Patterns in Fish Assemblages and Seagrass Herbivory in a Temperate Australian Seagrass Meadow

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Kirrily White (B.Env.Sc Merit Honours)
Student Number: 10569119

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ABSTRACT

While eutrophication of coastal waters has long been attributed as a major cause of seagrass decline, there is now emerging evidence from both tropical and temperate seagrass meadows that top down control of these benthic habitats is more important than previously thought. Overgrazing of seagrass by fish has been recorded in a wide range of locations and has been linked to interactions between multiple threats such as overfishing and eutrophication, yet little is known of the influence of herbivory on temperate Australian seagrass meadows. This study examined whether seagrass herbivory occurs in a large seagrass dominated temperate bay in Western Australia; how herbivory is influenced by nitrogen in seagrass leaves; and how herbivory and fish assemblages are influenced by depth and the spatial proximity of other habitats. Surveys to examine these questions included assessments of fish bite marks on seagrass leaves; collection of seagrass leaves for analysis of total nitrogen; sampling of fish using diver observations and stereo-baited remote under water video (BRUVs); and assessments of benthic habitat using video footage of the seafloor. Low levels of seagrass grazing was recorded, likely due to the low abundance of herbivorous fish in comparison to invertebrate and macroinvertebrate carnivores. An east - west geographic pattern was observed in the location of grazed sites and of herbivorous fish species that corresponded with mixed *Amphibolis griffithii* and *Posidonia sinuosa* seagrass meadows. Elevated nitrogen in seagrass leaves was not associated with grazed sites. Fish assemblages were diverse with 89 species from 34 families recorded. Many fish species were not seagrass associated, demonstrating a level of connectivity among seagrass and other habitats such as coral outcrops and limestone patch reefs. Given the low abundance of seagrass consumers, overgrazing of seagrass meadows by fish is unlikely to occur at the study location, yet the high diversity of fish assemblages found highlights the need for improved understanding of cross-habitat interchanges of fish biomass between seagrass and other habitats. Integrated marine management needs to extend not only to multiple threats, but also to the management of multiple connected habitats.

TABLE OF CONTENTS

FIGURES

TABLES

ACKNOWLEDGEMENTS

GENERAL INTRODUCTION

There is increasing evidence that fish herbivory is an important trophic pathway in seagrass systems, providing a direct food source and delivering top down control in some meadows (Valentine and Duffy 2006, Valentine et al. 2007). In tropical and in some temperate seagrass systems, grazing by fish can result in the removal of a substantial proportion of the above ground seagrass biomass, particularly in impacted meadows where nutrient enrichment has occurred (Ruiz et al. 2001, Boyer et al. 2004, Prado et al. 2010). Herbivorous and omnivorous fish also play an important role in removing epiphytes from seagrass leaves, improving resilience against nutrient loads (Gacia et al. 1999, Hily et al. 2004, Hays 2005). High levels of nutrients have long been thought to be a key driver of seagrass decline, with rapid epiphyte or macroalgal growth leading to over shading of seagrass leaves (Cambridge and McComb 1984, Hillman et al. 1991, Cansemi et al. 2003, Green and Short 2003). However, most studies of seagrass loss have occurred decades after overharvesting of primary consumers has dramatically altered the local food web (Heck and Valentine 2007). As a result, it is possible that important interactions between multiple pressures on these systems have not been accounted for.

Managers of impacted coastal systems have traditionally focused on nutrient loading, yet there are compelling reasons to examine the structure and function of fish assemblages in seagrass meadows, with a view to understanding herbivory and other trophic pathways. In order to predict impacts, and understand management implications for multiple disturbances such as overfishing, elevated nutrient inputs and physical disturbance in seagrass ecosystems, there is a particular need to develop a better understanding of the functional linkages between seagrass, fish, nutrients and invertebrates. This thesis primarily examines the first three of these components within a diverse and extensive temperate Western Australian seagrass meadow at Geographe Bay.

8

The first chapter of this thesis presents a review of the literature regarding seagrass establishment; human impacts on seagrass meadows; functional roles of seagrass as fish habitat; and seagrass herbivory. A detailed background of the importance of studying trophic linkages in seagrass ecosystems has been provided, highlighting the need for further research into temperate seagrass meadows, in which there has been less research in this area compared to tropical meadows.

The second chapter has used a comprehensive field survey to examine the presence of seagrass herbivory by fish; the nitrogen content of seagrass leaves; and the abundance of fish with potential to consume seagrass in Geographe Bay. Surveys were undertaken to test the hypothesis that herbivory of seagrass by fish does occur in temperate Australian seagrass meadows, and that elevated nutrients in seagrass leaves lead to increased herbivory. Patterns in seagrass herbivory were also investigated.

The third chapter examines patterns and linkages between benthic habitat and the assemblages of fish in Geographe Bay in more detail. Detailed surveys taken over two years assessed how fish assemblages in Geographe Bay vary spatially, and how connectivity between seagrass and other nearby benthic habitats influences these assemblages. The proportions of total fish abundance comprised by each trophic group, and the patterns in the distribution of potential seagrass grazers were also examined.

Finally, the implications of the key research outcomes from chapters two and three are discussed. This thesis does not attempt to examine all of the possible interactions between the multiple pressures that may exist in Geographe Bay, but rather assesses how herbivory may play a role in the system's response to specific pressures such as elevated nutrients and overfishing.

CHAPTER 1: LITERATURE REVIEW

Introduction

Seagrasses are a small group of flowering plants that grow submerged in shallow, near shore and estuarine environments, and frequently form extensive meadows. They occur in both tropical and temperate zones of the ocean, typically in sheltered and soft bottom environments, although a number of species have also adapted to rocky situations. The South West of Australia supports one third of all known species of seagrasses, of which 14 are endemic to the area.

As their name suggests, seagrasses have adapted to life in seawater, yet they retain a number of similarities with their ancestors, terrestrial flowering plants. The seagrass plant morphology includes leaves, roots and veins and they are able to reproduce with flowers and seeds. Unlike land plants, seagrasses do not use stomata for the exchange of gases, but rather they have a very thin cuticular layer over their leaves to enable direct exchange of oxygen and carbon dioxide with seawater (Edgar 2001).

Seagrass ecosystems are well recognized for providing a range of important and complex ecological, physical and chemical functions. Their three dimensional structure provides shelter for fish and invertebrates (Edgar and Robertson 1992) and seagrass leaves provide a substrate for algal growth, which is in turn a food resource for a range of organisms (Orth and Van Monfrans 1984). Detached seagrass leaf material also provides an important contribution of detritus to the food chain (Short 1987). Seagrass plants individually, and as meadows, stabilise and filter sediments and dampen wave energy, thereby contributing to improved water clarity and reducing shoreline erosion (Short and Short 1984, Daby 2003). In particular, *Posidonia* seagrass species have 50 - 90% of their biomass buried under the sediment in deep rooted rhizome mats that are highly resistant to wave action (Edgar 2001). Seagrass communities also play a key role in the nutrient cycle in near shore communities via direct uptake of nutrients from sediments,

absorption into leaves from the water column, and via nutrient uptake by the epiphytic algae that colonise their leaves (Short 1987, Hemminga et al. 1999).

Globally, seagrass communities have declined dramatically over the past few decades due to a range of anthropogenic influences such as eutrophication, increased sedimentation and physical disturbance (Waycott et al. 2009). In temperate systems, eutrophication has been a particularly common cause of decline. Elevated nutrients have resulted in an overgrowth of epiphytic algae on seagrass plants, thereby blocking sunlight and causing plant death (Hillman et al. 1991). High turbidity following sedimentation of near-shore waters has also reduced light availability, with similar impacts (Walker and McComb 1992, Spalding et al. 2003). While some instances of seagrass 'die back' have been attributed to natural causes (Seddon et al. 2000), there is still a very limited understanding of the degree to which other impacts, including global warming and contaminants such as herbicides and pesticides, may affect seagrass communities. Given the important role that seagrass communities play in the near shore environment, these recorded losses have the potential to impact on a wide range of other marine resources. In addition, seagrass recovery has been extremely slow in some temperate systems, often taking many decades before significant recovery takes place (Bryars and Neverauaskas 2004).

Many seagrass communities are affected by a combination of impacts including poor water quality, physical disturbance and over fishing. Within the past ten years, a number of researchers have undertaken investigations into the interactions between the activities of herbivores in seagrass communities, and impacts such as eutrophication and fishing (Jernakoff and Nielson 1997, Cebrian and Duarte 1998, Gacia et al. 1999, Heck et al. 2000, Goecker and Kall 2003, Alcoverro and Mariani 2004, Hays 2005). Herbivory has historically been considered a minor factor in temperate seagrass ecosystems, yet there is now evidence to the contrary. Seagrass decline has been attributed to overgrazing by herbivorous fish in response to elevated nutrient

contributions from aquaculture (Ruiz et al. 2001); and to heavy grazing by sea urchins in areas subject to fishing pressure (Alcoverro and Mariani 2004). Invertebrate herbivores that feed on epiphytes also play an important role in some areas by helping to reduce epiphyte loads (Jernakoff and Nielson 1997, Cebrian and Duarte 1998, Gacia et al. 1999, Heck et al. 2000, Goecker and Kall 2003, Hily et al. 2004, Hays 2005).

This literature review provides an account of the current understanding of environmental variables affecting seagrass establishment and persistence; herbivory processes and food webs in seagrass systems; and the interactions between eutrophication, grazing and physical disturbance in seagrass communities. These topics form the key concepts being investigated in this thesis; the links between these concepts are illustrated using a flow diagram in Figure 1.1.
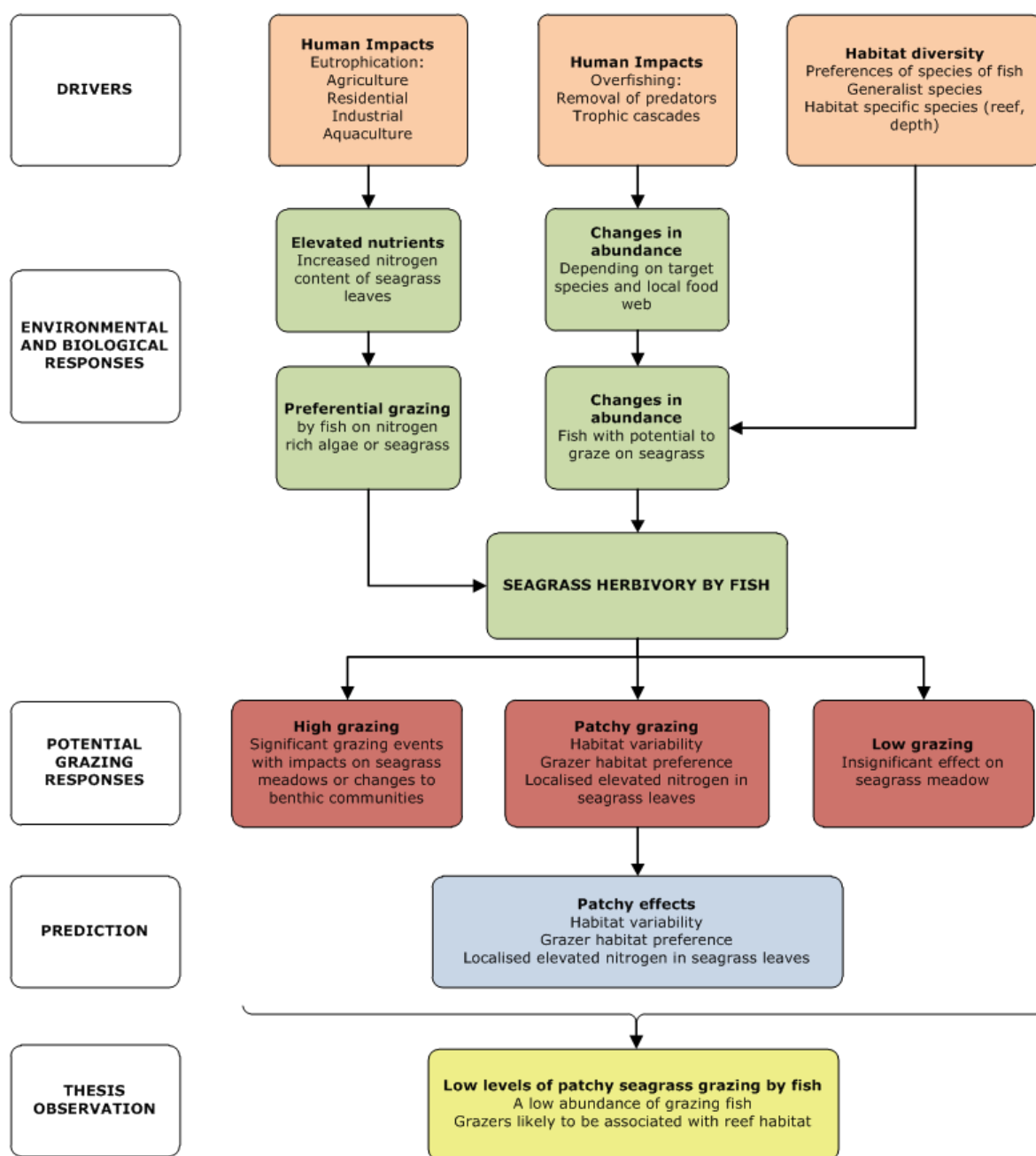
Figure 1.1: Flow diagram of thesis concepts.

Seagrass establishment

There are 60 species of seagrass known to occur worldwide, with 14 species found in south Western Australia (Spalding et al. 2003). Western Australia lacks the nutrient rich up welling of water found in other locations, hence very clear and naturally nutrient poor water are

characteristic in undisturbed areas. Large areas of the coastline are also sheltered from the prevailing swell by extensive areas of off shore reefs or by embayments such as Geographe Bay, that provide ideal shallow and soft bottom habitats in protected water. Seagrasses have very high light requirements for growth owing to their extensive system of non photosynthetic underground structures (Spalding et al. 2003); hence such high water clarity and sheltered conditions are favourable for their growth. These high light requirements strongly influence seagrass distribution by creating a lower depth limit of minimum light penetration required for photosynthesis (Walker 2003). This lower limit is combined with an upper limit associated with wave energy and desiccation, which may occur if seagrass leaves become exposed for long periods (Walker 2003).

Seagrasses have the ability to form extensive meadows, either as single species or a range of mixed species. Some such meadows are known to be highly dynamic, though the extent to which they establish in new areas or recover from disturbance varies considerably between species. The species *Halophila decipiens* relies on an established bank of seeds within the sediments for recolonisation, and is highly successful in sexual reproduction (Hammerstrom and Kenworthy 2003). Accordingly, *Halophila* species are well regarded as early colonisers following disturbance, though individual plants may easily be washed out during winter storm surge and are often replaced by other meadow forming species (Kirkman and Kuo 1990, Rasheed 2004). Other species, such as *Thalassia hemprichii,* seem unable to form a seed bank as the seeds do not remain viable for long under buried conditions, therefore these meadows rely on vegetative propagation for recovery and maintenance (Rollon et al. 2003). Species of the *Amphibolis* seagrasses release developed seedlings from mature plants that are able to snag onto the sea floor (Edgar 2001). Establishment and recovery of the Australian *Posidonia* seagrass species has been shown to take decades (Kirkman and Kuo 1990, Meehan and West 2000, 2004), though recolonisation and recovery have been recorded (Kendrick et al. 1999, Bryars and Neverauaskas 2004). In Jervis Bay, NSW large circular holes in a *Posidonia australis* meadow caused by seismic surveys undertaken in

1960s have recovered to only 56% of former cover over a period of some 30 years (Meehan and West 2000).

In addition to variations in the process of reproduction in seagrass species, the triggers for sexual reproduction appear to differ markedly between species. Flowering of *Posidonia australis* has been linked to changes in water temperature in Australia, with episodes of synchronous flowering of the species in a number of estuaries linked to an unusual occurrence of very cool autumn water temperature (Inglis and Lincoln Smith 1997). In the same study, the timing of flowering of *Zostera capricorni* varied greatly between and within estuaries, and appeared to be influenced by factors within meadows, rather than wider environmental conditions such as water temperature. *Posidonia coriacea* has been found to produce flowers every year, while *Heterozostera tasmanica* has displayed much less frequent and variable flowering occurrence (Campey et al. 2002).

Human impacts on seagrass

Seagrasses tend to occur in shallow, sheltered and (usually) sandy near shore environments such as embayments and estuaries, thus they occur in close proximity to sites of human settlement (Edgar 2001). With this proximity has come a host of human induced impacts on the near shore environment such as eutrophication, sedimentation, coastal development, overfishing and dredging. The need for adequate sunlight for photosynthesis means that seagrasses are vulnerable to any impact that substantially reduces water clarity. Elevated nutrients and sediment are among the most common cause of seagrass decline (Spalding et al. 2003), with both ultimately leading to reduced light availability to seagrass plants.

Losses of seagrass meadows can occur rapidly once threshold levels of algal growth are established and maintained. In Cockburn Sound, Western Australia, 77 % of seagrass meadow coverage was lost between 1967 and 1999, but the majority of losses occurred between 1967 and

1972 (Kendrick et al. 2002). Losses of seagrasses were primarily attributed to blooms of filamentous algae that responded to nutrient rich discharge from a wastewater treatment plant and a fertiliser plant (Cambridge and McComb 1984, Cambridge et al. 1986). The majority of losses in Cockburn Sound occurred over only a few years, soon after effluent disposal commenced, and subsequent losses have been attributed to a combination of physical disturbance from dredging activities, anchor damage, and an occurrence of over grazing by sea urchins (Kendrick et al. 2002). These time frames indicate that the levels of nutrient enrichment in Cockburn Sound quickly exceeded the ability of the system to assimilate them and the resulting algal growth. Very little recovery of seagrass meadows has occurred in Cockburn Sound, though localised increases in seagrass cover have been recorded on Success Bank (Kendrick et al. 2000).

Substantial losses of seagrass meadows were also recorded in Princess Royal Harbour and Oyster Harbour, Albany Western Australia between 1962 and 1981 followed by further rapid losses in Oyster Harbour between 1981 and 1984. These losses were due to large proliferations of macroalgae that smothered the seagrass meadows (Simpson et al. 1989, Hillman et al. 1991).

While eutrophication has been one of the most common causes of seagrass decline worldwide, seagrasses do need certain minimum levels of nutrients for growth. Most seagrass species are not well adapted to conserve nutrients given the consistent loss of senescing leaves and their very high production (Hemminga et al. 1999). Nutrients are taken up from the water column through leaves and from the sediments by rhizomes. The degree to which seagrasses respond positively to nutrients depends on the species and their reproductive strategies, possibly reflecting the levels to which certain species have adapted. An increase in seagrass cover, attributed to elevated nutrients, was observed at Green Island in the Great Barrier Reef between 1936 and 1994 (Waycott et al. 2005). Also, in the Bahamas, seagrasses surrounding patch reefs display a pattern of enhanced growth around a more narrow and central band of sand that immediately abuts the

reef structure (Alevizon 2002). The author linked the enhanced seagrass growth with aggregations of fish that colonise these reefs, thereby providing a supply of nutrient via their faeces.

Seagrass as habitat for fish

Seagrass meadows are highly productive systems and as such they can make a substantial contribution to the detrital food chain (Short 1987). Crustaceans, shrimps and amphipods feed on seagrass detritus (Hyndes and Lavery 2005) and then are consumed directly or produce pellets that are consumed by other invertebrates (Edgar 2001). Seagrass leaves also provide a substrate for the colonization of a suite of epiphytic algae that serve as an important food source for many groups of marine animals such as gastropods, amphipods, polychaetes and some fish (Orth and Van Monfrans 1984, Shaw and Jenkins 1992, Jernakoff and Nielson 1998, Edgar 2001). The presence of small invertebrates associated with seagrass meadows in turn provides a food source for a large number of fish species that feed on these epifauna (Connolly 1994b, a). Some fish species such as syngnathids and gobiids spend their entire life cycle in seagrass meadows (Jenkins et al. 1997), while others such as the commercially important King George whiting, *Sillaginoides punctata* and yelloweye mullet, *Aldichetta forsteri*, rely on seagrass habitats during the juvenile life cycle stage (Rotherham and West 2002, Nakamura and Sano 2004, Valesini et al. 2004). The structural diversity created by seagrass leaves also provides shelter from larger predators for a range of small fish, crustaceans, amphipods and molluscs, which in turn provide a food resource for larger fish (Edgar and Robertson 1992).

There is some debate as to whether seagrass habitats support higher species diversity and abundance of fish compared to bare sand, though it is likely that these aspects are highly site specific (Bostrom et al. 2006). A comparative study between seagrass and unvegetated habitats in Port Phillip Bay, Victoria, revealed higher abundance and biomass of fish in deep subtidal seagrass meadows compared to bare sand; higher species richness in seagrass beds during summer; and

higher abundance on sand adjacent to seagrass compared with sand remote from seagrass (Jenkins et al. 1997). The same study found little difference in fish communities between intertidal seagrass and bare sand (Jenkins et al. 1997). Overall, the species of fish that appeared strongly associated with seagrass habitat in this study were primarily small non-commercial species and juveniles of larger species. Examples include the six spine leatherjacket, *Meuschenia freycineti* blue rock whiting, *Haletta semifasciata* and grass flathead, *Platycephalus laevigatus* (Jenkins et al. 1997).

Fish have been found to respond to a range of different habitat variables within seagrass meadows, including seagrass species; exposure; and location within the seagrass canopy. A study of *Posidonia* seagrass meadows in Cockburn Sound during the 1970's found that fish used six spatial areas of the meadows, with all areas being vertically distributed (Scott et al. 1986). The spatial area categories were defined as bottom; bottom, middle and top; middle; middle and top; top; top and above. These categories coincided with the typical swimming behaviour and feeding position of groups of species. Six species of leatherjackets were found to occupy the middle and top layers of seagrass meadows typically swimming between the blades or with large species occurring above the canopy. These included the bridled leatherjacket *Acanthaluteres spilomelanurus*, spinytail leatherjacket *Acantheluteres brownii*, pygmy leatherjacket *Brachaluteres jacksonianus*, fan-bellied leatherjacket *Meuschenia chinensis*, toothbrush leatherjacket *Acantheluteres vittiger*, and rough leatherjacket *Scobinichthys granulatus*.

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McArthur and Hyndes (2001) also identified clear differentiation in the use of *Posidonia* versus *Amphibolis* seagrass meadows by fish in relation to body size, with a likely link to predation protection mechanisms. The rainbow fish *Odax acroptilus* was the largest species sampled and was restricted to *Amphibolis griffithii* that has large open spaces in the canopy. Other larger

bodied fish also preferred *Amphibolis* habitat including the orange spotted wrasse *Notalabrus parilus*, sea trumpeter *Pelsartia humeralis*, toothbrush leatherjacket *Acantheluteres vittiger* and eastern striped trumpeter *Pelates sexlineatus*. The smaller fish were more likely to be found in *Posidonia sinuosa* meadows, which form dense foliage near the substratum. These included gobbleguts *Apogon reuppellii*, bridled leatherjacket *Acanthaluteres spilomelanurus*, and the pygmy leatherjacket *Brachaluteres jacksonianus* (MacArthur and Hyndes 2001). Rotherham and West (2002) also found significant differences in fish assemblages between *Posidonia* and *Zostera* seagrass meadows on the east coast of Australia, but these differences were not consistent over a larger scale when a range of estuaries from different locations were sampled. The lack of consistency in such differences led the authors to conclude that other factors such as estuary geomorphology may sometimes be more important than seagrass species in structuring fish communities since these features such as width of estuary mouth have the potential to influence larval settling of fish (Rotherham and West 2002).

