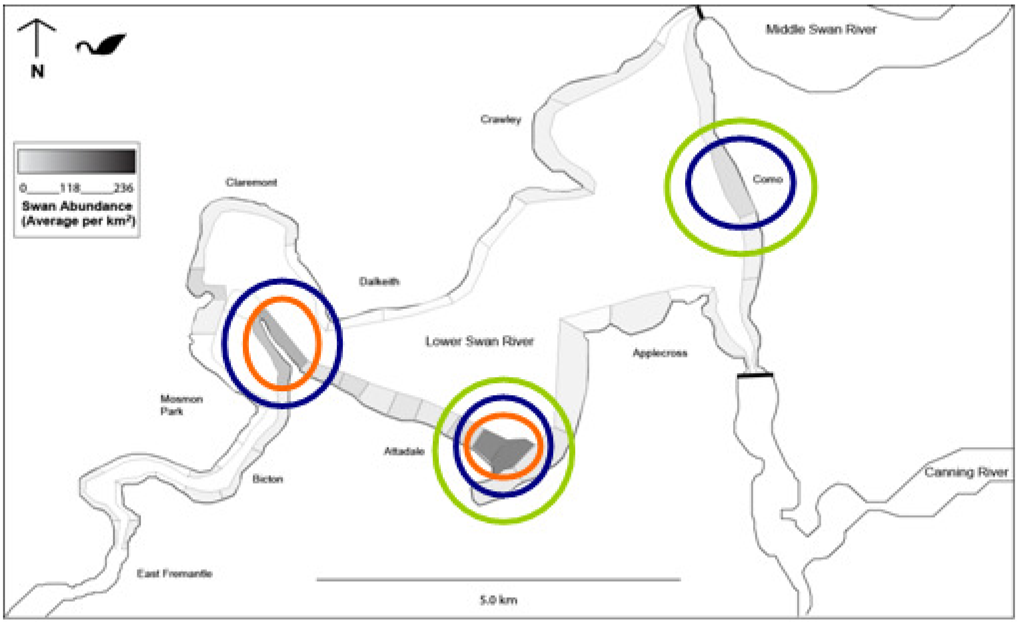


Figure 5.3 Swan hot-spots on the Lower Swan River estuary during spring and summer (orange), autumn (blue) and winter (green).

Based on the findings of this study, the key site and habitat characteristics that predict swan abundance include human disturbances (jetties and dogs), shoreline and submerged vegetation cover and condition, and the slope of the area available for foraging (Figure 5.4). Good vegetation condition and larger areas of natural vegetation along the shoreline protects swans from predators and other human disturbances when feeding and also breeding (Paracuellos & Telleria 2004, McKinney et al. 2006). Previous studies have shown that black swan abundance is affected by the amount and type of food present (Williams 1979, Congdon & McComb 1981, Mitchell & Wass 1996) and this study has shown swan abundance is most likely related to the swans' forage, in the amount, type and its distribution along a depth gradient is also important.

Other human disturbances such as the presence of jetties and dogs negatively affected black swan abundance. These factors reduce the local habitat quality for water birds and the carrying capacity of estuaries (Van den Bergh et al. 2005), by reducing the area available for feeding and breeding (Burton et al. 2002). Previous studies have also found increases in human disturbances such as ferries, boats, the presences of kite and wind surfers and increases in the number of walkers with dogs were significant factors reducing waterfowl abundance on the estuary (Creed & Bailey 2009).

Two swan hotspots, Alfred Cove and Como Foreshore are within Marine Parks (Alfred Cove Marine Park & Milyu Marine Park) and are protected from many of the characteristics that could negatively influence swan abundance. In these areas management appears to be appropriate for waterbird management. Based on these findings, protection should also be considered in the third hotspot (Point Walter) for conservation of the black swan and other water birds. Although not a marine park, Point Walter has important habitat characteristics for the black swan and other water birds and therefore warrants appropriate protection and management in conjunction with other management objectives.

The results of this study suggest water bird distributions are affected by a suite of habitat characteristics not just one in particular. This supports recent studies (Zhijun et al. 2010) and suggests water bird management requires integrated knowledge on the entire wetland ecosystem, particularly on factors that could potentially influence water bird distributions and temporal variability in water bird abundances. These factors should also be considered on multiple spatial scales as water birds move between habitats based on their breeding needs and forage availability.

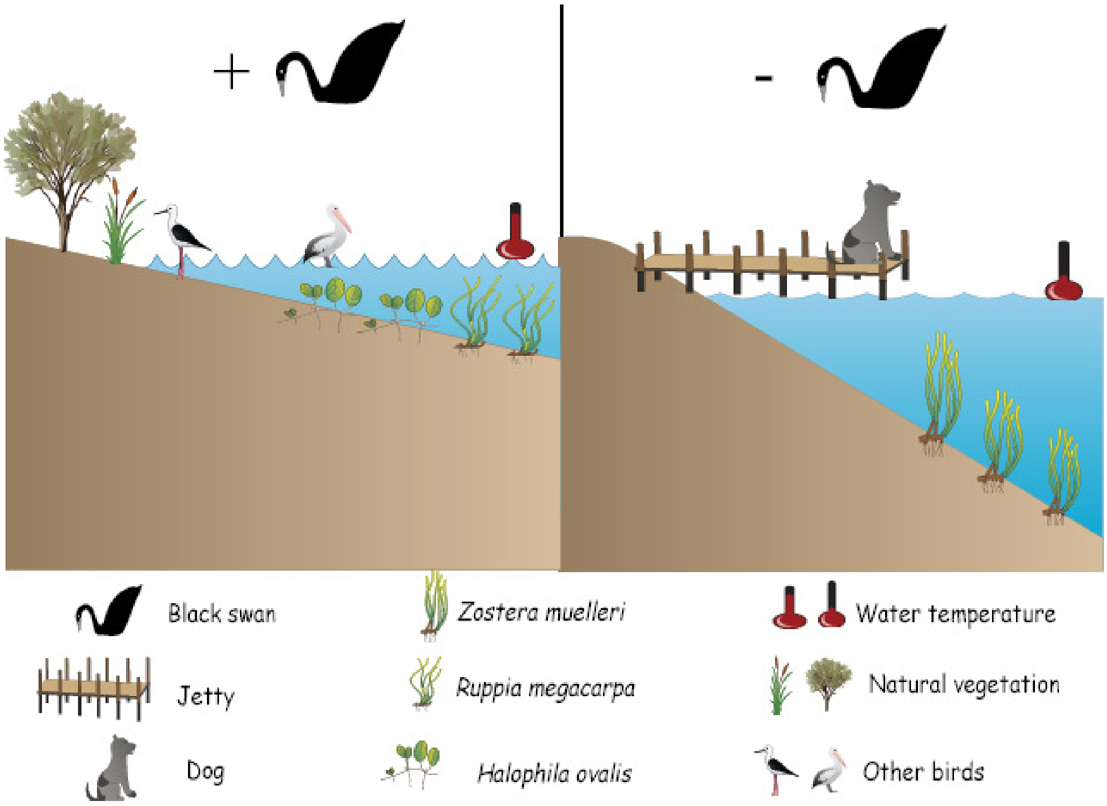


Figure 5.4 Factors potentially influencing black swan abundance on the Lower Swan River estuary (positive on the left, and negative on the right).

