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Herbivory by *Parma mccullochi* (Pomacentridae) : its role as an ecosystem engineer in temperate algal-dominated reefs

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Herbivory by *Parma mccullochi* (Pomacentridae): its role as an ecosystem engineer in temperate algal-dominated reefs.



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This thesis is presented in fulfilment of the requirements for the degree of Master of Science (biological sciences) by research at Edith Cowan University

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Abstract

Pomacentridae is one of the most representative families of herbivorous fishes inhabiting both tropical and temperate reefs, yet the vast majority of studies examining feeding within this family have been undertaken in tropical rather than temperate regions. Despite the high abundances of the pomacentrid *Parma mccullochi* in temperate waters of Western Australia, and their likely importance in removing algae from reefs in the region, there is a lack of information on their diet and their impact on the reef algal community. This study aims to determine the role of *Parma mccullochi* as an ecosystem engineer on temperate algal-dominated reefs in the metropolitan waters of Perth, Western Australia. To achieve this, the diet of *P. mccullochi* and any ontogenetic differences, and its impact on the reef in terms of algal composition and algal recruitment were determined. *P. mccullochi* in the temperate reefs of Western Australia was found to be a strict herbivore, with its diet comprising almost entirely red foliose and filamentous algae such as *Hypnea* spp., *Ceramium* sp. and *Brongniartella* sp., and showing no ontogenetic shift. Based on electivity indices, *P. mccullochi* showed a positive selection for specific algal taxa such as *Brongniartella* sp., *Dasyclonium* sp., *Hypnea* spp. and *Dictyopteris* spp. The species composition of macroalgae differed significantly between inside and outside *P. mccullochi* territories ($P = 0.010$), and a caging experiment in *P. mccullochi* territories indicated a moderate effect on the composition of recruiting algae ($P = 0.067$). Algal assemblages inside the territories were characterised by *Hypnea* spp. and *Dasyclonium* spp., while those outside the territories were characterised by the brown algae *Ecklonia radiata* and *Sargassum* spp., the foliose red alga *Rhodomenia sonderi* and the coralline red alga *Amphiroa anceps*. Total algal biomass was significantly lower ($P = 0.0126$) while species richness was higher ($P = 0.0114$) inside compared to outside territories. This study, therefore, provides the evidence to refute the theory that temperate Pomacentridae have a low impact on the temperate reefs (Jones 1992). *P. mccullochi* has the capacity to structure the benthic composition of reefs and maintain high biodiversity patches within kelp canopies. This effect is amplified by the high abundances of the species observed in Perth metropolitan waters, and can therefore be considered an ecosystem engineer/landscaper of temperate algal dominated reefs, highlighting its importance in ecosystem processes of temperate reefs in the region.

Declaration

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

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- ii. contain any material previously published or written by another person except where due reference is made in the text of this thesis; or
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Chapter 1

Introduction



Photograph: Adult *Parma mccullochi*

Chapter 1

Introduction

1.1 Herbivory

Herbivores are major consumers of primary producers in temperate and tropical ecosystems, making herbivory an important energy pathway in food webs (Huntly 1991; Levenbach 2008). Herbivory is a vital process in the natural environment and is one of the major forces controlling the evolution, distribution and abundance of plants in marine and terrestrial ecosystems (Huntly 1991). Herbivores can influence the abundance of sympatric primary producer species and create habitat separation in plant communities or cause morphological changes in plants (Holt 1984; Karban and Baldwin 1997; Ohgushi 2005). Among the factors that influence herbivory, the most important is the direct positive relationship with primary production (McNaughton et al. 1989).

1.2 Herbivory in marine ecosystems

Herbivory rates are much higher in the ocean than on land. For example, for a given level of primary production, aquatic herbivores showed to consume about 300% more food than terrestrial herbivores (Cyr and Pace 1993). Several factors influence this process in marine ecosystems. Firstly, herbivory increases rapidly when the most important factor, primary productivity, is high (McNaughton et al. 1989). Latitude is another influential factor, as the abundance and the richness of herbivorous species are inversely related to latitude, and directly related to the sea surface temperature (Floeter et al. 2005). Herbivory is also influenced by predation as, in presence of a strong trophic cascade, predators are more abundant and herbivory rates are lower (Hairston et al. 1960). For example, between 1950 and 1970 along the coast of southern California, the forests of giant kelp *Macrocystis pyrifera* collapsed because the predators of sea urchins, such as sheephead wrasse and spiny lobsters, had been overfished (Foster and Schiel 2010). Due to the low presence of predators, the abundance of sea urchins increased, such as the amount of kelp consumed, causing the collapse of the kelp forest. This is also a clear example of the impact that herbivores can have on the algal composition of the reef. In fact, high rates of herbivory have been shown to affect reef assemblages both in tropical and temperate environment (Andrew and Jones 1990;

Ceccarelli 2007; Doropoulos et al. 2011). For example, Doropoulos et al. (2011) showed that the exclusion of large herbivores in tropical coral reefs had a positive impact on algal recruitment. Moreover, high rates of herbivory can change the physiology of plants and induce morphological adaptations, or the production of secondary chemicals which can influence the palatability of a plant to herbivores or decrease herbivory rates by attracting predators (Price et al. 1980; Huntly 1991). The primary herbivores in marine systems are crustaceans, molluscs, fishes, echinoderms, reptiles, and mammals (Huntly 1991). A range of these groups, including herbivorous fishes, can play an important role in seagrass systems, particularly in tropical regions (Bjorndal 1980; Valentine and Heck 1999; Masini et al. 2001); (Valentine and Duffy 2006). Furthermore, herbivorous fishes are considered particularly important for coral-reef environments (Gaines and Lubchenco 1982), as their grazing activity can determine the biological structure of coral reefs and strongly influence carbon flow (Horn 1989; Verges et al. 2011). As Connel et al. (2007) showed, the high grazing activity of herbivorous fishes in tropical coral reefs plays a key role in the regeneration of corals, by controlling algal growth.

Most of the dietary and feeding activity studies on herbivorous fishes focus on tropical regions, where their main food resources comprise filamentous and turf seaweeds, epiphytic microalgae, invertebrates, other aquatic plants, associated meiofauna and detritus (Elliott and Bellwood 2003; Ceccarelli 2007; Castellanos-Galindo and Giraldo 2008; Kramer et al. 2013). This assemblage of materials is called the epilithic algal matrix (EAM) (Wilson et al. 2003); however, they may also ingest some animal material, which is a good protein source (Tolentino-Pablico et al. 2008). Herbivorous fishes in coral-reef systems have been categorised into four functional groups: scrapers/small excavators, large excavators/bioeroders, grazers/detritivores and browsers (Green and Bellwood 2009). The first functional group feeds on coralline algae, algal turf and epilithic algal matrix (EAM, sensu (Wilson et al. 2003), and includes scraping species such as parrotfishes (Bellwood et al. 2004). They take non-excavating bites and scrape material from the surface of the substratum. Large excavators/bioeroders are similar to the first group, but they also feed on coralline algae. Unlike scrapers, they take deeper excavating bites and remove greater parts of substrata with each bite (Bellwood and Choat 1990; Hoey and Bellwood 2008). This group includes all large individuals (>35cm SL) of excavating species of parrotfish such as

Bolbometopon muricatum and all species of the genus *Chlorurus* (Bellwood and Choat 1990). Grazers/detritivores feed on epilithic algal turf and detritus, and with their intense grazing activity they can limit the growth of macroalgae on the reef (Hughes et al. 2007). In contrast with excavators, they don't scrape or excavate the reef substratum when they feed (Green and Bellwood 2009). This group includes most species of rabbitfish, small angelfish such as *Centropyge* spp., and surgeonfish such as *Acanthurus* spp. (Green and Bellwood 2009). Grazers also include large vertebrates such as turtle and dugongs, which can have a strong impact on the biomass and species composition of tropical seagrasses in shallow water (Connell and Vanderklift 2007). The latter group, browsers, feeds on large fleshy macroalgae and foliose algae (Bennett and Bellwood 2011).

Compared to tropical systems, herbivory in temperate ecosystems is considered to be dominated by large invertebrates such as sea urchins, which graze intensively on erect algae (Foster and Schiel 2010), and gastropods, which feed on foliose algae (Connell and Vanderklift 2007). The number of herbivorous fish species is considered to be relatively low (Tolentino-Pablico et al. 2008), but they are likely to play an important role due to high number of herbivorous fishes present in temperate regions (Jones 1992). Despite this, few studies have been undertaken on this group of animals in temperate environments, highlighting a lack of understanding of fish herbivory in temperate systems.

1.3 Herbivory in temperate ecosystems

Key groups of herbivores appear to differ among different temperate ecosystems. In seagrass ecosystems, small invertebrates play a key role due to their high herbivory rates and huge abundance (Heck and Valentine 2006). Herbivorous fishes can also play an important role in these systems (MacArthur and Hyndes 2007; Wressnig and Booth 2008). The herbivorous fish *Sarpa salpa* in the Mediterranean Sea feeds mainly on the seagrass *Posidonia oceanica* (Prado et al. 2010). Labridae such as *Odax acroptilus* (MacArthur and Hyndes 2007) and Monacanthidae (Wressnig and Booth 2007; Wressnig and Booth 2008) also play an important role in the removal of seagrass and associated epiphytic algae in temperate seagrass systems. In comparison, intertidal rocky shores are dominated by gastropods, whose feeding impacts greatly on foliose algae, thereby playing a key role in the distribution of algae in this ecosystem

(Underwood 1980). In subtidal rocky habitats, sea urchin grazing activity is intense along the coast of California (Levenbach 2009) and eastern Australia (Fletcher 1987; Andrew 1993; Vanderklift and Kendrick 2004). For example, the black sea urchin *Centrostephanus rodgersii* removes virtually all erect algae along the coast of central and southern New South Wales (Fletcher 1987; Andrew 1993). Herbivorous fishes are also abundant in subtidal reefs and they prefer habitats with kelp or seagrasses than nearby habitat without vegetation (Harman et al. 2003; Thomson et al. 2012). These open-gaps between kelp canopies or other macroalgae are dominated by territorial species such as *Parma* spp. (Harman et al. 2003; Thomson et al. 2012). Within these patches they establish their territories defending them from the other herbivorous species competing for the same food sources, which usually are red filamentous and foliose algae (Jones and Norman 1986; Buckle and Booth 2009). Even though fish herbivory is lower in temperate reefs, compared to coral reefs, it still is still considered to play a key role in structuring the plant community (Andrew and Jones 1990). However, there is far less known about fish herbivory in temperate versus tropical reefs.

The most common and abundant families of herbivorous fishes in temperate reefs are Kyphosidae, Labridae, Aplodactylidae, Pomacentridae and Monacanthidae (Jones 1992; Meekan and Choat 1997). However, not all the species within these families are herbivorous. Kyphosidae and Pomacentridae are the most abundant families in algal reef systems and feed on different species of red and green turf algae (Jones 1992). In particular, Pomacentridae dominates the red algal zone in the patches among kelp canopy, where they establish their territories and chase other species, particularly those in Monacanthidae (leatherjacket) inhabiting the same area. On reefs, species of Monacanthidae feed on red algae in spaces between Pomacentridae territories and on epiphytic red algae growing on kelp (Jones 1992; MacArthur and Hyndes 2007). In comparison, Labridae feed directly on kelp (*Ecklonia radiata*) and seagrass, and are closely associated with the kelp forest (Jones 1992).

1.4 Ecology of Pomacentridae: their role in tropical and temperate reefs

The Pomacentridae is one of the most representative families of herbivorous fishes inhabiting both tropical and temperate reefs (Allen 1991; Aguilar-Medrano et al. 2011), though not all the species are herbivores (Ceccarelli 2007). Most species are tropical, but some species are very abundant in temperate waters and are distributed worldwide (Aguilar-Medrano et al. 2011). The family includes 29 genera and more than 350 species, which differ in habitat, feeding strategy and behaviour (Allen 1991; Aguilar-Medrano et al. 2011). The life cycle of Pomacentridae involves a planktonic larval stage resulting in pelagic dispersion, after which individuals settle into reef habitats (Leis et al. 2002).

