The Functional Importance of Herbivores

Tying the knot between fish biomass, parrotfish feeding and benthic structure on Kenyan coral reefs

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Abstract

Herbivory is considered a key ecosystem process on coral reefs as it enhances reefs resilience by preventing shifts to macroalgal states. In trying to understand mechanisms and consequences of such shifts, research have taken on a variety of approaches, from the effect of declining habitat condition on (herbivorous) fish communities to the roles of specific herbivore functional groups and size classes therein. This study aimed to incorporate these different foci by investigating the interplay between roving herbivore biomass (surgeonfish and parrotfish), parrotfish functional impact and a coral-macroalgal gradient, represented by four Kenyan reefs. The feeding function (here, the amount and type of algae removed) was measured at the parrotfish community level and an in-depth assessment was made of two target species (*Chlorurus sordidus* and *Scarus psittacus*) to determine the effect of benthic condition and fish size. Both herbivore biomass and the parrotfish community functional impact declined over the coral-macroalgal gradient, and the transition was found at herbivore biomass of ~300 kg ha\(^{-1}\). Interestingly, benthos appeared to only have limited effect on the function of individual parrotfish, whereas size was highly important as large fish were found to be functionally superior. It was the discussed how herbivore biomass and level of herbivory can be both cause and consequence of benthic community structure, and whether biomass can serve as a measure of function. Lastly, the question is raised on how to balance the trade-off between fish for food or fish for function, discussing management implications that can allow for fishing without undermining function provided.
Acknowledgements

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1. INTRODUCTION

It is broadly accepted in experimental and theoretical work that high species diversity provides resilience (Chapin et al. 2000, Loreau et al. 2001 Science). Resilience here is the ability of an ecosystem to absorb natural and/or human-induced shocks, reorganise and regenerate so as to maintain the same function and identity (Holling 1973, Gunderson 2000, Walker and Salt 2006). Coral reefs provide a paradox in this context; they are extremely diverse, yet they are crumbling under human impacts (Nyström et al. 2000, Hughes et al. 2003, Nyström 2006). In many areas coral reefs have switched to new alternative states dominated by macroalgae or other benthic organisms (Norström et al. 2009), so called regime or phase shifts. These new degraded states seem quite persistent (Mumby and Steneck 2008, Nyström et al. 2012) and can result in discontinued delivery of important ecosystem services (Moberg and Folke 1999).

Understanding the dynamics and mechanisms behind these shifts provides an important challenge for research, as coral-dominated reefs provide livelihood and are a source of food for many coastal populations around the world (Graham et al. 2013). It has been demonstrated that as habitat quality declines (i.e. to high macroalgal cover) so do both species richness and diversity of fish functional groups, resulting in a depauperate fish assemblage (Chong-Seng et al. 2012). Therefore, it is of critical importance to further our understanding of the type of ecosystem processes that underpin resilience and how they can be maintained.

Experimental (e.g. Hughes et al. 2007) and theoretical (Mumby et al. 2007) work clearly suggests that herbivory is a key process on coral reefs (Bellwood et al. 2004) by maintaining the balance between corals and algae (i.e. controlling recruitment and growth of macroalgae), and thereby preventing shifts to alternative states (Nyström et al. 2012). As shown by parameterized models of Caribbean reefs, 42% percent of the reef needs to be in a permanently grazed state to maintain coral dominion (Mumby et al, 2007). On the Great Barrier Reef areas of high macroalgal cover have been associated with low herbivore biomass (Wismer et al. 2009), indicating that a reduction in biomass means reduced grazing. The focus on biomass has been highlighted by work from the Western Indian Ocean, demonstrating specific thresholds of fish biomass under which ecosystem changes occur, such as increases in macroalgal cover (McClanahan et al. 2011). The authors broadly relates fish biomass to level of herbivory (McClanahan et al. 2011), however, determining specific levels of herbivore biomass may provide a better insight into the amount of grazing required to maintain healthy reefs.
Over the last decade, focus has turned to understanding the roles of specific species and functional groups within the herbivore guild. Despite its limitations functional groups have been put forward as a way to link the identity and diversity of species to ecosystem processes that underpin resilience (Bellwood et al. 2004, Nyström et al. 2008). Of herbivorous fish, parrotfish are regarded as one of the most important herbivore groups in preventing shifts to macroalgal dominion (Hoey and Bellwood 2007, Hughes et al. 2007) as their functional roles include both removal of algae and provision of clean substrata for coral recruitment (Bellwood et al. 2004, Mumby 2006). Their functional impact has been shown to increase with size (Bonaldo and Bellwood 2008, Lokrantz et al. 2008) and vary across shelves (Fox and Bellwood 2007), but few empirical comparisons have been made on the impact of different species. Studies have also focused on how phase shifts may influence fish behaviour and its feedbacks on the new ecosystem state (Bellwood et al. 2006, Hoey and Bellwood 2011), but little is known about how changing benthic condition may influence the functional impact of parrotfish or their dietary choices. A better understanding of such effects, as well as of species-specific functional traits, would help shed light on their relative abilities to act as preventers or reversers of shifts to macroalgal dominance.
1.2 Aim of the study

This study aims to link previous research on the relationship between fish and benthic structure and parrotfish function by examining the importance of roving herbivores (acanthurids and scarids) and the functional role of parrotfish across a variety of Kenyan coral reefs. The overall aim is to assess whether relationships exist between the benthic composition with a focus on coral and macroalgae, herbivore biomass and the feeding function provided by parrotfish. The following research questions will be answered:

1) On a gradient from coral to macroalgal dominance does a) herbivore biomass and b) parrotfish feeding function change?

2) Is there a relationship between the feeding function provided by parrotfish and the benthic community structure? Is the feeding function in turn affected by the benthos observed?

3) Is there a difference in the amount of algae removed (i.e. feeding impact) by different parrotfish functional groups, i.e. are some groups functionally more important?

The last two question will be answered by looking closer at a) the role of parrotfish size and biomass, b) bite sizes and feeding rates, and c) food preferences. The study will be looking at the parrotfish assemblage as a whole and also compare a few target species for more in-depth assessment of the feeding function so as to evaluate whether species specific traits exist.
2. THEORETICAL BACKGROUND

2.1 Resilience of coral reefs

Resilience has gained attention in recent years as a way to address global environmental degradation (Hughes et al. 2005, Folke 2006). Particularly, it has gained importance as a new approach to management of systems in which humans and nature are linked – coupled social-ecological systems – such as coral reefs (Cinner 2011).

Resilience is used within a variety of disciplines. It was originated within ecological sciences, by work of Holling (1973), but the meaning of the concept differs both between and within disciplines (Brand and Jax 2007) and ranges in degree of precision/vagueness (Strunz 2012). In coral reef research resilience has traditionally been measured as the time of recovery after disturbance, following Pimm (1984). This definition has been coined *engineering resilience* and assumes stable systems with one equilibrium state (Holling 1996). Thus, a resilient coral reef would have a swift recovery following a disturbance event, such as a hurricane (Nyström et al. 2008).

Holling (1996) provided a more comprehensive definition of resilience, namely *ecological resilience*, which has been widely used within lake ecology but only recently emerged within coral reef research (Nyström et al. 2008). It is defined as the ability of an ecosystem to absorb natural and human induced shocks, reorganise and regenerate so as to maintain the same function and identity (Holling 1973, Gunderson 2000, Walker and Salt 2006), and will be the definition used for this study. The focus on reorganisation challenges the old view that ecosystems merely return to a previous equilibrium state after disturbance (Folke 2006). If resilience is lost the system can be pushed into a less desirable state in which the system no longer provides the same ecosystem services (Daily 1997, in Folke 2006), which are benefits that nature provide to society (MA 2005). Such shifts, known as phase- or regime shifts, are often caused by external perturbation but can be facilitated by slow erosion of ecosystem resilience due to human activities (Sheffer et al. 2001). Hurricanes and bleaching events are stochastic events that can cause regime shifts in coral reefs, but ultimate causes are often a loss of reef resilience from actions such as overfishing, nutrient loading and sediment run-off (Bellwood et al. 2004). Coral reefs are known to shift to a variety of different states (Norström et al. 2009), although, the most common and well-studied shift is that from coral to macroalgal dominance (Ledlie et al. 2007, Mumby and Steneck 2008) (Box 1). Such shifts are difficult to
reverse once manifested since the new state is governed by a new set of feedback loops that maintains the system in macroalgal dominance (Nyström et al. 2012).