5.5 Significance of research

5.5.1 Ecological processes

Plant-grazer interactions are dynamic and complex. This study has revealed significant new findings about the seasonal nature of this relationship. Swan abundance on permanent and ephemeral water bodies appears to be influenced by a number of factors identified in Chapters 2 and 3. These factors include human disturbances and the presence and type of submerged and emergent vegetation (Chapter 3). Swan movement between ephemeral and permanent water bodies identified in Chapter 2 appears to change on a seasonal basis. This is likely to be due to the filling of ephemeral water bodies during winter, influencing characteristics including; water height, hydroperiod, food availability and the breeding needs of the black swan (Chapter 2). Drying of ephemeral habitats is estimated to result in the loss of 4804.1 ha of wetland area during summer and autumn, making permanent water bodies such as the Lower Swan River estuary an ideal habitat for swans to forage, (Chapter 3) with an expected increase in swan grazing pressure in these locations (Chapter 4). However, no change was seen in this study (Chapter 4). During summer and autumn when swan abundance is at its peak (Chapter 3), seagrass production is also at its peak (Chapter 4), so the seagrass is able to sustain under current levels of grazing, through changes in the expression of both growth and reproductive traits (Chapter 4) (Figure 5.5). The expression of traits associated with a tolerance strategy are dependent on the time of year grazing occurs. In this study *H. ovalis* showed traits of a tolerance strategy during summer but not in winter, when other factors could mediate the expression of these traits (temperature, light levels and nutrient inputs). In winter, lower light levels and water temperatures may result in less resources available for growth, so the energy fixed by seagrasses is used to maintain growth and less carbohydrates are stored, compared to summer (Moncreiff et al. 1992, Perez & Romero 1992). For this reason this study and recent studies emerging from terrestrial literature (Boalt et al. 2010, Bagchi & Ritchie 2011) highlights the importance of examining tolerance strategies at multiple times of year, particularly at those times with contrasting environmental conditions.

This study also identified an increase in sexual reproduction in *H. ovalis* after grazing, as a strategy that plants may use to cope with grazing. In this study, an increase in flowering intensity of *H. ovalis* was observed and a trend of increased seed production, corresponding with a significant positive relationship between flowering intensity and seed production with swan abundance. In seagrasses, little work has been done on changes in sexual reproduction after grazing, although some observational studies have suggested a positive relationship (Conacher et al. 1994, Peterken & Conacher 1997). Yet studies of other seagrass species have documented a negative response to grazing, a decrease in sexual reproduction (Lal et al. 2010). These contrasting results may be due to the different growth forms and life-history strategies of the plant. This study showed that *H. ovalis* was able to increase in sexual reproduction after grazing, suggesting that further research on this strategy should be considered.

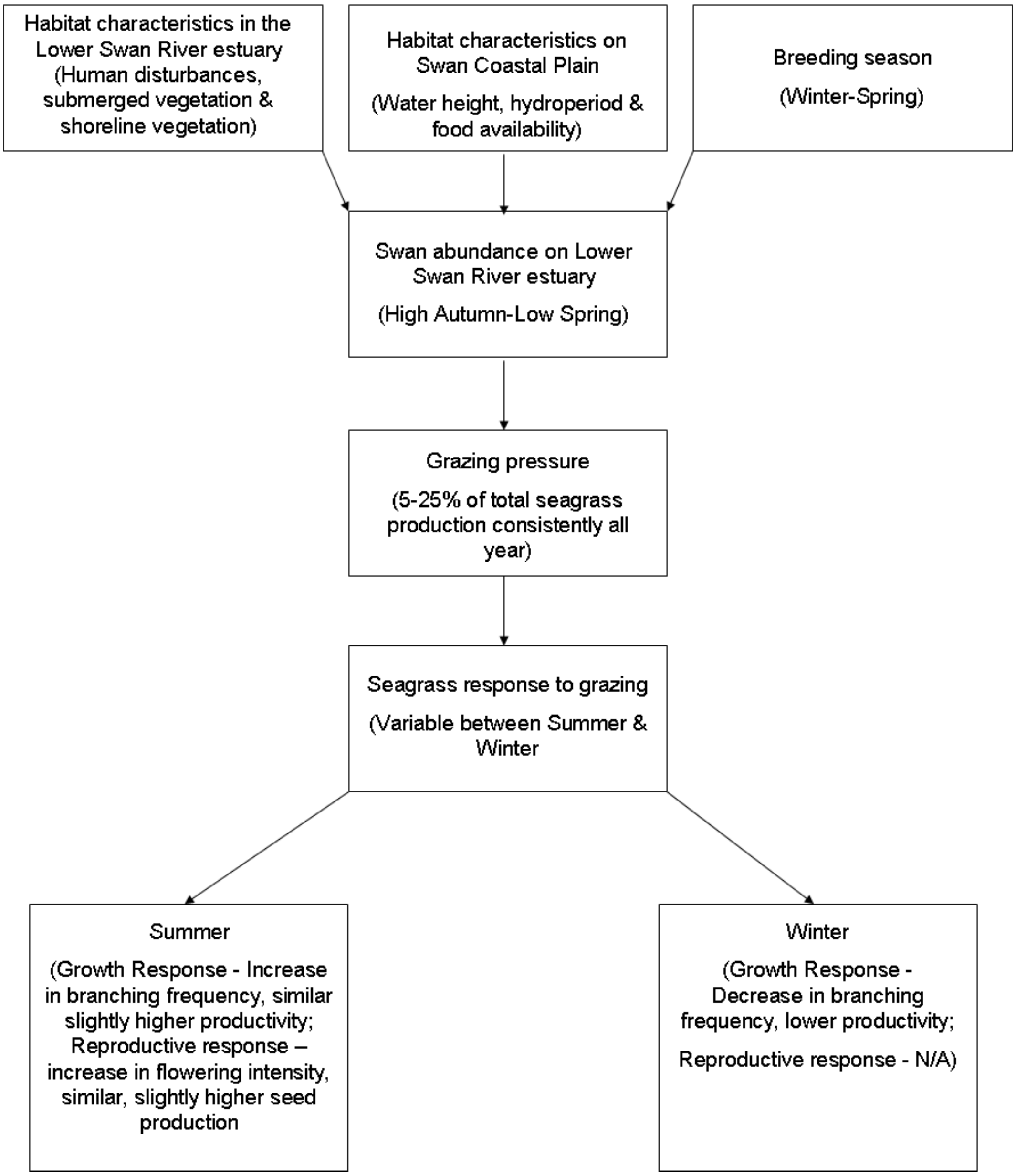


Figure 5.5 Conceptual model of how studies in this project inter-relate. A number of factors affect swan abundance on the estuary, which directly influence swan grazing pressure, and the time of year also influences plant responses to grazing. N/A = no data collected as flowering does not occur at this time.