Pomacentridae can be aggressive and territorial, protecting algal food sources and shelter in their territories (Low 1971), which can cover >50% of the substrata across a reef (Ceccarelli 2007). Tropical pomacentrid species are usually smaller compared to their temperate counterparts, and they feed within a smaller area (Ferreira et al. 1998; Hata and Kato 2004). For example, the temperate *Parma mccullochi* feed in an area of 9 m² (Saunders 2011), whereas the tropical *Stegastes fuscus* have a mean territory size of 2.1 m² (Ferreira et al. 1998), and *Microspathodon dorsalis* has a mean territory size of 0.51 m² (Montgomery 1980).

Pomacentridae play an important role in shaping benthic reef communities (Ceccarelli et al. 2001) and they can affect the algal composition of the reef in 3 different ways: (1) directly feeding on algae; (2) with their weeding and farming activities; and (3) indirectly excluding other competitive herbivorous fishes. For example, with their farming activities, territorial damselfishes allow turf algae to develop into bigger macroalgae within their territories (Hata and Kato 2004). Moreover, they can have a direct local impact on the reef because they exclude other herbivores from their territories (Brawley and Adey 1977) and can also exercise “farming activities” such as providing nutrient fertilization and selective weeding (Ceccarelli et al. 2001; Jones et al. 2006). In addition, their territorial behaviour facilitates survival of corals within the territories by chasing possible predators (Gochfeld 2010). The algal composition of Pomacentridae territories can vary between species, depending on their behaviour (Hata and Kato 2004). For example, Hoey and Bellwood (2010) showed that *S.*

nigricans removes the undesirable algae and chases other fishes from their territories. With this behaviour, each fish maintains a small territory (0.3 m²) dominated by *Polysiphonia sp.*, which is a red filamentous alga. In contrast, *Stegastes obreptus* does not “weed” undesirable algae from its territory and their chasing activity is lower than that of *S. nigricans*. Territories of this species are larger (6.3 m²) and contain a diverse assemblage of fleshy macroalgae (Hoey and Bellwood 2010). In addition, tropical Pomacentridae can have a strong impact on recruiting algae. In fact, their presence significantly increased turf algal cover whereas fleshy macroalgae were found in the herbivory exclusion treatment (Doropoulos et al. 2011). Due to these different behaviours affecting the structure of algae in the reef, territorial Pomacentridae could be compared to ecosystem-engineers or landscapers. Ecosystem engineers are organisms that have the capacity to modify the environmental conditions, and affect other species without direct trophic interactions (Jones et al. 1994). For example, the massive coral *Montastraea annularis*, which is a dominant frame-work builder of Caribbean coral reef, change the environment with its own physical structures (Foster et al. 2013). Seagrasses are also generally known as ecosystem engineers, as they modify the physical environmental parameters, for example reducing flow velocities in their canopies (Bos et al. 2007; Bouma et al. 2009). Pomacentridae, like ecosystem engineers, could shape temperate reef ecosystems through creating this characteristic patchy structure. Despite this, only one study has tested the effect of Pomacentridae on algae assemblages in temperate reefs, and didn’t show any significant effect (Saunders 2011).

The diet of Pomacentridae usually shifts from zooplankton as larvae (Leis et al. 2002), to a combination of zooplankton and/or macrophytes as juveniles and adults, depending on the species (Allen 1991). For example, juvenile *S. nigricans* feed on invertebrates and algae, while adults consume mainly red turf algae and detritus (Letourneur et al. 1997; Wilson and Bellwood 1997). The diet of tropical Pomacentridae can vary between different species (Letourneur et al. 1997; Ceccarelli 2007; Castellanos-Galindo and Giraldo 2008; Frederich et al. 2008), but they usually feed on red foliose and filamentous algae (Ceccarelli 2007; Feitosa et al. 2012). However, animal material and detritus can be also found in their diet (Letourneur et al. 1997; Ceccarelli 2007; Feitosa et al. 2012). Moreover, some species are selective towards certain food items indicating specialist feeding habits (Castellanos-Galindo and Giraldo 2008). The feeding rates of

territorial herbivorous fishes of tropical environments increase in the afternoon (“afternoon foraging”) (Horn 1989; Ferreira et al. 1998), probably because the nutritional content of algae on coral reefs is higher in the afternoon (Zemke-White et al. 2002). In comparison, *Parma* spp. in temperate reefs have not shown a shift in the feeding rates over the day (Buckle and Booth 2009) and different species of temperate Pomacentridae have similar diets, mostly comprising red filamentous and foliose algae (Jones and Norman 1986; Buckle and Booth 2009). In contrast with their tropical counterparts, animal material is mostly found in juvenile’s diet, with the percentage of ingested animal material negatively correlated with the body size (Buckle and Booth 2009). However, most studies on Pomacentridae have been done on species in tropical reefs, whereas the role of this family of fishes and its impact on temperate reefs has not been clearly studied and understood.

The most abundant genus of Pomacentridae inhabiting rocky temperate reefs is *Parma* (Moran and Sale 1977; Choat 1982). Due to their territorial behaviour and their high feeding rates, this genus of herbivorous fishes appears to play a vital role in this temperate habitat (Buckle and Booth 2009). The most common species of *Parma* inhabiting temperate reefs of Western Australia is *P. mccullochi*, in particular (Saunders personal communication), followed by *P. occidentalis*, *P. victoria* and *P. bicolor* (Allen 1991; Gommon et al. 1994). In comparison, *P. microlepis* and *P. unifasciata* are the most common species in temperate reef of eastern Australia (Moran and Sale 1977; Allen 1991; Gommon et al. 1994). Most of the studies on temperate Pomacentridae have focused on two species of *Parma*: *P. microlepis*, common in New South Wales, and *P. victoriae*, mainly in Victoria and South Australia (Moran and Sale 1977; Jones and Norman 1986). In contrast, few studies have focused on the most common *Parma* *mccullochi*.

1.5 *Parma* genus in temperate reefs

Parma species are limited in their distribution to Australasian waters (Allen and Hoese 1975). Like tropical Pomacentridae species, temperate *Parma* spp. are territorial and aggressive (Saunders 2011(Moran and Sale 1977)). Adults are mainly herbivores, feeding on algae and associated benthic invertebrates (Moran and Sale 1977). In contrast with most of the tropical species, *Parma* spp. seem to have a minimal effect on the algal composition of the reef. For example, Jones (1992) showed that the feeding

activity of *P. victoriae* doesn't have a significant impact on the species composition of the mixed algal turf. However, *Parma* spp. can affect the algal composition of the reef within the nesting sites through weeding activity (Saunders 2011).

The few studies that have been done on the diet and feeding ecology of *Parma* spp. in temperate regions showed that they feed mostly on red foliose algae, and the diet changes between juveniles and adults (Jones and Norman 1986; Buckle and Booth 2009). In fact, there is a positive correlation between the percentage of ingested algae and the body size (Buckle and Booth 2009). Furthermore, the bite rates decrease with body size but the feeding activity does not show significant differences during the day (Shepherd et al. 2008; Buckle and Booth 2009). Juveniles of *Parma* spp. appear to ingest more detritus and animal material, such as small invertebrates, than adults (Buckle and Booth 2009), probably to satisfy their energy and nitrogen demands (Choat 1991) and the difficulty in digesting macroalgae (Horn 1989). As Buckle and Booth (2009) showed, the diet of *Parma* spp. can vary between different species. For example, the diet of adults *P. microlepis* comprises 67% of algal material, 18% polychaetes, 10% molluscs and 5% crustaceans, which contrasts to the adults of *P. unifasciata* whose diet contains more algal material (94%), and a small percentage of animal material (4% polychaetes and 2% crustaceans).

1.6 Thesis aims and significance

Parma mccullochi is highly abundant in temperate waters of Western Australia, especially in the area around Perth (Saunders personal communication), and displays strong territorial and farming behaviour (Saunders 2011). As a result, this species is likely to have a significant influence on the algal composition on temperate reefs in the region. Despite this, there is a lack of information on its dietary composition and its impacts on reef algae. The broad aim of this study is, therefore, to determine the role of *P. mccullochi* as an ecosystem engineer on temperate algal-dominated reefs. The results of this study will provide a better understanding of the processes driving the diversity and productivity of macroalgal assemblages on temperate reefs that will feed into better management and planning of Marine Protected Areas of Western Australia. To achieve this, the study will address the following research questions:

- 1 What is the dietary composition of *P. mccullochi* and does it shift between life history stage and time of year?
- 2 Does the feeding activity of *P. mccullochi* affect the algal composition and recruitment on temperate reefs?

Chapter 2

Study sites and methods

2.1 Study Area

The study focused on marine waters adjacent to Perth, Western Australia, and specifically, in four different sites in the Marmion Marine Park (31°50'S, 115°42'E) (Fig. 2.1). The marine park is characterized by a series of parallel subtidal limestone reefs, dominated by the kelp *Ecklonia radiata*, associated with red algae inhabiting the understory (Toohey et al. 2004). The reef system runs parallel to the coast line for 15 km between 3 and 5 km offshore and is exposed to the swells coming from the open ocean, and also to the warm waters of the Leeuwin Current that flow south along the coast of Western Australia (Wernberg et al. 2003; Toohey et al. 2004). The reefs are separated by sandy patches and seagrass meadows dominated by *Posidonia* spp., *Halophila* spp. and *Amphibolis* spp. (Pearce 1991; Kirkman 1997). *Parma mccullochi* is an abundant species on the reefs in the region, where individuals maintain large territories chasing other species away (Saunders 2011).

Four sites (Fig. 2.1) were randomly chosen to represent the reef habitats where *P. mccullochi* is abundant. These four sites were used to address each aim of the study.

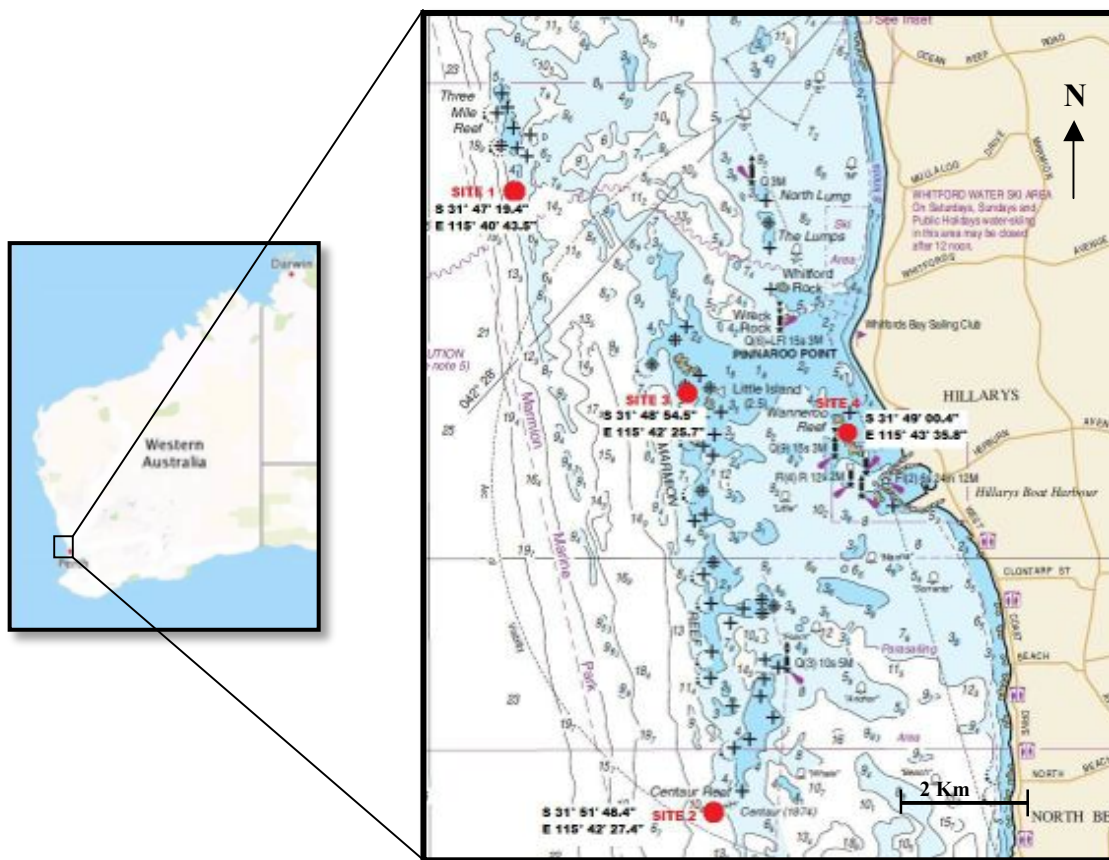


Fig. 2.1 Map showing the location of the Marmion Marine Park in Western Australia and the location of the Study sites in Marmion Marine Park (adapted from Department for Planning and Infrastructures W.A.)