**Box 1: Shifts from coral to macroalgal dominance**

Coral reefs as any natural systems are characterised by stabilising or destabilising ecological feedback mechanisms (Scheffer et al. 2001, Mumby and Steneck 2008). In a coral dominated state the system is characterised by feedbacks that perpetuates further coral dominion, such as ecological processes that control algal growth and enhance coral recruitment (Mumby and Steneck 2008). For example, grazing by herbivores reduces algal cover and opens up space for coral settlement (Nyström et al. 2012). Increased coral cover results in greater structural complexity, which in turn facilitates for fish recruitment (Öhman et al. 1998) and increased grazing intensity as algal resources become limited (Mumby 2006). Any weakening of these feedback mechanisms erodes resilience and can cause the system to flip to a macroalgae state following disturbance (Nyström et al. 2012). Climate change is considered the main global driver of system change on coral reefs, whereas the two main local drivers are overfishing and water quality (Graham et al. 2013). For example, a reduction in herbivores due to high fishing pressure will reduce the grazing intensity and allow algae to proliferate (Mumby and Steneck 2008). Poor water quality due to increased nutrients from e.g. coastal runoff can also promote algal growth, as well as smother coral (Graham et al. 2013). Once algae reach a certain canopy height they become unpalatable to most herbivores and are only consumed by a limited number of species (Hoey and Bellwood 2011). Furthermore, macroalgae can shade coral from light, and both physically and chemically inhibit settlement of new coral recruits (Diaz et al. 2010). This can result in coral mortality and a reduced structural complexity (Nyström et al. 2012), which has negative impact on fish assemblages (Chabanet et al. 1997) and further strengthens the macroalgal state.

2.2 A functional approach as means to understand resilience

A fundamental question is, what provides resilience to coral reefs? High biodiversity has been argued to provide insurance for ecosystem functioning (Chapin et al. 2000). More recently there has been an increased focus on the concept of functional groups as an important aspect of biodiversity, and their role in ensuring ecosystem resilience (Blondel 2003, Nyström 2006). Here, a functional group is defined as “a collection of species that perform a similar function, irrespective of their taxonomic affinities” (Bellwood et al. 2004). Species can be divided into functional groups according to what trophic guild they belong to (e.g. predators and herbivores) (Bellwood et al. 2004) or according to the ecosystem process they underpin (Naeem 1998), such as corals building reef structures and providing habitats for other marine organisms (Bellwood et al. 2004). Functional groups have been put forward as a way to link the identity
and diversity of species to ecosystem processes that underpin resilience (Bellwood et al. 2004, Nyström et al. 2008). Through the concepts of redundancy (Walker 1992) and response diversity (Elmqvist et al. 2003) a functional approach is able to quantify the value of species diversity (Nyström et al. 2008). However, functional groups are subjective, as there is no universal method of how to assign species to different groups. Therefore, it is up to the investigator to carefully define and decide what constitutes a specific functional group depending on which ecosystem process is under focus (Nyström et al. 2008).

It is imperative to maintain key functional groups in order to sustain coral reef resilience (Nyström 2006). Loss of such a group can be detrimental to ecosystem functioning (Naeem 1998), which eventually can result in a shift to alternate states. For example, removal of predators has shown to lead to disruption of whole food chains in a variety of ecosystems, including coral reefs (e.g. Nyström et al. 2012). Functional redundancy and response diversity are two aspects that can enhance ecosystem resilience by preventing loss of whole functional groups (Nyström 2006). Redundancy is when several species perform the same function and have the capacity to functionally replace each other should one species become locally extinct (Naeem 1998). Response diversity describes the variety of ways species within a functional group respond to disturbance (Elmqvist et al. 2003, Nyström 2006). Both are needed to bolster resilience; for example, high redundancy will be meaningless if all species respond to disturbance in a similar fashion.

2.3 Relationship between herbivore functional roles and reef structure

Herbivory is a key process on coral reefs as it controls succession of algae by removing algal cover, provide substratum for coral larval recruitment and hence prevents phase shifts (Bellwood et al. 2004). High grazing pressure yields a ‘mowed lawn’ of highly productive turf algae at low biomass. However, reefs with reduced herbivore density, from e.g. fishing, can shift to alternate states dominated by less productive and less palatable macroalgae (Hoey and Bellwood 2009). Recent studies have pointed towards the existence of a thresholds of fish biomass, under which reefs tend to move towards degradation (McClanahan et al. 2011, Norström et al. unpublished). Based on large empirical data sets from the Western Indian Ocean, McClanahan et al. (2011) fitted models on a range of reef parameters over a gradient of fishable biomass, to determine if the latter could provide reference points of where ecosystem changes occur. The earliest warning sign of change towards degradation occurred at fish
biomass at ~850 kg ha\(^{-1}\), whereby macroalgae tend to dominate coral cover. The most critical point, at fish biomass under 300 kg ha\(^{-1}\), a sequence of changes occurred, including a rapid decline in species richness (McClanahan et al. 2011). Degraded reefs are undesirable, as they are associated with depauperate fish assemblages and reduced functional diversity (Chong-Seng et al. 2012). Due to the diversity within and between coral reef systems it is of great importance to develop reef specific indicators, in order to help management prevent degradation (McClanahan et al. 2011). Determining such thresholds specific to herbivore biomass could help provide a direct insight into critical levels of grazing required to maintain reef healthy.

The herbivore functional group is commonly divided into browsers, grazers, scrapers, and bioeroders. The division depends on food preferences, morphological traits such as jaw structure (Bellwood and Choat 1990) and the action by which the algae is removed from the substratum, which underpin different ecosystem processes (Nyström 2006). Based on these criteria, this study defines 1) browsers as fish that primarily feed on macroalgae (Hoey and Bellwood 2009); 2) grazers prevent algal overgrowth whilst feeding on turf algae (Nyström 2006), but leave basal portions intact (Choat et al. 2002); 3) scrapers closely crop turf algae and remove sediments, thus facilitates for coral recruitment, and; 4) bioeroders remove a substantial part of the underlying substratum when feeding and therefore contribute to external erosion of dead coral cover (Hoey and Bellwood 2007) (Table 1). The latter two functional groups are primarily represented by parrotfishes, which indicate specific and important functional roles related to this family of herbivores. Planktivores are another group within the herbivore guild, but they differ markedly from the other groups as they feed on phytoplankton and thus, do not control benthic algae (Green and Bellwood 2009).

In this study herbivores will also be considered preventers or reversers with regards to the role they play in phase shifts to macroalgae dominance (Bellwood et al. 2006). Fishes that feed on turf algae are considered preventers, as they inhibit macroalgal propagules to become mature stands and promote coral recruitment (Mumby et al. 2007). Reversers are fishes that feed extensively on macroalgae, and in doing so, also have the ability to uproot large stands as this opens up space for coral recolonisation (Bellwood et al. 2006, Hoey and Bellwood 2011).
Table 1. A description of the functional groups used in the study.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Description</th>
<th>Genera and species in the study</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bioeroders</td>
<td>Bite into the substratum whilst feeding on benthic algae. Rework sediments and open up space for coral recruitment.</td>
<td>Parrotfishes within the <em>Chlorurus</em> genus. However, it is debated whether small individuals (&lt;35cm) act as scrapers instead.</td>
<td>Green and Bellwood (2009) Bellwood et al. (2012) Nyström (2006)</td>
</tr>
<tr>
<td>Browsers</td>
<td>Feed on and controls macroalgae growth.</td>
<td>Acanthuridae of the genus <em>Naso</em> (unicornfish). For <em>N. annulatus</em> and <em>N. brevirostris</em> only juveniles (&lt;20cm) act as browsers. Parrotfish species <em>Calotomus carolinus</em> and <em>Leptoscarus vaigiensis</em></td>
<td>Green and Bellwood (2009) Hoey and Bellwood (2009)</td>
</tr>
<tr>
<td>Grazers/detritivores</td>
<td>Feed on benthic algae such as turf but keep basal portions intact. Prevents algal overgrowth. Detritivores are included in this group since they often form schools that collectively can remove large amounts of algae despite their diet mainly consisting of non-algal detritus.</td>
<td>All species within the family Acanthuridae except for unicornfish (<em>Naso</em>).</td>
<td>Green and Bellwood (2009) Nyström (2006) Choat et al. (2002)</td>
</tr>
<tr>
<td>Planktivores</td>
<td>Feed on planktonic algae.</td>
<td>Large <em>N. annulatus</em> and <em>N. brevirostris</em> (&gt;20cm)</td>
<td>Green and Bellwood (2009)</td>
</tr>
</tbody>
</table>

2.4 Parrotfishes and their functional roles

Parrotfishes (family *Labridae*, previously *Scaridae*) are roving, or foraging as opposed to territorial, herbivores that have been identified as a key functional group in controlling algal growth and preventing phase shifts on coral reefs (Hoey and Bellwood 2007, Hughes et al. 2007). They are different from other herbivorous species (e.g. surgeon- and rabbitfishes) by having large dental plates that allows for a more comprehensive removal of algae (Bellwood and Choat 1990). Research from the Caribbean have shown that an unexploited parrotfish community are among the most important reef herbivores (Bruggemann et al. 1994) and can alone maintain 40 percent of the reef in a permanently grazed state (Mumby et al. 2007). The functional attributes of parrotfish are often species specific (Bellwood and Choat 1990) and dependent on size (Bonaldo and Bellwood 2008, Lokrantz et al. 2008). Lokrantz et al. (2008)
argue that parrotfish only reaches functional maturity at a specific size interval and that large parrotfish have disproportionately larger grazing impact. Since large parrotfish are often prime targets for fishers due to their high market prize (Thyresson et al. 2011), overfishing can have disproportionately large impact on the grazing function (Hoey & Bellwood 2009).