5.5.2 Management

This study has also built on our understanding of swan linkages and connections between water bodies, suggesting permanent water bodies, such as the Lower Swan River estuary, could be important refuges for swans while smaller ephemeral wetlands are dry. The movement of swans is likely due to a variety of factors including water height in ephemeral wetlands, food availability and the breeding need of the black swan, although more research is required to understand this better (See below).

5.6 Future research directions

5.6.1 Black swans

This study has identified the need for more comprehensive studies of connectivity among permanent and ephemeral water bodies by waterbirds. The connectivity between water bodies appears to be influenced by river flooding patterns and the filling of wetlands by groundwater, which is highly variable in arid countries like Australia. The understanding of these connections is important for conservation of waterbirds world-wide. If we can gain a better understanding of water bird movements, management can be directed into areas with high water bird abundances or particular important species of waterbird.

This study has also identified the need for further research into temporal and spatial patterns in swan abundance on lakes, wetlands and estuaries on the SCP. Out of the 210 sites on the SCP in the Birds Australia database, only a small subset (6) contained counts of swans with seasonal replication. The limited data highlights the need for more concerted data collection to be able to document temporal and spatial patterns in swan habitat use on the SCP. A particular focus should be the role of larger permanent water bodies, as these could provide a refuge for swans during summer and autumn when surrounding wetlands dry.

This study has identified hotspots on the Lower Swan River estuary where swans are found. Long term monitoring should be considered in these hotspots to determine whether seasonal patterns are consistent across years and whether increases in swans are observed on the estuary. If there is an increase in swan abundance across years, further studies may be considered to determine what impact this has on the seagrass. Identical surveys should be conducted on other permanent estuaries and water bodies such as the Peel Harvey estuary and

Leschenault Inlet to determine whether temporal patterns in swan abundance are similar to those observed on the Lower Swan River estuary, providing important information on whether these water bodies are important refuges for swans when surrounding wetlands dry out.

The black swan has specific habitat requirements for breeding, which have the potential to influence breeding success and clutch size. These requirements are more suited to smaller wetlands rather than water bodies, such as estuaries. If current climate models hold true, these smaller wetlands could dry out forcing the swans to move to these larger water bodies, such as estuaries as permanent areas to feed. Therefore it is important to investigate whether these estuaries could support the breeding needs of black swans to ensure the local survival of the species.

5.6.1 Seagrasses

In this study, *H. ovalis* has shown traits of a tolerance strategy allowing them to cope with grazing, however, some traits such as vegetative growth (branching and productivity) were not consistent across a year. The expression of these traits may be mediated by external factors inducing environmental conditions, including other stressors, such as light limitation. For example, Eklof et al. (2009) found *H. ovalis* was not as resilient to grazing following stress and depletion in carbohydrate reserves from short-term light reduction. Yet, this occurred in autumn when there were optimum conditions for tolerating grazing. Future studies should be conducted to determine what impact grazing and other stresses have on the seagrass when it is at its most vulnerable.

An important next step in the manipulative studies may be to increase the frequency of grazing. Recent studies have shown frequency can influence plant tolerance traits in contrasting ways (Mundim et al. 2011). Mundim et al. (2011) found that the reserves needed to flower were rapidly depleted by continuous grazing and dramatically reduced the plant fitness. It is clear from this study the frequency of damage can also exert a strong influence on plant response, therefore future studies should be conducted to manipulate the frequency and duration of grazing. Grazing should be simulated for a full year, to determine the effect on plant sexual reproduction, fitness and the success of new recruits.

6. References

Agrawal AA (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. Trends in Plant Science 5:309-313

Alberti J, Cebrian J, Casariego AM, Canepuccia A, Escapa M, Iribarne O (2011) Effects of nutrient enrichment and crab herbivory on a SW Atlantic salt marsh productivity. Journal of Experimental Marine Biology and Ecology 405:99-104

Alcoverro T, Manzanera M, Romero J (2001) Annual metabolic carbon balance of the seagrass *Posidonia oceanica*: the importance of carbohydrate reserves. Marine Ecology Progress Series 211:105-116

Alexandre A, Santos R, Serrao E (2005) Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. Marine Ecology Progress Series 298:115-122

Aschero V, Zquez DPV (2009) Habitat protection, cattle grazing and density-dependent reproduction in a desert tree. Austral Ecology 34:901-907

Bagchi S, Ritchie ME (2011) Herbivory and plant tolerance: experimental tests of alternative hypotheses involving non-substitutable resources. Oikos 120:119-127

Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386-400

Baldwin JR, Lovvorn JR (1994) Expansion of seagrass habitat by the exotic *Zostera japonica* and its use by dabbling ducks and brant in Boundary Bay, British Columbia. Marine Ecology Progress Series 103:119-127

Bancroft TG, Gawlik DE, Rutchey K (2002) Distribution of wading birds relative to vegetation and water depths in the northern everglades of Florida, USA. Journal of the Waterbird Society 25:265-391

Bechet A, Giroux JF, Gauthier G (2004) The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. Journal of Applied Ecology 41:689-700

Birkhead M, Bacon PJ, Walter P (1983) Factors Affecting the Breeding Success of the Mute Swan Cygnus olor. Journal of Animal Ecology 52:727-741

Boalt E, Arvanitis L, Lehtila K, Ehrlen J (2010) The association among herbivory tolerance, ploidy level, and herbivory pressure in *Cardamine pratensis*. Evolutionary Ecology 24:1101-1113

Bolduc F, Afton AD (2008) Monitoring waterbird abundance in wetlands: the importance of controlling results for variation in water depth. Ecological Modelling 216:402-408