2.2 Impact of the feeding activity of *P. mccullochi* on algal composition of reefs

The effect of *Parma mccullochi* feeding activity on the algal community was determined by examining the algal composition inside and outside *Parma* feeding territories (both adults and juveniles). While scuba diving, the observer (F. Vitelli) examined the presence of the fish and its feeding behaviour for 15 minutes (Altmann 1974; Saunders 2011) to identify the boundaries of a range of *Parma* feeding territories at the above four sites. Eight areas inside and eight areas outside eight different *Parma* feeding territories were randomly chosen within each site, and the biomass of different taxa of algae within each area was determined by collecting algae within a 25 x 25 cm quadrats from the 15th to the 26th of February 2012. All the algae present in each quadrat were removed manually, cutting all algae at the base with a knife and, if necessary, scraping with a wiper tool (Adey 1977). Each algae sample was placed in a cotton bag and returned to the boat, where it was placed on ice. On return to the laboratory, the samples were frozen for subsequent processing. Subsequently, each sample was rinsed with water to remove any sediment and spread on a white sheet. The algal taxa were separated, dried in an oven at a temperature of 80°C for 48 hours, and the biomass of each taxon was weighed to 0.001 g (dry weight).

Differences in the algal composition between inside and outside the territories were analysed using a nested PERMANOVA (Anderson et al. 2008), with sites (4 levels, random factor) nested in territory (2 levels, fixed factor). Analyses were conducted using 9999 permutations, based on a Bray-Curtis similarity matrix using square root transformed data. nMDS plots based on a Bray-Curtis similarity matrix were generated to visually represent relative similarities (Anderson et al. 2008) in algal composition between inside and outside territories. Nested PERMANOVA test, with sites (4 levels, random factor) nested in territory (2 levels, fixed factor) was used to test total biomass (all species together) and species richness differences between inside and outside territories and among sites. These univariate analyses were undertaken using Euclidean distance measures; which produces estimates of sums of squares equal to parametric ANOVA, but the use of permutation allows for significance to be tested without the assumption of normality (Anderson et al. 2008). All data were tested for homogeneity using a sphericity test (Mauckly-test). Biomass data were Log-transformed to achieve homogeneity. The algal species likely to be driving the algal composition of the

territories and outside the territories were determined by their correlations (Spearman correlation coefficient set at $r > 0.6$) with the canonical axes of the nMDS. All tests were conducted with PRIMER 6.

2.3 Dietary composition of juvenile and adult *Parma mccullochi*

Five juveniles (size class: 0-20 cm; recognisable for their shiny blue stripe on the back) and five adults (size class: >20 cm; totally black/dark brown with no blue stripes) fish were collected randomly from each of the four sites at the same time of day by spear fishing on two sampling occasions (April and September 2012). The fish were collected at a time of day just after their highest feeding activity (between 11:00 and 14:00, determined from pilot work for the feeding activity study, which represents the time when the gut fullness is greatest and dietary items are the least digested. Once on the boat, the fish were placed in a slurry of ice and returned to the laboratory for processing (Buckle and Booth 2009). In the laboratory, each fish had its total length (to the nearest 1 mm) and weight (to the nearest 0.1 g) recorded. Its stomach was then removed, weighed to the nearest 0.1 g and frozen for later examination. The stomach fullness was determined from the stomach weight index based on the stomach weight divided by the somatic weight of the fish and expressed as a percentage and also represented as an index from 1(empty) to 5 (full).

For dietary analyses, the stomach content was examined under a dissecting microscope to determine the taxa of algae present in each gut and their proportions following the procedures of (Buckle and Booth 2009). In summary, the material present in the stomach was placed into petri dish filled with water and the gut content was evenly spread on a grid. The taxon present at each of 100 systematically placed points was identified to species level when possible, and the percentage of each food item was determined. The percentage of each food item was expressed as percentage volume, based on the number of points on which it was found for each gut.

Feeding selectivity was also examined, based on comparing the percentage of each taxon of algae in the diets with the percentage of that taxon in the territories. The percentage of each taxon in each replicate quadrat in the territory at each site was determined by dividing the biomass of each taxon by the total biomass of all taxa in each quadrat and expressed as a percentage. The average percent of each taxon was then

calculated across all sites. This comparison used Ivlev's electivity index (Ivlev 1961) due to its simplicity and its suitability for dietary studies (Jones and Norman 1986). The formula is $E_i = (r_i - p_i) / (r_i + p_i)$, where r_i is the percentage of the "i" algal species in the diet and p_i is the percentage of the same "i" species in the field. Values of the index range from -1 (lowest selectivity for the species) to +1 (maximum selectivity). The value 0 indicates random feeding on the food item (Ivlev 1961).

Percent dietary data were compared between juveniles and adults (Life stage), and among sites (Site) nested in Life stage using PERMANOVA (Anderson et al. 2008). Life stage was considered as a fixed factor with two levels, while Site was considered as a random factor with four levels. All data were square root transformed to reduce the effect generated by different orders of magnitude in the percentage values and achieve homogeneity, and analyses were based on 9999 permutations from the Bray-Curtis similarity matrix (Anderson et al. 2008). Non-metric Multidimensional Scaling (nMDS) plots were run to visually represent relative similarity of samples from each factor. The algal species likely to be driving the diet composition of *P. mccullochi* were determined by their correlations (Spearman correlation coefficient set at $r > 0.6$) with the canonical axes of the nMDS. All tests were conducted with PRIMER 6.

2.4 Impact of feeding on algal recruitment

Within each of the four sites described above, 12 roughened PVC tiles (25x25 cm) (Smale et al. 2011) were set up inside the *Parma* territories (on tile for each territory) for a period of 6 months (from March 2011 to September 2012), which is a sufficient period of time needed for this type of experiment (Pech et al. 2002; Doropoulos et al. 2011). Each tile was attached to a concrete tile (40x40 cm) by 2 galvanised screws, which was fixed onto the reef by scuba divers using pegs and ropes. For the experiment, 4 tiles were caged (5 X 5 cm mesh size and 27.5 X 27.5 cm cage base by 40 cm height) to prevent feeding activity of *Parma*, 4 were without a cage and 4 were partially caged (with 2 sides of the cage open to let the fish go through it and feed on the tile) as cage controls (Fig. 2.2). During the 6-month deployment, tiles and cages were inspected and maintained (i.e. to replace cable ties) every 10 days (Smale et al. 2011). At the end of 6 months, all the panels were collected and returned to the laboratory, when a high-resolution digital image of each panel was taken for reference, and then

each panel was frozen for subsequent laboratory processing. For processing, each tile was thawed and rinsed with water to remove any sediment. The algae from each panel were scraped, and the different algal taxa separated and oven dried at 80°C for 48 hours, after which the biomass of each taxon was measured to 0.001 g (dry weight)

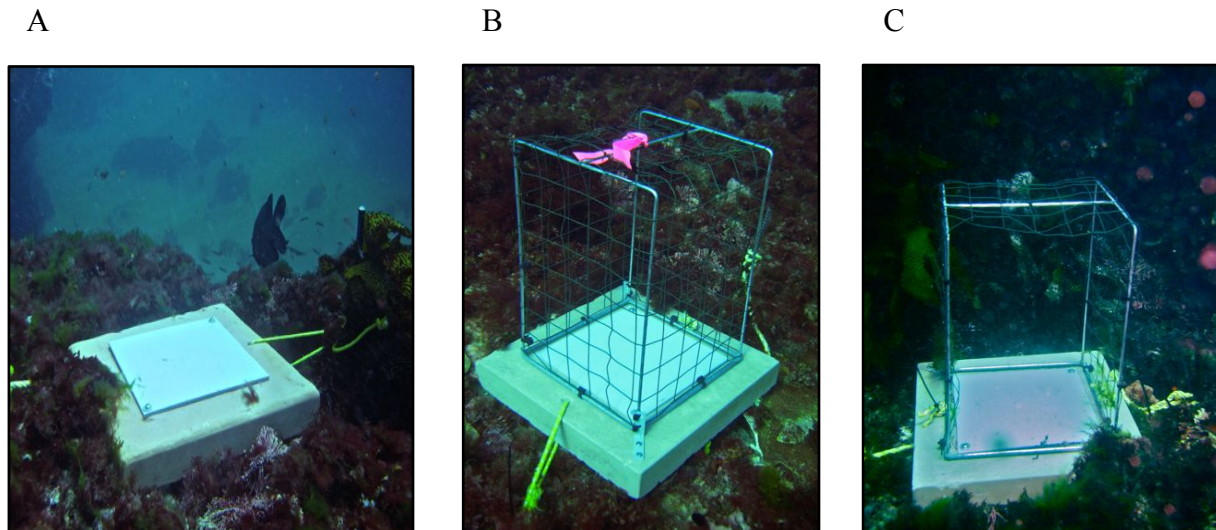


Fig. 2.2 Three different treatments for the recruitment experiment: Uncaged PVC tile (A), Caged (B) and half caged control (C). Tiles were deployed for a period of 6 months.

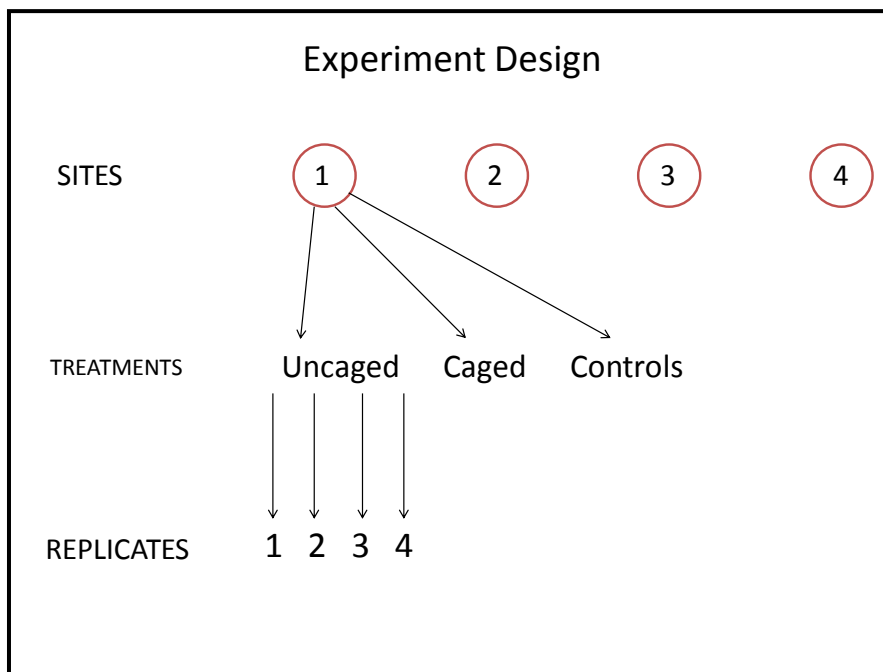


Fig. 2.3 Diagram of the recruitment experiment design.