Parrotfish functional role of removing algae is also dependent on their feeding preferences. Studies have shown that most species show strong preference for turf algae growing on dead hard coral surfaces and do not opt for macroalgae (Fox and Bellwood 2007, Lokrantz et al. 2008). However, Bruggemann et al. (1994) argue that certain species of macroalgae are targeted by parrotfish due to their high nutritional value. Furthermore, Mumby (2006) base his models of parrotfish grazing on a non-selective feeding strategy in terms of algae consumed. As such, there is a need for a better understanding of the parrotfish food preferences, as this can strongly determine their role in controlling algal growth.

2.5 Focus of this study

The aim of this study is to provide a link between studies on the relationship between benthic community structure, fish assemblages and herbivore biomass (McClanahan et al. 2011), on parrotfish functional role and the importance of size (e.g. Fox and Bellwood 2007, Bonaldo & Bellwood 2008, Lokrantz et al. 2008) and the link between food preferences and functional impact (Hoey and Bellwood 2009). It will also look deeper into potential differences between functional groups of parrotfish, using the detailed results on the feeding function by C. sordidus (bioeroders) and S. psittacus (scrapers). For the purpose of this thesis the feeding function incorporates both the amount and type of algae removed. However, it does not consider parrotfishes’ additional functional roles of bioerosion and sediment removal (Bellwood et al. 2011).
3. METHODS

3.1 Study sites

Four Kenyan reefs within government-managed fishing closures (Kisite, Mombasa 1 and 2, and Watamu) (Figure 1) were selected to represent a gradient of benthic community structures, spanning from high coral cover to high macroalgae cover (Table 2). The feeding function study required ample amount of parrotfish spanning from small to large individuals, and consequently no fished areas were chosen due to the low numbers of parrotfish at these sites and the weariness of the fish towards divers. The sites were located along approximately 250 km of the 500 km Kenyan coastline (Figure 1), in the lagoon or on the leeward side of the fringing reef and “are typical of Kenyan shallow coral reefs (<2,5m at low tide), dominated by live and dead hard coral, sand and seagrass” (McClanahan 2011). It should be noted that the two Mombasa sites are located within the same lagoon area, however, due to their contrasting benthic and fish communities they were treated as different study sites. The distance between sites is >500m whereby it can be assumed they represent different reef systems.

Table 2 Brief information on the study sites. Year of establishment, size of the MPA and benthic characteristics are given. The latter formed the basis for site selection. The area given in brackets represents the size of surrounding marine reserves, where fishing is allowed but within restrictions.

<table>
<thead>
<tr>
<th>Site</th>
<th>Established</th>
<th>MPA size</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kisite</td>
<td>1973</td>
<td>28 km²</td>
<td>High coral cover</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(11 km²)</td>
<td></td>
</tr>
<tr>
<td>Mombasa 1</td>
<td>1986</td>
<td>20 km² (&gt;200km²)</td>
<td>High macroalgae cover</td>
</tr>
<tr>
<td>Mombasa 2</td>
<td>1986</td>
<td>20 km² (&gt;200km²)</td>
<td>High turf cover</td>
</tr>
<tr>
<td>Watamu</td>
<td>1968</td>
<td>10 km² (213 km²)</td>
<td>High <em>Halimeda</em> cover</td>
</tr>
</tbody>
</table>

Figure 1 Map over the Kenyan coastline and the location of the study sites. The distances between the sites are >500m (Image source: Google Earth.)
3.2 Data collection

The study was conducted between November 2013 and January 2014. To evaluate the benthic composition four to five replicate 25m line-intercept transects were randomly placed at each site using a 50m measuring tape. The benthos intercepting the tape was measured to the nearest centimetre (McClanahan 1994) and placed into eight categories: hard coral, turf algae (fronds <1cm), macroalgae, *Halimeda* (green calcareous algae), crustose coralline algae (CCA), seagrass, sand and others (sponge, soft coral, anemones etc.). *Halimeda* is commonly grouped under the macroalgae complex (e.g. Mantyka and Bellwood 2007, Wismer et al. 2009, Adam et al. 2011) but since they represent different stages of the algae succession on Kenyan reefs, influenced by the type of herbivores present at the site (McClanahan et al. 1997), the decision was made to keep them separate. Urchins were counted in four circular 10m² quadrates, randomly placed within the area of each transect. Urchins were included in the study as they may explain distribution of algae (McClanahan et al. 1997).

The parrotfish (*Labridae*), surgeon- and unicornfish\(^1\) (*Acanthuridae*) families were chosen for the study since they represent more than 90 percent of the total roving herbivore community in Kenyan MPAs (McClanahan 2011). The community was sampled at each site, using 50mx5m (250m²) belt transects placed along the benthic transects of each site, in order to link the fish- and benthic communities (for details regarding the species sampled at each site see Appendix D). Fish greater than five cm were counted at species level and their size (total length, TL) was visually estimated to nearest centimetre as the transect tape was laid out. All censuses were conducted within two hours of high tide to minimize any tidal effects. All fish were thereafter divided into the functional groups browsers, scrapers, bioeroders, grazers (also including detritivores) and planktivores according to the algae they eat and the type of feeding mode they use (Table 1).

3.2.1 Parrotfish feeding function

Based on the fish census one to three of the most abundant scraping and bioeroding parrotfish species (Choat and Bellwood 1990) were chosen for assessing the feeding function at each site (Table 4). Feeding function here incorporates feeding impact (i.e. the amount of algae removed per unit time), feeding rate, bite size and food preferences. Browsing parrotfish (e.g. *Calotomus carolinus*) and all surgeonfish were not included since they do not leave a traceable scar on the

\(^1\)To note: henceforth, unicornfish are included when referring to surgeonfish unless specified.
grazed substrata. An initial pilot assessment of the parrotfish community (Källén, unpublished data) showed that *Chlorurus sordidus* and *Scarus psittacus* (Box 2) were commonly found across all reefs, and were thus chosen for the comparison of feeding function and food preferences at the individual level across sites.

To estimate the parrotfish feeding function, the feeding rate and bite sizes of individual fish were measured (Fox and Bellwood 2007; Bonaldo and Bellwood 2008; Lokrantz et al. 2008). The two assessments were done separately by one observer (J.K) using SCUBA. Each species was divided into three size classes (small, medium and large; Table 3) depending on intraspecific size ranges, and between 13-16 bites and feeding rates were sampled from each size class. To reduce the risk of subsampling, the fish chosen for observation was never of the same species and/or size class as the previous one. All fish observed were allowed a minimum of three minutes to get accustomed to the diver and if the fish showed any signs of stress (hiding or fleeing) the observation would be aborted (Lokrantz et al. 2008).

**Box 2. Introducing Scarus psittacus and Chlorurus sordidus**

*Scarus psittacus* and *Chlorurus sordidus*. The two focal species for the assessment of individual parrotfish feeding function, *Scarus psittacus* and *Chlorurus sordidus*. Both species belong to the Indo-Pacific region and inhabit reef flats, lagoons and drop-offs. *S. psittacus* (also known as Common parrotfish or Pale-nose parrotfish) is a scraper that reaches a total length of 30cm and primarily feeds on benthic algae. *C. sordidus* (Daisy parrotfish or Bullethead parrotfish) is larger, reaching 40cm total length (Froese and Pauly 2014), and belongs to the functional group bioeroders/excavators due to the ability of large individuals to bite into the substratum while feeding (Bellwood and Choat 1990). It is one of the most widespread parrotfishes in the region (Froese and Pauly 2014). Both species were among the most common parrotfishes on the Kenyan reefs surveyed. The pictures depict males, also called the terminal phase (Froese and Pauly 2014).
Parrotfish feeding rate and food preferences: All feeding rate data were collected between 10.00 and 15.00 to minimize the effect of time of day on feeding rates (Bonaldo and Bellwood 2008). The observer would swim along the reef until the first fish of a target species and size class was spotted whilst feeding. The TL of the fish was estimated and the number of bites taken were counted during a period of 2-3 minutes (Fox and Bellwood 2007), while recording the food chosen for each bite, with the categories of turf algae, macroalgae, Halimeda, live hard coral, CCA and others (e.g. seagrass, sand, sponge), to assess of food preference/selection.

Parrotfish bite size: The first feeding target individual spotted by the observer would be followed until the exact location of a bite could be seen. After, length and width of the bite scar was measured to the closest 0.1 mm using Vernier callipers and the bite size calculated (given as cm²) (Lokrantz et al. 2008). The percentage of bare substratum in the scar was visually estimated and multiplied with the bite size in order to get percentage algae removed. Henceforth, “bite size” will refer to the percentage algae removed.

Feeding impact of individual parrotfish: In order to compare the feeding impact, i.e. the amount of algal removed per unit time, of individual fish of C. sordidus and S. psittacus the average feeding rate was multiplied with the average area of algae removed (cm² min⁻¹) for each individual fish size at each site. Feeding impact was thereafter divided by the biomass of each individual fish to yield feeding impact per unit biomass (cm² min⁻¹ g⁻¹).