Bureau of Meteorology (2011a) Tide Predictions for Australia, South Pacific and Antarctica. Bureau of Meteorology

Bureau of Meteorology (2011b) Western Australia Climate Data. Bureau of Meteorology Perth

Boner ET, Halpern BS, Seabloom EW (2006) Asymmetry in community regulations: effects of predators and productivity. Ecology 87:2813-2820

Brearley A (2005) Swanland, Estuaries and Coastal Lagoons of South-wstern Australia, Vol 1. UWA Press, Perth

Burton NHK, Rehfisch MM, Clark NA (2002) Impacts of disturbance from construction work on the densities and feeding behaviour of waterbirds using the intertidal mudflats of Cardiff Bay, UK. Environmental Management 30:865-871

Campbell NA, Reece JB (2005) Biology, Vol 1. Pearson, Benjamin Cummings, Calif

Cebrian J, Duarte CM, Agawin NSR, Merino M (1998) Leaf growth response to simulated herbivory: a comparison among seagrass species. Journal of Experimental Marine Biology and Ecology 220:67-81

Chambers LE, Loyn RH (2006) The influence of climate variability on numbers of three waterbird species in Western Port, Victoria, 1973–2002. International Journal of Biometeorology 50:292-304

Chase JM, Leibold MA, Downing AL, Shrun JB (2000) The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81:2485-2497

Clarke K, Gorley R (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth

Conacher CA, Poiner IR, O'Donohue M (1994) Morphology, flowering and seed production of *Zostera capricorni* aschers in subtropical Australia. Aquatic Botany 49:33-46

Congdon RA, McComb AJ (1981) The vegetation of the Blackwood River Estuary, South-West Australia. Journal of Ecology 69:1-16

Cornelissen T, Stiling P (2005) Sex-biased herbivory: a meta-analysis of the effects of gender on plant-herbivore interactions. Oikos 111:488-500

Creed KE, Bailey M (2009) Continuing decline in wader populations at Pelican Point, Western Australia, since 1971. Stilt 56:10-14

Davis JL (2009) The Northwest Nature Guide, Vol. Timber Press, Portland

De Iongh II, Kiswara W, Kustiawan W, Loth PE (2007) A review of research on the interactions between dugongs (*Dugong dugon* Mu¨ ller 1776) and intertidal seagrass beds in Indonesia. Hydrobiologia 591:73-83

de Jong TJ, Klinkhamer PGI (2002) Sex ratios in dioecious plants, in Sex ratios: Concepts and research methods, Vol 1. Cambridge University Press, Cambridge

Department of Environment and Conservation (1999) Swan River estuary Marine Park and Adjacent Nature Reserves, Perth

Delph LF (2011) Sexual dimorphism in life history, in Gender and sexual dimorphism in flowering plants, Vol 1. Springer, New York den Hartog C, Kuo J (2006) Taxonomy and biogeography in seagrases, in Seagrasses: Biology, Ecology and Conservation, Vol 1. Springer, New York

Dennison WC (1985) Rhizome/ root production, in Seagrass Research Methods, Vol 1. UNESCO, Paris

Dingle H (2008) Bird migration in the southern hemisphere: a review comparing continents. Emu 108:341-359

Eklof JS, Gullstrom M, Bjork M, Asplund ME, Hammar L, Dahlgren A, Ohman MC (2008) The importance of grazing intensity and frequency for physiological responses of the tropical seagrass *Thalassia hemprichii*. Aquatic Botany 89:337-340

Eklof JS, McMahon K, Lavery PS (2009) Effects of multiple disturbances in seagrass meadows: shading decreases resilience to grazing. Marine and Freshwater Research 60:1317-1327

Forbs P, Damhoureyeh SA, Hartnett DC (1997) Effects of bison and cattle on growth, reproduction, and abundances of five tall grass. American Journal of Botany 84:1719-1728

Fourqurean JW, Manuel S, Coates KA, Kenworthy WJ, Smith SR (2010) Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to loss of seagrass meadows in Bermuda. Marine Ecology Progress Series 419:223-232

Gadgil M, Solbrig OT (1972) The concept of r-and K-selection: evidence from wild flowers and some theoretical considerations. The American Naturalist 106:14-31

Garcon JS, Moloney GJ, Hamann M (2010) Relative exposure index: an important factor in sea turtle nesting distribution. Aquatic Conservation: Marine and Freshwater Ecosystems 20:140-149

Globe (2003) Cloud Protocols. Atmosphere, p 16

Government of Western Australia (2000) Directory of Bush Forever sites, Department of Environmental Protection, Perth

Green AJ (1996) Analyses of globally threatened anatidae in relation to threats, distribution, migration patterns, and habitat use. Conservation Biology 10:1435-1445

Gruntman M, Novoplansky A (2011) Implications of local-scale productivity on compensatory growth in a semi-arid shrubland. Journal of Arid Environments 75:279-283

Hamilton AJ, Taylor IR, Hepworth H (2002) Activity budgets of waterfowl (*Anatidae*) on a waste-stabilisation pond. Emu 102:171-179

Hammerstrom KK, Kenworthy WJ, Fonseca MS, Whitfield PE (2006) Seed bank, biomass, and productivity of *Halophila decipiens*, a deep water seagrass on the West Florida continental shelf. Aquatic Botany 84:110-120

Hauxwell J, Osenberg CW, Frazer TK (2004) Conflicting management goals: manatees and invasive competitors inhibit restoration of native macrophyte. Ecological Applications 14:571-586

Hawkes CV, Sullivan JJ (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. Ecology 82:2045-2058

Heck KL, Valentine JF (2006) Plant–herbivore interactions in seagrass meadows. Journal of Experimental Marine Biology and Ecology 330:420-336

Hemminga MA, Duarte CM (2000) Seagrass ecology, Vol 1. Cambridge University Press, Cambridge

Hickman KR, Hartnett DC (2002) Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. Plant Ecology 159:23-33

Hillman K, McComb AJ, Walker DI (1995) The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the Swan/Canning Estuary, Western Australia. Aquatic Botany 51:1-54

Holm TE, Clausen P (2006) Effects of water level management on autumn staging waterbird and macrophyte diversity in three Danish coastal lagoons. Biodiversity and Conservation 15:4399-4423

Horwitz P, Sommer B, Hewitt P (2009) Chapter Five: Wetlands – Changes, Losses and Gains, in Biodiversity values and threatening processes of the Gnangara groundwater system, Edith Cowan University, Perth

Huntly N (1991) Herbivore and the dynamics of communities and ecosystems. Annual Review of Ecology, Evolution and Systematics 22:447-503