Herbivory in seagrass systems

Herbivory of seagrass plants

The bulk of research into food webs of southern Australian coastal ecosystems has found that seagrass material is not widely consumed, though certainly provides important habitat for a range of invertebrates, particularly small crustaceans such as amphipods that form an important component in the diet of many fish (Edgar and Shaw 1995). In tropical seagrass systems herbivory of seagrass plants (direct consumption) is driven by vertebrate grazers such as dugongs, turtles and fish (Edgar 2001) and also sea urchins (Valentine and Heck 1991, Alcoverro and Mariani 2004). Studies of the fate of seagrasses in temperate food webs have identified low percentages in the range of 3 to 10% of production being consumed by herbivores (Pergent et al. 1997). In these temperate systems, where vertebrate grazers such as turtles and dugongs are usually absent,

herbivory has generally been thought to play a minor role because of the relatively poor nutritive value of seagrass plants and the high cellulose content, which is difficult to digest. In some cases the presence of defensive phenolic compounds deters consumption by herbivores, with invertebrates such as gastropods and amphipods more likely to be affected than vertebrates (Valiela et al. 2004). Recent research indicates that herbivory may be a more dominant (though highly variable) process in seagrass communities than is commonly understood, with a number of cases documented in which such herbivory has led to reductions in seagrass cover and biomass (Valentine and Heck 1991, Cebrian and Duarte 1998, Kirsch et al. 2002, Alcoverro and Mariani 2004). For example, the fish species *Sarpa salpa* has been found to remove large quantities of *Posidonia oceanica* seagrass from shallow Mediterranean seagrass meadows in summer, while sea urchins at this location were also found to be significant seagrass herbivores (Tomas et al. 2005). In Florida, seagrass tethering experiments conducted to assess grazing of *Thalassia testudinum* by parrotfish revealed that biomass removal by this herbivore exceeded seagrass production at some sites, though not over prolonged periods (Kirsch et al. 2002). The same study revealed that grazing by these fish varied significantly over temporal and spatial scales, a factor which may have influenced prior study conclusions that seagrasses were not important as a primary food resource, given the high chance that field observations could miss these sporadic events.

Despite the potential to remove large amounts of biomass, some seagrass systems can assimilate the effects of herbivory, since grazing does not always reduce leaf growth rates, and many grazers consume less than 30% of leaf production (Cebrian et al. 1998). This is not always the case, however, as it appears that the presence of other impacts such as eutrophication may influence the rates and frequency of seagrass herbivory. In the Mediterranean, researchers assessing the impacts of nutrient loading from fish farms identified that light reduction and epiphytes could not have caused the observed seagrass meadow regressions, as measurements of these revealed little variance from controls. At these meadows the seagrass loss was attributed to a substantial

increase in the consumption of seagrasses by sea urchins, with grazing in the vicinity of the fish farms causing decreased shoot size and shoot growth and leading to mortality of seagrass plants (Ruiz et al. 2001). These results confer with studies undertaken in the Honduras, where nutrient enrichment increased consumption of seagrass by 30% (Boyer et al. 2004). Yet Cebrian and Duarte (1998) found that variability in seagrass grazing was more closely related to the population dynamics of herbivores themselves rather than the nutrient content of seagrass plants, though a similar study observed higher grazing pressure on seagrass species with a high 'leaf specific growth rate' compared with slower growing species (Cebrian et al. 1998). More recent research into the interactive affects of herbivory, light and nutrients found that herbivory had inconsistent effects on seagrass growth and biomass, indicating that this topic requires further research to fully elucidate the range of potential interactions in impacted environments (Ilbarra-Obando et al. 2004).

Patterns of seagrass herbivory in relation to proximity within reef systems have also been discovered. In the Maldives, the consumption of *Thalassia* seagrass was highest inside a sheltered reef atoll where fish density was lower than outside the atoll (Sluka and Miller 2001). The authors attributed this discrepancy to the fact that the fish within the reef atoll were smaller (being juveniles) compared with those outside the reef atoll. Clearly, there would appear to be potential for a range of factors including herbivore density, predation pressure on herbivores, eutrophication, availability of alternative food sources for herbivores, and suitable habitat for dominant herbivores to influence seagrass grazing pressure, of which the specific functional processes and relationships are currently poorly understood.

It is not only seagrass leaves that are targeted by herbivores, but also the reproductive material. Recent research at Rottnest Island, Western Australia, has revealed high levels of predation on the seeds of *Posidonia australis* by a portunid crab (*Nectocarcinus integrifrons*) (Orth et al. 2006a). In

this study, the losses of *Posidonia australis* seeds to predators were so high that the authors considered that seed predation is possibly a major obstacle to seedling establishment in seagrass meadows of this species. Herbivory of reproductive material has also been measured in the Mediterranean Sea where the herbivores were found to damage 84% of *Posidonia oceanica* flowers (Balestri and Cinelli 2002), and in Japan where a tanaid crustacean was found to bore into the seeds of *Zostera marina* and *Z. caulescens* (Nakaoka 2002). Heavy predation of seagrass flowers and seeds has the potential to influence the success of plant reproduction in species that rely on seedlings for establishment and recovery, though such a relationship between herbivores and seagrass recruitment success has not been thoroughly studied to date.

Indirect trophic linkages between seagrasses, invertebrates and fish have been examined by a number of authors using stable carbon and nitrogen isotopes combined with gut content analysis to trace dietary compositions in key species (Edgar and Shaw 1995, Smit et al. 2005). A recent study undertaken in Cockburn Sound examined the trophic linkages between transported seagrass wrack and fish in unvegetated near shore areas using these methods (Hyndes and Lavery 2005). This study found that transported seagrass wrack could contribute to unvegetated near shore webs to some degree, although brown algae were more dominant. The authors noted that this study did not assess seasonal variations, which are needed for a complete assessment of the overall importance of seagrass wrack as a food resource, particularly given that younger fish may be more likely to consume this material directly. Harpactacoid copepods and polychaetes were among consumers of seagrass wrack, and these formed important components in the diets of a number of fish from sand habitats (where seagrass wrack had accumulated), including long finned goby (*Favonigobius macrocephalus*), King George whiting (*Sillaginoides punctata*), three other whiting species (*Sillago vittata*, *S. burrus and S. schomburgkii)*), cobbler (*Cnidoglanis macrocephalus*) and elongate flounder (*Ammotreitis elongatus*) (Hyndes and Lavery 2005). Other

studies of food webs in seagrass systems have focused on commercial and recreationally targeted fish species, and have not included small non commercial fish species (Butler and Jernakoff 1999).

In temperate parts of Australia, evidence of direct grazing of seagrass plants is limited and patchy. Documented fish grazers of *Posidonia* seagrass include the two omnivorous leatherjackets *Monacanthus chinensis*, fan bellied leatherjacket and *Meuschenia freycineti,* six spine leatherjacket which have been recorded consuming appreciable quantities of seagrass material, and are notable for leaving semi-circular bite marks on the leaves (Bell et al. 1978). The southern sea garfish, *Hyporhamphus melanochir* also consumes seagrass during the day and switches to feeding on planktonic crustaceans at night (Edgar 1997), while the spider crab *Naxia aurita* and swimmer crab *Nectocacinus integrifrons* are also know to include large amounts of seagrass in their diet (Edgar 2001). Given that the majority of known consumers of seagrass in southern Western Australia are omnivorous, it is conceivable that many studies of food webs in these environments could easily have missed grazing events, particularly where herbivory varies on a seasonal basis. It is also interesting to note that many of the fish species that consume both plant material and invertebrates often occur in large numbers, possibly since their food resource is less limited (Edgar 2001).

In Cockburn Sound a number of episodes of overgrazing of *Posidonia* meadows by outbreak populations of the sea urchin *Temnopleurus michaelsenii* were recorded over 1972 and 1977-78, identified by the characteristic 'stripping' of leaf epidermis, resulting in jagged ribbons of remnant leaves (Cambridge 1979). In each case while the grazing event was relatively short lived, the resulting meadow decline was considered permanent (at least at the time of publication), given the overgrazed seagrass meadows did not regenerate. However, in all cases the sea urchin grazing occurred at sites where the seagrass meadow was already sparse either due to depth limitation or deterioration from (likely) eutrophication impacts, with no overgrazing events recorded within

dense seagrass canopy (Kendrick et al. 2002). While not studied in detail at the time, this observation seems to imply that the overgrazing events were linked with interactions between multiple impacts, possible including fishing pressure and eutrophication. The theme of threat interactions is discussed in more detail later in this review.

Herbivory of epiphytes

The accumulation of epiphytic algae has been implicated in the decline of many seagrass systems, yet under natural conditions the presence of these epiphytes are a normal component of the seagrass community, and are an important food source for a variety of benthic fauna that may be found within seagrass meadows (Bologna and Heck 1999). Researchers have surmised that natural levels of epiphytic growth on seagrass plants provide benefits to some seagrass species by reducing desiccation when leaves are exposed at low tides and minimising light stress (Orth and Van Monfrans 1984). The dynamics of seagrass primary production, involving the regular shedding of old leaves is believed to have the benefit of preventing over fouling of seagrass leaves under low to moderate nutrient conditions (Orth and Van Monfrans 1984). Some seagrass species are less susceptible to algal colonisation as their leaves are very narrow, thereby minimising the number of algal species that have small enough basal discs to be successful colonisers (Orth and Van Monfrans 1984).

Grazing of epiphytes is undertaken by a variety of organisms including molluscs, amphipods, polychaetes and fish (Orth and Van Monfrans 1984, Shaw and Jenkins 1992, Jernakoff and Nielson 1998). A number of researchers have examined this grazing function for its potential to regulate the level of epiphyte growth on seagrass plants (Jernakoff and Nielson 1997, Gacia et al. 1999, Goecker and Kall 2003, Hily et al. 2004, Hays 2005) and of macroalgae in estuaries (Balducci et al. 2001, Boyer et al. 2004). Certainly, grazing has been demonstrated to reduce epiphyte load on seagrass plants (Gacia et al. 1999, Hily et al. 2004, Hays 2005); have a positive effect on seagrass

plant growth (Hays 2005); and reduce seagrass mortality in exclosure experiments (Jernakoff and Nielson 1997). The efficiency of grazing to reducing the shading effect of epiphytes was emphasized by Hily et al (2003), who found that gastropod grazing was concentrated at the apex of seagrass plants, and that grazing activity actually increased when epiphyte biomass increased.

The degree to which grazing of algal epiphytes is an effective regulatory process for epiphyte growth in eutrophic conditions is highly dependent on a number of environmental and species specific factors. Gacia et al. (1999) found that the fleshy green algae species *Cladophora* and*, Enteromorpha,* which bloomed under nutrient rich conditions in Florida, were more heavily grazed by herbivorous fish than the coarser red algae epiphyte species. The authors concluded that fish played only a minor role in regulating the impacts of eutrophication given that they only consumed fleshy green algal species, thereby having a seasonal and opportunistic role. Other authors have found increased herbivory of macroalgae (Boyer et al. 2004) and epiphytes (Hays 2005) with high nutrient content, and increased seagrass growth under ambient high nutrient levels in the presence of herbivores (Hays 2005). Boyer et al (2004) concluded that herbivore populations may, therefore, play a compensatory role in the effects of elevated nutrients. Hays (2005) recorded significant differences in the strength of interactions between turtlegrass and herbivores based on the genetic differences between seagrass material of the same species collected from meadows of relatively close proximity. This research implies that seagrass responses to moderate levels of eutrophication may be population specific, and is an area that requires further exploration.

Interactions between herbivory and multiple threats

Many grazing invertebrates in seagrass systems provide links with species in higher trophic levels thereby transferring carbon produced by macrophytes to predators such as fish, crabs and birds that feed on them (Orth and Van Monfrans 1984, Vanderklift and Wernberg 2008). The temperate

seagrass community food web is highly complex, comprised of numerous linkages, few of which are considered to be dominant given that many of the consumers are generalists (Edgar 2001). With the increased understanding of the role of herbivory in seagrass communities, attention is now turning to the potential interactions between bottom up (eutrophication) and top down (fishing) impacts on seagrass systems (Burkepile and Hay 2006, Jorgensen et al. 2007, Moksnes et al. 2008, Olsen and Valiela 2010) and other ecological environments (Vasas et al. 2007, Smith et al. 2010, Faithfull et al. 2011). Of key interest are the potential consequences to the health and resilience of seagrass communities if trophic imbalances lead to increased herbivory of seagrass plants, or reduced herbivory of algal epiphytes.

Exploration of the interactions of trophic changes and other ecosystem impacts such as eutrophication is a growing area of interest. The majority of food web research has focused on strong trophic linkages and obvious consumers such as sea urchins. The cascading effects of fishing can be expected to be more easily measured where such strong interactions exist, since it is possible that systems with many weak trophic linkages may be much more stable, and therefore resilient, than those with few strong linkages because of the high number of generalist consumers (Worm and Duffy 2003). Nevertheless, losses of weak linkages in trophic structures can still damage natural communities because they play a vital stabilisation role (Berlow 1999).

The subject of trophic cascades, whereby removal of higher order predators results in a release of species in lower trophic levels with associated impacts on primary production, has received a substantial amount of research attention in coral reef environments (McCannes et al. 2000) and in tropical seagrass systems (Alcoverro and Mariani 2004). Fishing of piscivorous fish from reef flats where seagrass surround coral patches has been predicted to cause herbivorous fish to forage more widely from their coral shelters thereby creating larger halos of bare sand around the coral (Miller and Hay 1998). Over grazing of seagrasses by high populations of sea urchins has been

recorded from a number of locations around the world (Valentine and Heck 1991, Alcoverro and Mariani 2004) including Western Australia (Cambridge et al. 1986). There is also evidence that such trophic linkages may exist between seagrass and fish. Modelling of the indirect effects of fishing in Mediterranean rocky pools predicted that intensified fishing of large predatory fish would result in a 'release' of small fish species with a consequent decline in the abundance of small invertebrates such as amphipods on which they feed (Pinnegar and Polunin 2004). Given current knowledge regarding the role of herbivory in reducing epiphyte loads, such modelling raises the possibility that similar results could occur in seagrass systems with resultant reductions in algal grazing by the epifauna. A further possibility is that declines in the abundance of small invertebrates could lead to omnivorous fish known to feed opportunistically on seagrass, such as garfish and leatherjackets, consuming a higher proportion of seagrass as an alternative food source.

Heck et al (2000) assessed the combined effects of over fishing and eutrophication by stocking field enclosures with large numbers of small pinfish *Lagodon rhomboids*, thereby simulating the removal of large predatory fish and then added nutrient treatments to the ambient water. This study had two results. Firstly, high numbers of fish reduced mesograzer populations but did not eliminate them due to the dense cover of seagrass present. Secondly, epiphyte loads were reduced in the fish enclosures, apparently due to the fish feeding on epiphytes as well as the mesograzers. Of interest is whether more severe losses of mesograzers would occur under similar (high middle predator) conditions in seagrass meadows that were not pristine, i.e. would seagrass decline from other sources lead to an exacerbated top down impact on mesograzers? Also, would the same type of generalist fish feeding behaviour occur under natural (non enclosed) conditions when fish would be free to forage more widely for food? Furthermore, if these omnivorous fish turned to consuming epiphytes when their 'supply' of mesograzers was difficult to obtain, would a similar pattern occur with omnivorous fish that also consume seagrass plants?

Overall, the threads of research described above provide strong impetus for further exploration of the interactions of bottom up and top down impacts, but also emphasizes the difficulties in measuring such interactions within complex food webs. Heck et al (2000) commented that there is likely to be a connection between the density or biomass of seagrass meadows and their susceptibility to be impacted by such top down impacts. For instance, where there has already been some level of disturbance to seagrass meadows resulting in a sparser coverage, this would reduce the available shelter from predators for mesograzers. It could, therefore, be theorized that systems that are subject to multiple impacts, such as physical disturbance and / or sedimentation (resulting in sparse seagrass meadows), combined with over fishing (resulting in high number of predators of mesograzers), combined with high nutrient levels (resulting in high epiphyte growth and / or high seagrass leaf nutrient content) are likely to be much more vulnerable to overgrowth of epiphytes or overgrazing events than systems that receive only one of these impacts in isolation. When the evidence surrounding potential links between herbivory of seagrass plants and nutrients are considered in this context, it is possible that a complex web of threat interactions could exist.

To actually measure the interaction of a range of threats exerted on an ecosystem is quite complex and is influenced by a range of potential sources of error. For example, exclusion studies may be associated with cage artefacts, and in open coastal areas, trophic structures may be dominated by pelagic species that are transient. Invertebrate populations can be cyclic (Heck et al. 2000) and other physical factors such as storm frequency and ambient light levels can also influence seagrass growth and vigour. While some authors have compared fauna and plant communities in sanctuary (no take) and fished areas, there may still be potential problems with the validity of their observations. Myers and Worm (2003) point out that with the rise of industrialised fishing practices the loss of large predatory fish from ecosystems is now a worldwide problem. These authors estimate that large predatory fish biomass is likely to be only 10% of

levels before such intense fishing began, implying that comparative studies and current management practices that rely on recent data as benchmarks are likely to be misleading, since the structure of the communities they are measuring would have changed long before sanctuaries were established.

Summary

Overall, there is a need to develop a better understanding of the functional linkages between seagrass, fish, invertebrates and nutrients in order to be able to predict the impacts of multiple disturbances on these ecosystems. There is growing evidence that direct herbivory of seagrass plants in temperate coastal ecosystems is a more frequent, widespread and possibly more dominant process than was previously understood. A number of cases have been described identifying links between increased herbivory of seagrass plants and impacts such as eutrophication, physical disturbance and loss of predatory fish as a result of fishing pressure, though the functional processes associated with such links are generally poorly understood. Certainly these processes appear to affect different species of seagrass in different ways, though there have been a number of cases in which very high levels of herbivory have lead to losses of seagrass beds. The possibility that such outcomes could be a result of interactions between multiple impacts further strengthens the case for a more integrated approach to management of marine systems.

CHAPTER 2: GEOGRAPHIC PATTERNS IN FISH HERBIVORY IN A TEMPERATE AUSTRALIAN SEAGRASS MEADOW

Abstract

Seagrass grazing by fish was measured in a large seagrass-dominated temperate bay (Geographe Bay, Western Australia) to examine whether: (1) seagrass herbivory occurs; (2) the level of herbivory is influenced by nitrogen in seagrass leaves; and (3) how herbivory and herbivorous fish communities vary with water depth and seagrass species. Species and abundance of fish and herbivore bite marks on seagrass leaves were recorded from diver surveys of 23 sites of varying depth ranging from 1 m to 18 m. *Posidonia sinuosa, P. coriacea, Amphibolis griffithii, and A. antarctica* seagrass leaves were collected, dried and analysed for total nitrogen. Evidence for low levels of seagrass grazing (less than 5 bite marks per 25 m transect) was found at over half the sites surveyed, though high levels of grazing (greater than 35 bite marks per 25 m transect) were recorded at only one site. An east - west geographic pattern was observed in the location of grazed sites and of herbivorous fish species that corresponded with the general prevalence of patch reefs, indicating that reef associated fish assemblages may be responsible for the observed grazing. Total nitrogen was elevated in seagrass leaves associated with urban / agricultural drains, although increased nitrogen was not associated with increased grazing. While grazing was recorded in this temperate seagrass meadow, the abundance of herbivorous fish was low and the amount of biomass removed by them was small compared to the balance of the meadow remaining, and to seagrass grazing studies elsewhere.

Introduction

Seagrass communities worldwide are under increasing pressure from coastal urbanisation and agriculture (Kendrick et al. 2002, Orth et al. 2006b). Many seagrass meadows experience multiple impacts such as eutrophication (Kendrick et al. 2002, Spalding et al. 2003) sediment movement (Kendrick et al. 2000) over-fishing and physical disturbance (Valentine et al. 1994, Hastings et al. 1995, Kendrick et al. 2000). There is some debate as to whether top down effects (e.g. fishing), or bottom up effects (e.g. eutrophication), have been the main driver in the decline of some seagrass meadows (Heck and Valentine 2007). There is also potential for fishing and eutrophication impacts to interact by causing imbalances in the consumption of primary production (i.e. grazing of epiphytes and seagrass) by fish (Heck et al. 2000, Heck and Valentine 2007, Jorgensen et al. 2007). Understanding the trophic pathway in specific seagrass ecosystems is, therefore, important to clarify how such imbalances have the potential to cause flow on effects in these systems, and ultimately affect primary production (Hughes et al. 2005).

There is a significant body of research into the loss of seagrass meadows resulting from over growth of epiphytic algae caused by elevated nutrients (Orth et al. 2006b, Waycott et al. 2009), yet many such ecosystems have also been heavily fished for decades and subjected to physical impacts such as from anchors and dredging. Many investigations into the impacts of eutrophication on seagrass systems have been undertaken decades after heavy fishing has altered the trophic structure, with flow-on effects from predators potentially having similar impacts to those attributed to eutrophication (Heck and Valentine 2007). These top down impacts potentially include reduced grazing of epiphytes on seagrass due to a loss of herbivores from the system, or alternatively, an increase in direct consumption of seagrass due to a release of herbivore populations. Our understanding of the ways in which trophodynamics can influence primary production in marine systems has improved in recent years and, in particular, grazing of

seagrass and epiphytes by fish has been found to be important in some systems (Ruiz et al. 2001, Alcoverro and Mariani 2004, MacArthur and Hyndes 2007).

Until recently, it was generally accepted that few fish feed directly on living seagrass material in temperate meadows, but rather the role of seagrass in near shore food webs was only as detritus consumed by invertebrates and small fish (Burchmore et al. 1984, Pollard 1984, Hyndes and Lavery 2005). This contrasts with temperate reef food webs in which many fish species are known to feed on algae (Jones 1988), although their role in grazing is secondary to that of invertebrates such as sea urchins (Vanderklift et al. 2009). Low levels of seagrass herbivory have been attributed to their poor nutritive value (Zieman et al. 1984); leaf structural defences such as high cellulose content (Lawrence 1975, Thayer et al. 1984), which is difficult to digest; combined with the presence of phenolic compounds in some species that may deter grazers (Thayer et al. 1984, Valiela et al. 2004, Verges 2007). In tropical systems where seagrass grazing by some fish has been measured, the importance of carbon removal to the overall system was considered low owing to the comparatively high daily production of seagrass (Thayer et al. 1984). However, a review (Valentine and Duffy 2006) suggested that grazing may have been underestimated in the past, especially in tropical systems, since few studies have made direct measurements of daily biomass removal by grazers. Direct measurements of fish grazing have recorded large losses of daily seagrass production from tropical meadows of the Caribbean (Kirsch et al. 2002), the Indo-pacific (Unsworth et al. 2007), and in temperate northern hemisphere Mediterranean systems (Tomas et al. 2005). Kirsch et al. (2002) also noted that seagrass grazing varied significantly over temporal and spatial scales, a factor that may have influenced previous studies since sporadic grazing events may have been missed. These studies raise the possibility that seagrass grazing could also be significant in other regions, and lend support to the need to re-examine this trophic pathway in a variety of seagrass ecosystems. These include southern hemisphere temperate meadows, where there have been few studies of seagrass grazing by fish.

Elevated nutrients in seagrass have been shown to increase rates of grazing, both of seagrass and their epiphytic communities, at times leading to measureable losses from grazing events from tropical systems (Goecker and Kall 2003) and temperate seagrass meadows (Tomas et al. 2005). The link between grazing and nutrients has also been shown in coral reef systems, where herbivorous fish have been found to preferentially feed on nutrient rich algae (Boyer et al. 2004). These observations raise questions about what the combined effects of eutrophication and overfishing could be in locations where seagrass grazers are non-target species.