Table 3 The size classes and functional groups of each focal species. To note: S. falcipinnis was grouped into one size class due to relatively low abundance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Size class</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chlorurus sordidus</em></td>
<td>10-15cm</td>
<td>Medium</td>
</tr>
<tr>
<td><em>Scarus falcipinnis</em></td>
<td>N/A</td>
<td>13-20cm</td>
</tr>
<tr>
<td><em>Scarus frenatus</em></td>
<td>10-15cm</td>
<td>16-25cm</td>
</tr>
<tr>
<td><em>Scarus psittacus</em></td>
<td>10-14cm</td>
<td>15-20cm</td>
</tr>
</tbody>
</table>

Table 4 The species chosen at each site for assessment of the feeding function.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kisite</td>
<td><em>Chlorurus sordidus</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus frenatus</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus psittacus</em></td>
</tr>
<tr>
<td>Mombasa 1</td>
<td><em>Chlorurus sordidus</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus psittacus</em></td>
</tr>
<tr>
<td>Mombasa 2</td>
<td><em>Chlorurus sordidus</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus falcipinnis</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus psittacus</em></td>
</tr>
<tr>
<td>Watamu</td>
<td><em>Chlorurus sordidus</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus frenatus</em></td>
</tr>
<tr>
<td></td>
<td><em>Scarus psittacus</em></td>
</tr>
</tbody>
</table>
**Feeding impact of the parrotfish community:** To assess the feeding impact at community level, the average feeding rate was multiplied with the average algal removal of each size class of all focal species and multiplied with the number of individuals from the fish census. The feeding impact of each size class and species were summed to yield the total parrotfish feeding impact per site, given as the amount of algae removed per 250m². This was multiplied with the factor 60 to achieve hourly feeding impact and extrapolated to yield daily feeding impact assuming 12 hour of active feeding (Bellwood et al. 1995). Although this provides a crude estimate, it enables comparison to other studies using 12-hour estimates (e.g. Bonaldo and Bellwood 2008). It is also important to note that the community feeding impact is based on the feeding by 2-3 of the most common parrotfish species, which together comprise >60 percent of the biomass of all scrapers/bioeroders at each site. Thus, it is likely an underestimate as it does not give the total amount of feeding by parrotfishes at the sites.

### 3.3 Statistical analyses

A principal component analysis (PCA) was used to assess differences in benthic community structures across sites (Chong-Seng et al. 2012). The analysis was performed on percent cover at the transect level. The principal component axes representing the greatest variance in the data (PC1 and PC2) were extracted in order investigate relationships between the benthic gradient and herbivore biomass, and parrotfish community feeding impact and biomass of each functional group respectively, except for planktivores since they do not control benthic algae (Green and Bellwood 2009). For this, Spearman’s rank correlation was used as it allows for non-linear relationships and non-normal distributions (Townend 2002). To test if the community feeding impact differed between parrotfish functional groups (bioeroders and scrapers), a mixed effects model was fitted using lme function from the nlme package in R. Feeding impact was held as dependent variable and functional group as independent variable, with size as a covariate and site as random effect due to the nested design (i.e. it was assumed that data from within each site was similar than between sites) (Zuur et al. 2009).

In order to assess whether the feeding function differ between the sites and between different size of fish two-way ANOVAs were performed on the i) feeding rate, ii) bite size and iii) feeding impact using site and fish size class as independent variables of *C. sordidus* and *S.*
psittacus respectively. Type II sums of squares were used due to an unbalanced design and Tukey HSD post hoc test were performed in the case of significant results.

ANOVA could not be used to test the parrotfish food preferences. The assumption of independent observations is not met since the selection of one food type is likely dependent on the presence of others (Roa 1992). Thus, a combination of non-parametric Friedman’s test and Strauss’ Linear Selection Index was used (Mantyka and Bellwood 2007). The average bites taken on each food type for the two species combined was analysed using Friedman’s test, to assess if there are any general preferences for both species, followed by a Friedman post-hoc test to detect differences between the sites and species. This was complimented with Strauss’ Linear Selection Index, calculated from the average food selectivity per size class for each species and site respectively. The index takes into account the availability of each food type and is calculated as follows: \( L = (r_i - p_i) \) where \( r_i \) is the number of bites from food type \( i \) and the \( p_i \) is the average percent cover of the food type \( i \) present in the environment (Strauss 1979). The index ranges from +1.0 to -1.0 and 95% confidence intervals (CI) were calculated. Positive CI indicate active selection, negative indicate avoidance or no availability and CI that encompass zero indicate random selection (Mantyka and Bellwood 2007).

To test if the feeding rate, bite size and feeding impact differed between C. sordidus and S. psittacus mixed effects models were fitted on the variables respectively, using size as a covariate and site as a random factor due to the nested design (Zuur et al. 2009). Size as a continuous variable was used instead of size class, since the range within each class differs between the species (Table 2). The same model was also fitted on feeding impact per unit biomass to assess if biomass is a good indication of function and whether it differ between the two species. Before running the models the data was checked for collinearity of the explanatory variables by assessing the variance inflation factors (VIF) (Zuur et al. 2009). Using the residuals of the models the data was visually checked for normality and homogeneity. Bite size and feeding impact were transformed using Box-Cox power transformation so as to meet the assumptions (Townend 2002).
4. RESULTS

4.1 Benthic community structure

The benthic community structure varied between the different sites (for detailed figure please see Appendix C: A.C.1). Turf was the dominant organism across all sites (range from 26 % to 49 % ± 5.1 SE). Average percent coral cover was highest at Kisite (35% ± 4.8 SE), followed by Mombasa 2 (27% ± 6.2 SE), Watamu (23% ± 2.9 SE) and lowest at Mombasa 1 (13% ± 1.7 SE). Macroalgae cover was lowest in Kisite and Mombasa 2 at an average of 5% (± 1.9 SE) and 5% (± 3.3 SE) respectively, and highest in Mombasa 1 at 25% (± 3.2 SE). Mean macroalgae cover at Watamu was 11% (± 2.2 SE). Urchin density was greatest in Mombasa 1, 76.8 ± 20.8 SE indv. 10m⁻², and lowest at Watamu, 8.5 ± 2.9 SE indv. 10m⁻² (Appendix C: A.C.2).

The first principal component axis (PC1) from the benthic PCA represents the difference between individual transects across a gradient from high coral cover (up to 50% cover at transect level) and CCA (up to 18 %) to high macroalgae cover (up to 34 %) and sand (up to 24 %). This gradient explains 35.9 % of the variance between transects and the opposite ends were represented by transects at Kisite and Mombasa 1 respectively (Figure 2). The second principal component axis (PC2) represents a gradient from turf (up to 59%) and Halimeda (up to 29%), and explains 22.5% of the variance. For the purpose of this study only PC1 was used.

**Figure 2** The relationship between the benthic variables given by the principal component analysis. PC1 shows a transition from high coral/CCA cover (left, low values) and high macroalgae (MA)/sand cover (right, high values). PC2 represents a transition from high turf cover (high values) to high *Halimeda* cover (low values). The variance explained by each PC is given within brackets. The numbers at corresponding dots represents the distribution of individual transects along the benthic gradients. Colours represent different sites: Kisite (blue), Mombasa 1 (orange), Mombasa 2 (green), and Watamu (yellow).
4.2 Herbivore biomass

Both average abundance and biomass of roving herbivores were greatest at Kisite (74.9 ± 5.5 SE fish 250m$^{-2}$ and 11.0 ± 1.1 SE kg 250m$^{-2}$) and lowest at Mombasa 1 (27.8 ± 4.3 SE fish 250m$^{-2}$ and 2.9 ± 0.08 SE kg 250m$^{-2}$) (Figure 3; for detailed species biomass and abundance see Appendix D). Parrotfish had the highest mean biomass at all sites, ranging from 1.5 to 6.9 kg 250m$^{-2}$ (± 1.1 SE), whereas surgeonfish ranged from 1.3 to 4.1 kg 250m$^{-2}$ (± 0.6 SE), both of which were greatest at Kisite and lowest at Mombasa 1. Scrapers had the highest biomass (from 3.4 to 0.4 ± 0.7 SE kg 250m$^{-2}$) to out of the functional groups across all sites except for Mombasa 1, where grazer biomass was greatest. Grazer biomass ranged from 2.2 to 1.3 ± 0.2 SE kg 250m$^{-2}$, browsers from 1.8 to 0.6 ± 0.3 SE kg 250m$^{-2}$ and bioeroders from 3.0 to 0.6 ± 0.5 SE kg 250m$^{-2}$). All functional groups were found at lowest densities at Mombasa 1, whereas no site had the greatest densities of all groups (Figure 3).