Irwin DL, Aarssen LW (1996) Effects of Nutrient Level on Cost and Benefit of Apical Dominance in *Epilobium ciliatum*. American Midland Naturalist 136:14-28

Jacobs RPWM, Den Hartog C, Braster BF, Carriere FC (1981) Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). Aquatic Botany 10:241-259

Jaensch R (2009) Floodplain wetlands and waterbirds of the channel country, South Australian Arid Lands Natural Resources Management Board

Jongman RHG, Ter Braak CJF, Van Tongeren OFR (1995) Data analysis in community and landscape ecology, Vol 1. Cambridge University Press, Cambridge

Kear J (2005) Ducks, Geese and Swans: General chapters, species accounts (Anhima to Salvadorina), Vol 1. Oxford University Press, Oxford

Kingsford RT, Norman FI (2002) Australian waterbirds – products of the continent's ecology. Emu 102:47-69

Kingsford RT, Roshier DA, Porter JL (2010) Australian waterbirds: time and space travellers in dynamic desert landscapes. Marine and Freshwater Research 61:875-884

Kingsford RT, Wong PS, Braithwaite LW, Maher MT (1999) Waterbird abundance in eastern Australia, 1983-92. Wildlife Research 26:351-366

Kirkman H, Kirkman J (2000) Long-term seagrass meadow monitoring near Perth, Western Australia. Aquatic Botany 67:319-332

Kuiper-Linley M, Johnson CR, Lanyon JM (2007) Effects of simulated green turtle regrazing on seagrass abundance, growth and nutritional status in Moreton Bay, south-east Queensland, Australia. Marine and Freshwater Research 58:492-503

Lal A, Arthur R, Marba N, Lill AWT, Alcoverro T (2010) Implications of conserving an ecosystem modifier: Increasing green turtle (*Chelonia mydas*) densities substantially alters seagrass meadows. Biological Conservation 143:2730-2738

Lane JAK, Clarke AG, Pearson GB, Winchcombe YC (2007) Waterbirds of the Vasse-Wonnerup wetalnds in 1998-2000, Including Ramsar stuatus and comparisons with earlier data. , Department of Environment and Conservation, Perth

Lazo L, Markham JH, Chapman ARO (1994) Herbivory and harvesting: Effects on sexual recruitment and vegetative modules of *Ascophyllum nodosum*. Ophelia 40:95-113

Leferve CD, Bellwood DR (2011) Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. Marine Ecology Progress Series 422:239-251

Liu H, Yu F, He WM, Chu Y, Dong M (2007) Are clonal plants more tolerant to grazing than co-occurring non-clonal plants in inland dunes? Journal of Ecological Research 22:502-506

Liu H, Yu F, He WM, Chu Y, Dong M (2009) Clonal integration improves compensatory growth in heavily grazed ramet populations of two inland-dune grasses. Flora 204:298-305

Macia S (2000) The effects of sea urchin grazing and drift algal blooms on a subtropical seagrass bed community. Journal of Experimental Marine Biology and Ecology 246:53-67

Marba N, Hemminga MA, Mateo MA, Duarte CM, Mass YEM, Terrados J, Garcia E (2002) Carbon and nitrogen translocation between seagrass ramets. Marine Ecology Progress Series 226:287-300

Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand and Antarctic Birds, Vol 1. Oxford University Press, Melbourne

Marell A, Ball JP, Hofgaard A (2002) Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Levy flights. Canadian Journal of Zoology 80:854-865

Martin K, Wiebe KL (2004) Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. Integrative and Comparative Biology 44:177-185

Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: the Influence of plant association, nutrient availability, and timing. The American Naturalist 134:1-19

McKinney RA, McWilliams SR, Charpentier MA (2006) Waterfowl–habitat associations during winter in an urban North Atlantic estuary. Biological Conservation 132:239-249

McMillan C (1983) Sulfated flavonoids and leaf morphology of *Halophila ovalis-H.minor* complex (Hydrocharitaceae) in the Pacific Islands and Australia. Aquatic Botany 16:337-347

Mitchell SF, Wass RT (1995) Food consumption and faecal deposition of plant nutrients by black swans (*Cygnus atratus* Latham) in a shallow New Zealand lake. Hydrobiologia 306:189-197

Mitchell SF, Wass RT (1996) Grazing by black swans (*Cygnus atratus Latham*), physical factors, and the growth and loss of aquatic vegetation in a shallow lake. Aquatic Botany 55:205-215

Moles AT, Bonser SP, Poore AGB, Wallis IR, Foley WJ (2010) Assessing the evidence for latitudinal gradients in plant defence and herbivory. Functional Ecology 25:380-388

Moncreiff CA, Sullivan MJ, Daehnick AE (1992) Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. Marine Ecology Progress Series 87:161-171

Moran KL, Bjorndal KA (2005) Simulated green turtle grazing affects structure and productivity of seagrass pastures. Marine Ecology Progress Series 305:235-247

Mundim FM, Bruna EM, Viera-Neto EHM, Vasconcelos HL (2011) Attack frequency and the tolerance to herbivory of Neotropical savanna trees. Oecologia 168:2088-2096

Musil P, Fuchs R (1994) Changes in abundance of water birds species in Southern Bohemia (Czech Republic) in the last 10 years Hydrobiologia 279:511-159

Mutikainen P, Walls M (1995) Growth, reproduction and defence in nettles: responses to herbivory modified by competition and fertilization. Oecologia 104:487-495

Nakaoka M, Aioi K (1999) Growth of seagrass *Halophila ovalis* at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. Marine Ecology Progress Series 184:97-103

Nienhuis PH, Groenendijk AM (1986) Consumption of eelgrass (*Zostera marina*) by birds and invertebrates: an annual budget. Marine Ecology Progress Series 29:29-35

Nolet BA (2004) Overcompensation and grazing optimisation in a swan–pondweed system. Freshwater Biology 49:1391-1399

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society 271:59-64

Olsen YS, Valiela I (2010) Effect of sediment nutrient enrichment and grazing on turtle grass *Thalassia testudinum* in Jobos Bay, Puerto Rico. Estuaries and Coasts 33:769-783

Owens MK, Launchbaugh KL, Holloway JW (1991) Pasture characteristics affecting spatial distribution of utilization by cattle in mixed brush communities. Journal of Range Management 44:118-123

Paracuellos M, Telleria JL (2004) Factors affecting the distribution of a waterbird community: the role of habitat configuration and bird abundance. Waterbirds: The International Journal of Waterbird Biology 27:446-453

Perez M, Romero J (1992) Photosynthetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. Aquatic Botany 43:51-62