Seagrass diversity in Western Australia (WA) is among the highest in the world, with 19 of the 50 known species of seagrasses occurring, of which 14 are endemic (Carruthers et al. 2007). Despite this, there have been few studies of seagrass herbivory from the region. Many seagrass meadows in temperate WA receive large annual nutrient loads from agricultural and urban sources (Walker and McComb 1992, Kendrick et al. 2000) and are subjected to heavy fishing pressure (Sumner and Willamson 1999). Few studies have sought to explore the role that elevated nutrients may play within the trophodynamics of seagrass ecosystems in WA. This is despite recorded cases of sea urchins over grazing seagrass meadows impacted by elevated nutrient loads, leading to measureable losses on a meadow scale (Cambridge 1979, Kendrick et al. 2002). The aforementioned gaps in knowledge combined with evidence for fish herbivory in temperate seagrass meadows add weight to the need to further explore the relationship between seagrass, fish and nutrients in temperate seagrass systems.

Three key questions were posed by this study: Does herbivory of seagrass by fish occur at the study location? Is herbivory related to the nitrogen concentration in seagrass leaves? And, does seagrass herbivory vary with water depth? Non – destructive survey techniques were used to test these questions.

Materials and methods

Study area

A survey of 23 sites covering 30 km from west to east in Geographe Bay was undertaken during spring in 2006. Sampling was designed to test for differences in grazing; the abundance and assemblage structure of fish communities; and the nutrient content of seagrass leaves. The sampling design accounted for a range of water depths, seagrass species, proximity to reef, and a broad geographical spread across Geographe Bay.

Geographe Bay (hereafter the Bay), located 270 km south of Perth in Western Australia, is a large sheltered marine embayment of approximately 134 km^2 in size with 70% coverage of seagrass (McMahon and Walker 1998). A variety of habitats are present in the Bay with the potential to influence the structure of fish communities. The predominantly sandy base of the Bay is underlain by limestone, which protrudes in some areas to create small limestone patch reefs. In the western corner of the Bay (near Cape Naturaliste) these outcrops are more prolific, and small coral bommies also occur throughout the Bay (Veron and Marsh 1988, Westera et al. 2009). A ridge of reef occurs off shore at approximately 18 metres depth (Geographe Bay Ridge). This ridge runs parallel to the shore for most of the length of the Bay. At depths below 18 metres the centre of the Bay has very little reef though there are extensive limestone reef outcrops extending along the eastern shores in the vicinity of Forrest Beach and Peppermint Beach (McMahon et al. 1997). With exception of these reef areas, the majority of the embayment has been colonised by extensive *Posidonia* and *Amphibolis* seagrass meadows (McMahon and Walker 1998). These meadows are among the largest and most continuous meadows of temperate seagrasses in Australia, with over ten different seagrass species recorded (McMahon et al. 1997). The dominant seagrass species is *Posidonia sinuosa*, which has formed large mono-specific meadows, particularly in shallow areas. In deeper waters *P. sinuosa* is often mixed with *Amphibolis griffithii* and *A.*

antarctica. Seven other seagrass species have been recorded in Geographe Bay (Walker and McMahon 1994), these include: *Posidonia angustifolia*, *P. ostenfeldii, P. coriacea, P. kirkmanii, Thalassodendron pachyrhizum, Halophila ovalis and Syringodium isoetifolium.*

Geographe Bay receives large annual loads of nutrients (225 tonnes of nitrogen annually) in winter primarily from agricultural sources (McMahon and Walker 1998) and is subjected to high recreational fishing during summer (Sumner and Willamson 1999). The Bay forms part of a proposed marine park area and supports a wide diversity of fish species, including those that have potential to graze on seagrass (Scott 1981). These include records of the two weed whiting species *Neodax radiatus* and *N. semifasciatus*; and four leatherjacket species *Scobynichthys granulatus*, *Acanthaluteres spilomelanurus*, *Brachaluteres jacksonianus* and *Meuschenia freycineti* (Scott 1981). Gut content studies of all of these species have shown that seagrass can form at least a component in the diet of these fish (Burchmore et al. 1984, Scott et al. 1986, MacArthur and Hyndes 2007). The combination of diversity in both seagrass and fish species together with the presence of high nutrient loads make Geographe Bay a suitable location to investigate interactions among seagrass grazing, nutrients and habitat.

Site selection and sampling design

Sites were selected across four depth ranges (Figure 2.1), these included ten shallow sites at 1-2 m; seven near shore sites located at 3 - 8 m depth; three mid shore sites located at 10 m depth and three off shore sites located at 18 m depth. Sites were geographically spread across four locations within the Bay, which were described in terms of their proximity to Cape Naturaliste, Dunsborough, Busselton and Wonnerup (west to east) (Figure 2.1). Two shallow sites (Old Dunsborough and Dunsborough North) and three near shore sites (Toby Inlet, Vasse Diversion Drain and Vasse Wonnerup) were located near urban / agricultural drains, and therefore had potential to be influenced by elevated nutrients. The design was unbalanced since additional near shore and shallow sites were sampled in order to sample drains and inshore mixed reef / seagrass habitat.

Seagrass species present at each site varied across the bay. *P. sinuosa* was present at all sites except the two western most shallow sites, Bunker Bay and Eagle Bay, while *P. coriacea* was present only at Wonnerup and Dunsborough South. *A. antarctica* had a widespread distribution and was absent only from Old Dunsborough, Dunsborough North, Dunsborough Mid and Offshore 3. The distribution of *A. griffithii* was more patchy with this species absent from transects at Dunsborough North, Dunsborough Mid, Quindalup, Toby Inlet, Siesta Park, Vasse Diversion Drain, Busselton, Forrest Beach, Wonnerup Beach and Offshore 1.
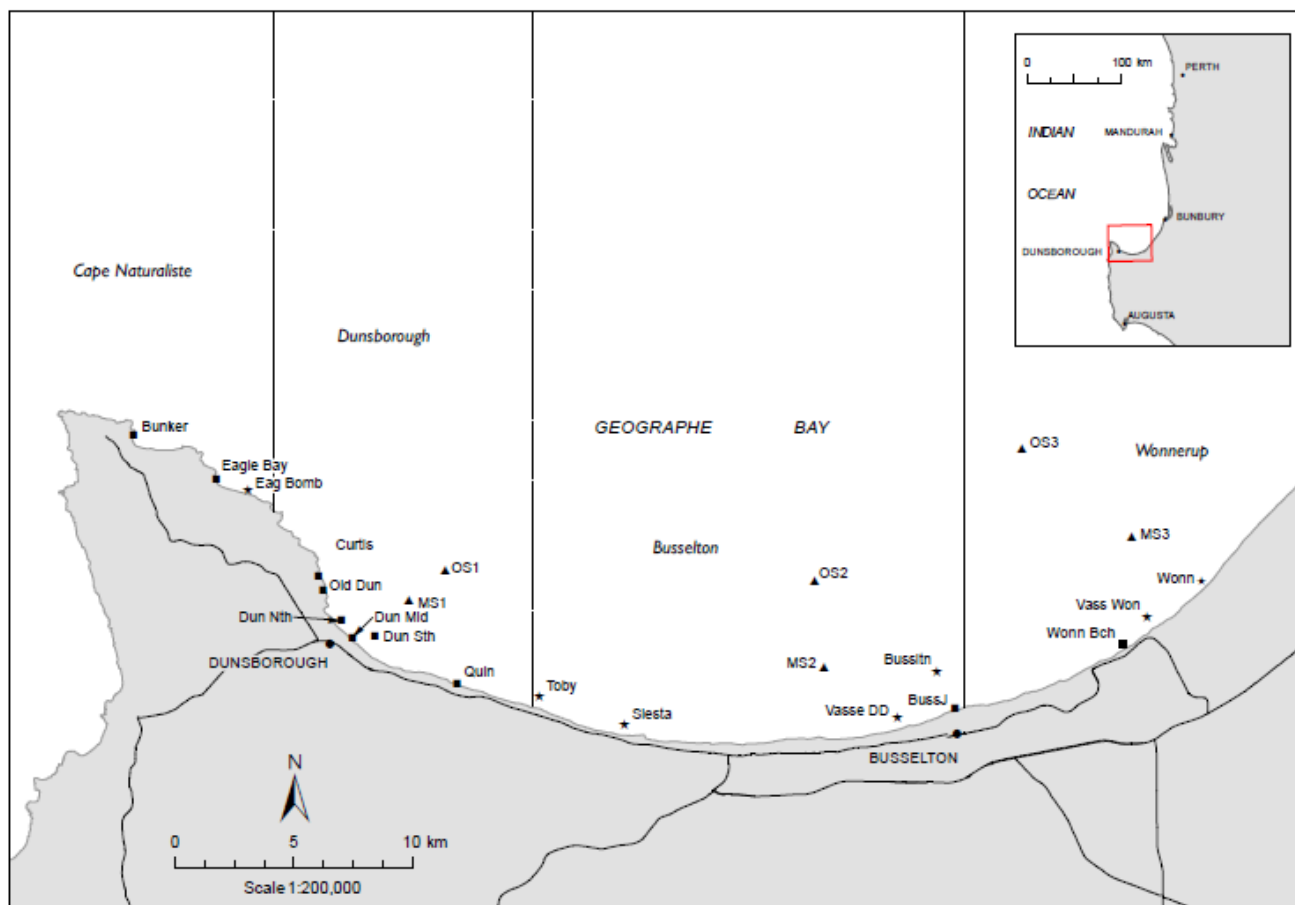
Figure 2.1: Study location and sampling sites in Geographe Bay (▲ off shore and mid shore: Off shore 1 (OS1), Off shore 2 (OS2), Off shore 3 (OS3), Mid shore 1 (MS1), Mid shore 2 (MS2) and Mid shore 3 (MS3); * near shore sites: Eagle Bay Bommie (Eag Bomb), Toby Inlet (Toby), Siesta Park (Siesta), Vasse Diversion Drain (Vasse DD), Busselton, Vasse Wonnerup (Vasse Won) and Wonnerup (Won) ■ shallow sites: Bunker Bay (Bunker), Eagle Bay (Eagle), Curtis Bay (Curtis), Old Dunsborough (Old Dun), Dunsborough North (Dun Nth), Dunsborough Mid (Dun Mid), Dunsborough South (Dun Sth), Quindalup (Quin), Busselton jetty, (Buss J) and Wonnerup Beach (Won Bch))

Survey regime

Grazing assessments

Evidence for damage or consumption of seagrass leaves by fish was assessed by conducting diver surveys of four haphazardly placed 25 x 1 m transects at each site. Divers swam along each transect and searched for seagrass leaves showing distinctive semi-circular bite marks left by herbivorous fish (approximately five minutes was allocated per transect). Such bite marks are known to be specific to herbivorous fish (Alcoverro and Mariani 2004, Tomas et al. 2005). All leaves found with fish bite marks were collected in the field and then each bite mark and leaves with marks were counted for each transect. Marks that were irregular or not completely consistent with a semicircular shape were not counted in order to reduce the risk of mistaking marks made by invertebrate grazers, leaf tears or necrosis of leaves. Divers were shown photographs of example seagrass bite marks prior to field work being undertaken. Example bite marks are illustrated in Figure 2.2.

Estimates of the proportion of seagrass biomass removed from within Geographe Bay were made. The average wet weight of an individual bite mark was estimated at 0.02 g. This estimate was obtained by weighing pieces of *P. sinuosa* that were equivalent in size (70 mm^2) to the average bite marks recorded. Seagrass leaves with bite marks were collected from the field and photographed over a 1cm by 1cm grid to obtain this estimate of bite mark area. The average biomass of seagrass removed per square metre was calculated using this estimate and the average bite marks over all transects. These figures were then compared to estimates of the total cover (94 km^2) and biomass (3.0 x 10^{10} g) of seagrass from the same study area made by McMahon and Walker (1998). Since the age of individual bite marks could not be determined

these estimates are based on biomass removed during the summer / autumn season (prior to senescence of leaves), and are therefore likely to be underestimated.

a   b   c
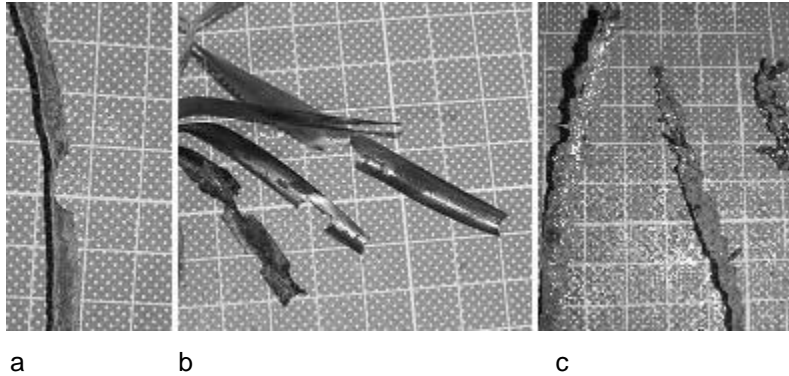
Figure 2.2: Photographs of fish bite marks on a) *P. sinuosa* seagrass leaf, b) *A. antarctica* leaves and c) multiple bite marks on *P. sinuosa* leaves. Leaves have been photographed over a 1cm grid.

Fish census

An underwater visual census (UVC) was conducted at all sites to test whether seagrass grazing was correlated with the abundance of herbivorous or omnivorous fish species with previous records of seagrass consumption. Fish species and abundance were measured by the same diver via visual census along four replicate 25 m transects at each site. Divers were familiar with local fish species. All fish species within visual range of the diver were counted and recorded on a slate while swimming along the transect. A maximum time of 5 minutes was spent at each transect. Horizontal visibility was recorded throughout the survey and remained within 15 to 20 m at all sites. A literature search identified that fish species in the (previous) Odacidae (now included within the family Labridae), Monacanthidae, Tetraodontidae and Girellidae families had potential to graze on seagrass (Burchmore et al. 1984). Abundances of fish within these groups were therefore analysed separately to the total species abundance data. Total species abundance was recorded so that herbivorous species abundance could be compared to the balance of the fish population.

Nitrogen content of seagrass leaves

Seagrass leaves of each species were collected for laboratory nitrogen analysis in order to assess linkages between seagrass nitrogen content and the occurrence of grazing pressure. Divers randomly selected 30 leaves from a 100 m transect at each site. All leaves were frozen following collection then three sub-samples of ten leaves of each species were dried, weighed and analysed for total kjeldahl nitrogen (TKN).

Statistical analysis

Multivariate data

Multivariate analyses were undertaken using the PRIMER 6 and PERMANOVA + statistical package (PRIMER E LTD 2005) to examine the abundance and assemblage structure. Raw data were treated with a square root transformation prior to analysis to down weight the influence of high abundance species. A Bray-Curtis resemblance matrix was constructed within PRIMER, using a dummy variable (+1). The data set contained a high proportion of blank samples and samples with only one species recorded. Without the use of a dummy variable, a Bray-Curtis matrix would have produced undefined similarities where no species were recorded in two compared samples, and highly varied similarities where only one species was recorded in the two samples. The adjustment of the dummy variable moderates these effects (Clarke et al. 2006). Data from the different depth and location groups were then compared using a two factor (depth, location; both fixed) and three factor (depth, location (both fixed), seagrass species (random)) PERMANOVAs (Anderson 2001). To address the unbalanced design the type three partial sums of squares was used.

Univariate data analysis

Since there was an unbalanced number of sites across treatments, univariate PERMANOVA (Anderson 2001, McArdle and Anderson 2001) were used to test for differences between depth, location and drains / no drains groups within the seagrass grazing and seagrass nutrient data using the same approach as used for the multivariate fish data.

Results

Herbivory assessments

Herbivory, measured as bite marks on leaves, was low. Damage of seagrass leaves attributed to fish bite marks was found at 69.6% of the sites surveyed. The mean number of bite marks found per transect across all sites was 2.6 ± SE 0.9, and was less than 5 for each site with the exception of Curtis Bay (Curtis) where an average of 37 bite marks were recorded (Figure 2.3). The majority those recorded at Curtis Bay were comprised of multiples bite marks on individual leaves of *P. sinuosa* and *A. griffithii.* Bite marks were recorded on *P. sinuosa* leaves at 12 of the 23 sites and on *P. coriacea* leaves at Wonnerup Beach. Bite marks were recorded on *A. griffithii* leaves at six sites (Figure 2.3), while a single bite mark was found on an *A. antarctica* leaf at the western most mid shore site.

The observed herbivory measurements displayed an obvious geographical pattern across the Bay. Bite marks were recorded at all sites west of Quindalup with the exception of Bunker Bay and at all sites within the eastern most Wonnerup location (Figure 2.3). In contrast bite marks were found at only two sites in the central Busselton location (at Vasse Diversion Drain and at Off shore 3). Grazing, measured as bite marks, was found at all three off shore sites, 80% of shallow sites, 66% of near shore sites and 66% of mid shore sites.

The influence of distance from shore on the fish and grazing data was inconsistent across the depth ranges. Grazing was found at all off shore sites regardless of their location, but only at those near shore and mid shore sites that were close to reef. For the shallow group of sites grazing was found at a wider range of locations.
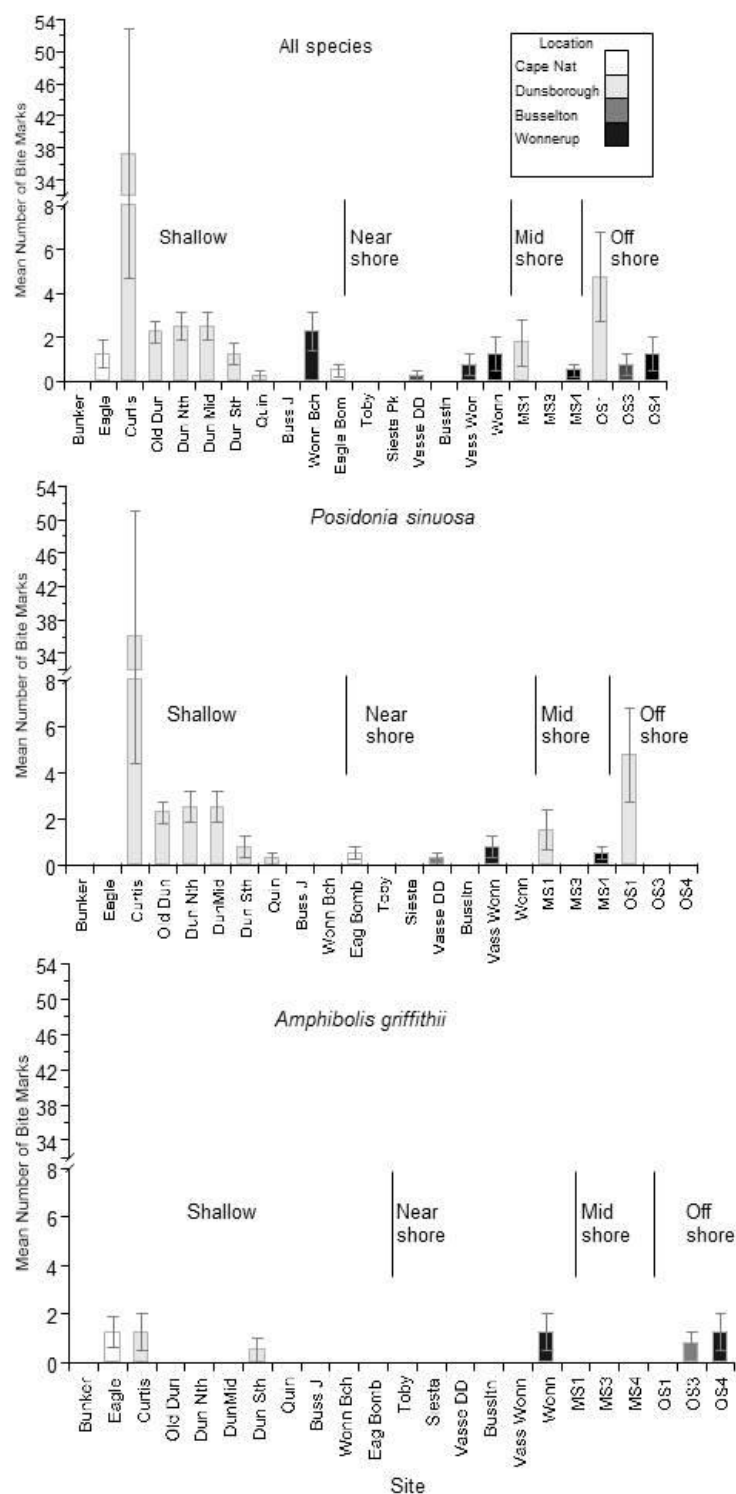
Figure 2.3: Mean number of fish bite marks (±SE) per transect on seagrass species; *P. sinuosa* and *A. griffithii* leaves and from all seagrass species surveyed in Geographe Bay.

A two factor PERMANOVA showed a significant difference for the factor location but no significance for the factor distance from shore (Table 2.1). Pair-wise analyses revealed significant differences between grouped sites within the locations Cape Naturaliste and Dunsborough; Cape Naturaliste and Busselton; Dunsborough and Busselton; and Busselton and Wonnerup (Table 2.1).

Extrapolated estimates of the total biomass and total percent of seagrass biomass removed from Geographe Bay were 1.95 kg and 0.00065% respectively. These estimates were based on the following:

Calculated in this study

Transect size	25 m^2
Average bite marks per transect	2.6 bites
Estimated wet weight per bite mark	0.02 g
Average biomass removed by grazing	0.00208 gm^{-2}
Estimated total biomass removed in study area	1955.2 g
Proportion of total biomass grazed in study area	0.00065 %

Calculated by McMahon and Walker (1998) for the same study location

Area of study	134 km^2
Average seagrass cover in area [a]	70%
Area of *P. sinuosa* cover	94 km^2
Mean maximum biomass	320 gm^{-2}
Total biomass in study area	3 x 10^{10} g

a: based on Walker et al (1987);Conacher et al (1993)

Table 2.1: Results of a two factor PERMANOVA to test for the effect of location and distance from shore on the numbers of fish bite marks on seagrass leaves. Pair wise analyses for the location groups are also shown. Note: bold text indicates significant differences (p < 0.05).

Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Location	3	7247	2415.7	5.4801	**0.001**
Distance from Shore	3	1248	416.2	0.9441	0.418
Distance x Location	6	1245	207.4	0.4706	0.872
Residual	82	36587	440.8		
Total	95	54077			
Pair wise groups (location)	*t*	*P(perm)*			
Cape Naturaliste, Dunsborough	2.1404	**0.031**			
Cape Naturaliste, Busselton	2.5188	**0.017**			
Cape Naturaliste, Wonnerup	1.3737	0.181			
Dunsborough, Busselton	3.4767	**0.001**			
Dunsborough, Wonnerup	1.0868	0.284			
Busselton, Wonnerup	*3.3818*	**0.002**			

Fish assemblages

Thirty six species of fish from 24 families were recorded during the UVC. The most frequently observed species were *Pseudocaranx dentex* (Skipjack trevally), *Apogon rueppellii* (Gobbleguts) and *Coris auricularis* (Western king wrasse). The mean abundance of all fish per transect was greatest at the Eagle Bay Bommie and at the Busselton Jetty. These sites also displayed high variability as evidenced by the error bars. This variability was created by records of large schools of fish at some replicates. For example, *Trachurus novaezelandiae* (Yellow tail scad) was abundant at the Busselton Jetty (Figure 2.4).