The gradient from high coral to high macroalgae cover given by PC1 was correlated with a decline in total herbivore biomass (rho = -0.56, P < 0.01; Figure 4a), parrotfish biomass (rho = -0.55, P < 0.05; Figure 4b) and surgeonfish biomass (rho = -0.52, P < 0.05; Figure 4c). Of the functional groups there was a significant decline in bioeroders (rho = -0.66, P < 0.01; Figure 4d) and scrapers (rho = -0.47, P < 0.05; Figure 4e) but not browsers (rho = 0.16, P > 0.05; Figure 4f) and grazers (rho = 0.15, P > 0.05; Figure 4g).

![Figure 3](image-url)  
**Figure 3** Average biomass and abundance per 250m$^2$ of parrotfish (P) and surgeonfish (S) at each site respectively. The functional groups within each genera is given by the different colours. Error bars indicate standard error of the mean for parrotfish and surgeonfish respectively.
Figure 4 The relationship between herbivore biomass (kg 250 m$^{-2}$) along PC1 (i.e. coral to macroalgae dominance). The y-axes represents biomass of a) main herbivore assemblage, b) parrotfish, c) surgeonfish, and of the functional groups: d) bioeroders, e) scrapers, f) browsers and g) grazers. A significant negative correlation was found between all variables and the benthic gradient, except for browser and grazer biomass.
4.3 Parrotfish community feeding impact

Parrotfish feeding impact at the community level is negatively correlated with the transition from coral to macroalgae dominance (rho = -0.67, P < 0.01; Figure 5). It was found highest at Kisite at an average of 85.5 ± 12.8 cm² min⁻¹ 250m² and lowest at Mombasa 1 at 19.0 ± 2.0 cm² min⁻¹ 250m². This translates to a daily algal removal of 6.15 m² of each 250m² at Kisite, compared to 1.37 m² at Mombasa 1. Furthermore, community feeding impact appears to correspond to the recorded community biomass (Figure 6). At functional groups level, bioeroders were found to be the primary contributors of the feeding impact (t (335) = -1.97, P < 0.05) contributing to more than 50 percent of the feeding impact at each site (Figure 6), which is solely attributed to C. sordidus.

![Figure 5](image_url) **Figure 5** The negative relationship between parrotfish feeding impact at community level and PC1.

![Figure 6](image_url) **Figure 6** The average parrotfish community feeding impact per 250m² at each site and the community biomass. Feeding impact is the amount of algae removed and the relative contribution of scrapers (orange) and bioeroders (blue). The latter contribute on average more than 50 percent of the community feeding impact across sites. Error bars indicate standard error of the mean for the whole community impact. To note: biomass here does not include the whole parrotfish assemblage at the sites but only the species upon which the feeding impact was calculated.
4.4 Feeding function at individual level

4.4.1 Food preferences

The main food type of Chlorurus sordidus and Scarus psittacus was turf algae, shown by a significant Friedman’s test for the two species and sites combined ($x^2(4) = 1140, P < 0.001$; Figure 7) and a positive Strauss’ Linear Selection Index at all sites (Figure 8). Friedman’s post-hoc test showed no significant difference between turf and Halimeda at Watamu ($P > 0.05$), which means they were equally preferred at the site. However, according to the selection index the affinity for Halimeda was only attributed to S. psittacus and small C. sordidus (Figure 8 g, h). No other food item was actively selected by either species. Interestingly, random selection of macroalgae was recorded for small S. psittacus at Mombasa 1 and Mombasa 2, and for large ones at Watamu. Furthermore, the only strong avoidance for macroalgae for both parrotfishes was found at Kisite.

![Figure 7](image-url)

*Figure 7.* The food preferences of C. sordidus (Sord) and S. psittacus (Psi) at each site. The graph represents proportion of bites taken of each food type. Turf is preferred by both species at all sites. A different pattern can be observed at Watamu, where there was no difference in the preference for turf and Halimeda.
Figure 8. The selection index (mean ± 95% CI) of each size class given per species and site respectively. Positive numbers indicate selection, negative numbers indicate avoidance and zero indicate no selection. Sample size (n) is given for all size classes collectively.
4.4.2 Feeding rate

Size class had a significant effect on feeding rate for both species (C. sordidus: \( F_{(2)} = 42.08, P < 0.001; \) S. psittacus: \( F_{(2)} = 9.06, P < 0.001; \) Table 5), with feeding rate decreasing with increasing size (Figure 9a). This was more pronounced in C. sordidus where feeding rates differed significantly among all three size classes (\( P < 0.001; \) Figure 10c); average rate for small individuals was 25.0 ± 0.92 SE bites min\(^{-1}\), compared to 21.1 ± 0.71 SE bites min\(^{-1}\) for medium and 17.1 ± 0.65 SE bites min\(^{-1}\) for large ones. For S. psittacus only small and large individuals had significantly different feeding rates (\( P < 0.001; \) Figure 10d), at 26.6 ± 1.1 SE bites min\(^{-1}\) compared to 21.5 ± 0.96 SE bites min\(^{-1}\) respectively. Feeding rate also differed among sites (C. sordidus: \( F_{(3)} = 7.82, P < 0.001; \) S. psittacus: \( F_{(3)} = 13.70, P < 0.001; \) Table 5); for both species feeding rates were significantly higher at Kisite than both Mombasa 1 and Watamu, and higher at Mombasa 2 than Watamu (Figure 10c,d). There was also a significant interaction between size class and site for S. psittacus (\( F_{(6)} = 2.51, P < 0.05 \)) and was dependent on differences in the relationship between size classes across sites (Figure 10d). Feeding rate did not differ significantly between the two species (\( t_{(354)} = -0.26, P > 0.05; \) Figure 9a), but size was highly significant (\( t_{(354)} = -9.72, P < 0.001 \)), thus corroborating the results from the ANOVA.

4.4.3 Bite size

Bite size increases substantially and non-linearly with fish size (Figure 9b). Size class had a significant effect on bite size (C. sordidus: \( F_{(2)} = 46.62, P < 0.001; \) S. psittacus: \( F_{(2)} = 178.85, P < 0.001; \) Table 5) and differed significantly between all size classes for both species (Figure 10e,f). Large C. sordidus removed on average 0.43 ± 0.022 SE cm\(^2\) algae in one bite, compared to 0.15 ± 0.0080 SE cm\(^2\) for medium individuals and 0.037 ± 0.0048 SE cm\(^2\) for small. Mean bite size for large S. psittacus was 0.23 ± 0.016 SE cm\(^2\), 0.085 ± 0.0073 SE cm\(^2\) for medium individuals and 0.020 ± 0.0026 SE cm\(^2\) for small ones. Bite size of neither species was affected by site and there was no interacting effect between site and size class (Table 5). From the mixed effects model there was a significant difference between the species (\( t_{(345)} = -3.11, P < 0.01 \)), with C. sordidus removing more algae on average in one bite (0.19 cm\(^2\)) than S. psittacus (0.11 cm\(^2\)). Size also had an effect (\( t_{(345)} = 13.89, P < 0.001 \)) and there was an interacting effect between size and species (\( t_{(345)} = 4.87, P < 0.001 \)), which was interpreted as bite size has a greater increase with fish size for C. sordidus than for S. psittacus. As shown in Figure 9b the curve for C. sordidus has a steeper slope than for S. psittacus.
Figure 9. The relationship between a) feeding rate, b) bite size, c) feeding impact, d) feeding impact per unit biomass, and fish size for *C. sordidus* and *S. psittacus*. Feeding impact and bite size increases with increasing fish size, whereas feeding rate decreases. The feeding impact and bite size of *C. sordidus* are significantly greater than those of *S. psittacus*. The orange markers and corresponding lines represents *S. psittacus*, and the blue represent *C. sordidus*. The figures show the untransformed data.

### 4.4.4 Feeding impact of an individual

The feeding impact of both *C. sordidus* and *S. psittacus* increases appears to increase exponentially with size (Figure 9c). This is corroborated by size class having a significant effect on the feeding impact of both species (*C. sordidus*: $F_{(2)} = 207.91$, $P < 0.001$; *S. psittacus*: $F_{(2)} = 162.89$, $P < 0.001$; Table 5). It differs significantly between all size classes (Figure 10a,b), and is lowest among small individuals and highest for large individuals. Large *C. sordidus* remove on average $7.50 \pm 0.39$ SE cm$^2$ min$^{-1}$, making the impact twice that of medium individuals, $3.6 \pm 0.2$ cm$^2$ min$^{-1}$, and more than 7 times the impact of small ones, $1.02 \pm 0.13$ SE cm$^2$ min$^{-1}$. Similar pattern was observed for *S. psittacus* where the average algal removal of large
individuals was 4.7 ± 0.4 SE cm$^2$ min$^{-1}$, roughly twice the impact of medium individuals, 2.0 ± 0.2 SE cm$^2$ min$^{-1}$, and 9 times greater than small ones, 0.5 ± 0.06 SE cm$^2$ min$^{-1}$.

Feeding impact did not differ significantly between the four sites (C. sordidus: $F_{(3)} = 0.97$, $P > 0.05$; S. psittacus: $F_{(3)} = 1.1$, $P > 0.05$; Table 5), however, there was a significant interaction between site and size class for S. psittacus ($F_{(6)} = 2.75$, $P < 0.05$; Table 5). Post hoc test showed that the relationship between small, medium and large individuals does not hold across all sites (Figure 10b).