Perrow MR, Schutten JH, Howes JR, Holzer T, Madgwick FJ, Jowitt AJD (1997) Interactions between coot (*Fulica atra*) and submerged macrophytes: the role of birds in the restoration process. Hydrobiologia 342:241-255

Peterken CJ, Conacher CA (1997) Seed germination and recolonisation of *Zostera capricorni* after grazing by dugongs. Aquatic Botany 59:333-340

Petrie SA, Wilcox KL (2003) Migration chronology of eastern-population Tundra Swans. Canadian Journal of Zoology 81:861-870

Phillips RC, Grant WS, McRoy CP (1983) Reproductive strategies of eelgrass (*Zostera marina*). Aquatic Botany 16:1-20

Pickering CM, Hill W (2002) Reproductive ecology and the effect of altitude on sex ratios in the dioecious herb *Aciphylla simplicifolia* (Apiaceae). Australian Journal of Botany 50:289-300

Piippo S, Hellstrom K, Huhta A, Raulto P, Tuomi J (2009) Delayed flowering as a potential benefity-decreasing cost of compensatory regrowth. Botany 87:837-844

Pilson D (2000) Herbivory and natural selection of flowering phenology in wild sunflower, *Helianthus annuus.* Oecologia 122:72-82

Polis GA, Strong DR (1996) Food Web Complexity and Community Dynamics. The American Naturalist 147:813-846

Powell GN, Fourqurean JW, Kenworthy WJ, Zieman JC (1991) Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. Estuarine, Coastal and Shelf Science 32:567-579

Quentin AG, Beadle CL, O'Grady AP, Pinkard EA (2011) Effects of partial defoliation on closed canopy *Eucalyptus globulus Labilladière*: growth, biomass allocation and carbohydrates. Forest Ecology and Management 261:695-702

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists, Vol 1. Cambridge University Press, Melbourne

Quinn JA (1998) Ecological aspects of sex expression in grasses, Vol 1. Cambridge University Press, Cambridge

Quiroga RE, Golluscio RA, Blanco LJ, Fernandez RJ (2010) Aridity and grazing as convergent selective forces: an experiment with an Arid Chaco bunchgrass. Ecological Applications 20:1876-1889

Robertson H, Barrie H (2005) The field guide to the birds of New Zealand, Vol. Penguin NZ, Auckland

Roshier DA, Robertson A, Kingsford RT (2009) The availability of wetland habitat for waterbirds in arid Australia, National Wetlands Research and Development Program

Saab V (1999) Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135-151

Scott A (1997) Relationships between waterbird ecology and river flows in the Murray Darling Basin, CSIRO

Semeniuk V, Semeniuk C (1994) Ecological Assessment and Evaluation of Wetlands in the System 5 Region, V & C Semeniuk Research Group Perth

Simms EL, Stowe KA, Marquis RJ, Hochwender CG (2000) The evolution ecology of tolerance to consumer damage. Annual Review of Ecological Systems 31:565-595

SPSS (2008) SPSS statistics: Version 18 for windows. IBM, Chicago

Stephenson AG, Lau TC, Quesada M, Winsor JA (1992) Factors that Affect Pollen Performance, in Ecology and Evolution of Plant Reproduction, Vol 1. Chapman & Hall, New York

Storey AW, Vervest RM, Pearson GB, Halse SA (1993) Waterbird usage of wetlands on the Swan Coastal Plain, Department of Conservation and Land Management Perth

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends in Ecology and Evolution 14:179-185

Thayer GW, Bjorndal KA, Ogden JC, Zieman JC (1994) Role of larger herbivores in seagrass communities. Estuaries 7:351-376

Tiffin P (2000) Mechanisms of tolerance to herbivore damage: what do we know. Evolutionary Ecology 14:523-536

Trumble JT, Kolodny-Hirsch DM, Ting IP (1993) Plant compensation for arthropod herbivory. Annual Review of Entomology 38:93-119

Tulip I, Schekkerman H (2008) Has prey availability for arctic birds advanced with climate change? hindcasting the abundance of Tundra Arthropods using weather and seasonal variation. Artic 61:48-60

Twilley RR, Kemp WM, Staver KW, Stevenson JC, Boynton WR (1985) Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities*. Marine Ecology Progress Series 23:179-191

Underwood AJ, Chapman. MG (1997) Statistical program GMAV.5 for windows. Institute of Marine Ecology. University of Sydney, Sydney

Valentine JF, Duffy JE (2006) The Central Role of Grazing in Seagrass Ecology, in Seagrasses: Biology, Ecology and Conservation, Vol 1. Springer, New York

Valentine JF, Heck KL (1998) Seagrass herbivory: evidence for the continued grazing of marine grasses. Marine Ecology Progress Series 176:291-302

Valentine JF, Heck KL, Busby J, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. Oecologia 112:193-200

Valentine JF, Heck KL, Kirsch KD, Webb D (2000) Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadow in the Florida Keys (USA). Marine Ecology Progress Series 200:213-228

Valesini V, Hourston M, Wildsmith MD, Coen NJ, Pottern IC (2010) New quantitative approaches for classifying and predicting local-scale habitats in estuaries. Estuarine, Coastal and Shelf Science 86:665-664

Van den Bergh E, Ysebaret T, Meire P (2005) Water bird communities in the Lower Zeeschelde: long-term changes near an expanding harbour. Hydrobiologia 540:237-258

Van Donk E, Otte A (1996) Effects of grazing by fish and waterfowl on the biomass and species composition of submerged macrophytes. Hydrobiologia 340:285-290

Varga S, Kytoviita MM, Siikamaki P (2009) Sexual differences in response to simulated herbivory in the gynodioecious herb *Geranium sylvaticum*. Plant Ecology 202:325-336

Verges A, Perez M, Alcoverro T, Romero J (2008) Compensation and resistance to herbivory in seagrasses: induced responses to simulated consumption by fish. Oecologia 155:751-760

Viejo RM, Martinez B, Arrontes J, Astudillo C, Hernandez L (2011) Reproductive patterns in central and marginal populations of a large brown seaweed: drastic changes at the southern range limit. Ecography 34:75-84

Warnock SE, Takeawa JY (1996) Wintering site fidelity and movement patterns of western sandpipers (*Calidris maun*) in the San Francisco Bay estuary. Ibis 138:160-167

Whitman TG, Maschinski J, Larson KC, Paige KN (1991) Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms, Vol 1. John Wiley and Sons, New York

Williams M (1979) Status and management of black swans *Cygnus atratus,* Latham at Ellesmere since the 'Wahine' storm, April, 1968. New Zealand Journal of Ecology 2:34-41