Eight fish species, that were potential seagrass grazers, were recorded in low abundances. At least one of these species was recorded at nine of the sites: Curtis Bay, Dunsborough Mid, Dunsborough South, Busselton Jetty, Wonnerup Beach, Eagle Bay Bommie, Mid shore 1 and Off shore 1 (Figure 2.5). The most abundant grazing species recorded were *Odax acrophilus* (herring cale) and *Odax cyanomelas* (rainbow cale). Both species were recorded in highest abundance at

Curtis Bay. Other grazing species recorded included *Girella zebra* (zebra fish), *Siphonognathus beddomei* (pencil weed whiting), *Meuschenia hippocrepis* (horseshoe leatherjacket), *Scobinichthys granulates (*rough leatherjacket), *Polyspina piosae* (orange barred pufferfish) and *Torquigener pleurogramma* (weeping toado). Only the western most sites within the near shore, mid shore and off shore groups recorded any grazing species. Abundance of potential grazing species was not related to total abundance of all species. A two factor PERMANOVA did not show any significant differences for the factors location and distance from shore across or within groups. With the exception of the Busselton Jetty, all sites where potential grazing fish were recorded corresponded to sites where fish bite marks were also recorded.
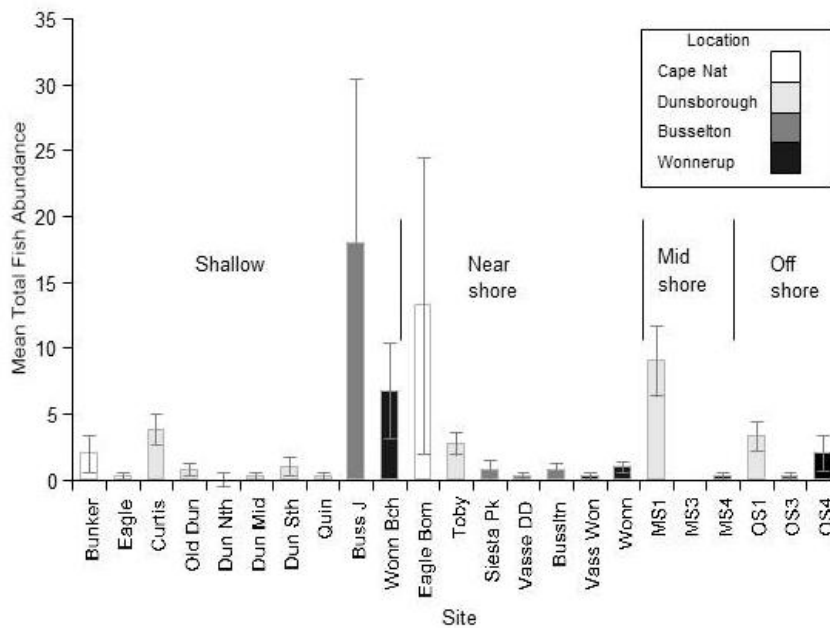
Figure 2.4: Mean abundance of all fish (± SE) species recorded in Geographe Bay by UVC per transect.
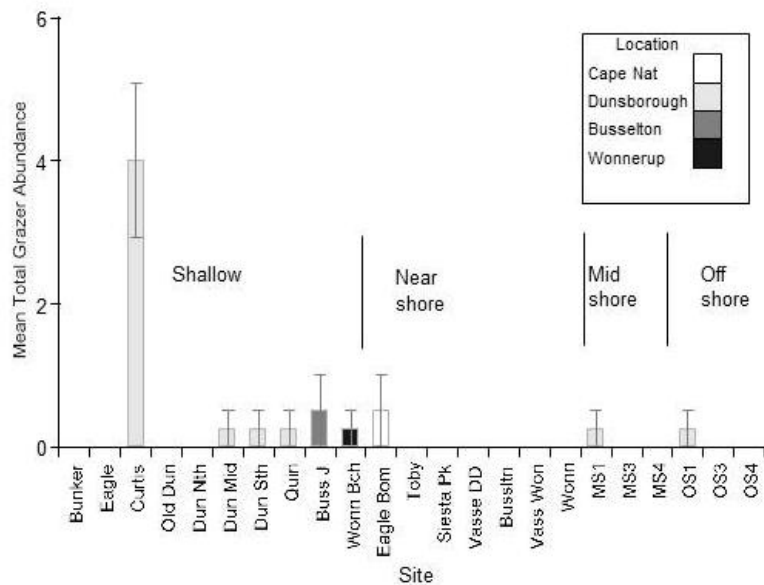
Figure 2.5: Mean abundance of potential herbivorous fish species (± SE) (from the families Odacidae, Monacanthidae, Tetraodontidae and Girellidae) by UVC per transect.

Nitrogen content of seagrass leaves

The nitrogen content (as TKN) of *P. sinuosa* and *A. antarctica* leaves collected from shallow and near shore sites was slightly elevated compared to samples collected from the mid shore and off shore (Figure 2.6). In *A. griffithii*, nitrogen was elevated in leaves collected from off shore sites compared with mid shore, near shore and shallow sites. *P. coriacea* leaves were only collected from one site (Wonnerup). Nitrogen content in these samples was comparable with that measured in *A. antarctica* leaves at the same site.

A three factor PERMANOVA showed a significant effect on TKN of seagrass leaves for the factor depth group (Table 2.2). Pair wise analyses revealed significant differences between sites in the shallow and near shore; shallow and mid shore; and mid shore and near shore depth groups (Table 2.2). The off shore group of sites did not differ significantly from any other group. There

was no significant effect for the factors location and seagrass species; however, significant differences in the effect of seagrass species were recorded by a single factor PERMANOVA, demonstrating all species do not retain the same pools of nitrogen. A second set of pair wise analyses revealed significant differences in TKN content between the pairs of species *P. sinuosa* and *A. griffithii*; *A. griffithii* and *A. antarctica*; and *A. griffithii* and *P. coriacea* (Table 2.2). There were no significant differences between *P. sinuosa* and *P. coriacea*; *P. sinuosa* and *A. antarctica*; and *A. antarctica* and *P. coriacea*.

The subset of shallow and near shore sites was analysed separately since some of these sites are exposed to seasonal pulses of elevated nutrients from rural and urban drains. A two factor PERMANOVA identified a significant interaction between species and drains suggesting a difference in the response of individual species to elevated TKN. The main effects of species and drains were also significant (Table 2.2), although the effect varied between the four drain sites Dunsborough North, Toby Inlet, Vasse Diversion Drain and Vasse Wonnerup. TKN in *P. sinuosa* and *A. antarctica* leaves from the Vasse Diversion Drain and Toby Inlet drain sites were lower than other sites while *P. sinuosa* seagrass from the Dunsborough North and Vasse Wonnerup drain sites were elevated. The Busselton, Busselton Jetty, Wonnerup Beach and Wonnerup sites (all non drain sites) also had consistently elevated TKN.
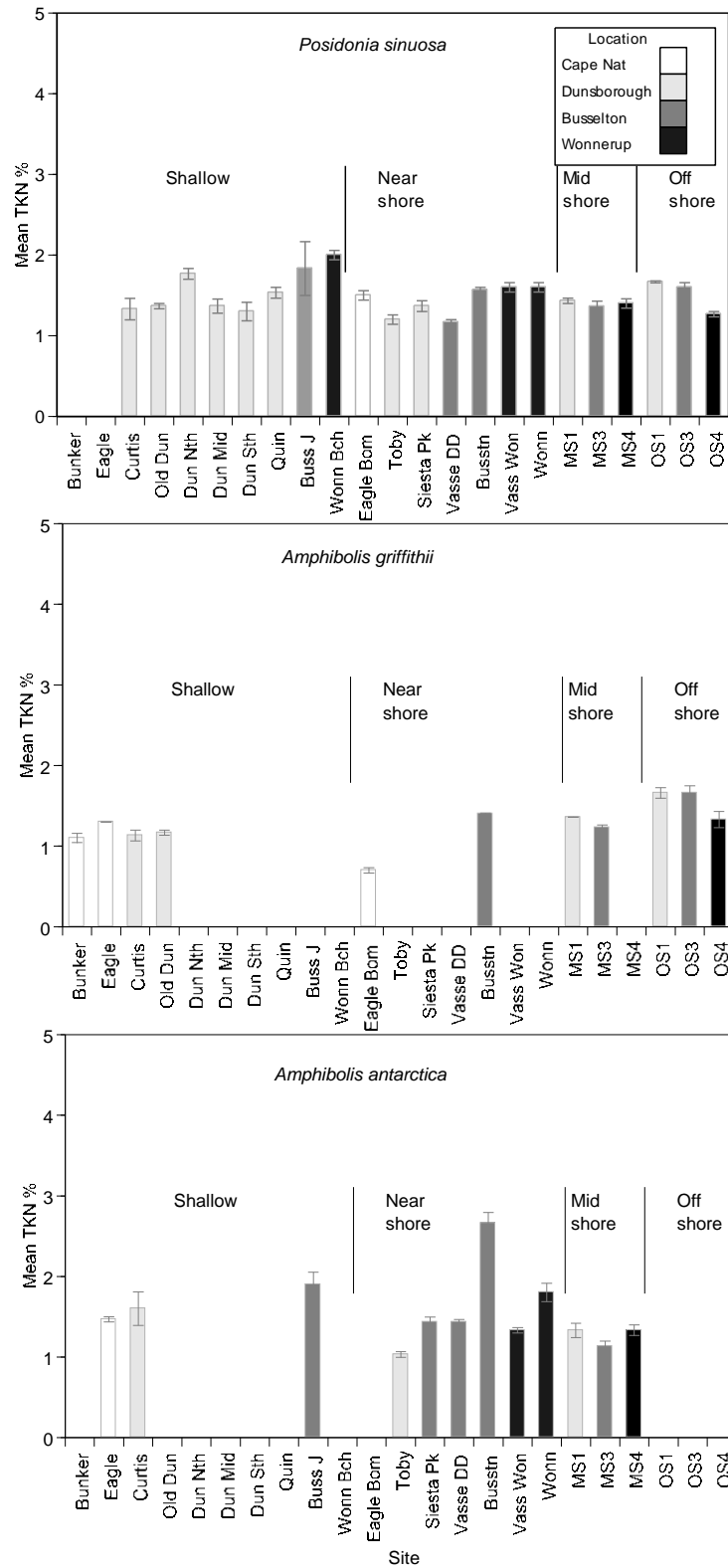
Figure 2.6: Mean TKN (± SE) of *P. sinuosa*, *A. griffithii* and *A. antarctica* seagrass leaves collected per site.

Table 2.2: Results of PERMANOVA analysis to test for differences in depth, location and seagrass species on TKN of seagrass leaves. Pair wise analyses for location and seagrass species groups are also shown. Bold text indicates significant differences.

3 factor PERMANOVA: Depth, Location, Species					
Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Depth group	3	15.023	5.007	5.560	**0.037**
Location	3	0.1899	0.063	0.384	0.777
Species	3	2.9575	0.986	1.430	0.249
Depth x Location	5	15.575	0.907	1.317	0.066
Depth x Species	5	4.5375	0.039	0.056	0.997
Location x Species	5	0.1948	0.175	0.254	0.782
Depth x Location x Species	2	0.3506	0.175	0.254	0.782
Res	108	0.6890			
Total	134	134			
Pair wise groups (location)	T	P (perm)			
Shallow, Mid shore	2.7405	**0.015**			
Shallow, Off shore	0.6450	0.595			
Shallow, Near shore	4.9447	**0.003**			
Mid shore, Off shore	2.2121	0.264			
Mid shore, Near shore	2.7148	**0.027**			
Off shore, Near shore	0.5049	0.682			
Single factor PERMANOVA: Species					
Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Species	3	11.617	3.872	4.145	**0.008**
Res	131	122.38			
Total	134	134			
Pair wise groups(seagrass species)	T	P (perm)			
P. sinuosa, A. griffithii	2.8563	**0.007**			
P. sinuosa, A. antarctica	0.2536	0.809			
P. sinuosa, P. coriacea	1.8871	0.077			
A. griffithii, A. antarctica	2.3692	**0.025**			
A. griffithii, P. coriacea	3.3419	**0.002**			
A. antarctica, P. coriacea	1.3439	0.235			
Two factor PERMANOVA: Species and drains					
Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Species	3	8.4453	2.815	3.976	**0.015**
Drains	1	9.1873	9.187	12.978	**0.001**
Species x Drains	2	5.5912	2.796	3.949	**0.026**
Res	86	60.882	0.708		
Total	92	92			

Discussion

Seagrass leaves were grazed by fish in Geographe Bay, but the amount of grazing was at extremely low levels, representing a small proportion of the total seagrass biomass in the Bay (0.00065%). Elsewhere, the reported rates of seagrass grazing by fish have varied widely, yet some examples have demonstrated large biomass removal (Table 2.3). For example, direct measurements of seagrass grazing using tethering techniques identified losses that were close to or exceeded daily production in the Florida Keys (Kirsch et al. 2002, Valentine et al. 2007) and in the Medes Island Marine Reserve in Spain (Tomas et al. 2005). In these examples, and those listed in Table 2.3, the fish species responsible for grazing were schooling species found in high abundance. In comparison, the abundance of herbivorous fish recorded in this study was very low. Only eight potential grazing species were recorded, and half of these were single sightings. These results are consistent with temperate seagrass meadows from Australia, where herbivore abundance is considered low (Edgar and Shaw 1995). While Mediterranean temperate meadows also have few grazing species, the fish *Sarpa salpa* occurs in large schools in *Posidonia oceanica* meadows and has been shown to consume large quantities of seagrass (Tomas et al. 2005). Large schools of herbivores such as *Scarus guacamaia* also occur in tropical seagrass meadows (Valentine and Duffy 2006) and can graze heavily on *Thalassia testudinum* seagrass. Grazing by larger schools of herbivores would have a more measureable impact on the overall seagrass meadow.

Table 2.3: Comparison of estimates of seagrass biomass removal by grazing fish from the international literature.

Author	Location	Grazing fish	Seagrass species grazed	Observed grazing
Valentine et al (2007)	Florida Keys	*Sparisoma radians*	*Thalassia testudinum*	Ranged from 48% removal of above ground production to grazing exceeding production
Tomas et al (2005)	Medes Island Marine Reserve. NE coast of Spain	*Sarpa salpa*	*Posidonia oceanica*	65 – 100% of shoots with bite marks. Removal of leaf biomass by fish exceeded production.
Alcoverro and Mariani (2004)	Kenyan coast	*Calotomus carolinus*	*Thalassodendron ciliatum*	For older leaves in fishing protected areas between 50 and 100% of leaves with bite marks.
Kirsch et al (2002)	Florida Keys	Parrot fish *Sparisoma radians*	*Thalassia testudinum*	Up to 80% of above ground biomass removed by fish
(Cebrian and Duarte 1998)	Medes Island Marine Reserve. NE coast of Spain	*Sarpa salpa*	*Posidonia oceanica*	0 to 50% above ground leaf production removed.

Our results show that in *P. sinuosa* meadows, grazing of seagrass by fish does not appear to be as important as that reported elsewhere, as the biomass of seagrass removed represents a small overall area of meadow. When the average consumption per unit areas is extrapolated to the whole of Geographe Bay it represents an estimated total of 1.9 kg annum^{-1} of seagrass biomass, though it is noted that this removal is undertaken by relatively few grazing fish. These results contrast with work from a *Posidonia australis* meadow in eastern Australia in which seagrass material was found to comprise between 29% and 63% of the gut contents of monocanthid fish (Burchmore et al. 1984). Similarly, a study from the south west of Western Australia that found large quantities of seagrass material were consumed by two species (*Odax acroptilus* and *Haletta semifasciata)* (MacArthur and Hyndes 2007). The authors concluded that grazing of seagrass and algae in off shore meadows could be underestimated in Western Australia where

large numbers of omnivorous monacanthid, labrid and terapontid fish occur (MacArthur and Hyndes 2007). However, the results of this study also demonstrate that fish grazing in predominantly *P. sinuosa* meadows in temperate Australia are not influential in the growth and structure of seagrass since the proportion removed by grazing is so small.

Bite marks on seagrass leaves were elevated near the far western (Cape Naturaliste and Dunsborough) and eastern (Wonnerup Beach) locations compared to the central Busselton location of the Bay. Although not statistically significant, the same geographic pattern also occurred in the abundance of herbivorous fish. It is likely that differences in benthic habitat characteristics of the Busselton location explain this pattern. In the central Busselton area there is generally less relief in the form of coral bommies and / or limestone outcrops and at near shore and shallows sites the meadows were comprised of *P. sinuosa* and *A. antarctica* seagrass rather than *P. sinuosa* and *A. griffithii*. The seagrass leaves grazed in this study were almost exclusively *P. sinuosa* and *A. griffithii*, and while these were certainly the most common species recorded, there was a clear preference away from grazing of *A. antarctica*. Benthic habitat variables, including seagrass species and presence of reef are known to influence fish (Ayvazian and Hyndes 1995, MacArthur and Hyndes 2001, Rotherham and West 2002) and invertebrate (Tuya et al. 2010) assemblages within temperate Australian seagrass meadows. For example, McArthur and Hyndes (2001) identified clear differentiation in the use of *Posidonia* versus *Amphibolis* seagrass meadows by fish in relation to body size, with a likely link to predation protection mechanisms. In their study *Odax acroptilus* was restricted to *A. griffithii* which has large open spaces in the canopy allowing space for this larger species to forage. The results of this study also supports the work of Macarthur and Hyndes (2007), who found high levels of grazing within other Western Australian mixed meadows of *P. sinuosa* and *A. griffithii* and noted that grazing is likely to vary with fish assemblages among different seagrass meadows. The

53

structure of fish communities in the western locations of Geographe Bay may be influenced by a cross habitat exchange with the adjacent high energy environment beyond Cape Naturaliste, where diverse near shore and deeper off shore reefs are prevalent. The fact that no grazing was recorded at the two western most sites at Bunker Bay and Eagle Bay appears to be an exception to this rule. However, these sites also differed in their benthic habitat from all other sites in the absence of *Posidonia sinuosa*, and this factor may have influenced both grazing and fish assemblages. Clearly, while the seagrass grazing and the abundance of herbivorous fish recorded in this study were both very low, a positive influence of the presence of reef and of mixed *P. sinuosa* and *A. griffithii* seagrass meadows is a logical explanation for the geographic patterns displayed. However, further assessment of the fish and habitat variables using more intensive sampling techniques would be required to confirm this observation.

The concentration of nitrogen in seagrass leaves did not follow the aforementioned geographic pattern, and nitrogen was elevated in *P. sinuosa* seagrass leaves in near shore and shallow sites. While *P. sinuosa* was certainly the most common species grazed, it was also by far the most abundant and widespread seagrass species. Elevated nitrogen (predominantly in *P. sinuosa*) in seagrass leaves from the near shore and shallow sites indicate that seagrass may be taking up nitrogen delivered via surface drains and groundwater flow that discharge to the near shore area. It is also possible that nitrogen may be pooling in leaves at locations where higher epiphyte growth reduces leaf growth. Other sites with elevated nitrogen were those that are known to attract large schools of fish, such as at the Busselton Jetty and the Eagle Bay Bommie, where faecal matter from schooling fish may have contributed additional nitrogen to the sediments (Ruiz et al. 2001, Alevizon 2002). There was not, however, a relationship between sites with elevated nitrogen and sites with elevated grazing. These results contrast with those from the Florida Keys where *Sparisoma radians* have shown a strong preference for seagrass

leaves with high nitrogen content compared with non enriched leaves. In the field these species have been recorded removing a large proportion of daily biomass of seagrass (Goecker and Kall 2003). The link between grazing and nutrients has also been shown in coral reef systems, where herbivorous fish have been found to preferentially feed on nutrient rich algae (Boyer et al. 2004). The dynamic nature of nitrogen in *Posidonia* seagrass leaves, which can vary with seedling age, leaf age and stage of senescence (Hocking and Cambridge 1981) may have complicated the assessment of this variable, especially considering the very low rates of grazing that were being compared.

The most abundant grazing species recorded in this study was *Odax acroptilus,* and its highest abundance occurred at the same location with the greatest grazing. Macarthur and Hyndes (2007) noted that *Odax acroptilus* consumed the most plant material of all species in their study, with seagrass and algae comprising over half of its diet. A more detailed examination of the distribution of this and the other herbivorous species recorded using other methods may help to explain the observed patterns in herbivory.

Curtis Bay was the only location surveyed where high levels of grazing occurred. This site also had the highest abundance of potential herbivorous fish species in addition to large loads of epiphytes on the seagrass leaves. Epiphytes were not specifically measured as part of the survey, but field notes were made providing visual descriptions of these factors. Long and fleshy green epiphytes were observed on the leaves of *P. sinuosa* leaves at Curtis Bay. It is possible that herbivorous fish may have preferentially been feeding on the seagrass leaves at Curtis Bay in order to obtain more nutritious algae as a food source, as observed by Wressnig and Booth (2007) in their study of monacanthid fish grazing of *P. australis* leaves with high epiphyte loads.

The UVC data suggest that grazing fish may be relatively uncommon in depth ranges of 4 to 10 m in Geographe Bay, except where influenced by reef. However, sampling was more intensive inshore and the fish abundances were small making statistical inference difficult. More survey work examining fish communities would also help to clarify these issues

Overall, these results confirm that seagrass grazing by fish does occur in temperate Australian meadows, but at relatively low levels. Potential drivers of seagrass grazing are likely to be more strongly related to fish communities rather than to the nitrogen content of seagrass leaves, at least at the meadow scale. The strong geographic gradient of herbivory warrants further work to explore the role of depth gradients and exposure as well as the nature of habitat factors such as rocky shorelines, patch limestone reefs and coral bommies in structuring fish assemblages in seagrass systems.

CHAPTER 3: CONNECTIVITY AMONG SUBTIDAL HABITATS INFLUENCE SEAGRASS ASSOCIATED FISH ASSEMBLAGES

Abstract

The spatial distribution of fish within seagrass meadows can be influenced by their level of connectivity to adjacent reef and sand habitats. This has been demonstrated in spatially fragmented seagrass habitats. In this study, we have focused on a continuous temperate seagrass meadow covering 134 km^2 to ask the question: "How are fish assemblages influenced by depth and the spatial proximity of other habitats?" Fish and benthic habitat were recorded in a large seagrass-dominated temperate bay (Geographe Bay, Western Australia) to examine how a) fish assemblages; and b) species identified as potential seagrass grazers; vary with depth, proximity to reef, seagrass species and algal cover. Fish species and abundance were recorded at 25 sites in depths varying from 1m to 18m using baited remote underwater stereo-video (stereo-BRUV) systems. Benthic habitat variables at these sites were classified from seafloor video footage taken along six randomly chosen 25 m transects. Fish assemblages were diverse with 89 species from 34 families recorded. Fish species and abundance were significantly influenced by the presence or absence of hard substrata, and different combinations of the mean percent cover of the seagrasses *Posidonia sinuosa*, *Amphibolis griffithii* and *A. antarctica*. Benthic habitat and fish assemblages were both strongly structured by depth. At near shore locations, large drains were associated with a different benthic habitat and a different assemblage of fish compared to other near shore and deeper sites. The number of fish that were herbivorous or omnivorous, and included seagrass in their diet, was less than four percent of the total fish abundance. The diversity of habitat present within the seagrass meadow afforded by patch reefs, coral outcrops and variations in seagrass species influenced the high diversity of fish recorded. These findings emphasise the importance of understanding the connectivity between critical habitats within seagrass meadows when undertaking marine planning.