C. sordidus has a greater feeding impact than S. psittacus ($t_{(170)} = 3.85$, $P < 0.001$; Figure 6a). On average C. sordidus removes almost twice the amount of algae as S. psittacus: 215 cm$^2$ h$^{-1}$ compared to 137 cm$^2$ h$^{-1}$. For both species size had a significant effect ($t_{(170)} = 22.79$, $P < 0.001$). Feeding impact per unit biomass was also significantly greater for C. sordidus than S. psittacus ($t_{(172)} = 3.72$, $P < 0.001$). It was not affected by size ($t_{(172)} = -0.46$, $P > 0.05$), however, a significant interaction between size and species ($t_{(172)} = -2.36$, $P < 0.05$) was interpreted as feeding impact per unit biomass decreases with increasing size for C. sordidus (Figure 9d).

Table 5 A summary table of 2-way ANOVAs on feeding impact, feeding rate and bite size as response variables, with site and size class as explanatory variables. The results are given for each explanatory variable and C. sordidus and S. psittacus respectively. (SS: Sum of squares; Df: degrees of freedom; $F$: the f-statistic of the test; $P$: p-value. Significance is annotated with * = $p<0.05$, ** = $p < 0.01$, *** = $p < 0.001$, and non-significance NS = $p > 0.05$)

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Explanatory variable</th>
<th>C. sordidus</th>
<th>S. psittacus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SS</td>
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Figure 10. The average a), b) feeding rate, c), d) bite size and e), f) feeding impact of each size class for *C. sordidus* and *S. psittacus* respectively. The coloured lines represent values per site. Error bars represent standard error of the mean (SE). The figures show the untransformed data.
4.4.5 Feeding impact of C. sordidus and S. psittacus at community level

The majority of the parrotfish community feeding impact was attributed to C. sordidus at all sites; 64% at Kisite, 66% at Mombasa 1, 53% at Mombasa 2 and 64% at Watamu. S. psittacus contributed to approximately one third of the community feeding impact at Mombasa 1 (34%) and Mombasa 2 (38%), but only 10% at Kisite and 14% at Watamu. The difference between the contribution of the two species was significant (t(210) = 4.95, P < 0.001).
5. DISCUSSION

Phase shifts in coral reefs have become increasingly commonplace (Hughes et al. 2010), the most prevalent being a switch from coral to macroalgae dominance (Norström et al. 2009). Because of their potential socioeconomic consequences (Graham et al. 2013) a better understanding of what paves way for and triggers phase shift, and how to reverse them once manifested, is critical (Hughes et al. 2010, Nyström et al. 2012). There is ample evidence that herbivory is a key ecosystem process in this context (Bellwood et al. 2004, McClanahan et al. 2011). Some broad research strains related to coral reef phase shifts include studies of; i) the interplay between habitat quality and (herbivorous) fish community (i.e. “what drives what”) (e.g. Graham et al. 2006, Chong-Seng et al. 2012), ii) the relationship between perturbation and herbivorous fish biomass (i.e. different threshold analysis) (Mumby et al. 2007, McClanahan et al. 2011, Jouffray et al. in press), iii) the relationship between biodiversity and ecosystem resilience (Nyström et al. 2000, Nyström 2006), embracing iv) dissection of specific species functional role (Bellwood et al. 2003, 2004) and how it may change with life-stage/size (Lokrantz et al. 2008, Bonaldo and Bellwood 2008). More recently studies have also investigated how phase shifts may influence fish behaviour and how this in turn feeds back on the dynamics of the new ecosystem state (Bellwood et al. 2006, Hoey and Bellwood 2011). This study incorporates several of these research foci and demonstrates a negative interplay between herbivore biomass, parrotfish feeding impact and a transition from high coral to high macroalgae cover, as well as highlighting the importance of large parrotfish in provision of function on the reefs under study.

5.1 Relationship between herbivores and benthos

5.1.1 What drives what?

A negative correlation was found between herbivore fish biomass and macroalgae abundance (i.e. coral cover decreases with decreasing fish biomass), which corroborates findings from modelling (Mumby 2006), experimental (Williams et al. 2001) and observational studies (Wismer et al. 2009). The pattern can be a consequence of different levels of herbivory, as this is directly related to the amount and density of herbivores on a reef (Mumby and Steneck 2008). The decline in feeding impact of the parrotfish community further supports this argument. Herbivores are known to be able to shape benthic communities by continuous grazing of algae.
(Burkepile and Hay 2006). For example, level of grazing can influence algal community succession; intense grazing yields lawns of turf algae whereas low levels lead to development of slow growing macroalgae such as *Sargassum* (McClanahan et al. 1997). In an experimental study on Kenyan reefs Mörk et al. (2009) demonstrated that herbivory is the most important process regulating algal growth and showed that exclusion of herbivores resulted in a 77% increase in algae cover. This is comparable to the recorded levels of feeding impact provided by the parrotfish community, as the lowest levels were found at high macroalgal cover. It supports the notion that reduced grazing pressure can undermine reef resilience and can pave way for phase shifts to macroalgae dominance (Bellwood et al. 2004).

Interestingly, parrotfish community feeding impact corresponded well with the biomass of the same parrotfish assemblage. McClanahan et al. (2011) demonstrate specific thresholds of fishable biomass in the Western Indian Ocean (WIO) under which reefs tend to move towards a degraded state dominated by macroalgae. An increase in macroalgae was found at fish biomass below 1,130 kg ha\(^{-1}\); at levels below 850 kg ha\(^{-1}\) macroalgae tend to increasingly dominate coral cover; and high macroalgae cover (>30%) was found when biomass fell below ~500 kg ha\(^{-1}\) (McClanahan et al. 2011). Although this measure is inclusive of the whole reef fish assemblage the authors suggest that it broadly relates to level of herbivory (McClanahan et al. 2011). The present study demonstrates that just below 8 kg 250m\(^{-1}\), or ~300 kg ha\(^{-1}\), of roving herbivores the study reefs move towards increased macroalgal dominance. Recorded levels of parrotfish and surgeonfish biomass show that they contribute to roughly 35 percent of the total fish biomass within Kenyan closures (McClanahan 2011), which includes the MPAs from the present study. Assuming that this is representative for these reefs, a simple calculation yields a total fish biomass of ~860 kg ha\(^{-1}\) at ~300 kg ha\(^{-1}\) surgeon- and parrotfish biomass. This implies that the result from this study falls within the same range as the thresholds recorded for the WIO region, and if crossed, macroalgae become increasingly dominant, as the amount of grazing would be reduced. However, in order to establish accurate thresholds of herbivore biomass an extensive data set it required, including a multitude of reefs and a complete herbivore assemblage, and thus, this study provides a rough estimate and an indication of where such thresholds may lie.

Benthic communities can also influence associated fish assemblages and consequently also rates of herbivory through provision of habitat and food (Chabanet et al. 1997). Herbivore biomass were markedly higher at Kisite (reef crest) than the lagoon sites. Herbivore biomass and level of herbivory is generally greater on outer reefs and reef crests compared to lagoons.
(Green and Bellwood 2009, Hoey and Bellwood 2009, Vergés et al. 2011) as the former provides greater structural complexity and coral cover (Vergés et al. 2011). Structural complexity offers refuge from predation and facilitates for settlement of fish larvae (Öhman et al. 1998), which would enhance the abundance and biomass of herbivorous fish. This creates a feedback in which coral dominance is maintained (Nyström et al. 2012), particularly since high coral cover augments grazing intensity (i.e. the amount of grazing that occurs on any given patch of reef) due to greater competition for limited algal resources (Mumby 2006). Conversely, intensity will decline from either removal of herbivores or disturbance-induced coral loss (Mumby 2006). This is likely an underlying cause for the observed pattern at the study reefs. For example, the 1998 bleaching event caused extended coral mortality on Kenyan reefs (McClanahan et al. 2001), which may have affected the sites differently. Moreover, poaching in Kenyan MPAs has been observed in the past (McClanahan and Obura, 1995), but more recent studies suggest improved and even strong compliance within the same parks (McClanahan et al. 2009). Despite this, the recovery rate of herbivores can be slow. Studies from Kenya and elsewhere, indicate that biomass and some key target species are likely to recover on the scale of more than 10 years and possibly as much as 40 years following closures (Russ et al. 2005, McClanahan et al. 2007, McClanahan and Humphries 2012). Fishing in surrounding areas can also be critically important for estimating recovery rates (Daw et al. 2011). Hence, it is likely that the investigated reefs suffer from a lag-effect (Graham et al. 2006), and that the recorded levels of biomass, parrotfish feeding impact and coral cover are far from recovered. This may be particularly prominent for Mombasa 1, which only received full protection in 1991 (McClanahan and Graham 2005), and is situated in close proximity to fished areas where incidences of illegal fishing were observed (Källén, pers. obs.), potentially indicating non-compliance. Although, this could explain the low herbivore biomass and high macroalgal cover at the site, a lack of data on disturbance history suggests an enquiry that rather focuses on what mechanisms maintain this pattern today.