Zhijun M, Yinting C, Bo L, Jiakuan C (2010) Managing wetland habitats for waterbirds: an international perspective. Wetlands 30:15-27

Zimmerman M (1988) Nectar production, flowering phenology, and strategies for pollination, in Plant Reproductive Ecology, Vol 1. Oxford University Press, New York

Zimmerman RC, Kohrs DG, Alberte RS (1996) Top-down impact through a bottom-up mechanism: the effect of limpet grazing on growth, productivity and carbon allocation of *Zostera marina* L. (eelgrass). Oecologia 107:560-567

7. Appendixes

7.1 Seasonal and spatial variation in the behaviour of swans

There was significant spatial variation in the proportion of the 6 main behaviours exhibited by swans on the Lower Swan River estuary. However, changes were dependent on time of year and time of day (Table 7.1, Season x Time of day, Site Time of Day and Site x Season interaction: $p<0.05$, Figure 7.1). The black swan exhibited two main behaviours on the Lower Swan River estuary, grazing and loafing. During spring, summer and autumn a greater proportion of black swans were observed loafing during the morning (0.13 ± 0.02; 0.20 ± 0.03 & 0.21 ± 0.03) compared to the afternoon (0.07 ± 0.01; 0.15 ± 0.02 & 0.09 ± 0.02). Fewer swans were observed grazing in the morning (0.08 ± 0.02; 0.11 ± 0.02 & 0.19 ± 0.02) compared to the afternoon (0.14 ± 0.03; 0.18 ± 0.02 & 0.23 ± 0.03); however, during winter there was no significant difference in swan behaviour between morning and afternoon.

Blackwell Reach North South, Burke Drive West B, Troy Park, Dee Road and Freshwater Bay B (sites 11, 17, 22, 25, 43) were the only sites to have variation in the behaviour of swans. More swans were observed grazing in the afternoon compared to the morning (0.2 ± 0.02 vs. 0.15 ± 0.02) and also more swans were observed loafing in the morning compared to the afternoon (0.19 ± 0.01 vs. 0.12 ± 0.03).

Fifteen sites had no swans present during the entire study period (sites 2, 3, 5, 6, 10, 12, 26, 33, 34, 37, 38, 39, 40, 44, 45) and were not included in this analysis. Of the sites included in the analysis, 11 sites showed significant seasonal variation (sites 11, 13, 14, 15, 16, 19, 22, 23, 24, 25, 32). The nature of the variation varied with site. For example, at Blackwell Reach North South, Burke Drive Centre B, Troy Park Alfred Cove and Dee road a greater proportion of swans were observed grazing and loafing during summer (0.18 ± 0.02 & 0.21 ± 0.02) and autumn (0.25 ± 0.02 & 0.19 ± 0.02) compared to spring (0.14 ± 0.01 & 0.12 ± 0.01). During summer, Blackwell Reach North south had a greater proportion of swans observed loafing than autumn (0.21 ± 0.02 & 0.19 ± 0.02), however, a greater proportion of swans were observed grazing at this site (0.25 ± 0.02 & 0.18 ± 0.02). Point Walter South, Point Walter North, Troy Park and Cunningham Street had a greater proportion of swans observed grazing and loafing during summer compared to winter (0.18 ± 0.02; 0.21 ± 0.02 & 0.15 ± 0.02; 0.12 ± 0.02). Finally, Blackwell Reach North South, Point Walter Café, Burke Drive Centre B and Troy Park (sites 11, 15, 19, 22) had more swans observed grazing and loafing compared to winter (0.21 ± 0.02; 0.19 ± 0.02 & 0.15 ± 0.02; 0.12 ± 0.02).

Finally, at significant swan use sites (Sites 13, 14, 15, 21, 22 & 23), there were significant variations in the proportion of the 6 main behaviours exhibited by swans, however, variations were dependent on the time of year. Sites 14, 15 & 22 had a significantly greater proportion of swans observed grazing and loafing than site 13 (0.16 ± 0.05; 0.12 ± 0.05) during three of the four seasons. Site 14 had significantly more swans grazing and loafing during spring, summer and autumn (0.51 ± 0.06; 0.39 ± 0.05), site 15 had significantly more swans grazing and loafing in spring, autumn and winter (0.51 ± 0.06; 0.36 ± 0.05), site 22 had significantly more swans grazing and loafing in summer, autumn and winter (0.50 ± 0.06; 0.32 ± 0.05), while site 23 had significantly more swans grazing and loafing in all four seasons (0.55 ± 0.05; 0.51 ± 0.05). During spring, summer and autumn site 14 had a significantly higher proportion of swans observed grazing and loafing than site 24 (0.51 ± 0.06; 0.39 ± 0.05 vs 0.10 ± 0.03; 0.16 ± 0.04) and site 15 had significantly higher proportion of swans observed grazing and loafing than site 24 (0.51 ± 0.06; 0.36 ± 0.05 vs 0.10 ± 0.03; 0.16 ± 0.04). Site 21 had a significantly higher proportion of swans observed grazing and loafing than site 23 (0.26 ± 0.06; 0.27 ± 0.06 vs 0.55 ± 0.05; 0.51 ± 0.05) during summer, autumn and winter.