Introduction

Temperate seagrass meadows are highly productive ecosystems that support diverse assemblages of fish (Burchmore et al. 1984, Ayvazian and Hyndes 1995, Edgar and Shaw 1995, Jenkins et al. 1997, Carruthers et al. 2007). Seagrass meadows offer protection from predators in addition to foraging opportunities within the canopy for invertebrates and attached algae (Pollard 1984, Edgar and Shaw 1995), while for some species of fish the seagrass leaves are also a food resource (Valentine and Duffy 2006, Heck Jr and Valentine 2007, MacArthur and Hyndes 2007). Seagrasses also provide important linkages with adjacent habitats, with some reef associated fish foraging or sheltering in nearby seagrass meadows during critical life stages (Heck Jr et al. 2008). Understanding how fish are distributed within, and adjoining, seagrass meadows in relation to environmental gradients, is important for clarifying the interaction between top-down and bottom-up trophic linkages in the ecosystem; making predictions about potential impacts of benthic habitat changes; and designing marine reserves. Building knowledge about the processes that connect seagrass meadows and other local habitats i.e. the movement of animals across habitat boundaries is vital for the management of these complex systems.

Research into the influence of habitat on fish assemblages has identified clear differentiation in temperate fish assemblages associated with distinct habitats such as seagrass, reef, bare sand and surf zones (Ayvazian and Hyndes 1995, Jenkins et al. 1997, Nakamura and Sano 2004, Valesini et al. 2004), and with depth (Hyndes et al. 1999). We propose that this separation of habitats is a construct of the design of the studies and method used, and does not address the potential connectivity among depths, habitats and within species of seagrasses. Such connectivity ensures important contributions, both in terms of animal and plant biomass,

58

between seagrass meadows and a variety of adjacent habitats including reefs, beach zones, continental shelves and mudflats (Heck Jr et al. 2008). Within seagrass meadows themselves, seagrass species and density (MacArthur and Hyndes 2001, Rotherham and West 2002, Hyndes et al. 2003), substrate (Chatfield et al. 2010), and the size and patchiness of seagrass beds (Jelbart et al. 2007) have also been shown to play a role in structuring fish assemblages. However, our understanding of the way in which combinations of different benthic habitat variables influence fish assemblages is still limited within seagrass systems, given the high degree of variability in regional fish associations and benthic habitat characteristics of seagrass meadows from different areas (Burchmore et al. 1984, Edgar and Shaw 1995, Vanderklift and Jacoby 2003, Chatfield et al. 2010).

Fish from different trophic guilds are likely to respond differently to variations in seagrass species, substrate and depth depending on the degree to which food availability or shelter from predators drive choices in habitat. A large proportion of seagrass associated temperate fish consume small crustaceans, which are in turn influenced by seagrass biomass (Edgar and Shaw 1995) and seagrass species (Jernakoff and Nielson 1998). It is therefore logical that these habitat variables also influence the habitat choices made by these fish. Non-seagrass associated fish that leave their primary habitats to forage within seagrass meadows may also respond to similar cues. There has been less work on the role of benthic habitat in structuring herbivorous fish assemblages compared to other trophic groups, although MacArthur and Hyndes (2007) found herbivorous labrid, monacanthid and terapontid fish favoured off shore *Posidonia sinuosa* and *Amphibolis griffithii* meadows. Similarly, work from chapter 2 of this thesis identified a strong geographic gradient in seagrass herbivory and herbivorous fish, with an apparent link to depth and patch reefs in the study location. These findings prompted further work to explore the role of depth, hard substrate and other habitat variables in structuring these fish

59

assemblages, and emphasised the potential importance of connectivity among adjoining habitats in this system.

Most studies of fish assemblages in Australian seagrass systems have used beam trawl methods for sampling (Scott 1981, Jenkins et al. 1997, MacArthur and Hyndes 2001, Rotherham and West 2002, Hyndes et al. 2003, Valesini et al. 2004, Jelbart et al. 2007). Beam trawls require a destructive sampling approach, favour sampling of small sedentary or cryptic fish species, and do not enable fine scale sampling of habitats since a single sampling event may cross a number of habitat boundaries (Cappo et al. 2004). Alternative sampling methods such as baited remote underwater stereo-video (stereo-BRUV) systems have been used to sample a wide variety of habitats (Cappo et al. 2004, Harvey et al. 2007, Moore et al. 2009), but relatively few seagrass meadows (Stoner et al. 2008, Chatfield et al. 2010). In reef environments stereo-BRUVS have a tendency to record a wider range of larger and more mobile species, and although they are baited they attract a suite of non carnivorous fish (Cappo et al. 2004, Harvey et al. 2007). The use of BRUVS to investigate habitat preferences of fish within seagrass meadows therefore has the potential to identify differences in seagrass utilisation by fish species across changes in depth and habitat.

In this study I sought to examine habitat preferences of fish within a large (134 km^2) seagrass meadow dominated by *Posidonia sinuosa*, but containing representative areas of predominantly *Amphibolis antarctica*, *A. griffithii* and patch reefs. I was primarily interested in examining how fish assemblages at the study location are influenced by depth and the spatial proximity of other habitats. A secondary aim of the study was to assess how species identified as potential seagrass grazers vary with depth, proximity to reef, seagrass species and algal cover.

Materials and methods

Study location

The study area included the seagrass meadows of southern Geographe Bay along 57 km of shoreline between Eagle Bay in the west (latitude -33.5558, longitude 115.0639) and Forrest Beach to the east (latitude -33.5585, longitude 115.4691) in water depths of 3 to 20 m (Figure 3.1).

Geographe Bay (hereafter the Bay), located 270 km south of Perth in Western Australia, is characterised by extensive (134 km^2) *Posidonia* and *Amphibolis* seagrass meadows (McMahon and Walker 1998). Patchy limestone reef outcrops occur within the continuous seagrass meadow. The dominant seagrass species is *Posidonia sinuosa*, which has formed large mono-specific meadows, particularly in shallow areas. In deeper waters *P. sinuosa* is often mixed with *Amphibolis griffithii* and *A. antarctica* (Walker and McMahon 1994)*.*

Experimental design

Sampling was conducted over two consecutive years. During the summer of 2006/2007 sampling was undertaken at four types of sites in Geographe Bay based on their distance from shore (or depth); and their proximity to drains (Table 3.1, Figure 3.1).

1. Near shore and near to agricultural and residential drains and estuaries

2. Near shore and away from agricultural and residential drains

3. Mid shore

4. Off shore

These included 12 near shore sites in 3 to 8 m of water depth and 350 to 600 m off shore, of which six were close to drains; five mid shore sites in 8 to 12 m of water depth and 2.5 to 4.5 km off shore; and five off shore sites in 15 to 18 m of water depth and 4.5 to 8.5 km from shore.

Some minor amendments were made to the sampling design for the summer of 2007/2008. Eagle Bay was not sampled in this second year since it was not considered to be representative of the wider near shore environment across Geographe Bay owing to the presence of a very large coral outcrop. Four additional sites were sampled in 2007/2008. These included two to provide a better geographical spread across the bay (Quindalup and Broadwater); and two in 1-2 m water depth to investigate fish assemblages in the very shallow areas of Geographe Bay near Dunsborough (Dunsborough Lagoon and Quindalup Beach). The latter two sites were sampled only for fish.

Table 3.1: The location, short name, proximity to drains, distance from shore and depth for each study site in Geographe Bay. [a] Dunsborough Lagoon and Quindalup Beach were sampled for fish only in 2007/2008 only. [C] Quindalup and Broadwater were sampled in 2007/2008 only.

Location	Short name	Proximity to Drains	Distance from Shore	Depth
Dunsborough Lagoon [a]	Dun Lg	Far	Shallow	1-2 m
Quindalup Beach [a]	Quin Bch	Far	Shallow	1-2 m
Eagle Bay [b]	Eag Bomb	Far	Near	3-5 m
Dunsborough	Duns	Far	Near	3-5 m
Quindalup [c]	Quin	Far	Near	3-5 m
Toby Inlet	Toby	Near	Near	3-5 m
Siesta Park [c]	Siesta	Far	Near	3-5 m
Buayanyup	Buay	Near	Near	3-5 m
Broadwater	Broad	Far	Near	3-5 m
Vasse Diversion Drain	Vasse DD	Near	Near	3-5 m
Busselton	Bssltn	Far	Near	3-5 m
Port Geographe	PortGeo	Near	Near	3-5 m
Vasse Wonnerup	Vass Won	Near	Near	3-5 m
Wonnerup Beach	Wonn	Far	Near	3-5 m
Forrest Beach	Forr Bch	Far	Near	3-5 m
Mid shore Site 1	MS1	Far	Mid	8-12 m
Mid shore Site 2	MS2	Far	Mid	8-12 m
Mid shore Site 3	MS3	Far	Mid	8-12 m
Mid shore Site 4	MS4	Far	Mid	8-12 m
Mid shore Site 6	MS6	Far	Mid	8-12 m
Off shore Site 1	OS1	Far	Off	15-20 m
Off shore Site 2	OS2	Far	Off	15-20 m
Off shore Site 3	OS3	Far	Off	15-20 m
Off shore Site 4	OS4	Far	Off	15-20 m
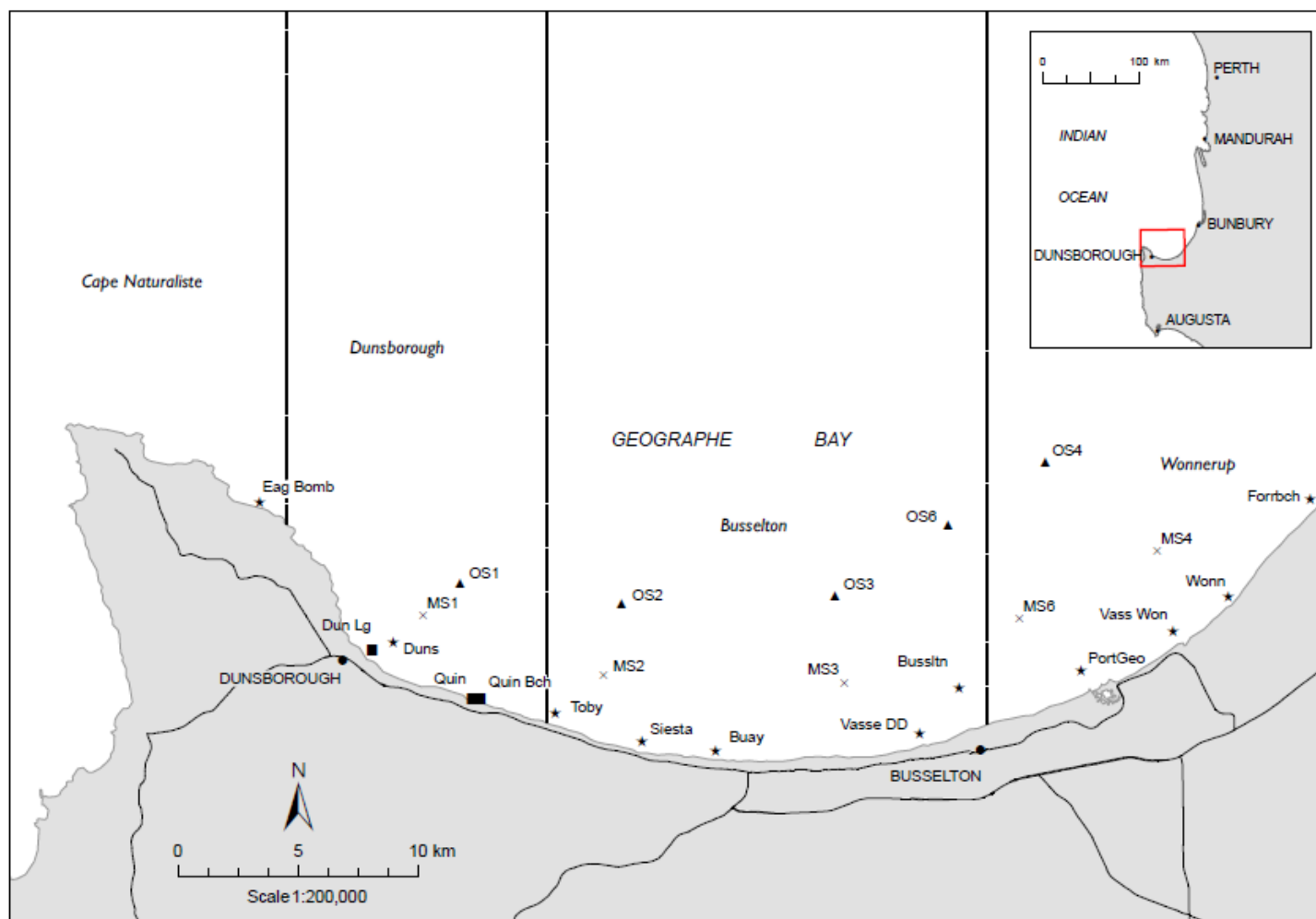
Figure 3.1: Study location and sampling sites in Geographe Bay (▲ off shore sites , X, mid shore sites * near shore sites ■ shallow sites)

Sampling of fish

Fish assemblages were sampled at five replicate locations at each site in December 2006 and December 2007 using baited remote underwater stereo-video (stereo-BRUVs) systems as described by Watson et al (2005). Information on the design and calibration of the stereo BRUVs can be found elsewhere (Harvey and Shortis 1996, Harvey and Shortis 1998, Harvey et al. 2001, Harvey et al. 2002). This system used two SONY HC 15E handy-cams with 0.6 wide-angle lens in underwater housings. The housings and cameras were separated on a base bar by 0.7 m and inwardly converged to provide an overlapping field of view from approximately 0.5 m in front of the cameras. The field of view sampled by this system was from 0.5-8 m inclusive from the cameras. Bait consisted of 800 g of pilchards (*Sardinops sajax*) in a plastic-coated wire mesh basket that was suspended 1.2 m in front of the two cameras. Each deployment was separated by 300 m to reduce the likelihood of fish moving between replicates within the sampling period. Video footage was filmed for a minimum of 45 minutes.

Video footage was captured using Adobe Premiere Pro 2 in an avi (Audio Video Interleaved) format. The right hand video of each stereo-pair was used to determine the relative abundance of the fish seen on the video tape using EventMeasure (http://www.seagis.com.au/event.html) software. This program is used for logging and reporting events occurring in digital video imagery, and was used in this study to manage data collected from the field operations and video tapes, to record the timing of events and capture reference images of the seafloor and fish in the field of view.

A search of literature identified that fish species in the (previous) Odacidae (now included within the family Labridae), Monacanthidae, Tetraodontidae and Girellidae families had potential to graze on seagrass (Burchmore et al. 1984). Abundances of fish within these groups were

therefore analysed separately to the total species abundance data to address the question relating the abundance and distribution of potential grazing fish.

The trophic categories of each fish species was identified using data from Ford (2011). These data were then used to compare the proportions of fish abundance from each trophic category comprising the total fish abundance.

Sampling of benthic cover

Benthic cover was recorded at each site using underwater videography taken 50 cm above the canopy or sea floor along six haphazardly chosen 25 m transects. The video footage was analysed on computer and sites classified based on the percentage cover of 21 different benthic categories (Table 3.2). Categories were based on the lowest practicable taxonomic level possible from the footage. For each transect the percentage cover of each benthic category was estimated by allocating the category under each of 10 points in 15 randomly selected frames (a total of 150 points per transect). The number of rocky reef patches recorded at each transect were estimated by counting the total number of patches along the entire transect (the entire transect was analysed since patch reefs were relatively sparse).

Table 3.2: Benthic categories identified in video transects.

Seagrass	Algae	Invertebrates	Inorganic
Amphibolis antarctica	*Caulerpa spp.*	Ascidians	Bare reef
A. griffithii	*Cystophora racemosa*	Corals	Rubble
Halophila spp.	*Padina australis*	Sponges	Shell grit
Posidonia australis	*Sargassum* spp.	Unidentified invertebrates	Sand
P. sinuosa	*Udotea* spp.		
Dead rhizomes / stems	Unidentifiable algae		
Seagrass wrack			

Statistical analysis

Untransformed data were used for the multivariate analyses of benthic cover, while square-root transformed data were used for multivariate analyses of fish assemblages to account for rare species. Bray-Curtis similarity matrices were calculated for both the fish and benthic habitat data sets. Non-metric multidimensional scaling (hereafter referred to as MDS; Clarke 1993) was used to illustrate patterns of differences among sites. Three factor PERMANOVAs were used to test differences in benthic habitat and fish assemblages among year of sampling (random), distance from shore (fixed) and site (random, nested in distance from shore); and in benthic habitat among year of sampling (random), proximity to drains (fixed) and site (random, nested in proximity to drains). Since we were interested in the general patterns of fish assemblages in relation to habitat, data were pooled across the two sampling years (Anderson et al. 2008) to ensure the full range of species that utilised the habitat were included in the total analysis regardless of individual differences between years. Where differences were significant, pair wise analyses were then performed. SIMPER (Clarke, 1993) was used to identify particular taxa or variables that contributed most to differences between groups of sites.

The RELATE procedure (Clarke 1993) was used to test the correlation between fish matrices and the benthic habitat matrix. Data from both data sets were first averaged on a site basis to enable sites to be compared at the appropriate scale, and to ensure site names were matched. The two shallow sites, where benthic habitat had not recorded, were omitted from this analysis. One near shore site at (EagBom) was also omitted since this site differed from all others in the presence of a very large coral outcrop. The BVSTEP procedure (Clarke 1993) was used to identify the subset of benthic habitat variables that best explained a) the wider fish assemblages and b) the subset of potential grazing fish species. Six key habitats were then identified by

differentiating between the averaged benthic habitat variables that were identified by BVSTEP

as having the best correlation with the fish assemblages. These habitats were then used as a

factor within the PRIMER data set to identify the range of fish species that were recorded within

these habitats. A single factor PERMANOVA was undertaken to test for the significance of

differences in fish assemblages within each habitat type.

Results

Benthic habitats

There were significant differences in benthic cover among depths (Table 3.3). SIMPER indicated that this was driven by *Posidonia sinuosa* and *Amphibolis antarctica*, which were both dominant at near shore sites (Figure 3.2). The abundance of *A. griffithii* and rocky reefs increased with distance from shore. Off shore sites were dominated by algal assemblages in both sampling years (Figure 3.3), and in the second year of sampling only, were also more common at mid shore compared with near shore sites

Within the near shore group of sites, there were significant differences in the cover of *A. griffithii* among sites near to and far from residential and agricultural drains (Table 3.4), with less *A. griffithii* occurring in all sites close to drains, except the Vasse Diversion Drain. Proximity to drains did not significantly affect the other individual benthic categories or the overall benthic assemblage.

At near shore sites, reefs only occurred at Eagle Bay and Dunsborough in the west and at Wonnerup in the east of the bay, while *A. griffithii* was also more common in the far western and eastern sampling sites compared with those in the centre of the Bay. Two sites (Broadwater and Siesta Park) were entirely dominated by *P. sinuosa* while mixed species' occurred at all other sites. Sponges were recorded at all off shore sites in addition to mid shore site 1, indicating the presence of hard ground at these locations. Small coral outcrops were recorded at the mid shore sites 1 and 2 in addition to off shore sites 1 and 4.
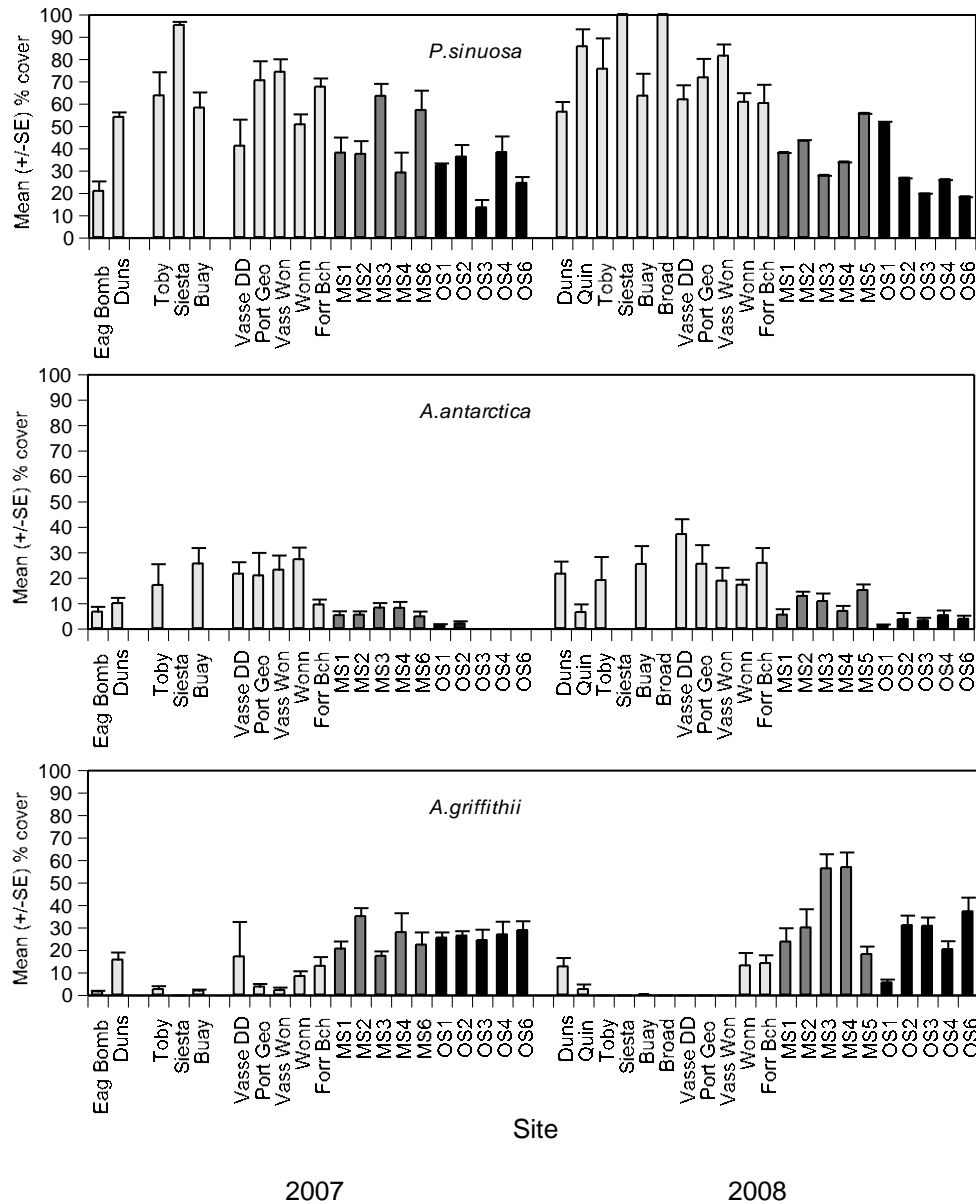
Figure 3.2: Mean percent cover (± standard error; n=6) of seagrass species recorded in Geographe Bay (near shore sites are represented in light grey bars, mid shore sites in dark grey bars and off shore sites in black bars; sites are presented from west to east within each depth group).

Figure 3.3: Mean percent cover (± standard error; n=6) of algal assemblages and rocky reef recorded in Geographe Bay (near shore sites are represented in light grey bars, mid shore sites in dark grey bars and off shore sites in black bars; sites are presented from west to east within each depth group).

Table 3.3: Results of three factor PERMANOVAs to test for the effect of site (Si(Di)), year of sampling (Ye) and distance from shore (Di) on the percent cover of each benthic habitat variable. Note: bold text indicates significant differences (p < 0.05).