The low herbivore biomass at high macroalgal cover can be consequence of to the algae’s ability to inhibit herbivory (Hoey and Bellwood 2011), as macroalgae is only consumed by a limited number of species (Hoey and Bellwood, 2009). Moreover, in contrast to corals, the structural complexity offered by dense macroalgae is flexible in nature, which has shown to deter herbivores, as these environments impedes the ability to detect predators (Hoey and Bellwood 2011). Reefs with dense macroalgal stands have shown to support less species richness and functional diversity (Graham et al. 2006, Chong-Seng et al. 2012). Of the
functional groups both scrapers and bioeroders declined over the benthic gradient but, interestingly, not browsers and grazers. Similar patterns have been noted on the GBR (Wismer et al. 2009). Conversely, Chong-Seng et al. (2012) found that browser biomass increased slightly over a similar gradient. A possible explanation is that browsers are supported by reefs with high macroalgal cover, but not scrapers/bioeroders since these primarily feed on turf algae (Bonaldo and Bellwood 2008, Green and Bellwood 2009). However, the relationship between browsers and macroalgae is poorly understood. Counterintuitively, reefs dominated by macroalgae often have low functional redundancy in the browsers assemblage (Hoey and Bellwood 2009) which is consistent with the low species richness (only two species in total) within the browser group at Mombasa 1. Coral cover, complexity or other environmental aspects may thus have a greater influence on the presence of browsers than availability of their preferred food choice. As Hoey and Bellwood (2011) demonstrated, even browsers avoid dense macroalgal stands due to lack of predation refuge, thus creating a feedback in which macroalgal dominance is maintained. Furthermore, only one scraper and one bioeroder species were recorded at the Mombasa 1. Consequently, this site appears to have low functional redundancy within the functional groups that are both responsible for preventing as well as reversing shifts to macroalgae. Noteworthy is that this site also supported the highest density of sea urchins. It has been shown that sea urchins can replace grazing by herbivorous fish (Hay 1984, Hughes 1994, Lokrantz et al. 2009), but they can erode reef structure at high densities (Graham et al. 2013), which could feed back to reduced fish recruitment.

5.1.2 Limitations to determining cause and effect

It is beyond the scope of this study to explain ultimate causes behind the patterns observed on the study sites, and it should be stressed that correlation only indicates relationships and not causality. Furthermore, this study only includes surgeon- and parrotfishes, and although these are the most numerous on Kenyan reefs (McClanahan 2011) there are other important herbivores (e.g. rabbitfishes and urchins) to be considered. Environmental factors such as nutrient input, sedimentation, water flow and connectivity to other reef systems are other aspects determining coral and macroalgal cover (Green and Bellwood 2009) and were not measured in this study. Such confounding biophysical factors may well result in observed differences between the sites, particularly between Kisite and the lagoon sites, but also between the latter as they differ in distance to shore and to outer reefs. Nonetheless, numerous studies have shown that coral reefs are primarily top-down driven; that herbivores are more important

5.2 Benthic impact on the feeding function of individual parrotfish

Despite the negative relationship between feeding by the parrotfish community and the benthic gradient, benthic composition appeared to only have limited impact on the function provided by individual parrotfish. Only food preferences, albeit slightly, and feeding rate were affected by benthos.

5.2.1 Food preferences

Turf was the preferred food type for both Chlorurus sordidus and Scarus psittacus across all sites, which has been observed elsewhere (e.g. Ledlie et al. 2007, Bonaldo and Bellwood 2008, Lokrantz et al. 2008). They largely avoided macroalgae, despite occasional feeding by primarily small S. psittacus individuals at Mombasa 1 and 2, which may be a result on the fish feeding on small epiphytes on the macroalgae. The only non-browsing parrotfish known to feed on macroalgae are species belonging to the genus Sparisoma (Bruggemann et al. 1994) and evidently this does not translate to behaviour among Indo-Pacific Scarus and Chlorurus. Due to their preference for turf algae and rejection of macroalgae (Ledlie et al. 2007), parrotfish of these genera are considered preventers rather than reversers of shifts from coral to macroalgal dominance (Wismer et al. 2009). Interestingly, S. psittacus and small C. sordidus actively selected Halimeda at Watamu. Selection for calcareous Halimeda by parrotfishes has been recorded in experiments (Mantyka and Bellwood 2007) and this study demonstrates that this occurs under natural conditions as well. Parrotfishes’ specialised dental and jaw morphologies and a lack of acidic stomach allows for ingestion of calcareous algae (Bellwood and Choat 1990, Mantyka and Bellwood 2007), which otherwise deters herbivory by browsers lacking such attributes (Mantyka and Bellwood 2007). By feeding on Halimeda, S. psittacus and C. sordidus act as browsers, which indicate that a change in benthic conditions can alter (parrot)fish functional roles (Bellwood et al. 2006) and may in this regard be considered a “sleeping functional group” (Bellwood et al 2006), i.e. species that change their functional role in response to changes in benthic conditions. However, from a phase shift perspective, their ability to reduce Halimeda cover and provide space for coral is likely limited, as the fish were never observed to uproot mature stands when feeding. In fact, the presence of Halimeda at this
site may be a result of the feeding by parrotfish, as parrotfish tend to promote calcareous algal growth on Kenyan reefs (McClanahan et al. 1997).

5.2.2 Feeding rate

Feeding rate for both species was found to be higher at Kisite and Mombasa 2 and lower at Mombasa 1 and Watamu. Foraging behaviour in fishes is influenced by a range of factors, such as food availability and quality (Bruggemann et al. 1994), predation, habitat condition and competition (Nash et al. 2012). In a study on two scarid species on the GBR Nash et al. (2012) found that increased coral cover and competition reduce inter-foray distances. High coral cover could explain high feeding rates at Kisite and Mombasa 2, as a reduction in inter-foray distances would result in increased feeding rates as less time is spent travelling between foraging sites. High feeding rates at the two sites also fits well with optimal foraging theory, which states that foraging is concentrated where resources are plentiful (Börger et al. 2008), in this case turf algae. As such, both high coral and turf cover may help concentrate the functional impact of parrotfishes (Mumby 2006, Nash et al. 2012). Greater competition can also explain high feeding rates at Kisite, where roving herbivore abundance and biomass were highest, but cannot explain the difference between Mombasa 2 and Watamu. The low feeding rates at Watamu may be linked to low availability of turf, but may also be an indication that Halimeda has higher nutritional value, which would reduce the need for intense foraging. This has been observed in the Caribbean where parrotfish leave their territories and swim further in order to feed on certain species of macroalgae with greater nutritional value (Bruggemann et al. 1994).

5.3 Parrotfish feeding function in relation to fish size

5.3.2 Bite size and feeding impact

Bite size and feeding impact increased non-linearly with fish size for both C. sordidus and S. psittacus, whereas feeding rate decreased. It implies that bite size is the determinant factor of the amount of algae removed, regardless of differences in feeding rates due to size or benthic impact. This is likely a morphological trait, as larger fish have stronger jaws that facilitates a bigger bite (Bellwood and Choat 1990) and consequently a greater functional impact. This study shows that large C. sordidus (>25cm) remove on average close to seven times more algae per minute than small individuals (10-15cm), and for S. psittacus the difference was nine times (>20cm and 10-14cm respectively). Lokrantz et al. (2008) also found a non-linear relationship between size and function and concluded that parrotfish become functionally mature when
reaching a size of 15-20 cm, which appears to fall in line with the present study. The importance of large individuals have been reported elsewhere (Bruggemann et al. 1994, Bonaldo and Bellwood 2008). However, this study also shows that the function provided per unit biomass is the same for large and small parrotfishes, with regards to amount algae removed. The feeding impact per unit biomass was not affected by size for *S. psittacus* and declined slightly for *C. sordidus*, meaning that measured biomass would be a good indicator for function. As such, the differences in the feeding impact at the community level is likely to be a function of varying parrotfish biomass between the sites, rather than a direct effect of benthos on parrotfish feeding. However, equating biomass with function may not be straight forward. For example, Bonaldo and Bellwood (2008) demonstrated that parrotfish functional roles may differ between different sizes of fish, as large individuals scrape the surface and open up space for new coral recruits, whereas small individuals crop the algae and thus, are functionally similar to grazers. Biomass may therefore only be an indication of function provided by medium to large parrotfish, if considering both algal removal and provision of clean surface, particularly since they had disproportionally bigger bites than small ones.

A greater feeding impact per unit biomass may also help explain why *C. sordidus* on average removed more algae than *S. psittacus*. Being a bioeroder, *C. sordidus* has a stronger jaw structure than *S. psittacus* (Choat and Bellwood, 1990), which also indicate that this species is particularly important in providing space for coral recruitment (Bellwood et al. 2011). *S. psittacus* has been coined a “sand-sucker” – a group of scrapers with relatively weak jaws that occasionally feed on detritus in the sand (Choat and Bellwood 1990) – and therefore, a comparison between other scraper species and *C. sordidus* may not have yielded the same results. In fact, small to medium bioeroders (<35cm) are considered to provide the same function as scrapers in terms of controlling algae and opening up substratum for coral recolonisation (Green and Bellwood 2009). The results from this study point towards a greater functional impact of individual *C. sordidus* than that of *S. psittacus*, but this may not be equated to comparison with other scrapers.