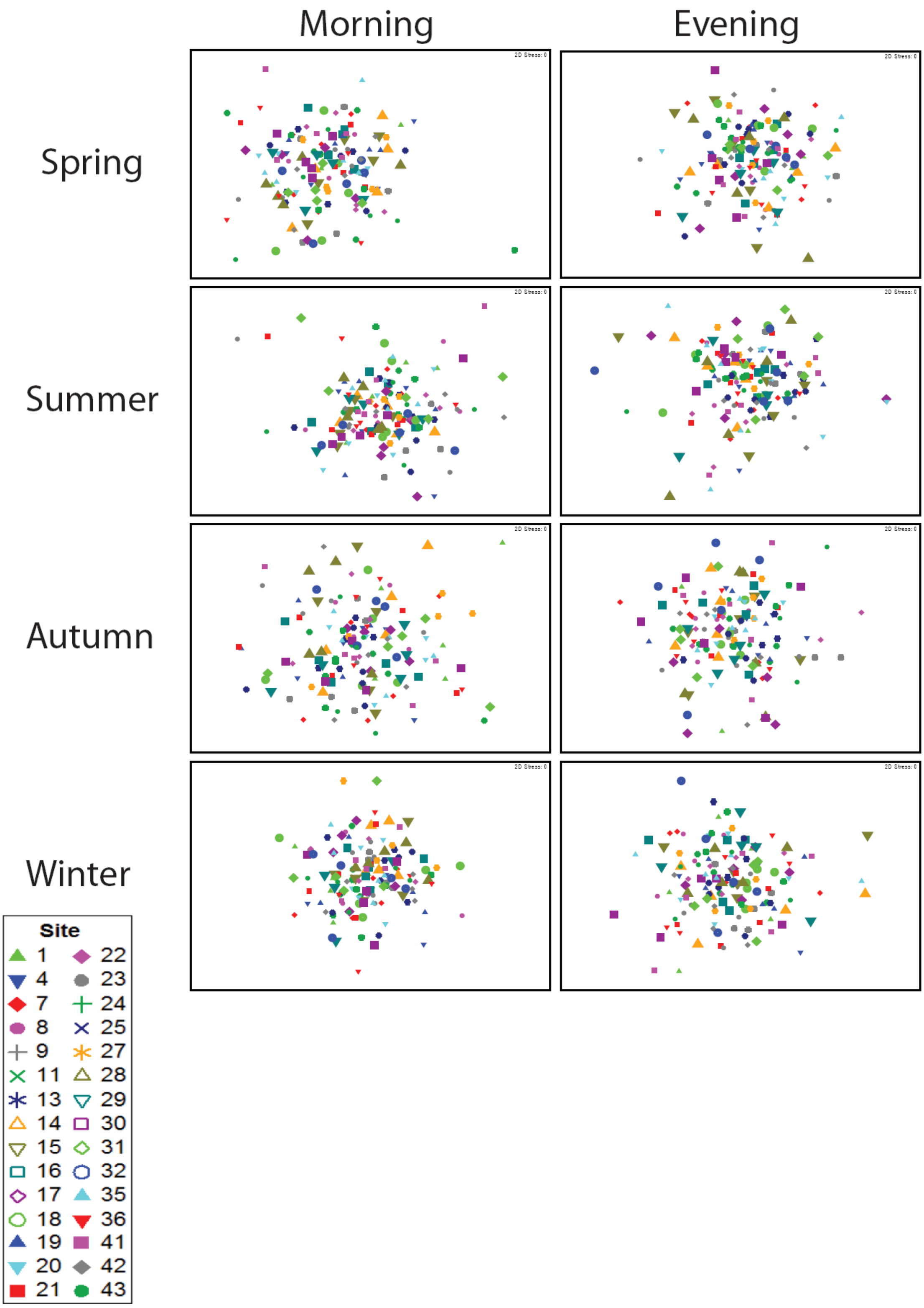


Figure 7.1 MDS plot comparing different swan behaviours (grazing, loafing, transiting, across sites, sleeping, and other behaviours) between site (45 sites), season (spring, summer, autumn and winter) and time of day (morning and afternoon) on the Lower Swan River estuary.

Table 7.1 Summary of PERMANOVA testing for differences in spatial (45 sites), temporal variation (inter-annual) (spring, summer, autumn and winter) and daily (morning and afternoon) in six behaviours of swans (grazing, loafing, transiting, across sites, sleeping, and other behaviours).

	Sum of squares	**Df**	**Mean Square**	**F**	**P**
Site	1.12	29	3855.10	14.44	0.00
Season	8515.5	3	2838.50	10.63	0.00
Time of day	3071.2	1	3071.20	11.50	0.00
Site X Season	47718	87	548.48	2.05	0.00
Site X Time of day	10364	29	357.37	1.34	0.04
Season X Time of day	1847.9	3	615.97	2.31	0.04
Site X Season X Time of day	20294	87	233.27	0.87	0.90
Residual	2.56	960	266.98		
Total	4.60	1199			

7.2 Swan grazing pressure table

Table 7.2 Summary of total *H. ovalis* seagrass production, swan grazing parameters (surface area grazed, biomass removed of *H. ovalis* removed, production removed) and biomass of *H. ovalis* meadow for all sites (three per season) and seasons (spring, summer, autumn and winter).

Site/ Season	**Surface area grazed (% day^{-1})**	**Biomass removed *H. ovalis* (g DW m^{-2} day^{-1})**	**Production removed (% of daily production)**	**Total seagrass production (g DW m^{-2} day^{-1})**	**Biomass of *H. ovalis* meadow (g DW m^{-2})**
Spring	0.28 ± 0.04	1.05 ± 0.20	10.1 ± 0.79	12.12 ± 1.37	280.93 ± 45.77
Freshwater Bay A	0.14 ± 0.02	0.66 ± 0.06	8.1 ± 1.28	8.62 ± 0.65	322.34 ± 103.43
Point Walter South	0.44 ± 0.05	1.35 ± 0.15	18.06 ± 0.61	9.57 ± 1.84	330.99 ± 81.05
Burke Drive East B	0.26 ± 0.01	1.15 ± 0.01	10.22 ± 1.97	12.1 ± 1.05	189.47 ± 39.84
Summer	0.64 ± 0.07	2.58 ± 0.84	15.01 ± 1.18	17.06 ± 2.31	561.08 ± 81.85
Burke Drive East B	0.55 ± 0.08	1.78 ± 0.34	13.06 ± 1.8	14.26 ± 2.64	107.63 ± 37.35
Point Walter South	0.87 ± 0.17	4.25 ± 0.40	27.71 ± 2.91	14.73 ± 1.61	513.72 ± 106.86
Freshwater Bay A	0.5 ± 0.06	1.70 ± 0.30	10.41 ± 1.04	16.04 ± 2.15	1061.88 ± 139.96
Autumn	0.81 ± 0.08	3.02 ± 0.33	14.56 ± 1.88	19.48 ± 1.78	328.00 ± 63.62
Burke Drive East B	0.81 ± 0.14	3.63 ± 0.56	23.2 ± 1.5	15.68 ± 2.41	171.85 ± 53.81
Point Walter South	0.55 ± 0.13	2.95 ± 0.78	10.95 ± 1.21	17.09 ± 4.93	687.86 ± 146.75
Cunningham Street	1.06 ± 0.05	2.48 ± 0.43	24.18 ± 1.46	10.92 ± 1.45	124.30 ± 24.29
Winter	0.28 ± 0.03	0.44 ± 0.17	5.68 ± 0.55	13.64 ± 1.89	323.38 ± 46.68
Burke Drive East B	0.24 ± 0.04	0.64 ± 0.10	17.51 ± 2.95	5.43 ± 1.35	274.00 ± 66.72
Troy Park	0.28 ± 0.07	0.10 ± 0.02	14.97 ± 2.95	5.04 ± 0.92	413.78 ± 65.16
Como Mid B	0.34 ± 0.15	0.57 ± 0.21	8.43 ± 3.77	6.57 ± 2.94	323.39 ± 105.41