Biomass differences in the algal composition among treatments (caged, partially caged and uncaged tiles) were analysed using nested PERMANOVA+ (Anderson et al. 2008), with sites (4 levels, random factor) nested within treatment (3 levels, fixed factor). Analyses used 9999 permutations, based on a Bray-Curtis similarity matrix from square root transformed data. Data were square root transformed to reduce the effect generated by different orders of magnitude in the values and achieve homogeneity. nMDS plots, based on a Bray-Curtis similarity matrix, were generated to visually represent relative similarities in algal composition among treatments (caged, uncaged and controls, and sites). Nested PERMANOVA test (Anderson et al. 2008), with treatments (3 levels, fixed factor) and sites (4 levels, random factor) nested in treatments was used to test total biomass (all species together) and species richness differences between treatments and between sites. These univariate analyses were undertaken using Euclidean distance measures; which produces estimates of sums of squares equal to parametric ANOVA, but the use of permutation allows for significance to be tested without the assumption of normality (Anderson et al. 2008). The algal species likely to be driving the algal composition on the recruitment tiles were determined by their correlations (Spearman correlation coefficient set at $r > 0.6$) with the canonical axes of the nMDS. All data were tested for homogeneity using a sphericity test (Mauckly-test). All data were Log-transformed to achieve homogeneity. All tests were conducted with PRIMER 6.

Chapter 3

Results



Photograph: Juvenile *Parma mccullochi*

3.1 Gut contents and diet analysis.

The range of collected fish sizes for juveniles was 10.5-19.8 cm, and for adults 22-30.4 cm. All stomachs of *Parma mccullochi* were found full (mean fullness ≥ 4), with a mean gut weight index exceeding 2 % of the somatic weight of fish (Table 3.1), and food items inside were not digested. As a consequence, food items were easily identified, apart from some of the smallest fragments of algae, which were grouped under broad categories such as red, brown or green and filamentous or foliose algae. A variety of red (Rhodophyta), green (Chlorophyta) and brown (Phaeophyta) algae were found inside the stomachs of both juvenile and adults *P. mccullochi* during the two sampling occasions (April and August). The most frequently consumed species was *Hypnea* spp., followed by *Ceramium* sp., *Champia* spp., *Derbesia* sp., *Dictyopteris* sp., *Dasyclonium* sp., *Hinksia* sp., red foliose algae, and *Ulva lactuca* (Table 3.1).



Fig. 3.1 Stomach contents of *P. mccullochi*.

PERMANOVA showed that there were significant temporal differences in the diet of *P. mccullochi* (Table 3.2). This was also highlighted by a clear separation of samples from April and August in the nMDS plot (Fig. 3.2). PERMANOVA also showed that there was no significant difference in the dietary composition between juvenile and adult *P. mccullochi*, but there was a significant difference among sites (Table 3.2). This was highlighted by a general separation of samples from sites 3 and 4 and from sites 1 and 2 from each other (Fig. 3.5A and B). Based on Spearman rank correlations, in April, the most recurrent species of algae found in the stomachs were *Hypnea* spp., *Derbesia* Sp. and *Dasyclonium* spp.; these three dominant food items were still present in the stomach contents from August but with a smaller percentage. In comparison, *Ceramium* sp. and red foliose algae were the most characteristic algae in the diets during August (Fig. 3.2).

The main differences in the diets were found between offshore (1 and 2; 12 m deep) and inshore (3 and 4; 5 m deep) sites. Based on Spearman rank correlations, in April, *Dasyclonium* spp. was the species characterizing the diet of the fish collected within

sites 1 and 2 (offshore). On the other hand, *Hypnea* spp. and *Ulva lactuca* were characteristic of inshore sites (3 and 4) (Fig. 3.3A). In August, *Dasyclonium* spp. and red foliose algae were characterizing the diet of the fish collected within offshore sites (1 and 2), and *Ceramium* sp. was characteristic particularly within the inshore shallow site 3 (Fig 3.3B).

In April, the main differences in the diets between offshore (1 and 2; 12 m deep) and inshore (3 and 4; 5 m deep) sites were the percentage of the two dominant food items *Hypnea* spp. and *Dasyclonium* spp. (Fig. 3.3B). The first was more abundant in the stomachs of fish collected at sites 3 and 4 (inshore), and *Dasyclonium* was much less abundant, while fish collected within sites 1 and 2 (offshore) consumed more *Dasyclonium* spp. reducing the percentage of *Hypnea* spp. Ingested (Figs 3.3 and 3.4). The species driving the differences between sites 3 and 4 was *Ulva lactuca*, which was found more abundant at site 3 (Fig. 3.4A). In August, *Hypnea* spp. showed relatively consistent contribution to the diets across sites, whereas *Brongniartella* sp. ranged from 59.96-52.04 % at sites 1-2 compare to 0 % at sites 3-4 (Fig. 3.4B). Fish collected within inshore sites 3 and 4 were shown to feed more on red foliose algae (max: 58.09% - site 3) and *Ceramium* sp. (max: 88.55% - site 4) (Fig. 3.4B).

Feeding selectivity of *P. mccullochi*

Ivlev's electivity index, calculated on percentage of algal species in the stomachs of *Parma mccullochi* and their percentages inside the territories from the first sampling occasion (April), showed that certain species were preferred to others (Table 3.1). In fact, species with a high electivity index, such as *Brongniartella* sp., *Dasyclonium* sp., *Hypnea* spp. and *Dictyopteris* spp. (Table 3.1), also made the greatest contributions to the diet of fish in April (Fig. 3.4). However, species found in low biomass in the *Parma* territories (e.g. *Heterodoxia* sp., *Champia* spp.) and in low percentages in the guts showed a high electivity index (Table 3.1). In contrast, species such as *Pterocladia lucida*, *Dictyomenia* spp. and *Ceramium* sp., which were present in high biomass in territories but low proportions in stomachs, had electivity indices close to -1 (Table 3.1).

Table 3.1 Mean percentage volume (%V), frequency of occurrence (%F) and Ivlev's Electivity index (E_i) of dietary items in the stomachs of juvenile and adult *Parma mccullochi*, with mean gut index as a weight standard and gut fullness. Data have been pooled from two sampling occasions (April and August) and four sites.

	JUVENILES			ADULTS		
Gut weight index (%)	2.7671±0.002			2.3317±0.001		
Gut fullness (1-5)	4±0.2			4.5±0.2		
Species	% F	% V	E_i	% F	% V	E_i
Rhodophyta	<u>72.52</u>	<u>86.34</u>		<u>80.19</u>	<u>89.54</u>	
Foliose	22.8	31.67		22.58	16.18	
<i>Dictyomenia sonderi</i>	11.1	0.47	-0.56	23.1	1.53	-0.44
<i>Dictyomenia tridens</i>	13.9	3.17	0.27	0	0.10	-1
<i>Heterodoxia</i> sp.	16.7	1.91	0.89	23.1	2.19	0.88
<i>Rhodomenia sonderi</i>	30.6	1.51	-0.37	30.8	1.13	-0.39
Unidentified	41.7	24.60	0	35.9	11.24	0
Corticated	26.38	17.4		35.03	30.18	
<i>Asparagopsis</i> sp.	5.6	0.28	-0.73	20.5	1.50	-0.08
<i>Botrocladia</i> sp.	8.3	0.37	-0.36	5.1	0.08	-0.81
<i>Champia</i> spp.	33.3	2.33	0.87	61.5	3.14	0.81
<i>Hypnea</i> spp.	<u>91.7</u>	<u>13.89</u>	<u>0.4</u>	<u>92.3</u>	<u>24.02</u>	<u>0.64</u>
<i>Pterocladia lucida</i>	8.3	0.25	-1	10.3	0.55	-0.31
<i>Pterocladia rectangularis</i>	11.1	0.28	0.57	20.5	0.88	0.83
Filamentous	23.34	37.27		22.58	43.18	
<i>Ceramium</i> sp.	38.9	9.53	-1	43.6	18.06	-1
<i>Brongniartrella</i> sp.	38.9	15.97	0.6	15.4	20.35	0.62
<i>Dasyclonium</i> sp.	13.9	10.94	0.98	2.6	1.26	0.77
<i>Polysiphonia</i> sp.	11.1	0.52	0.39	12.8	0.51	0.05
<i>Erythrimenia minuta</i>	13.9	0.32	-0.13	38.5	3.00	0.83
Phaeophyceae	<u>64.87</u>	<u>6.79</u>		<u>53.8</u>	<u>6.63</u>	

Foliose	23.17	3.67		28.2	5.18	
<i>Dictyota dichotomia</i>	13.9	1.02	-0.56	15.4	0.48	-0.08
<i>Dictyopteris</i> sp.	50	2.46	0.39	56.4	4.31	0.66
<i>Sargassum</i> spp.	5.6	0.20	-1	12.8	0.39	-1
Filamentous	41.7	3.12		25.6	1.45	
<i>Hinksia</i> spp.	41.7	3.12	0	25.6	1.45	0
<u>Chlorophyta</u>	<u>80.5</u>	<u>6.87</u>		<u>76.9</u>	<u>3.73</u>	
Foliose	33.3	5.01		48.7	2.56	
<i>Ulva</i> spp.	33.3	5.01	0.59	48.7	2.56	0.16
Filamentous	47.2	1.86		28.2	1.17	
<i>Cladophora</i> sp.	47.2	1.86	0.98	28.2	1.17	0.98
<u>Seagrasses</u>	<u>0</u>	<u>0</u>		<u>10.2</u>	<u>0.1</u>	
<i>Amphibolis</i> spp.	0	0	-1	10.2	0.10	-1

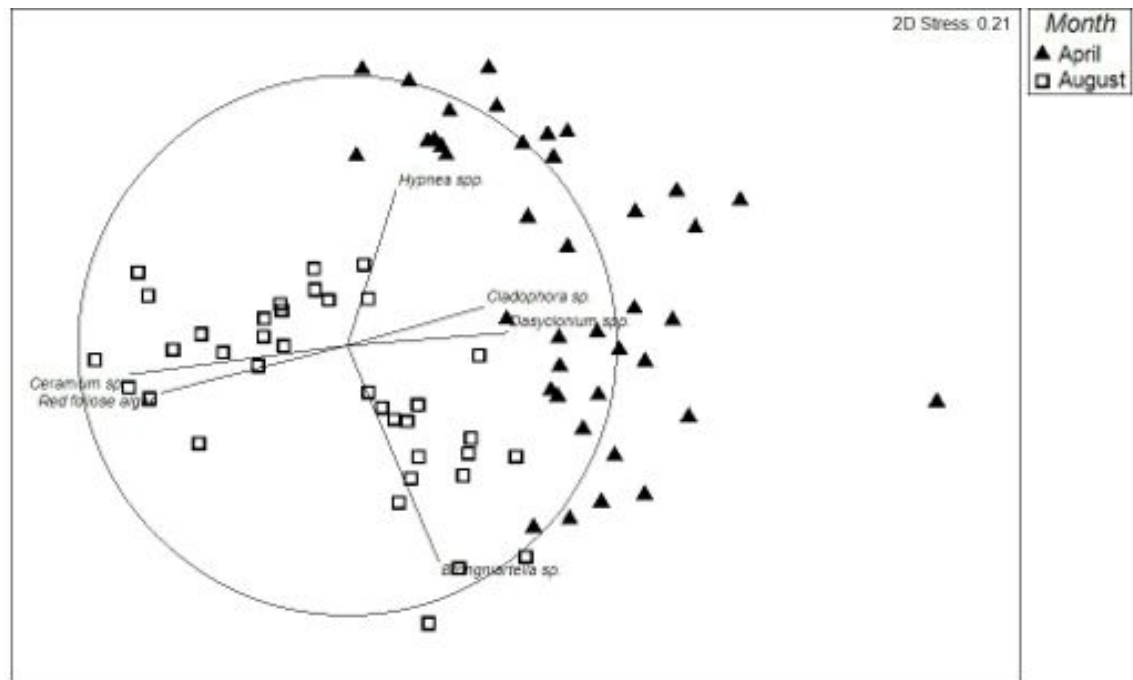
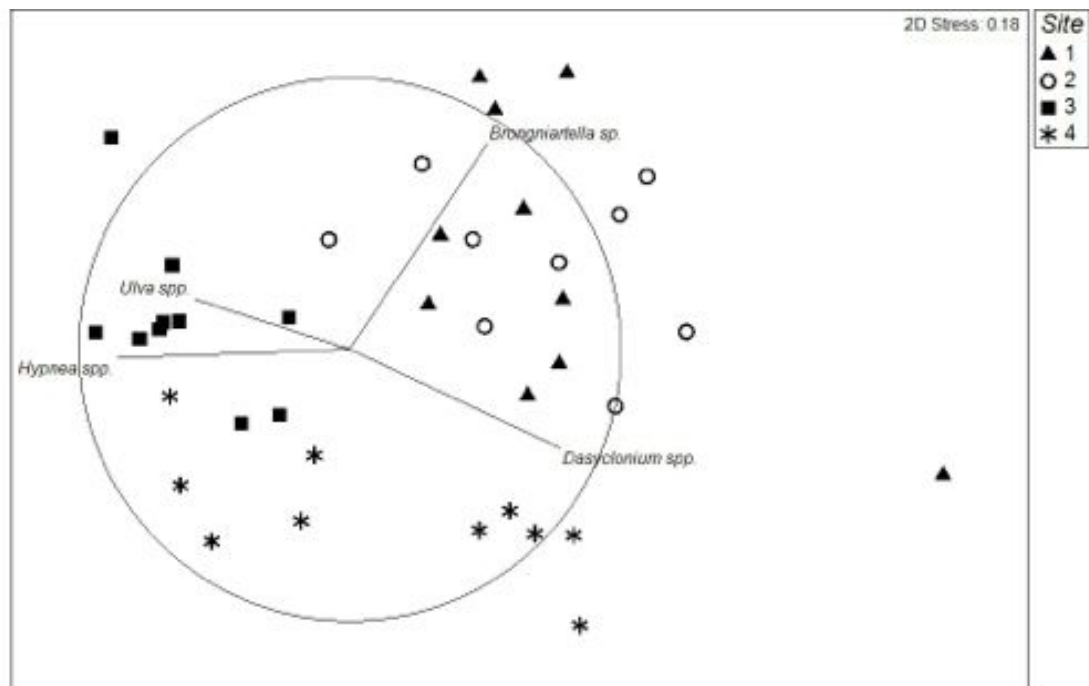