Benthic assemblages					*Posidonia sinuosa*		
Source of variation	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Ye	1	3423.0	2.10	0.131	46.3	0.05	0.829
Di	2	31935.0	7.08	**0.002**	20984.0	11.28	**0.001**
Si(Di)	11	3352.1	2.06	**0.010**	1740.5	1.86	0.146
Ye x Di	2	1391.6	0.85	0.512	202.8	0.22	0.814
Ye x Si	11	1631.1	3.60	**0.001**	937.3	4.63	**0.001**
Res	140	453.7			202.5		
Total	167						
A. antarctica					*A. griffithii*		
Source of variation	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Ye	1	559.0	4.31	0.063	627.6	0.85	0.406
Di	2	1889.9	5.85	**0.011**	6322.4	5.09	**0.011**
Si(Di)	11	334.2	2.57	**0.046**	584.8	0.79	0.661
Ye x Di	2	11.2	0.09	0.930	804.5	1.08	0.380
Ye x Si	11	129.9	3.35	**0.001**	742.6	5.25	**0.001**
Res	140	38.8			141.4		
Total	167						
Algal assemblage					Rocky reefs		
Source of variation	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Ye	1	634.2	3.89	0.081	1.90	0.49	0.488
Di	2	4960.3	6.07	**0.010**	128.30	17.65	**0.002**
Si(Di)	11	436.0	2.68	**0.053**	7.18	1.86	0.136
Ye x Di	2	407.7	2.50	0.127	0.30	0.08	0.947
Ye x Si	11	162.9	2.40	**0.009**	3.86	2.41	**0.012**
Res	140	68.0			1.61		
Total	167						

Table 3.4: Results of three factor PERMANOVAs to test for the effect of site (Si(Pr)), year of sampling (Ye) and proximity to drains (Dr)on the percent cover of each benthic habitat variable. Note: bold text indicates significant differences (p < 0.05).

Benthic assemblages						*Posidonia sinuosa*		
Source of variation	df	MS	Pseudo-F	P(perm)		MS	Pseudo-F	P(perm)
Ye	1	4404.1	11.071	**0.010**		488.47	5.283	0.052
Pr	1	4104.4	1.937	0.166		3.0885	<0.0001	1.000
Si (Pr)	7	2408.1	6.074	**0.007**		2475.1	26.802	0.001
Ye x Pr	1	92.826	Negative			86.576	0.947	0.355
Ye x Si (Pr)	7	396.48	0.943	0.492		92.347	0.287	0.960
Res	88	420.53				322.16		
Total	105							
A. antarctica						*A. griffithii*		
Source of variation	df	MS	Pseudo-F	P(perm)		MS	Pseudo-F	P(perm)
Ye	1	416.080	1.5044	0.242		12.941	0.887	0.387
Pr	1	2346.100	4.3377	0.068		1854.900	6.780	**0.037**
Si (Pr)	7	596.320	2.1603	0.155		219.640	14.951	**0.005**
Ye x Pr	1	6.220	<0.0001	0.897		55.299	3.760	0.090
Ye x Si (Pr)	7	276.040	1.3892	0.200		14.691	0.382	0.883
Res	88	198.710				38.465		
Total	105							
Algal assemblage								
Source of variation	df	MS	Pseudo-F	P(perm)				
Ye	1	1990.700	18.889	**0.006**				
Pr	1	50.138	1.068	0.478				
Si (Pr)	7	142.340	1.355	0.335				
Ye x Pr	1	2.815	<0.0001	0.888				
Ye x Si (Pr)	7	105.010	3.792	0.002				
Res	88	27.691						
Total	105							

Fish

Total assemblage

Eighty-nine species of fish (from 69 genera and 34 families) and one species each of cuttlefish, squid, crab and octopus were recorded on the stereo-BRUVS (Appendix A). The schooling species *Pelates sexlineatus*, *Trachurus novaezelandiae* and *Pseudocaranx spp*. were the most abundant recoded. Of these, only *Pseudocaranx spp*. was widely distributed among depths throughout the bay. This species, in addition to *Parequula melbournensis and Notolabrus parilus,* was recorded at all 25 sites over the two-year sampling period*.* Rays were also recorded at the majority of sites (23 and 22 sites respectively). In contrast, *Pelates sexlineatus* and *Trachurus novaezelandiae* were primarily recorded only at near shore sites. Two thirds of the fish species were recorded in low abundances (usually singular sightings) at five or less sites.

Each fish species recorded was assigned a trophic category (Ford 2011) (Appendix A). When proportions of the total abundance of fish from each category were compared, the most dominant were invertebrate carnivores, generalist carnivores and species that consumed both invertebrates and algae (Figure 3.4). A very small proportion of the overall fish abundance recorded were either herbivorous fish (0.48 %) or omnivorous species known to include seagrass within their diet (3.41 %). Similarly, piscivorous fish and zooplanktivores comprised a very low proportion of the total fish abundance in Geographe Bay (0.91 and 2.84 % respectively).
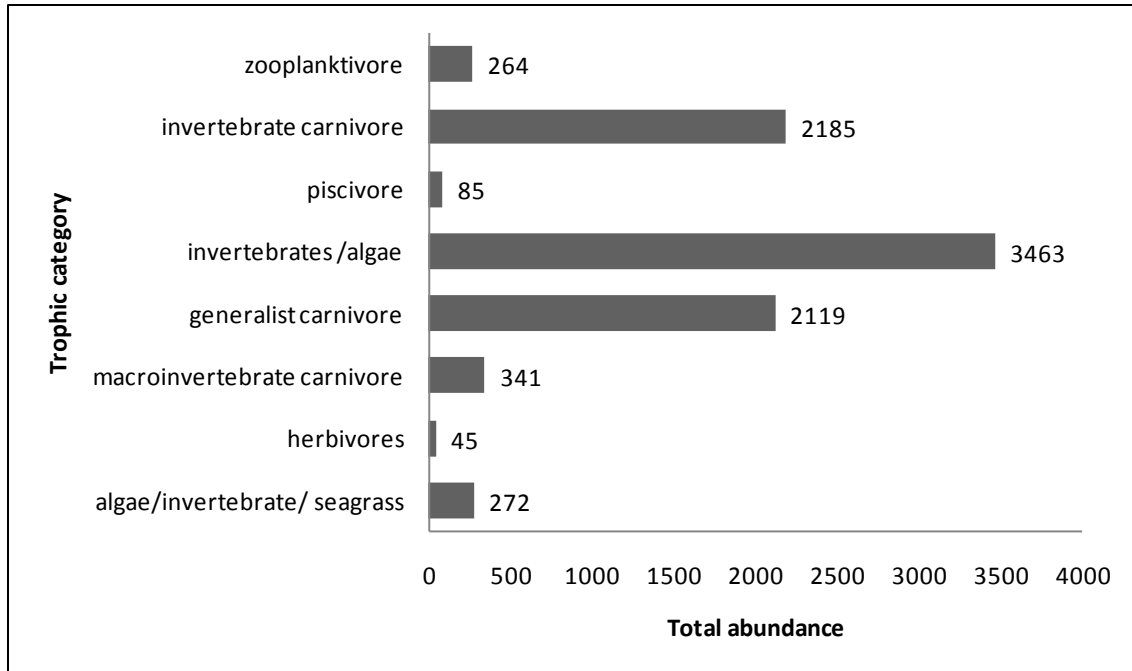
Figure 3.4: Total abundance of fish recorded from each trophic category in Geographe Bay (pooled data for both years of sampling).

An MDS of fish assemblages displayed a clear pattern with increasing distance from shore (Figure 3.5) with a change from shallow and near-shore sites to mid shore to off shore sites. The observed differences in fish assemblages between depth groups were statistically significant when tested using a three factor PERMANOVA (Table 3.5). SIMPER identified that *Apogon ruepellii*, *Pelates sexlineatus*, *Pseudocaranx* spp., *Trygonorhina fasciata*, *Paraquula melbournensis*, *Coris auricularis*, *Ophthalmolepis lineolatus* contributed most to variability in assemblages among sites and times. The former three species were recorded in greatest abundance at near shore sites, while the latter three were more abundant at off shore sites. *Trygonorhina fasciata* was recorded in all depth groups, but was generally less abundant at mid shore sites compared to other depth groups.

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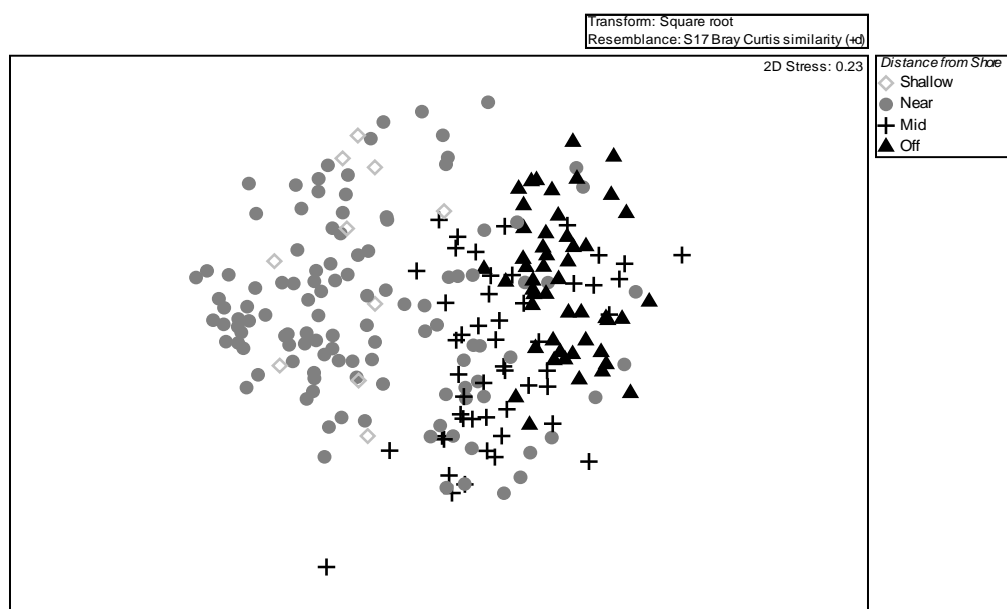
Figure 3.5: MDS ordination illustrating differences in assemblages of fish in replicate stereo-BRUVs at each site.

Table 3.5: Results of a PERMANOVA to test for differences in distance from shore (Di), site (Si(Di)) and year of sampling (Ye) on fish assemblages in Geographe Bay.

Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Ye	1	5152.4	5152.4	2.3004	**0.018**
Di	3	< 0.0001	34973	4.5317	**0.001**
Si(Di)	21	< 0.0001	6091.1	2.7195	**0.001**
Ye x Di	2	6618.9	3309.5	1.4776	0.109
Ye x Si (Di)	17	38076	2239.8	1.4066	**0.001**
Residual	180	< 0.0001	1592.3		
Total	224				

Relating general fish assemblages and benthic habitat

RELATE identified a significant correlation between averaged benthic habitat variables and the wider fish assemblages (P=0.1%, *p*: 0.58). Use of the BVSTEP procedure identified the variables *A. antarctica, A. griffithii, P. sinuosa*, bare sand and shell as providing the best correlation with the total fish assemblage data (*p*: 0.655). An alternative selection of only two variables: ascidian

and sponge (both indicating the presence of hard ground) provided a slightly lower correlation of p: 0.589. Given that seagrass species also varied with depth the near shore sites were also analysed separately. BVSTEP identified *A. griffithii, P. sinuosa, Halophila* sp and wrack as providing the best correlation, (p: 0.309) with fish assemblages at these near shore sites.

Five key fish habitat classes were identified using interpretation of the averaged benthic habitat data (Appendix B) regarding seagrass species and substrate using variables derived from the BVSTEP routine. Groupings of sites that supported these habitats were also influenced by depth and the location of the mouths of drains or estuaries (Table 3.6). A single factor PERMANOVA identified a significant difference for the effect of these classified habitat classes on fish assemblages (Table 3.7). The total abundance of each species of fish recorded in each habitat and their respective trophic categories are presented in Appendix A. A list of the fish species grouped according to each habitat is presented in Appendix C.

The largest range of fish species were recorded at benthic category type 5 (*P. sinuosa* mixed with *A. griffithii* (> 10% of each) with patches of hard substrata (reef, coral or rubble)). This category encompassed all of the off shore sites in addition to the two western most mid shore sites. Many of the fish species recorded here were reef associated species that are not necessarily associated with seagrass habitat (Appendix C and D).

Pair wise analyses revealed significant differences between each pair of habitat classes except Type 3 and Type 6. These two categories were both characterised by a mixture of *P. sinuosa*, *A. antarctica* and *A. griffithii* and were separated only by the presence of hard substrata in Type 6. Three species of fish: *Meuschenia hippocrepis, Trygonoptera personata and Mustelus antarctica* were exclusively recorded in these two habitat types. Three other species of reef-associated fish (*Parma mccullochi*, *Meuschenia scaber* and *Enoplosus armatus*) also recorded in these two

habitat types were not found in other habitats except for habitat Type 5 (*P. sinuosa* mixed with

A. griffithii (> 10% of each) with patches of hard substrata (reef, coral or rubble)).

Table 3.6: Fish habitat classes derived from averaged benthic habitat data; the sites where these habitats were recorded; and a geographic description of these locations.

Habitat Class name	Description	Sites with this habitat	Geographic location of these sites
Type 1	Greater than 80% cover of *P. sinuosa* on sand.	Quindalup Siesta Park Broadwater	Near shore sites near the centre and slightly to west of the Bay. No influence of drains or estuaries.
Type 2	*P. sinuosa* meadow mixed with *A. antarctica* on sand (> 10% of each)	Toby Inlet Buayanyup Vasse Wonnerup Vasse DD Port Geographe	Near shore sites with a broad geographical spread across the Bay. All directly influenced by drains or estuary mouths or a marina.
Type 3	Mixture of *P. sinuosa*, *A. antarctica* and *A. griffithii* on sand (> 10% of each)	Dunsborough Forrest Beach Mid shore 6	Near shore sites at extreme west and east of the Bay, mid shore site at extreme east of Bay
Type 4	*P. sinuosa* mixed with *A. griffithii* on sand (> 10% of each)	Mid shore 3 Mid shore 4	Mid shore sites in the centre of the Bay.
Type 5	*P. sinuosa* mixed with *A. griffithii* (> 10% of each) with patches of hard substrata (reef, coral or rubble)	Mid shore 1 Mid shore 2 Off shore 1 Off shore 2 Off shore 3 Off shore 4 Off shore 6	All off shore sites in addition to the two western most mid shore sites.
Type 6	Mixture of *P. sinuosa*, *A. antarctica* and *A. griffithii* (> 10% of each) with patches of hard substrata (reef, coral or rubble)	Busselton Jetty Wonnerup	Near shore sites in centre and east of the Bay

Table 3.7: Results of a single factor PERMANOVA to test for the effect of habitat class on fish assemblages. Pair wise analysis for each habitat type are also shown. Note: bold text indicates significant differences (p < 0.05).

Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Habitat	5	< 0.0001		29142	**0.001**
Residual	209	< 0.0001		1938	
Total		< 0.0001			
Pair wise groups (Habitat type)	t	P(perm)			
2, 6	2.9834	**0.001**			
2, 3	3.4343	**0.001**			
2, 5	3.4343	**0.001**			
2, 4	4.3624	**0.001**			
2, 1	1.4254	**0.049**			
6, 3	1.0873	0.308			
6, 5	3.6649	**0.001**			
6, 4	1.8773	**0.001**			
6, 1	2.2874	**0.001**			
3, 5	3.6995	**0.001**			
3, 4	1.8564	**0.001**			
3, 1	2.4908	**0.001**			
5, 4	3.1715	**0.001**			
5, 1	5.1925	**0.001**			
4, 1	3.3993	**0.001**			

Potential grazing fish species

Of the 89 fish species recorded, 16 species were identified as being potential seagrass grazers. These included two Odacidae, three Tetraodontidae, and 11 Monacanthidae. Of these *Torquigener pluerogramma* was the most abundant species followed by *Meuschenia freycineti* and *Acanthaluteres spilomelaneurus*. A two factor PERMANOVA identified significant differences in depth groups for all grazing fish in addition to the groups of monacanthid, odacid and tetraodontid fish (Table 3.8).

RELATE identified a significant correlation between the grazing fish assemblages and benthic habitat variables (P=0.1%, *p*: 0.301). When the subset of grazing fish was analysed separately a

second BVSTEP routine identified ascidian, sponge, and coral (all indicating the presence of hard ground) as providing the best correlation with these species, providing a correlation of *p*: 0.391. When the subset of near shore sites was selected BVSTEP identified *A. griffithii, P. sinuosa, Halophila* sp, wrack, bare sand and bare reef as providing the best correlation for grazing fish species (*p*: 0.393).

Clear geographic patterns were displayed by a number of grazing fish, with some species favouring particular depth groups or habitat classes (Figures 3.6 and 3.7, Table 3.9). *Meuschenia galii, M. flavolineata, Scobinichthys granulatus*, and *M. hippocrepis* and were almost exclusively recorded at mid shore or off shore sites, favouring habitat class 5. *M. freycineti* and *Acanthaluteres spilomelanures* were recorded at a wide variety of habitats both in shore and off shore, though *A. spilomelanures* was abundant in habitat classes 3, 4, 5, and 6. *A. vittiger* was also found almost exclusively in the far western and eastern locations of the bay and was recorded across all depth groups in habitat classes 1, 5 and 6.

Parika scaber was recorded at two off shore sites and two near shore sites (Busselton Jetty and Wonnerup beach). Reefs or reef like structures are present at all four of these sites. A single record of *Eubanichthys mosaicus* was made at off shore site 6, located in the far east of the bay.

Two odacid species were recorded exclusively in shallow or near shore sites. A single record of *Haletta semifasciata* was recorded only at Buayanyup while *Odax cyanomelas* was recorded only in the most shallow and western sites the Dunsborough Lagoon. Within the tetraodontid group, *Torquigener pleurogramma* was recorded exclusively at near shore and shallow sites and was most abundant in the Dunsborough Lagoon. A single record of *T. pallamaculatus* was made at Buayanyup, while *Contusus brevicaudus* was recorded at the near shore eastern Vasse Wonnerup site and the central mid shore 2 site.

Table 3.8: Results of a three factor PERMANOVA to test for the effect of year (Ye), distance from shore (Di) and site (Si(Di)) on grazing fish. Pair wise analysis for the distance from shore groups are also shown. Note: bold text indicates significant differences (p < 0.05).

Source of variation	Degrees of Freedom	SS	MS	Pseudo F	P (perm)
Ye	1	2012	2011.8	3.050	**0.021**
Di	3	14956	4985.4	2.453	**0.002**
Si(Di)	21	44866	2136.5	3.239	**0.001**
Ye x Di	2	814.84	407.4	0.618	0.761
Ye x Si (Di)	17	11213	659.6	0.920	0.7
Residual	180	< 0.01	717.1		
Total	224	<0.0001			
Pair wise groups (Distance from Shore)	t	P(perm)			
Near, Mid	1.283	0.121			
Near, Off	1.761	**0.016**			
Near, Shallow	1.712	**0.044**			
Mid, off,	1.450	0.086			
Mid, Shallow	1.862	**0.043**			
Off, Shallow	1.491	0.110			
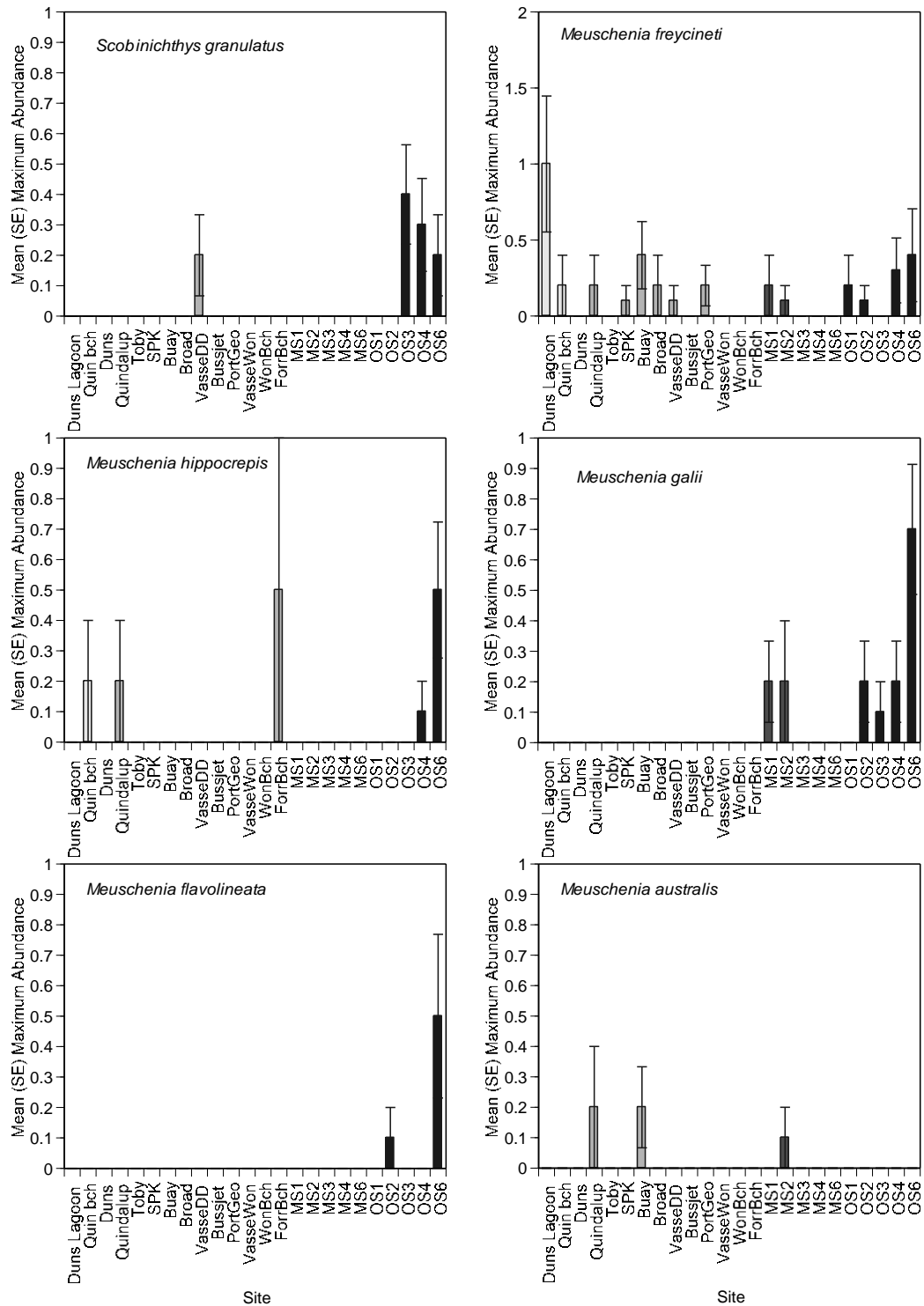
Figure 3.6: Mean abundance (± standard error, n=5) of potential seagrass grazing fish: *Scobinichthys granulatus, Meuschenia freycineti, Meuschenia hippocrepis, Meuschenia flavolineata, Meuschenia australias,* and *Meuschenia galii* (pooled data for both years of sampling).
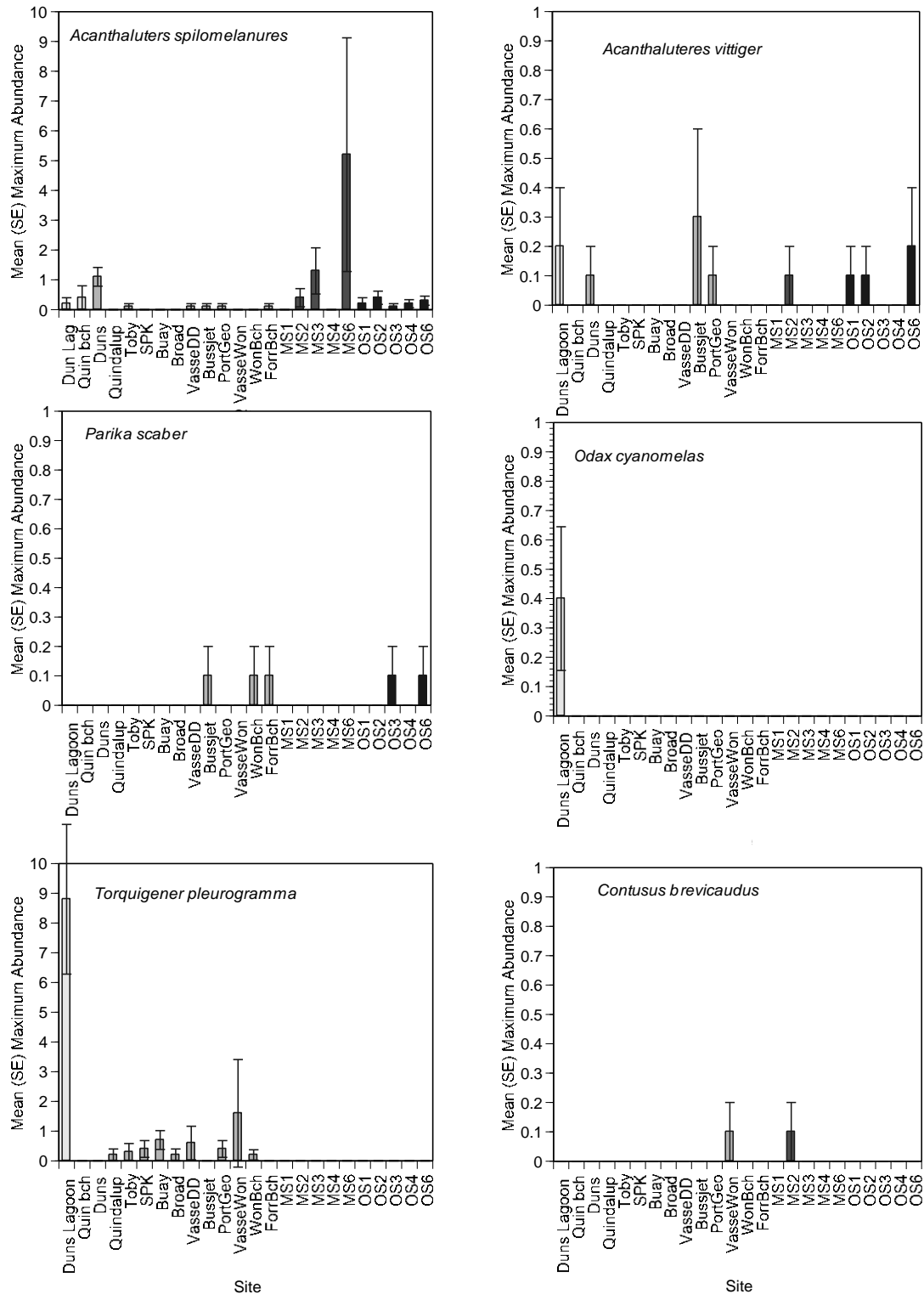
Figure 3.7: Mean abundance (± standard error, n=5) of potential seagrass grazing fish: *Acanthaluteres spilomelanures*, *Parika scaber*, *Acanthaluteres vittiger*, *Torquigener pleurogramma*, *Odax cyanomelas* and *Contuses brevicaudus* (pooled data for both years of sampling). Note: scales differ among species.