Fig. 3.2 nMDS plots based on a Bray-Curtis similarity matrix of stomach contents of *Parma mccullochi* collected in April and August 2012, highlighting differences between the two sampling occasions. Vectors represent the species characterizing the composition of the diet during the two sampling occasions (April and August 2012), (Spearman correlation=0.6). Data were square root transformed.

Table 3.2 Results of nested PERMANOVA testing life stage (juveniles or adults) and temporal differences in the diet of *Parma mccullochi*. Mixed design with sites (Random factor, 4 levels) nested in treatments (Fixed factor, 2 levels), and time of the year (Fixed factor, 2 levels). Fish were collected in April and August 2012, data were square root transformed.

	df	MS	Pseudo-F	P(perm)	perms	Comp Var
Life Stg (L)	1	4913.5	0.54617	0.6253	1667	-112.17
Month (M)	1	33726	8.7986	0.0023	9946	821.27
S(L)	6	9084.8	7.8285	0.0001	9880	861.12
L x M	1	4681.7	1.2214	0.3139	9954	46.631
S (L)x M	6	3863.3	3.3291	0.0001	9826	587.42
Res	59	1160.5				

A



B

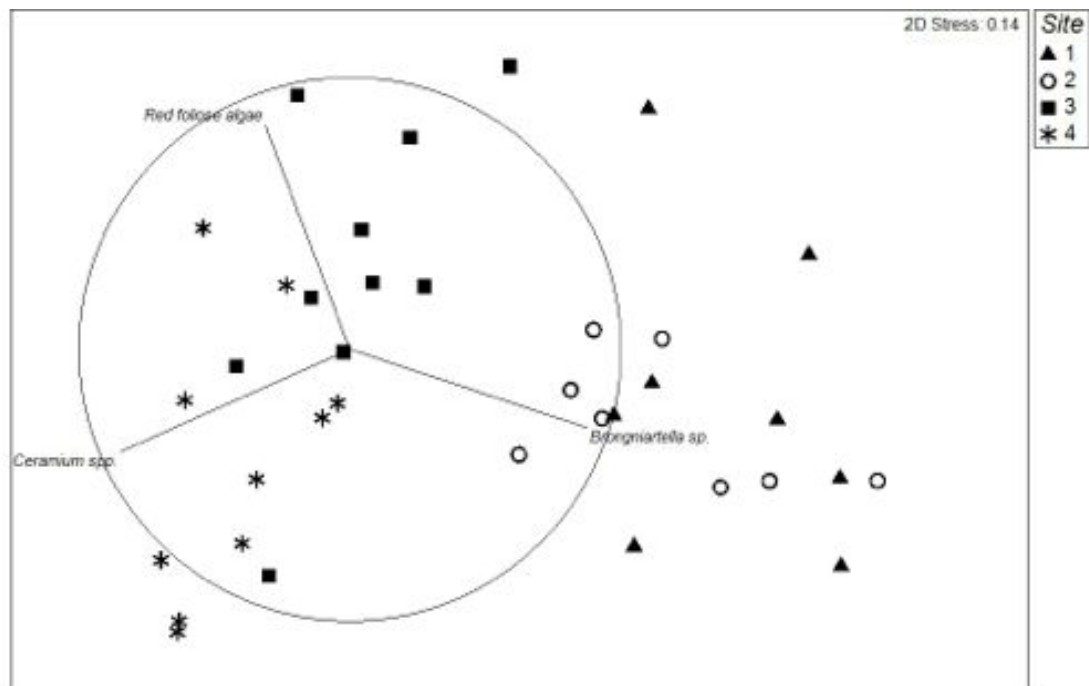
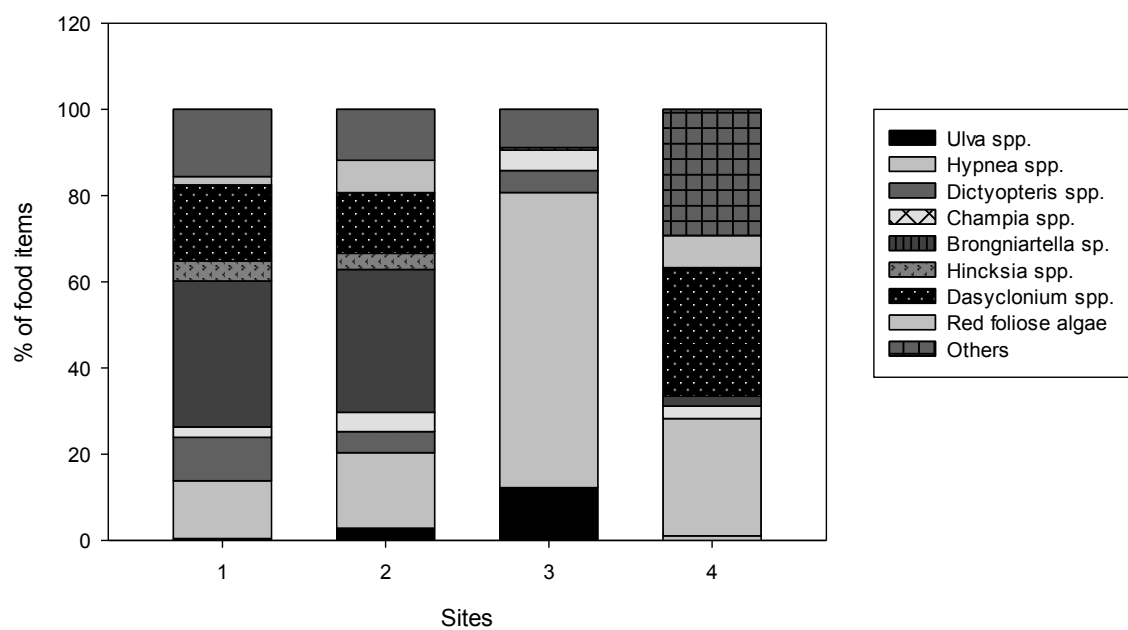


Fig. 3.3 nMDS plots based on a Bray-Curtis similarity matrix representing stomach contents of *Parma mccullochi* collected in April 2012 (A) and August 2012 (B), highlighting the differences between sites. Vectors represent the species characterizing the composition of the diet (Spearman correlation=0.6). Data were square root transforme

(A)



(B)

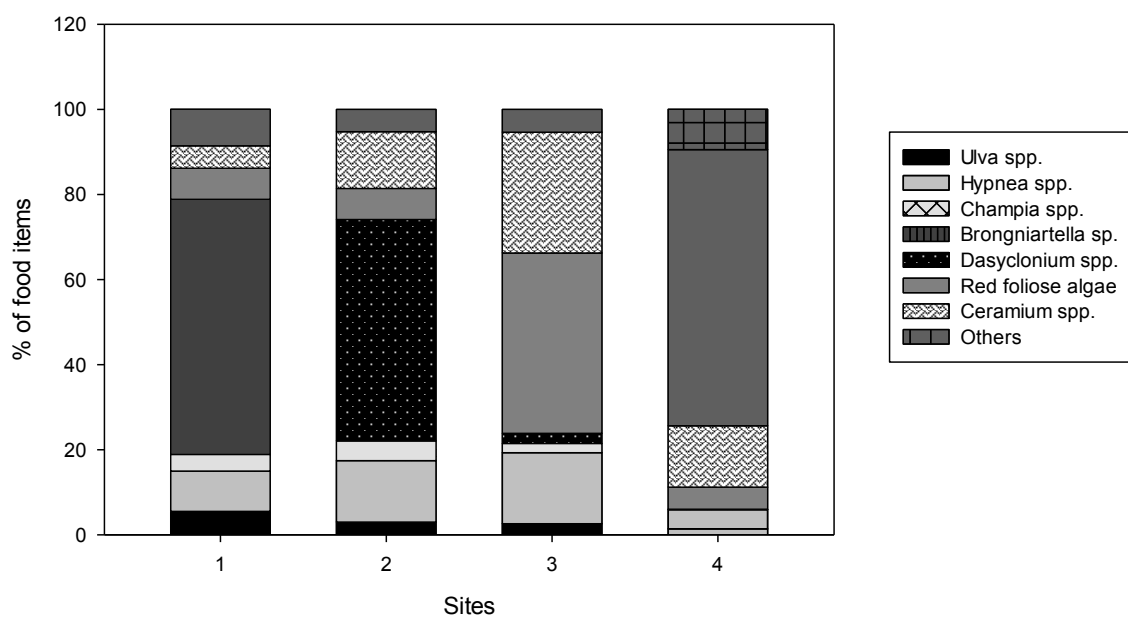


Fig. 3.4 Mean percentage contribution of the various algal species to the diet of *Parma mccullochi* collected in April (A) and August (B) 2012, within each of the four sites.

3.2 Impact of the feeding activity of *P.mccullochi* on the algal composition of the reef

PERMANOVA showed that the species composition of macroalgae differed significantly between inside and outside *Parma mccullochi* territories (Table 3.3) and this was supported by samples representing the species composition generally forming clusters associated with inside or outside territories on the nMDS plot (Fig. 3.5). Algal assemblages inside the territories were characterised by *Hypnea* spp. and *Dasyclonium* spp., while those outside the territories were characterised by the brown algae *Ecklonia radiata* and *Sargassum* spp. and the foliose red alga *Rhodomenia sonderi* (Fig. 3.5). The coralline red alga *Amphiroa anceps* also displayed a high correlation, but this was not associated with a pattern in the species composition between inside and outside territories. Species composition also differed among the four sites (Table 3.3).

Total algal biomass was significantly lower inside compared to outside the territories of *P. mccullochi*, but there was no significant difference among sites within treatment (Table 3.4, Fig. 3.6). In comparison, species richness was higher inside than outside the territories, but again, there was no difference among the four sites (Table 3.4, Fig. 3.6).