Table 3.9: Habitat classes in which grazing fish species were recorded.

1: Greater than 80% cover of *P. sinuosa* on sand, near shore sites near centre of bay

2: *P. sinuosa* meadow mixed with *A. antarctica* on sand, near shore sites close to drains;

3: Mixture of *P. sinuosa, A. antarctica* and *A. griffithii* on sand, western and eastern near shore and eastern mid shore sites.

4: *P. sinuosa* mixed with *A. griffithii* on sand, central mid shore sites;

5: *P. sinuosa* mixed with *A. griffithii* with patches of hard substrata, all off shore and western mid shore sites;

6: Mixture of *P. sinuosa*, *A. antarctica* and *A. griffithii* with patches of hard substrata, central and eastern mid shore sites.

Grazing fish species	*Habitat Classes*					
	1	**2**	**3**	**4**	**5**	**6**
Haletta semifasciata		*				
Odax cyanomelas	*					
Contusus brevicaudus		*			*	
Torquigener pleurogramma	*	*				*
Torquigener pallimaculatus	*	*				
Meuschenia australis		*				
Acanthaluteres spilomelanurus			*	*	*	*
Meuschenia galii					*	
Meuschenia flavolineata					*	
Scobinichthys granulatus		*			*	
Meuschenia freycineti	*	*			*	
Meuschenia hippocrepis	*		*		*	
Meuschenia scaber					*	*
Acanthaluteres vittiger		*	*		*	*
Eubalichthys mosaicus						*
Bigener brownii				*		

Discussion

Fish diversity and reef-seagrass connectivity in Geographe Bay

A highly diverse suite of fish species was recorded in this study, totalling 89 species. This compares with 92 species recorded in surf zones by a seine net over a much larger area that included sites on both the south and west coasts of Western Australia (Ayvazian and Hyndes 1995). The south western tip of Western Australia, where Geographe Bay is located, has been identified as a transition zone for tropical and temperate fish (Ayvazian and Hyndes 1995, Westera et al. 2009), and is the southernmost location where some tropical fish species have been recorded (Ayvazian and Hyndes 1995). However, only 19 species of fish were recorded by an earlier study of the fish fauna of Geographe Bay using a beam trawl (Scott 1981). This previous study did not sample beyond a depth of 7 m, however, and therefore would not have sampled the off shore areas close to the Naturalise Ridge reef formation where the highest diversity of species was recorded in this study. Over 66 % of the fish recorded at off shore sites in this study were reef associated species. Although small patches of coral, reef or rock were recorded at each of these off shore sites, the high abundance and diversity of reef associated fish recorded implies a strong cross habitat exchange of fish biomass between the nearby (larger) Naturaliste Ridge reef formation system and the deeper seagrass meadows of Geographe Bay. Differences between this study and that conducted by Scott (1981) could also be partly due to the different sampling techniques, yet evaluations of stereo-BRUVs have found that they may miss the smaller cryptic and less mobile fish (Harvey et al. 2007). If this is the case then the diversity of fish in Geographe Bay may be even greater than was recorded by this study. The apparent exchange of fish biomass between the reef and seagrass communities implies a level of connectivity between these two habitats, yet in the context of this thesis as a

correlative study, it is acknowledged that the definition of connectivity (i.e. the movement of animals between separate habitats) is limited. Further experimentation at both habitats is needed to confirm the cause and degree of such connectivity.

As for off shore sites, there is evidence that fish assemblages recorded in the eastern and western near shore and mid shore sites were also influenced by their proximity to hard substrata. Limestone platform reefs occur to the far east of Geographe Bay while rocky shorelines and coral outcrops are prevalent at the western end of Geographe Bay. The only two habitat types that did not support statistically different fish associations were habitat types 3 and 6. Both habitat types were characterized by mixed meadows of *P. sinuosa, A. griffithii* and *A. antarctica*; and were separated only by the presence of hard substrata at habitat type 6. These habitats were both recorded in the far west and east of the bay and shared records of reef associated fish such as *Parma mccullochi*, *Meuschenia scaber, M. hippocrepis and Enoplosus armatus* that were not recorded in other habitats, except type 5 (comprising all of the off shore sites). Although hard substrate was not specifically measured at habitat type 3, it is likely that reef and rocky shorelines that are known to occur nearby have influenced the fish associations there to the degree that they were not statistically distinguishable from habitat 6.

Depth as a driver of fish assemblages

Fish assemblages and benthic habitat were both strongly structured by depth; yet the specific influence of benthic habitat and depth cannot be completely separated. *Amphibolis griffithii* and rocky reefs both increased with distance from shore and, at near shore sites, were also more abundant at the eastern and western ends of the Bay. Of the 65 fish species recorded at the off shore sites (at depths of 15 to 20 m), 26 species were not recorded at lower depth. It is

likely that the combination of depth and reef was the main driver of this fish assemblage since the typical habitat for 12 of these species was off shore reefs, while another seven species are known to prefer coastal reefs. Many fish species were recorded in a variety of depths and very few fish species (five) were found exclusively in near shore locations (*Meuschenia australis, Odax cyanomelas, Torquigener pleurogramma, Sillago ciliata* and *Mustelus antarcticus*). Of these fish, *Torquigener pleurogramma* was the only species known to be specifically associated with shallow water habitats.

The interlinked influence of both depth and benthic habitat is supported by research from the south west of WA, which found the best discrimination between fish assemblages was determined by exposure; steepness of bathymetry; distance to the first off shore reef; and the areas of bare sand, subtidal reef and seagrass in near shore areas (Valesini et al. 2003). These factors were not all measured in this study, but they could explain the dominance of some species at the far western end of Geographe Bay where contours drop off sharply and where reefs are closer to shore. Similarly, Chatfield et al. (2010) found that in the Recherche Archipelago, substrate type had the greatest influence on fish assemblages, but water depth and macroalgal species were also important factors. The authors of that study noted that interactions of multiple drivers of fish assemblages may have been previously misinterpreted as singular influences such as a depth driven response.

Seagrass species and meadow structure as a driver of fish assemblages

Seagrass species and bare sand were the benthic habitat variables that had the greatest influence in structuring the wider fish assemblages. While the patchiness of seagrass meadows was not measured in this study, to some extent this is implicit in the recorded areas of bare sand. Fish assemblages in patchy seagrass beds have been found to differ from those in

continuous meadows in south Western Australian estuaries (Jelbart et al. 2007). For example *Pelates sexlineatus* was more abundant in patchy compared to continuous meadows in that study, while more cryptic species such *Acanthalutures spilomelanures* were more abundant in continuous meadows. Both species were also abundant in Geographe Bay, therefore similar patterns may explain the importance of bare sand as a driving habitat variable. Jelbart et al. (2007) also found a greater density of fish in small patches of seagrass than in wide dense continuous cover. Potential explanations proposed for these findings included increased predation of fish by the Blue Swimmer crab in larger meadows since small patches could not support the adult crab; greater abundance of some fauna at the edges of seagrass meadows (there is a greater chance of sampling the edge of a meadow where patchiness occurs); and differences in the recruitment settlement of fish larvae in patchy as compared to continuous seagrass meadows. While these are also potential explanations for the observed effect of bare sand on fish assemblages in Geographe Bay, they would all require more detailed sampling, including assessments of other invertebrate fauna, to be confirmed.

The influence of seagrass species on fish assemblages has a number of potential explanations. Jernakoff and Nielson (1998) found a greater abundance and diversity of epifaunal invertebrates and epiphytic algae in meadows of *Amphibolis griffithii* compared to *Posidonia sinuosa*. The stems of *A. griffithii* are longer lived and therefore support more epiphytes and associated grazing epifauna than those of *Posidonia* (Jernakoff and Nielson 1998). These differences may have a direct influence on fish species that feed directly on algae and/or invertebrates associated with the epiphytes of seagrass leaves. An alternative or additional explanation is that differences in the leaf structure of *Amphibolis* and *Posidonia* influence the preferences of different size classes of fish since larger spaces are created by *Amphibolis* species. MacArthur and Hyndes (2001) found that larger bodied fish such as *Odax acroptilus* were restricted to

Amphibolis griffithii meadows while smaller species such as *Apogon reuppellii, Acanthaluteres spilomelanurus, and the Brachaluteres jacksonianus* favoured *Posidonia* meadows. Either theory could help to explain the distribution of species such as *A. vittiger* that, in near shore areas, strongly favored the extreme west and east of the bay where *A. griffithii* was more prevalent. MacArthur and Hyndes (2001) recorded fewer species overall within the *P. sinuosa* meadows, a finding not supported by this study. Although the highest diversity of species was recorded in habitat class five (mixed *P. sinuosa* and *A. griffithii* with patches of hard substrata), the depth and presence of reef at these off shore sites are likely to have had a strong influence on the fish assemblages there. Also, when sandy near shore sites were compared, meadows that consisted almost entirely of *P. sinuosa* recorded a comparable or greater range of fish species compared to habitats with mixed species of seagrass. It should be noted that since seagrass species changed with depth and the influence of depth was analysed separately to that of the benthic habitat variables, a proportion of the observed influence of seagrass species on fish assemblages is likely to have actually been a depth driven response. The importance of depth as a driving factor in structuring fish assemblages is species dependent. For example some species that were abundant only in near shore areas (and therefore recorded mainly in dense *P. sinuosa* meadows) such a *Torquigener pluerogramma* are known to be shallow water species that favor estuaries and near shore areas of coastal embayments (Hutchins and Thompson 1995). This species was also recorded in greatest abundance at the most shallow site sampled: Dunsborough lagoon. Overall these results confirm that while any singular environmental variable is unlikely to be solely responsible for structuring diverse fish assemblages, seagrass species do play an important role.

Drivers of potential grazing fish assemblages

Benthic habitat variables associated with hard ground (ascidian, sponge, and coral) provided the best correlation for the subset of potential grazing fish species. This is likely to be due to the prevalence of reef associated monacanthid species that were included in the analysis, noting that the selection of seagrass grazers was a family based selection of all monacanthids, odacids and tetraodontids. Five monacanthids in particular favoured the off shore sites, including *Meuschenia galii, M. flavolineata, M. hippocrepis , P. scaber* and *Scobinichtys granulates*. These species are all reef associated fish (Hutchins and Thompson 1995, Kuiter 1996). When categorised into trophic groups on a species level, these fish were all either macroinvertebrate carnivores, invertebrate carnivores or species that consumed both algae and invertebrates (Ford 2011). In contrast, other monacanthid species that displayed a more widespread distribution throughout Geographe Bay such as *Meuschenia freycineti, Acanthaluteres spilomelanures* and *A. vittiger* were all recognised as including seagrass in their diet and were categorised as either herbivores or generalist consumers feeding on invertebrates, algae and seagrass. It is logical, that given the ample and widespread availability of both seagrass and algae (as seagrass epiphytes) across Geographe Bay, species that are either herbivorous or generalist consumers might be less restricted in their choice of feeding habitat compared to those that feed primarily on a specific range of invertebrate species. In contrast, however, a cluster analysis of fish species with different diets from 13 Caribbean islands found no clear distinction between the various seagrass bed and sandy seabed sites (Nagelkerken and van der Velde 2004). The authors concluded that trophic groupings are poor discriminators of different habitat types since many sites with different types of habitat clustered together owing to the dominance of invertebrates as the primary food source for the majority of fish species.

The influence of drains on fish and benthic habitat

The distribution of biota that define the benthic habitats and fish assemblages were both influenced by their proximity to a number of large and (mainly) artificial drains. These drains deliver large volumes of turbid fresh water to the near shore areas of Geographe Bay during winter. The habitat class close to drains was characterised by a mixture of *P. sinuosa* and *A. antarctica*, with very little *A. griffithii* recorded from these areas. In near shore areas *A. griffithii* was restricted to sites away from drains and where cover of *P. sinuosa* was less than 80% (at Dunsborough, Forrest Beach and the Busselton Jetty). Both *Amphibolis* species have the ability to grow where swell and current is prevalent (Carruthers et al. 2007) and can therefore persist where hydrodynamic disturbance occurs. These species are often found colonising the edges of blow outs within *Posidonia* meadows (Kirkman and Kuo 1990). It is possible that low light conditions associated with the outlet of these drains may explain the absence of *A. griffithii* from these areas. *A. griffithii* has been identified as being sensitive to reductions in light since the rhizome sugar stores of this species can support less than one days respiration (Carruthers and Walker 1997). In a recent study of the effects of light reduction on this species, all shading treatments (three, six and nine months) negatively impacted the meadow, and experimental plots that were shaded for more than three months failed to recover even up to two years after the experiment was conducted (McMahon and Lavery 2008). Low light conditions occur near the outlet of drains in Geographe Bay (Barnes et al. 2008) during the period that they flow (May to November) (White 2010). Regardless of the cause of observed patterns in benthic habitat near drains, these results indicate that anthropogenic shoreline changes, such as the construction of artificial drains, has potential to influence fish assemblages by changing benthic habitat variables.

Trophic categories of fish

The dominance of invertebrate carnivores and generalist carnivores that was identified in the total abundance of fish in Geographe Bay is considered typical of temperate Australian seagrass meadows (Burchmore et al. 1984, Pollard 1984) and seagrass meadows elsewhere (Elliot and Dewailly 1995, Nagelkerken and van der Velde 2004). It should be noted that over 97 % of the abundance of fish that consumed both invertebrates and algae was derived from large schools of *Pelates sexlineatus* that frequented the near shore areas of the bay. Similarly, within the invertebrate carnivore group, large schools of *Trachurus novaezelandiae* and *Parequula melbournensis* contributed strongly to the total abundance, though individuals of *Trygonorrhina fasciata* were also recorded at the majority of sites through the bay. Of interest was the very low proportion of herbivores and fish that consumed invertebrates, algae and seagrass. Together these comprised less than 4 % of the total fish abundance, though herbivores were the smallest group of all trophic categories. The only schooling species that included seagrass in their diet were *Torquigener pluerogramma* and juveniles of *Acanthaluteres spilomelanures,* both generalist consumers that also feed on algae and invertebrates (Ford 2011). In contrast, large schools of the herbivorous fish *Sarpa salpa* are supported in Mediterranean temperate seagrass meadows (Cebrian and Duarte 1998, Tomas et al. 2005) while the herbivore *Sparisoma radians* also schools in large numbers in the tropical meadows of the Florida keys (Kirsch et al. 2002, Valentine and Duffy 2006).

Changes in the composition of fish assemblages in Geographe Bay

In a study of the fish fauna of Geographe Bay undertaken in 1984 using a beam trawl, the odacid species *Neoodax radiatus* (now named *Siphonognathus radiatus*) was the most abundant and widespread species sampled (Scott 1981). At the time of that study, this species comprised over 52 %of the total fish abundance sampled in Geographe Bay. However, this species was not

recorded at all in the current study, though was recorded by Ayvazian and Hyndes (1995). It is likely that differences in sampling methods may partly explain the absence of this species in the current study. Nevertheless, given previous abundance and widespread distribution of *Neoodax radiates*, it is also possible that changes to the fish assemblages in Geographe Bay have occurred over the past two decades, resulting in the absence of this species. Other species recorded by Scott (1984) and not by this study include *Neoodax semifasciatus*, *Stigmatophora argus*, *Syngnathid poecillaemus, Cristiceps australis, Heteroclinus adelaidae* and *Brachaluteres jacksonianus*; however, *Stigmatophora argus*, and *Heteroclinus adelaidae* were also sampled during the Ayvazian and Hyndes 1991/92 survey of Geographe Bay. These species were all recorded in much lower abundances, and given that many are small cryptic species that are less likely to respond to the attraction of a baited camera, their absence in this study can probably be explained by sampling bias (Cappo et al. 1994).

Summary

Overall these results support the recent literature that emphasise the importance of understanding connectivity among habitats and interactions between environmental variables that may influence fish associations both on a species and a wider community level. Depth; seagrass species; bare sand; reef and, in near shore areas, the presence of drains all influenced fish assemblages in Geographe Bay. Of these, depth and the presence of reef had the greatest influence, with some species making clear preferences based on these two variables. The importance of seagrass species in structuring fish assemblages highlights the need to understand how changes to near shore environments may influence seagrass species dynamics. The high diversity of fish recorded in this location was unexpected and many fish species were not seagrass associated, but clearly utilise multiple habitats. These findings emphasise the

importance of understanding the cross-habitat energy exchange between seagrass and other habitats such as reefs and rocky shorelines. The low proportion of herbivorous fish and generalist consumers that include seagrass in their diet confirms that herbivory is a small component of the trophodynamics of temperate seagrasses in this area.

GENERAL DISCUSSION

Patterns in seagrass grazing and grazer abundance

This study found evidence for low levels of patchy seagrass grazing by fish in Geographe Bay and a low abundance of fish with potential to consume seagrass. Geographic patterns observed in the location of grazed seagrass leaves, recorded in Chapter 2, were reflected by patterns in benthic habitat recorded in Chapter 3. These benthic habitats were characterised by mixed *A. griffithii* and *P. sinuosa* seagrass meadows and, in most cases, were located nearby reefs or rocky shorelines. The potential grazing monacanthids: *A. vittiger*, *A. spilomelanures*, *M. scaber* and *M. hippocrepis* also displayed similar patterns in their distribution. It is therefore likely that grazing of seagrass leaves by these fish species contributed to the observed patterns in leaf herbivory, yet further research would be needed to confirm the specific role that these species play in the grazing of seagrass meadows.

It is possible that some of the observed patterns in grazing occurred as a result of specific feeding behaviours, rather than intended seagrass consumption. While *A. spilomelanures* (Scott 1981, Ayvazian and Hyndes 1995) and *A. vittiger* both feed on seagrass along with algae and/or invertebrates, the primary diet of *M. scaber* is invertebrates, and *M. hippocrepis* consumes both invertebrates and algae (Ford 2011). Bell (1978) proposed that monacanthids consume seagrass primarily as a means to obtain encrusting material such as algae or invertebrates, and noted that they have specialised teeth to bite off pieces of encrusted seagrass, of which only the epiphytic mass is actually digested. Wressnig and Booth (2007) also recorded a feeding preference for epiphyte covered blades of *P. australis* by two monacanthids (*M. freycineti* and *M. trachylepsis*). Such feeding behaviours would help to explain the highly sparse nature of the

recorded seagrass bite marks, and the lack of correlation between grazed sites and elevated nitrogen content of seagrass leaves. Grazing fish are less likely to respond to elevated nitrogen content of seagrass leaves if their primary feeding intent is to obtain epiphytic material. The high levels of grazing recorded at Curtis Bay, where observed epiphyte loads were also larger than at other sites, may have resulted from a preferred feeding pattern such as that described by Wressnig and Booth (2007).

Overall the proportion of potential grazing fish recorded in Chapter 3 was very small (less than 4 %) compared to the total fish abundance. This contrasts with temperate seagrass meadows in eastern Australia where the abundance of algae and seagrass consumers are high, with records of this trophic group exceeded only by fish that feed on crustaceans (Burchmore et al. 1984). Monacanthids comprise the majority of those consumers and, in Port Hacking, the density of monacanthids in seagrass meadows was recorded as one fish per 7 m^2 (Bell et al. 1978). In the Mediterranean, the herbivorous fish *Sarpa salpa* has been recorded at densities of up to 100 fish per 100 m^2 (Tomas et al. 2005) and in these high densities can exert strong grazing pressure on *Posidonia oceanica* meadows (Tomas et al. 2005, Prado et al. 2010).