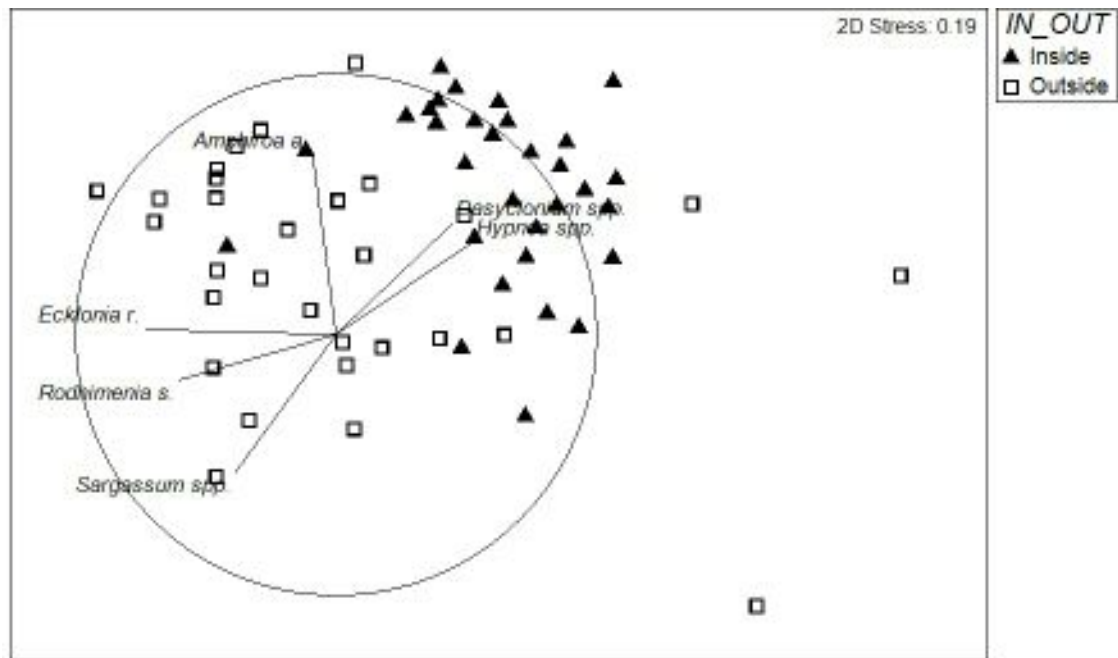


Fig. 3.5 nMDS plots based on a Bray-Curtis similarity matrix representing the algal composition inside (triangles) and outside (squares) the territories of *Parma mccullochi*. Vectors represent the genera characterizing the algal composition of the samples (Spearman correlation=0.5). Data were square root transformed.

Table 3.3 Results of nested PERMANOVA testing the differences in terms of algal composition between inside and outside *Parma mccullochi* territories. Nested design with Sites (Random factor, 4 levels) nested in Treatments (Fixed factor, 2 levels). Data were square root transformed.

	<i>DF</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>
Treatments	1	33892	7.723	0.0103
Sites (Treat)	6	4397.2	1.6031	0.0022
Residual	53	2742.8		

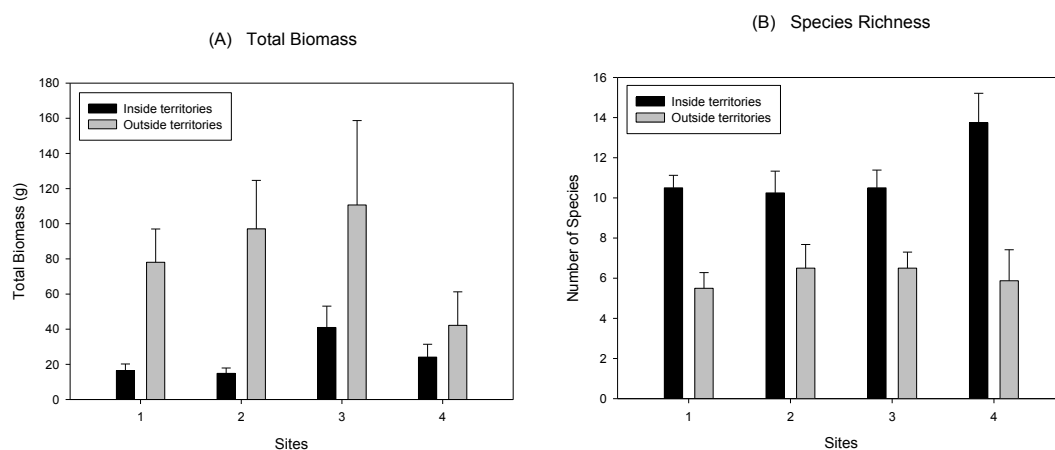


Fig. 3.6 Mean total biomass (A) and species richness (B) of algae inside and outside the territories of *Parma mccullochi* at four different sites. Error bars to one SE.

Table 3.4 Results of nested PERMANOVA testing the differences in terms of total biomass and species richness of algae inside and outside *Parma mccullochi* territories. Nested design with sites (Random factor, 4 levels) nested in treatments (Fixed factor, 2 levels). Species richness data were square root transformed, and biomass data were Log (X+1) transformed.

		Total Biomass			Species richness		
		<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>
Treatments	1	3382.3	18.161	0.0126	3228.3	36.832	0.0114
Sites (Treat)	6	186.18	208.4	0.5123	87.654	1.017	0.4325
Residual	54	208.4			86.187		

3.3 Impact of *Parma mccullochi* feeding activity on algal recruitment.

Due to adverse weather conditions, including storms producing 5-6 m swell, the results of this experiment have been heavily compromised. The strong swell destroyed many cages, and therefore, several replicates (14) were lost. A storm on August 2012 produced a 6 m swell and 40 knot wind, which resulted in the metal mesh of many cages falling apart and scratching the surface of the PVC tiles. Therefore, to better represent the real impact of the feeding activity of *Parma mccullochi* on the recruitment of algae, only those tiles scratched over <15% of the surface area were included in the analyses. Biomass and percentage cover were calculated from the sections of tiles that were not scratched. This experiment is being repeated during the summer/autumn (January to May 2013) when the weather is likely to be less extreme. However, the data were not available for this thesis, and rely on the earlier, compromised experiment.

Total biomass of algae did not differ among treatments or sites within treatment (Table 3.5). In terms of species richness, PERMANOVA showed significant differences among sites within treatment, but not among treatments (Table 3.5). However, algal composition was close to being significantly different among treatments ($P = 0.066$) and significantly different among sites (Table 3.6). This was highlighted by the overlap of samples from caged, uncaged and controls in the nMDS plot (Fig. 3.8A), but a general separation of samples from sites 1 and 3 (Fig. 3.8B).

Based on the Spearman rank correlations, *Laurencia* sp. *Hypnea* spp., *Hinksia* sp. and *Ceranium* sp. provided the highest correlations with the samples in the nMDS (Fig. 3.8 A-B). However, these species did not reflect any of the patterns across treatments or sites in that plot. Furthermore, the biomass of all three of these species did not differ significantly among treatments, and only *Hinksia* spp. differed among sites (Table 3.7). *Hinksia* sp. tended to have greater biomass at the inshore sites 3 and 4 (Fig. 3.9).

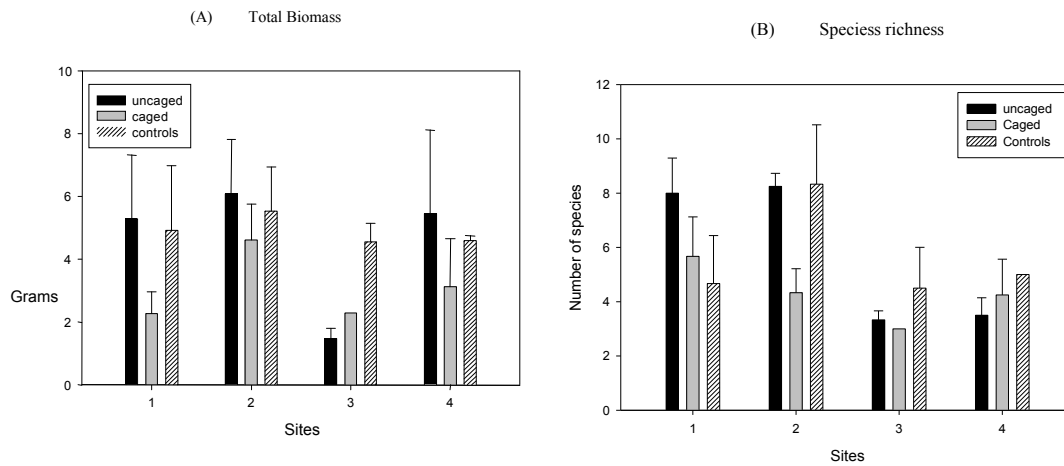
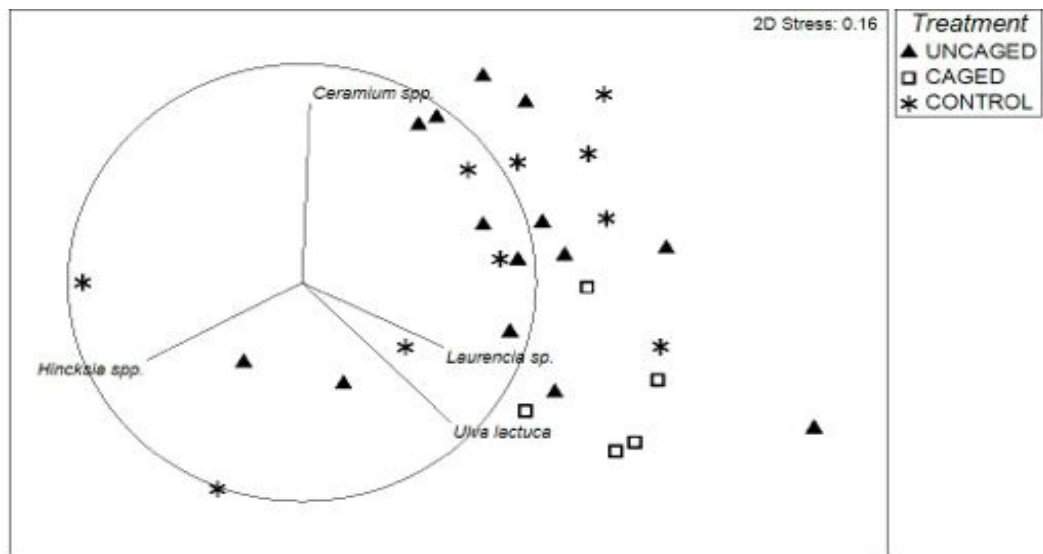


Fig. 3.7 Mean (+SE) total biomass of algae (A) and species richness (B) on recruiting algae on tiles within caged, uncaged and controls at four sites in Marmion Lagoon, examining the effect of *Parma mccullochi* feeding activity on recruiting algae. Error bars to one SE.

Table 3.5 Results of nested PERMANOVA testing the effect of *Parma mccullochi* feeding activity on recruiting algae. Nested design with Sites (Random factor, 4 levels) nested in Treatments (Fixed factor, 3 levels). Species richness data were square root transformed, and biomass data were Log transformed.

		Total Biomass			Species richness		
	<i>DF</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>
Treatments	2	388.22	1.0259	0.39	118	0.48853	0.6242
Sites (Treat)	9	387.02	1.2803	0.2837	256.03	2.2628	0.0476
Residual	24	302.29			113.15		

A



B

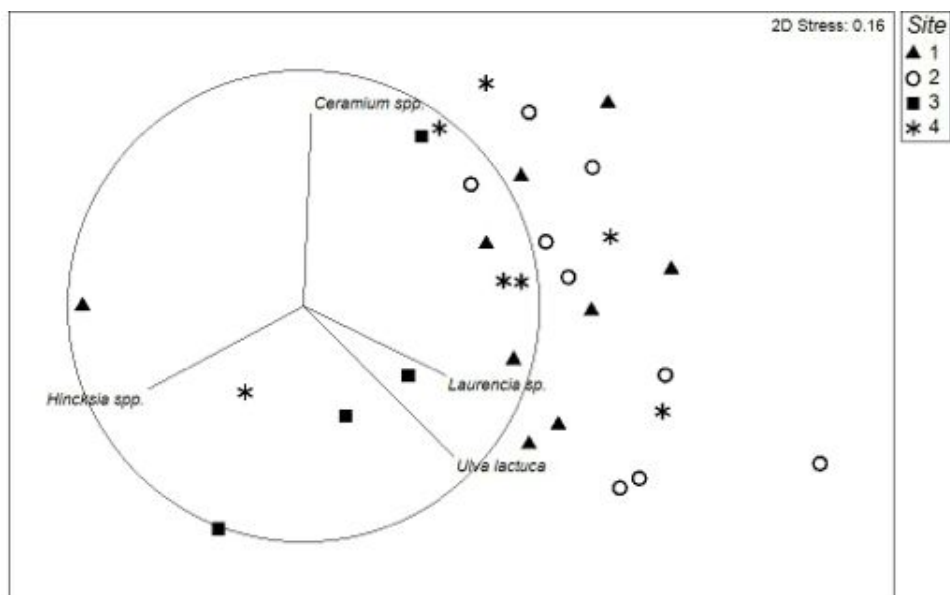


Fig. 3.8 nMDS plots based on a Bray-Curtis similarity matrix representing the species composition of algal recruits on PVC tiles, highlighting the differences among treatments (A) and sites (B). Vectors represent the species characterizing the algal composition (Spearman correlation > 0.6). Data were square root transformed.