The low abundance of seagrass grazers suggests it is highly unlikely that severe overgrazing by fish could occur in Geographe Bay, even under conditions of elevated nutrient loading. There was a general lack of schooling species in the group of grazing fish, and the majority of these were generalist feeders with abundant alternative food sources. If preferential grazing of epiphyte encrusted seagrass leaves is occurring, this process is more likely to contribute a net benefit to the seagrass meadows rather than an impact. Grazing would remove a proportion of accumulated epiphytes, therefore helping to prevent overshading of individual plants by these epiphytes. Yet given the low grazing rates, such a benefit may be small in comparison to other

grazers in the system such as invertebrates and other fish species that include algae (including

epiphytes) in their diet, but exclude seagrass material. Barnes (2008) recorded low abundances

of non cryptic (> 2 cm) invertebrates in Geographe Bay and, therefore, these probably have little

effect on seagrass productivity. We found the abundance of fish that feed on algae and

invertebrates to be far greater than fish from other trophic categories. These fish have potential

to play an important role in removing epiphytes on seagrass leaves in Geographe Bay, yet they

may also exert control on the abundance of smaller (< 2 cm) invertebrates that have been

shown in other seagrass systems to be important in managing epiphyte growth (Jorgensen et al.

2007, Moksnes et al. 2008, Olsen and Valiela 2010).

The results of this study support the findings of Cebrian and Duarte (1998) who found that

variability in seagrass grazing was more closely related to the population dynamics of herbivores

themselves rather than the nutrient content of seagrass plants. However, while nitrogen

content of seagrass did not influence patterns of grazing in Geographe Bay, the nitrogen and

phosphorus content of *P. sinuosa* is low (C/N atomic ratio of 36) (McMahon and Walker 1998)

compared to other seagrass species such as *P. oceanica* (C/N atomic ratio of 17) (Cebrian and

Duarte 1998), which can be intensely grazed. The slow growth of *P. sinuosa* (Kirkman and Kuo

1990) also fits with the observation that low grazing rates are typically observed on slow

growing seagrass species (Cebrian et al. 1998). These results are in contrast to recent studies of

herbivory of other canopy forming species such as temperate algae. Vanderklift et al. (2009)

found exposure had a greater influence on herbivory of the kelp *Ecklonia radiata* than

productivity. They recorded no grazing at all at off shore sites, while grazing by fish was intense

at one off shore reef, and sea urchin grazing occurred at all inshore reefs (Vanderklift et al.

2009). Similarly, in New Zealand the temperate brown algae *Durvillaea antarctica* was strongly

structured by grazing by the herbivorous fish *Odax pullus* in sheltered locations, and the effect

of exposure on grazing was so strong that this species of algae could only persist in highly exposed locations (Taylor and Schiel 2010). The importance of exposure has also been found in studies of herbivory of Mediterranean temperate seagrass, where losses of the *Cymodocea nodosa* were five times greater in sheltered locations compared to exposed sites (Cebrian et al. 1996). However, meta-analyses of seagrass herbivory studies have found herbivory may be influenced by a variety of factors, including latitude, productivity, exposure, and herbivore dynamics (Cebrian et al. 1998, Burkepile and Hay 2006). The high variability of potential influences emphasises the importance of undertaking local studies of individual systems, so that the significance of seagrasses as a local resource for the specific populations of grazing fish (and other grazers); and the potential effects of grazing on seagrass meadows can be evaluated at an appropriate scale.

Fish diversity, habitat connectivity and ecosystem resilience

The high diversity of fish assemblages recorded in Geographe Bay and the apparent influence of nearby reef on the spatial distribution of fish highlights the important role that cross habitat connectivity may provide within this system, though further experimental work would help to confirm such connectivity. The similarity in geographic patterns between the distribution of some grazing fish species; the observed grazed sites; and the location of sites in proximity to reef implies that connectivity between seagrass and reef habitats may have multiple flow on effects for the trophodynamics of the local system. Managers of the proposed marine park area, which includes Geographe Bay, need to account for the interlinked role that occurs between these seagrass meadows and other habitats.

In Geographe Bay, most fish fed on invertebrates, and there were very few piscivorous fish, suggesting there may not be strong top down control of fish abundance, but more top down

control of invertebrates by fish. Disturbance to seagrass meadows has the potential to enhance

predation of invertebrates by fish since refuge from predation is reduced in sparser meadows

(Heck et al. 2000). In this scenario there is potential for an interaction to occur between fishing

effects, which may either reduce abundance or cause a release of fish that feed on invertebrates

(Pinnegar and Polunin 2004), and eutrophication, which may alter the benthic habitat structure

(Orth et al. 2006b). Such interactions may have occurred in the overgrazing of Western

Australian *Posidonia* meadows by sea urchins in Cockburn Sound, since only the sparse or

impacted meadows were affected and the urchin population had temporarily increased

dramatically (Cambridge 1979). Further investigations of these potential interactions would

involve assessments of invertebrates and their relationship between seagrass, algae and fish

using additional techniques to the surveys presented in this thesis, such as gut content analysis,

lipid analysis and stable isotope analysis.

The high species diversity of fish in Geographe Bay may provide improved resilience against

disturbance. This diversity, combined with the large number of generalist consumers in

Geographe Bay, is suggestive of a system with many weak trophic interactions and few strong

interactions, that may provide improved resilience against human induced imbalances such as

trophic cascades (Worm and Duffy 2003). In the absence of the important exchange of fish

biomass between reefs and the seagrass system, a less diverse and therefore potentially less

resilient community may have developed. However, fish assemblages in Geographe Bay are

likely to have already significantly changed compared to those present prior to European

settlement, since recreational fishing pressure in summer is equivalent to that near the Western

Australian capital city of Perth (Sumner and Willamson 1999). In addition, there were a number

of (non target) fish species that were absent from the current study that were previously

abundant some 20 years prior (Scott et al. 1986), the cause of which is unknown. Despite the

apparent absence of significant impacts on benthic plant communities in Geographe Bay, the potential influence of disturbance of existing ecological processes would need to be evaluated on a species level since some species may have specific functional roles in the ecosystem. Even in a diverse community, losses of such species may have important flow on effects that are not yet understood (Farmer and Wilson 2010).

A potential limitation of this research is that it was undertaken in only one general location, and this may limit the applicability of conclusions drawn here to other areas. However, other research has shown that the diets of fish can vary widely, depending on individual locations, and much can be learned by a detailed analysis of individual sites and species (Farmer and Wilson 2010). This study was undertaken in an extensive seagrass meadow that receives a large annual load of nutrients and supports a highly diverse assemblage of fish. While insignificant impacts of grazing on the meadow were found, we have pointed to the possible importance of grazing (by fish and / or invertebrates) in moderating the effects of eutrophication. Testing of this paradigm requires additional research, involving of a range of other locations with varied fauna and benthic habitat assemblages, physical characteristics and nutrient loads, in addition to techniques such as isotope analysis and exclusion studies that were not included in this thesis.

General conclusions

The low abundance of grazers and lack of a grazing response to seagrass leaves with elevated nitrogen content suggests that overgrazing of seagrass by fish is unlikely to occur at this location, even under conditions of elevated nutrient loads. Although grazing of seagrass by fish was the initial focus of this study, the evidence that some level of cross subsidy of fish biomass occurs between temperate reef and seagrass habitats at the study location was an important finding. Such connectivity between nearby reef and mixed *P. sinuosa and A. griffithii* meadows

may have influenced the observed geographic patterns in leaf herbivory, as these were similar to the distribution of reef associated monacanthid fish with potential to graze on seagrass. The high number of reef-associated fish that utilised the seagrass habitat emphasises the critical ecological role that seagrass meadows provide. In addition, the high abundance of fish that feed on both algae and invertebrates highlights the possible importance of fish in moderating the effects of eutrophication, or possibly controlling the abundance of mesograzers at this location.

Managers of temperate marine systems need to understand and respond to the connectivity between habitats, rather than considering and managing each habitat as discrete entities. In Geographe Bay, it is possible that preservation of the current diversity and abundance of fish (and possibly small invertebrates) will be important to maintain the system's resilience against future high nutrient loads. In this regard, off shore reefs may contribute substantially to the overall diversity (and abundance) of fish recorded in the seagrass meadows, while seagrass meadows provide important habitat for non-seagrass associated species. Both habitats require long-term management and protection, therefore representative areas of both habitats, including variations in seagrass species, need to be included in future sanctuary zones of the proposed marine park area. An improved understanding of the contribution of algal epiphytes to the total food web of Geographe Bay is also needed. Future work involving stable isotope, lipid analaysis and gut content studies of the wider fish community and invertebrates of Geographe Bay; combined with experimental nutrient enrichment and grazer exclusion studies would help to confirm the importance of fish and small grazing invertebrates in mediating the effects of elevated nutrient loads at this location.

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APPENDICES

Appendix A: The trophic categories, typical habitat and total abundance of fish species recorded from each benthic habitat class in Chapter 3

Habitat classes: 1: Greater than 80% cover of *P. sinuosa* on sand, near shore sites near centre of bay; **2**: *P. sinuosa* meadow mixed with *A. antarctica* on sand, near shore sites close to drains; **3**: Mixture of *P. sinuosa, A. antarctica* and *A. griffithii* on sand, western and eastern near shore and eastern mid shore sites; **4**: *P. sinuosa* mixed with *A. griffithii* on sand, central mid shore sites; **5**: *P. sinuosa* mixed with *A. griffithii* with patches of hard substrata, all off shore and western mid shore sites; **6**: Mixture of *P. sinuosa*, *A. antarctica* and *A. griffithii* with patches of hard substrata, central and eastern mid shore sites.

Note to reader: Common names have been removed from the text of chapter 3 since they are all provided in the table below. In all other chapters, common names for fish have been retained within the text for ease of reading and interpretation and since many of those species may not appear in the table below.

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Apogon rueppellii	Apogonidae	gobbleguts	macroinvertebrate carnivore	sand and weed in estuaries and embayments	59	87	7		3	4
Unknown Apogonidae spp	Apogonidae		macroinvertebrate carnivore			3				
Anoplocapros lenticularis	Aracanidae	white-barred box fish	generalist carnivore	off shore reefs		2		1		
Arripis georgianus	Arripidae	herring	piscivore macroinvertebrate carnivore	coastal waters	9	50	7		1	10
Pseudocaranx dentex	Carangidae	skipjack trevally	generalist carnivore	coastal waters and estuaries						2

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Pseudocaranx spp	Carangidae	trevally sp	generalist carnivore	coastal waters and estuaries	227	195	678	58	334	586
Seriola hippos	Carangidae	samson fish	piscivore	off shore reefs	2				20	1
Trachurus novaezelandiae	Carangidae	yellow tail scad	invertebrate carnivore	coastal waters	28	236	533			2
Chelmonops curiosus	Chaetodontidae	truncate coral fish	invertebrate carnivore	coastal reefs					3	
Nemadactylus valenciennesi	Cheilodactylidae	queen snapper	invertebrate carnivore	off shore reefs					4	
Sardinella lemuru	Clupeidae	Scaly mackerel	zooplanktivore	embayments and mouths of estuaries			23			
Dactylophora nigricans	Dactylophora	dusky morwong	invertebrates/algae	coastal seagrass and adjacent reefs	1	2			4	1
Dasyatis brevicaudata	Dasyatidae	smooth stingray	macroinvertebrate carnivore	all benthic habitats, preference for sand	4	7	3		9	1
Dinolestes lewini	Dinolestidae	long-finned pike	piscivore	coastal waters near reefs					28	13
Diodon nicthemerus	Diodontidae	slender-spined porcupine fish	invertebrate carnivore	off shore reef and weed	2	2				1
Enoplosus armatus	Ecoplosidae	old wife	invertebrate carnivore	reef and weed			4		3	1
Parequula melbournensis	Gerreidae	southern silverbelly	invertebrate carnivore	protected coastal sand, weed and reef	11	94	155	52	242	53
Glaucosoma hebraicum	Glaucasomatidae	West Australia dhufish	piscivore macroinvertebrate carnivore	off shore reef					1	

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Hyporhamphus melanochir	Hemiramphidae	Southern sea garfish	herbivore	coastal waters		1				
Heterodontus portusjacksoni	Heterodontidae	Port Jackson Shark	macroinvertebrate carnivore	coastal reef and adjacent sand and weed	1	1	2	2	12	
Kyphosus sydneyanus	Kyphosidae	buffalo bream	herbivore	off shore reefs	3					
Achoerodus gouldii	Labridae	western blue groper	macroinvertebrate carnivore	coastal reefs					2	
Austrolabrus maculatus	Labridae	black-spotted wrasse	generalist carnivore	coastal reefs					10	
Bodianus frenchii	Labridae	western fox fish	generalist carnivore	off shore reefs					3	
Choerodon rubescens	Labridae	baldchin groper	macroinvertebrate carnivore	off shore reefs					2	
Coris auricularis	Labridae	western king wrasse	generalist carnivore	off shore reefs and adjacent sandy areas	10	1	20	12	267	5
Dotalabrus aurantiacus	Labridae	Castelnaus wrasse	invertebrate carnivore	shallow protected seagrass beds					1	
Eupetrichthys angustipes	Labridae	Snakeskin wrasse	invertebrate carnivore	shallow protected weed and sand near coastal reefs and off shore reefs	1				2	
Notolabrus parilus	Labridae	brown-spotted wrasse	generalist carnivore	coastal reef and weed	14	13	45		92	22
Ophthalmolepis lineolatus	Labridae	maori wrasse	invertebrate carnivore	off shore reefs			11	11	216	1

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Pictilabrus laticlavius	Labridae	senator wrasse	generalist carnivore	off shore reef and weed	1				2	1
Pictilabrus viridis	Labridae	false senator wrasse	generalist carnivore	shallow off shore reefs			1		1	
Pseudolabrus biserialis	Labridae	red banded wrasse	invertebrate carnivore	off shore reefs					47	4
Unknown Labridae spp	Labridae									1
Acanthaluteres spilomelanurus	Monacanthidae	bridled leatherjacket	invertebrates/algae/seagrass	shallow protected seagrass beds	1	3	77	13	16	47
Acanthaluteres vittiger	Monacanthidae	Toothbrush leatherjacket	herbivore	shallow protected reef and weed	1	1	1		5	3
Acanthaluteres brownii	Monacanthidae	spiny tailed leatherjacket	generalist carnivore	protected coastal reefs, juvelines in seagrass beds			1	1		
Eubalichthys mosaicus	Monacanthidae	Mosaic leatherjacket	invertebrates/algae	off shore reefs					1	
Meuschenia australis	Monacanthidae	Southern leatherjacket	invertebrates/algae	coastal embayments on algae and sponge reefs	1	2			1	
Meuschenia flavolineata	Monacanthidae	yellow-striped leatherjacket	invertebrates/algae	off shore reefs					6	
Meuschenia freycineti	Monacanthidae	six spined leatherjacket	herbivore	coastal reefs, juveniles in seagrass beds in coastal embayments and mouths of estuaries	8	7			13	
Meuschenia galii	Monacanthidae	blue-lined leatherjacket	invertebrates/algae	off shore reefs					16	

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Meuschenia hippocrepis	Monacanthidae	horseshoe leatherjacket	invertebrates/algae	off shore reefs, juveniles in reef and weed areas	1		5		6	
Meuschenia scaber	Monacanthidae	velvet leatherjacket	invertebrate carnivore	deep off shore waters			1		2	2
Scobinichthys granulatus	Monacanthidae	rough leatherjacket	macroinvertebrate carnivore	coastal seagrass and adjacent reefs		2			9	
Unknown Monocanthidae spp	Monacanthidae					1		2	2	2
Upeneichthys vlamingii	Mullidae	blue-spotted goatfish	invertebrate carnivore	shallow protected sandflats to deep off shore waters	2	4	14	5	88	10
Myliobatis australis	Myliobatidae	eagle ray	macroinvertebrate carnivore	sand and weed inshore and off shore	1	8	18	4	14	9
Octopodidae spp	Octopodidae	Octopus	generalist carnivore				1	1		
Haletta semifasciata	Odacidae	blue weed whiting	invertebrates/algae/ seagrass	seagrass beds in coastal embayments		2				
Odax cyanomelas	Odacidae	herring cale	invertebrates/algae/ seagrass	seagrass beds	2					
Orectolobus sp	Orectolobidae	wobbegong	piscivore	coastal reef and weed					1	
Anoplocapros amygdaloides	Ostraciidae	western smooth boxfish	invertebrates/algae	coastal and off shore reefs, juveniles in coastal embayments		2				
Aracana aurita	Ostraciidae	shaws cow fish	invertebrates/algae	inshore and off shore seagrass beds		1	1	1	1	
Pempheris klunzingeri	Pempheridae	rough bullseye	invertebrate carnivore	coastal reefs					8	

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Pempheris multiradiata	Pempheridae	common bullseye	zooplanktivore	coastal reefs					23	217
Paristiopterus gallipavo	Pentacerotidae	Yellow spotted boarfish	generalist carnivore	off shore reefs					1	
Paraplesiops meleagris	Plesiopidae	western blue devil	generalist carnivore	coastal and off shore reefs					1	
Chromis klunzingeri	Pomacentridae	black headed puller	invertebrates/algae	deep off shore reefs	1				156	6
Parma bicolor	Pomacentridae	bicolor scalyfin	invertebrates/algae	deep off shore reefs					1	
Parma mccullochi	Pomacentridae	McCullochs scalyfin	invertebrates/algae	coastal reefs			2		3	1
Unknown Parma spp	Pomacentridae		invertebrates/algae							1
Trygonorrhina fasciata	Rhinobatidae	fiddler ray	invertebrate carnivore	sand adjacent to coastal reefs	23	42	37	13	37	19
Neosebastes pandus	Scorpaenidae	gurnard perch	generalist carnivore	off shore waters and sand and weed near coastal reefs					3	
Microcanthus strigatus	Scorpididae	Stripey	invertebrates/algae	shallow protected reefs					2	
Neatypus obliquus	Scorpididae	footballer sweep	invertebrate carnivore	off shore reefs					71	
Scorpis aequipinnis	Scorpididae	sea sweep	zooplanktivore	off shore reefs					1	
Tilodon sexfasciatus	Scorpididae	moonlighter	invertebrate carnivore	off shore reefs	2				2	
Sepia sp	Sepia	Cuttlefish	generalist carnivore						3	
Sepioteuthis sp	Sepia		generalist carnivore		7	10	11	3	7	10

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Hypoplectrodes nigroruber	Serranidae	banded sea perch	piscivore macroinvertebrate carnivore	coastal reefs					1	
Othos dentex	Serranidae	harlequin fish	piscivore	off shore reefs					1	
Sillaginodes punctata	Sillaginidae	King George whiting	invertebrate carnivore	coastal embayments	37	8	3		5	1
Sillago bassensis	Sillaginidae	school whiting	invertebrate carnivore	coastal embayments	2	1	3			
Sillago ciliata	Sillaginidae	sand whiting	invertebrate carnivore	coastal embayments		1				
Unknown Sillago spp	Sillaginidae		invertebrate carnivore	coastal embayments		3				
Pagrus auratus	Sparidae	Silver seabream	macroinvertebrate carnivore	coastal waters					5	
Rhabdosargus sarba	Sparidae	Tarhwine	macroinvertebrate carnivore	sandy areas adjacent to coastal reefs	5		4			44
Sphyrna sp	Sphyrnidae	hammerhead shark	piscivore	off shore waters					1	
Pelsartia humeralis	Terapontidae	sea trumpeter	invertebrate carnivore	seagrass in coastal embayments	12	8	3		1	1
Pelates sexlineatus	Terapontidae	six lined trumpeter	Invertebrates/algae	seagrass in coastal embayments	762	1671	112	2	1	586
Contusus brevicaudus	Tetraodontidae	Prickly pufferfish	invertebrates/algae/seagrass	seagrass beds and adjacent sandy areas		1			1	
Torquigener pallimaculatus	Tetraodontidae	orange barred pufferfish	invertebrates/algae/seagrass	sandy bottoms off coastal beaches		1				
Torquigener pleurogramma	Tetraodontidae	common blowfish	invertebrates/algae/seagrass	estuaries and coastal inshore waters	49	36				2

Species	Family	Common Name	Trophic category	Typical habitat	Species abundance in each benthic habitat class					
					1	2	3	4	5	6
Mustelus antarcticus	Triakidae	gummy shark	piscivore	off shore waters			1			1
Trygonoptera ovalis	Urolophidae	striped stingaree	generalist carnivore	off shore reef, weed and sand, particularly off shore	1	2	10	3	7	4
Trygonoptera personata	Urolophidae	masked stingaray	generalist carnivore	shallow reef, sand and weed			1		1	1

Appendix B: Mean percent cover of benthic habitat variables at each site from Chapter 3

(Pooled data for both years of sampling).

Site	*A.antarctica*	*A. griffithii*	*P. sinuosa*	*P. australis*	Bare sand	Bare reef	Rocks / rubble	Shell	*Padina australis*	Algal assemblage	Wrack	Ascidian	Sponge	Coral
Dunsborough	15.67	14.06	55.06	0.00	3.39	0.00	0.00	0.56	0.28	7.06	2.61	0.00	0.00	0.00
Quindalup	6.33	2.44	85.56	0.00	1.78	0.00	0.00	0.00	0.00	0.22	3.67	0.00	0.00	0.00
Toby Inlet	17.88	1.33	68.97	0.00	0.48	0.00	0.00	1.76	0.00	9.27	0.30	0.00	0.00	0.00
Siesta Park	0.00	0.00	97.56	0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.00	0.00	0.00	0.00
Broadwater	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buayanyup Drain	25.33	0.94	60.78	0.00	3.28	0.00	0.00	0.00	0.00	4.78	3.72	0.00	0.00	0.00
Vasse Diversion Drain	29.22	0.56	59.33	0.00	1.06	0.00	0.00	0.00	0.00	8.00	0.22	0.00	0.00	0.00
Busselton Jetty	34.94	12.44	38.17	0.00	0.61	0.00	0.17	0.00	0.50	7.56	0.00	0.00	0.00	0.00
Port Geographe	22.85	1.94	70.91	0.00	1.45	0.00	0.00	0.00	0.00	2.55	0.24	0.00	0.00	0.00
Vasse Wonnerup	20.83	1.00	77.72	0.00	0.11	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00
Wonnerup Beach	22.11	10.61	55.61	0.00	0.61	0.22	0.00	0.00	0.17	10.50	0.06	0.00	0.00	0.00
Forrest Beach	17.50	13.39	63.78	0.00	0.39	0.00	0.00	0.00	0.00	4.78	0.06	0.00	0.00	0.00
Mid shore 1	5.22	22.00	38.00	0.00	18.67	0.00	0.17	0.06	0.22	11.33	1.78	0.00	0.56	0.50
Mid shore 2	9.00	32.39	40.28	0.00	2.50	0.00	0.00	0.06	0.00	13.83	1.06	0.00	0.00	0.50
Mid shore 3	9.39	36.67	45.61	0.00	1.94	0.00	0.00	0.11	0.06	5.89	0.33	0.00	0.00	0.00
Mid shore 4	5.72	39.44	45.44	0.00	0.33	0.00	0.00	0.00	0.00	6.17	0.00	0.00	0.00	0.00

Mid shore 6	11.50	22.89	42.33	0.00	9.06	0.00	0.00	4.67	0.17	7.17	1.44	0.00	0.00	0.00
Off shore 1	1.17	15.39	41.72	0.17	18.94	0.00	0.06	0.33	0.61	10.39	0.17	0.00	0.72	0.67
Off shore 2	2.72	28.56	31.39	0.00	8.06	0.06	0.00	1.44	4.44	19.78	0.06	0.06	0.33	0.00
Off shore 3	1.56	27.39	16.44	0.00	4.61	0.56	0.28	3.50	8.11	33.61	0.67	0.00	0.17	0.00
Off shore 4	2.56	24.44	25.17	0.00	6.72	0.17	0.17	0.17	9.44	27.94	1.17	0.00	0.22	0.61
Off shore 6	1.83	31.89	28.22	0.00	7.00	0.33	0.06	0.06	0.94	26.11	0.67	0.00	0.06	0.00