Table 3.6 Results of nested PERMANOVA testing the differences in the composition of recruiting algae on tiles among treatments (caged, uncaged and controls) and sites. Nested design with sites (Random factor, 4 levels) nested in treatments (Fixed factor, 3 levels).

	<i>DF</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>
Treatments	2	4671.6	1.6627	0.0664
Sites (Treat)	8	2996.5	1.7643	0.0025
Residual	18	1698.4		

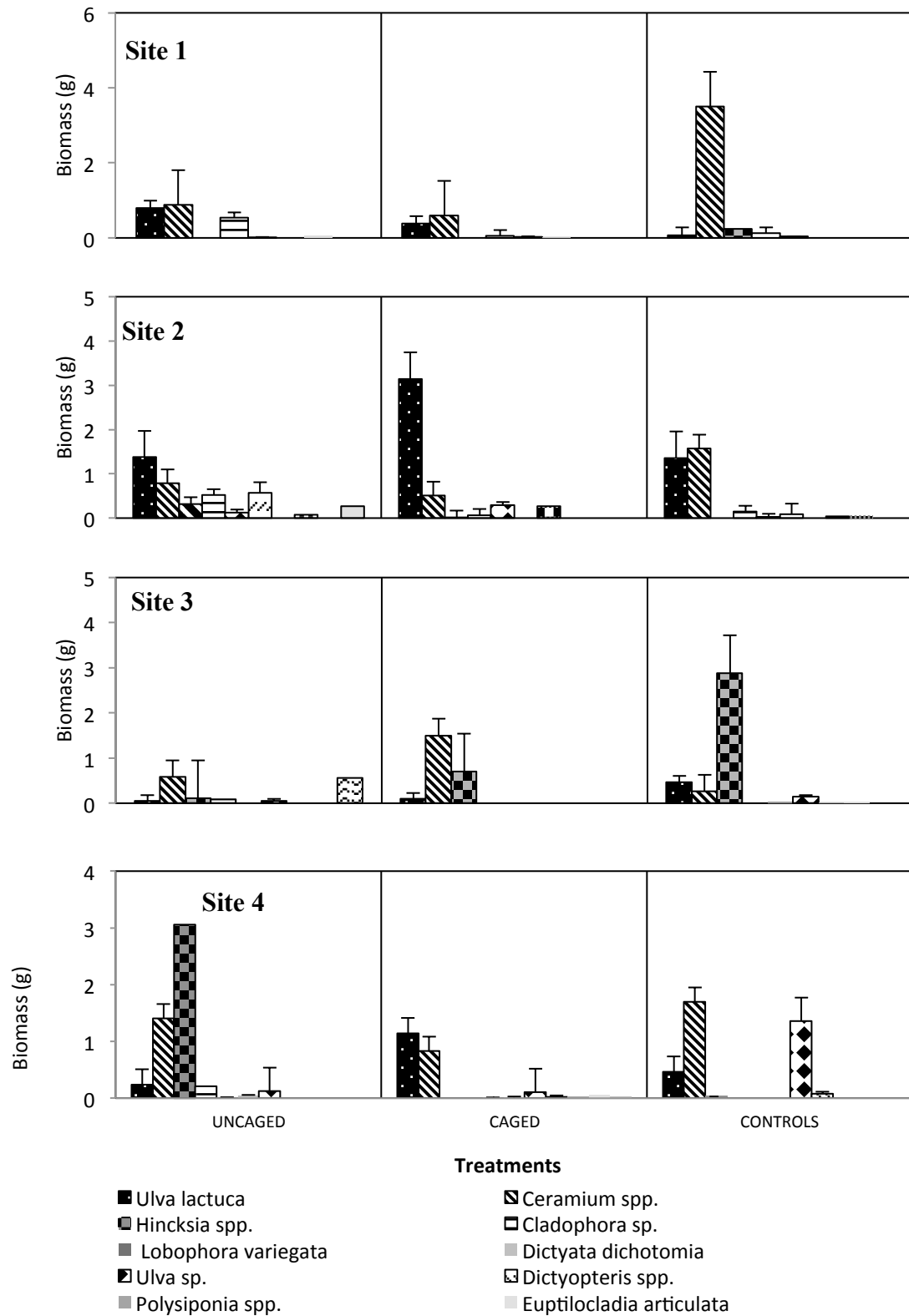


Fig 3.9 Mean biomass (g) of the different algae species found on the PVC tiles in treatments (caged, uncaged and controls) deployed inside *Parma mccullochi* territories at four different sites on the reef for a period of 6 months. Error bars to one SE.

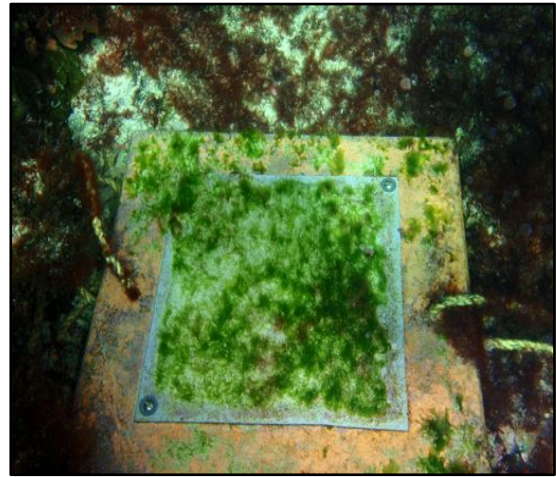
Table 3.7 Results of nested PERMANOVA testing the differences in the biomass of the three characteristic species of algal recruits (*Ulva lactuca*, *Ceramium* spp. and *Hinksia* spp.) among sites (Fixed factor, 4 levels) nested in treatments (Fixed factor, 3 levels).

		<i>Ulva lactuca</i>			<i>Ceramium</i> spp.			<i>Hinksia</i> spp.		
	<i>DF</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>	<i>MS</i>	<i>Pseudo- F</i>	<i>p</i>
Treatments	2	5.765	9.42	0.9165	0.45134	1.6303	0.2432	0.82771	0.89526	0.409
Sites (Treat)	9	0.6173	1.4064	0.2215	0.27542	0.84954	0.5813	0.94096	2.479	0.0338
Residual	26	0.43893			0.3242			0.37957		

A



B



C

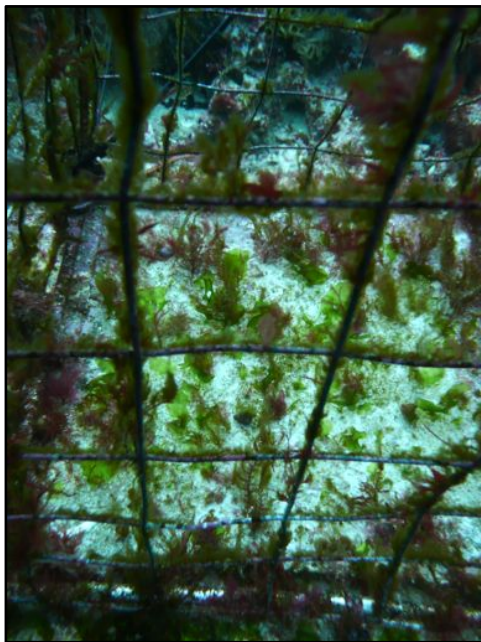


Fig. 3.10 Visual differences in representative replicates for the treatments of the algal recruitment experiment two months after deployment: differences in the algal recruits can be noticed between uncaged (B), controls (A) and caged (C) PVC tiles.

Chapter 4

Discussion

4.1 Diet of *Parma mccullochi*

This study provides one of the few accounts of the diets of Pomacentridae in the temperate environment. *Parma mccullochi* in the temperate reefs of Western Australia is predominantly an herbivore, with its diet mostly comprising red foliose and filamentous algae such as *Hypnea* spp., *Ceramium* sp. and *Brongniatrella* sp. This was similar to the diets of the few species of Pomacentridae whose diets have been examined in temperate reefs (Jones and Norman 1986; Buckle and Booth 2009). For example, the diet of *Parma victoriae* was mostly composed of the red algae *Champia* spp., *Hypnea* sp., *Rhodoglossum* sp., and *Dictyomenia* sp. (Jones and Norman 1986), and *Parma microlepis* and *P. unifasciata* also fed on red foliose algae (Buckle and Booth 2009). Animal material was also found in the diet of temperate Pomacentridae, especially in the juveniles (Buckle and Booth 2009). For example, Buckle and Booth (2009) showed that the diets of adult *P. microlepis* comprised 67% algal material and 33% of animal material. In contrast, only a minimum percentage of animal material was found in the stomachs of *P. mccullochi*, probably ingested by mistake while feeding on algae. This was similar to *P. unifasciata* in temperate eastern Australia, which ingested 95% plant material (Buckle and Booth 2009). Thus, *P. mccullochi* appears to be essentially a strict herbivore in temperate reefs of Western Australia, and therefore one of the few herbivorous fish species in temperate environments, where only 3% of fish species are considered to be herbivorous (Tolentino-Pablico et al. 2008). In comparison, other temperate herbivorous fish families such as Blennidae and Kyphosidae feed selectively on filamentous and fleshy turf algae (Tolentino-Pablico et al. 2008). For example, the diets of *Girella* spp. (Kyphosidae) and *Sarpa salpa* (Sparidae) have been shown to mostly comprise Chlorophyceae of the genera *Cladophora*, *Enteromorpha* and *Ulva*, while *Kyphosus* spp. (Kyphosidae) consumed Phaeophyceae in the genera *Sargassum* and *Dictyota* (Tolentino-Pablico et al. 2008). However, *Sarpa salpa* in the Mediterranean Sea feeds mainly on the seagrass *Posidonia oceanica* (Prado et al. 2010). Labridae such as *Odax acroptilus* (MacArthur and Hyndes 2007) and Monacanthidae (Wressnig and Booth 2007; Wressnig and Booth 2008) also play an important role in the removal of seagrass and associated epiphytic algae in temperate seagrass systems,

but less is known about their role in temperate reefs. Moreover, the diet of *P. mccullochi* is also different from herbivorous invertebrates, such as sea urchins, which feed mostly on laminarian algae such as kelp (Foster and Schiel 2010).

Like *Parma mccullochi* in temperate Western Australia, foliose red algae such as *Hypnea* are the most dominant genus in the diet of many species of tropical Pomacentridae (Ceccarelli 2007). However, their diet can vary between different species (Letourneur et al. 1997; Ceccarelli 2007; Castellanos-Galindo and Giraldo 2008; Frederich et al. 2008). For example, Ceccarelli (2007) showed that different species of tropical Pomacentridae in the same fish community ranged from being herbivores to detritivores and omnivores. Many tropical Pomacentridae also ingest large quantities of invertebrates (Letourneur et al. 1997). For example, animal material such as amphipods and copepods make up a significant contribution to the diet of *Stegastes nigricans* in Reunion island (Letourneur et al. 1997) and *Abudefduf concolor* in the western coast of Colombia (Castellanos-Galindo and Giraldo 2008), and few species of *Pomacentrus* (Ceccarelli 2007).

No significant ontogenetic differences were found in the diet of *Parma mccullochi*. This is in contrast with other tropical and temperate Pomacentridae (Letourneur et al. 1997; Castellanos-Galindo and Giraldo 2008; Buckle and Booth 2009). For example, the proportion of algae in the diet of *P. microlepis* and *P. unifasciata* was positively related to the body size (Buckle and Booth 2009). In tropical Pomacentridae, the amount of animal material ingested was significantly higher in the juveniles compared to adults of *Stegastes nigricans* (Letourneur et al. 1997). Head shape and mouth morphology are two key factors influencing the feeding behaviour and diet of Pomacentridae (Frederich et al. 2008; Aguilar-Medrano et al. 2011). Furthermore, species can display an ontogenetic increase in the length of digestive tract as they display an ontogenetic shift in their diet to macroalgae (Buckle and Booth 2009). Thus, the mouth morphology and relative gut length of juvenile and adult *P. mccullochi* may be similar and might help juveniles ingest and digest red foliose and filamentous algae. Collection of such morphometrical data would be required to test this hypothesis, but no studies have been done on this topic for *P. mccullochi* yet. Juvenile herbivorous fishes ingest more detritus and animal material, such as small invertebrates, than algae to satisfy their energy and nitrogen demands (Choat 1991) and overcome the difficulty in digesting this material

(Horn 1989). In contrast, animal material was not present in the stomachs of juvenile *P. mccullochi*. This study provides the first evidence of temperate Pomacentridae species being herbivorous as both juveniles and adults. It is possible that this reflects sufficient food availability due to the high abundance of food present in the territories. In addition, it is possible that both juvenile and adult *P. mccullochi* have endogenous enzymes that help them digest rhodophytes. This occurs in other herbivorous species, such as *Kyphosus sydneyanus*, which rely on endogenous enzymes for the digestion of chlorophytes and rhodophytes for their energy (Moran and Clements 2002). However, no studies have shown these enzymatic activities in *P. mccullochi*.

Temporal differences were found in the diet of *Parma mccullochi*; they still consumed red foliose and filamentous algae, but the species ingested differed slightly between April and August. Temporal differences in their diet may suggest a shift in availability of different foliose and filamentous species in the territories during the year. However, seasonal differences in algal composition were found to be small in Marmion Lagoon (Wernberg et al. 2003), where this study was carried out. Similar patterns in temporal dietary shifts were found in tropical territorial Pomacentridae (Letourneur et al. 1997). However, Castellanos (2008) showed that there were no temporal differences in the diet of *Abudefduf concolor*, suggesting that different species exhibit different feeding behaviour. Indeed, as stated earlier, tropical Pomacentridae display highly diverse diets and algal compositions within territories (Ceccarelli 2007).

4.2 Impact of *Parma mccullochi* on temperate reefs

In this study, *Parma mccullochi* had a significant impact on the algal community of temperate reefs, by influencing the algal assemblages in their territories and algal recruitment (even if it was only close to being significant). *P. mccullochi* maintained a higher species richness and a different algal species composition inside compared to outside territories, which is similar to tropical Pomacentridae. For example, tropical territorial damselfish *Eupomacentrus planifrons* have a direct impact on the algal composition of the reef by excluding other herbivorous fish from their territories, where they maintain a higher algal biomass and biodiversity, while the algae on flat reef outside the territories are heavily grazed by the other herbivorous species (Brawley and Adey 1977). In contrast, the biomass of algae inside *P. mccullochi* territories was lower

compared to outside the territories, which is dominated by the kelp *Ecklonia radiata*. This suggests that *P. mccullochi* has an impact on the algal community of the reef by maintaining patches with high algal diversity within the canopy of the kelp. These open-gap patches within kelp canopies are usually created by natural events such as storms (Kennelly 1987), and previous studies have shown that the abundance of territorial Pomacentridae increases within these open-patches, where they establish new territories on cleared patches (Jones 1992; Thomson et al. 2012). In contrast, Saunders (2011) showed that the exclusion of *P. mccullochi* from their algal feeding area did not have any significant effect on the algae. However, this exclusion experiment was run for only 6 weeks, which is likely to be too short to see an effect on algal composition.

Feeding activity of *Parma mccullochi* was shown to have a moderate effect on recruitment of algae, with the effect close to being significant ($P = 0.06$) in the caging experiment. The loss of cages and tiles during a winter storm reduced the number of replicates (48 to 34), and therefore, reduced the power of the test to detect a significant effect at $P < 0.05$. Thus, it is highly likely that the experiment would have produced a significant effect at this level if all replicates were retained. No studies have been done on the impact of temperate Pomacentridae on algal recruitment. However, tropical Pomacentridae have a large impact on recruiting algae, significantly affecting the algal composition on recruitment tiles (Doropoulos et al. 2011). We suggest that *P. mccullochi* could have the same role in the temperate environment. This could have a significant impact on temperate algal dominated reefs, especially when *P. mccullochi* establishes new territories on cleared patches. As the results on the impacts of feeding activity on algal recruitment were only close to being statistically significant in this study, further investigation should be done to test this hypothesis.

Based on electivity indices, *Parma mccullochi* could show a positive selection for specific algal taxa such as *Brongniartella* sp., *Dasyclonium* sp., *Hypnea* spp. and *Dictyopteris* spp., and this is one of the mechanisms considered to promote the growth of the preferred algae inside territories (Klumpp et al. 1987; Jones 1992). The abundance of prominent species such as the kelp *Ecklonia radiata* inside the territories was very low, and no kelp was found in the diet of *P. mccullochi*. Therefore, this could be a strong indication that gardening is taking place. In support, Saunders (2011) showed that *P. mccullochi* exercised farming activities such as scraping the reef, tidying, and weeding unwanted algae from their territories. This study supports the role

of *P. mccullochi* as a landscaper/engineer of temperate reefs, and I suggest that *P. mccullochi*, with their feeding and farming activities, maintain distinct algal communities inside the territories. In support, other temperate territorial Pomacentridae have a highly selective diet and showed similar farming behaviours (Montgomery 1980; Jones et al. 2006; Ceccarelli 2007). In fact, Jones and Norman (1986) showed that *Parma victorae* fed mostly on a few preferred red algae species and this selectivity increased with the territory size. In addition, the tropical Pomacentridae *Stegastes nigricans* maintains a monoculture of *Polysiphonia* sp. inside the territories, which is also the most abundant food item in the diet (Hata and Kato 2004).

This study provides the evidence to refute the theory that pomacentrid fishes have a low impact on temperate reefs (Jones 1992). Indeed, feeding and farming activities of territorial *Parma maccolluchi* have an impact on reefs that is similar to territorial species of Pomacentridae in tropical reefs, where they have been shown to be an important factor in shaping benthic communities (Barneche et al. 2009). *P. mccullochi* can be compared to an engineer/landscaper of temperate algal dominated reefs, showing the capacity to structure the benthic composition of the reef and maintaining these high biodiversity patches within the kelp canopy. In addition, its effect on the reef is amplified and highly noticeable due to their large abundance, especially in Perth metropolitan waters, where they reach a mean abundance of 53.6 fish/1000 m² (Saunders 2011; Turco, not published). Considering that each *P. mccullochi* feeds in an area of 9 m² (Saunders 2011), they impact approximately half of the reef's substrata (482 of 1000 m²). As a consequence, the structure, morphology and, overall biodiversity of temperate algal dominated reefs of Western Australia are most likely strongly influenced by *P. mccullochi*. The term "Engineer of the reef" can suit other herbivorous animals such as sea urchins, which can also have the capacity of modelling the algal structure of the reef (Ling et al. 2010). However, the impact of sea urchins has been shown to be minimal in temperate reefs of Western Australia, as they consume mainly detached kelp (*Ecklonia radiata*) (Vanderklift and Wernberg 2008). In addition, Vanderklift et al. (2009) showed that their abundance and intensity of herbivory was very low, especially within offshore reefs (Vanderklift et al. 2009). In contrast, the abundance of *P. mccullochi* is high in both inshore and offshore reefs (Turco, unpublished data) and the current study has shown a similar impact on algal composition in both inshore and offshore reefs. In conclusion, like tropical

Pomacentridae, *P. mccullochi* has an impact on the benthic community of the temperate reefs, and this impact could be via three different ways that are not mutually exclusive: (1) directly feeding on algae; (2) weeding and farming activities; and/or (3) excluding other competitive herbivorous fishes (Brawley and Adey 1977; Hata and Kato 2004; Hoey and Bellwood 2010; Saunders 2011).

Implications and future research

In summary, this study showed that *Parma mccullochi* is essentially a strict herbivore, feeding mainly on red foliose and filamentous algae. These forms of algae also contribute to the diets of other temperate Pomacentridae, but in contrast to those species, *P. mccullochi* did not show any ontogenetic differences in the diet. Moreover, this species had a local impact on the algal composition, and a likely impact on algal recruitment, on temperate reefs. The species maintains patches with high species richness of algae within kelp canopies, and therefore plays an important role as an ecosystem engineer or landscaper of reefs by maintaining a high biodiversity and lower biomass of macroalgae in its territories on temperate algal dominated reefs through their feeding and territorial behaviour.

This study provides a better understanding of the ecological importance of the abundant *Parma mccullochi* in the temperate reefs of Western Australia. These results will allow management authorities, such as Department of Environment and Conservation (DEC) to include this new knowledge of *P. mccullochi* and its associated ecological processes in the management of marine parks of temperate Western Australia. In fact, one of the most important strategic objectives of conservation for DEC in marine parks is ‘maintaining marine biodiversity and ecological integrity’ (Kendrick et al. 2010). Moreover, DEC’s research priorities in relation to enhancing knowledge of marine biodiversity for conservation are:

- Describing WA’s marine biodiversity;
- Understanding the patterns of WA’s biodiversity, both spatially and temporally, and what is causing these patterns;
- Understanding the key ecological processes that sustain WA’s marine biodiversity; and
- Understanding human use (including climate change impacts) on and benefits of WA’s marine biodiversity (Kendrick et al. 2010).

Given the potentially broad impact of *Parma mccullochi* herbivory on algal communities at a landscape scale, this species is likely to provide a key ecological process that influences temperate algal-dominated reefs of WA, in particular by sustaining marine biodiversity. Therefore, this species should be considered an important component of the ecosystem, and needs to be considered in the planning and management of temperate marine reserves where these fishes and algal communities are prominent. In addition, given the high abundance of *P. mccullochi* on temperate reefs of WA, and their role in sustaining biodiversity of the reef, this study could give a positive input to DEC to expand the size of existing sanctuary zones or creating new zones. It is vital that future DEC management plans for marine reserves aim to provide management zoning that ensures protection of adequate algal-dominated temperate reefs and their associated flora and fauna to ensure the conservation of this key ecological process. However, additional information on the likely direct and indirect human impacts to this herbivory process would be required, in to ensure the most appropriate type of zoning be implemented to best protect this process.

Future studies should be undertaken to better understand the ecology of *Parma mccullochi* on a larger temporal scale, to understand whether or not its impact on the reef is significant throughout the whole year, and if there are any significant seasonal differences in the diet of this species. In fact, the impact study was carried out only in one time of the year, but the diet showed temporal differences. Moreover, since this study only analysed the diet during two times during the year (April-August), a broader temporal analysis of the diet throughout the whole year would be useful to gain a more comprehensive understanding of its diets. Another point which future studies should focus on is to understand why there are no ontogenetic differences in the diet of *P. mccullochi*. A study of the head and mouth morphology, gut length and digestive processes, which typically shift with size of herbivores (Frederich et al. 2008), could provide an understanding of the reasons for a lack of ontogenetic differences in the diets of the species. In addition, a comprehensive study on the abundance of temperate Pomacentridae across a broad spatial and temporal scale would be extremely helpful to determine the actual extent of their impact on temperate reef of Western Australia. Due to the importance of *P. mccullochi* in maintaining biodiversity in temperate algal dominated reefs, and to their high abundance, it is critical to determine the interactions of this species with other key species occupying reefs in the region, particularly those

species that predate on *P. mcccullochi*. Shifts in predator abundance have been shown to have top-down impacts on the lower-order consumers and ecosystem processes (Foster and Schiel 2010). Thus, any top-down effect could have an impact on the ecological processes by which *P. mcccullochi* influences WA's marine biodiversity.

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