Nonetheless, *Chlorurus sordidus* alone contributed to more than 50 percent of the measured community feeding impact at each site. Although this is likely an overestimation as community feeding impact does not consider the whole parrotfish assemblage, *C. sordidus* is one of the most abundant species and stand for 34-58 percent of the total scraper/bioeroder biomass and close to 20 percent of the biomass of all herbivores sampled at each reef. It can thus be assumed
that this species is highly important in controlling algal growth on the studied reefs, and thereby play an important role in preventing shifts to alternate states.

5.4 Fish for food or fish for function?

Fish is an important ecosystem service provided by coral reefs, as it offers a cheap source of protein, and as a commodity underpins livelihoods for many coastal populations around the world, particularly in poor, developing countries (Thyresson et al. 2011, Johnson et al. 2012). On the other hand, as this study demonstrates, fish provide key ecosystem functions, or supporting ecosystem services, which ensure that reefs can continue to provide fish for consumption. Overfishing is a pressing issue, and by fishing down the food chain (Pauly et al. 1998), herbivores become increasingly targeted as the availability of higher taxa is reduced (Aswani and Sabetian 2010). Countries have the right to develop, but unfortunately, research have shown that the relationship between development and reef health is U-shaped (Cinner et al. 2009a), meaning that at low and high levels of development impact on resources is low. However, on the path between, fishing pressure increases due to improved gears. As fish, such as important herbivores, decline important functions are reduced, resulting in degraded reefs that no longer provide the same ecosystem services, which in turn perpetuates poverty (Cinner et al. 2009a, Steneck 2009). As such, there appears to be a trade-off between provisioning and supporting ecosystem services, i.e. either fish for food or fish for function, as well as between development in the short-term compared to the long-term. These trade-offs need to be carefully balanced to avoid such socio-ecological traps (Cinner et al. 2009a), and allow for fishing without undermining continued ecosystem functioning.

The present study demonstrate that herbivore biomass could be used as an indicator of benthic changes on coral reefs. Levels should be maintained above ~300kg ha⁻¹ to avoid increases in macroalgal cover, which is concurrent with findings from the greater WIO region (McClanahan et al. 2011). Such targets have been suggested to act as guidelines for management, to allow for sustainable extraction whilst avoiding phase shifts (McClanahan et al. 2011). Biomass has been used as a proxy for ecosystem functioning (Mora et al. 2011) and this study shows that for parrotfish, biomass may well be indicative of the function they provide, at least in terms of algal control. However, this should be treated with caution since only a select few species were studied and more encompassing assessments are required in order to determine the relationship between parrotfish biomass and function. Furthermore, it is debatable whether it is prudent to
use biomass targets for fishing, especially at the lower end, as it may render fishing that inevitably pushes reefs close to, or beyond, critical thresholds. Also, to assume that biomass equates function may render missed information on functional diversity and redundancy, or presence of key species at a reef. For parrotfish both size and species are important factors to consider. Interestingly, Bellwood et al. (2011) demonstrated that algal control by parrotfishes is resilient to fishing, as a reduction of both large parrotfish and predators promote an increase in smaller size classes and species of parrotfish. However, recruitment is dependent on good habitat quality with high coral cover (Öhman et al. 1998) and thus, this may not be the case on reefs already showing signs of degradation. Furthermore, large fish are considered particularly important for recruitment due to greater fecundity and larvae of better quality than smaller fish (Birkeland and Dayton 2005), thus in this regard they may not be functional compensated for by smaller fish.

A variety of management solutions have been proposed to allow for fishing whilst maintaining function. For example, a ban on gears that specifically targets critical functional groups can enhance reef resilience (Cinner et al. 2009b). This is often specific to the region (Graham et al. 2013), and in Kenya would include large fish traps and spear-guns as these target larger fish size (McClanahan et al. 2009). Slot size management (Steneck et al. 2009), with a minimum and maximum size limit, would both allow for small fish to reach reproductive size as well as protecting vital function provided by e.g. large parrotfish. Such solutions could be combined with monitoring of fish or herbivore biomass in order to detect warning signs of ecosystem change (McClanahan et al. 2011). However, studies have shown that in order to successfully reduce exploitation, management needs to consider underlying socioeconomic drivers and issues of non-compliance. For example, market forces such as increasing prices as fish become scarce, can provide an irresistible incentive for continued unsustainable fishing (Thyresson et al. 2011). Addressing such drivers is likely key to balance the trade-off between fish for food and fish for function.
6. CONCLUSION

To revisit the aims of the study, it has been clearly demonstrated that both herbivore biomass and functional impact of parrotfish decreases over a gradient of high coral cover to high macroalgae cover. Determining causality in this regard is difficult, as herbivore biomass and level of herbivory can be both cause and consequence of benthic community structure. Furthermore, benthic structure appeared to only have limited impact on the function provided by individual parrotfish. Rather, a reef dominated by macroalgae can indirectly influence algal control by parrotfishes, by supporting less abundance and biomass of fish. This study also demonstrated that large parrotfish are functionally superior to small individuals and that there may be differences in functional impact between different species. Algal control by herbivores in general, and parrotfish in particular, is critical to enhance coral reef resilience in the phase of change. A better understanding of the impact of specific species, and the relationship between fish biomass and function provided, is needed in order to develop sound management practices that can allow for fishing without undermining the resilience of coral reefs and their vital function to deliver important ecosystem services to humans.
7. REFERENCES


APPENDIX

Appendix A: Extended study site description

The criteria for study site selection included 1) a gradient of benthic community structures, from high coral cover to high macroalgal cover, had to be covered by the sites; 2) they needed to display a range of parrotfish sizes in order to meet the requirements for the study on parrotfish feeding; and 3) the depth may not exceed 5m to increase sampling time and reduce risk of diving-related illnesses. From a pilot study four sites (Kisite, Mombasa 1 and 2, and Watamu) were chosen based on the aforementioned criteria. All sites are located within marine parks, run by the Kenyan Wildlife Service (KWS), a government institution that manages wildlife and its conservation in Kenya, as well as enforces related regulation. Kenyan marine parks are often divided into a park where fishing is not allowed and a reserve where fishing is restricted to hook-and-line and baited traditional fish traps. Compliance is generally high (McClanahan et al. 2009), however, incidences of poaching has been observed (McClanahan and Obura 1995, Källén, pers. obs.). The aim was not to discriminate between no-take zones and fished areas, however, due to depauperate parrotfish populations within the latter all sites were located within government-run MPAs. Below follows a detailed description of each site.

Kisite

The site is located within the Kisite Marine Park – a 28km$^2$ no-take area adjacent to an 11km$^2$ marine reserve. Out of the 28km$^2$ approximately 10km$^2$ is coral reef and the rest comprised of sandy areas (McClanahan and Graham 2005). The park and reserve, Kisite Mpunguti Marine Park, is comprised of four small islands surrounded by coral reefs and seagrass beds on the coast outside the village Shimoni close to the Tanzanian border. The no-take zone was established in 1973 and regazetted in 1976 to include the reserve (McClanahan and Graham 2005). It is a popular tourist attraction.

Kisite was chosen to represent reefs with high coral cover. The reef runs along Kisite Island, a small grass island approximately 7-8km from shore surrounded by a ~ 5 km reef, out of which roughly 1.1km comprised the study site. Since Kisite is the largest continuous stretch of reef in this study, a total of 7 transects were used to sample the fish and benthic communities. All data was collected from the outer reef flat and the reef crest on the leeward side of the island at a maximum of 4m during high tide. The crest and outer flat was characterised by pockets of continuous hard coral in-dispersed between areas of coral rubble, turf-laden coral rock and sand,
compared to the continuous coral cover along the reef slope. Such fragmentation was similar to the lagoon reefs, and thus the crest and outer flat was chosen for the study instead of the reef slope. It should be noted that this site is not located within the lagoon and as such offers differing conditions compared to the other study sites. Although all data was sampled from the less wave exposed inner area of Kisite Island, exposure is likely higher than at the lagoon sites, which can have an effect on ecosystem dynamics. Nonetheless, the site has been compared to Kenyan lagoon areas in previous studies (e.g. McClanahan and Graham 2005, McClanahan et al. 2009, McClanahan 2011).

**Mombasa**

The two Mombasa sites are both located within the Mombasa Marine National Park, within close proximity of Mombasa Town. The park is 10km², stretches from the lagoon out to the fringing reef and is surrounded by a reserve of approximately 200km². The reserve and park were gazetted in 1986, but fishing was only fully restricted in 1991 (McClanahan and Graham 2005). The two study sites are can be found at each end of the marine park with a distance of approximately 550m between them. They differ in benthic composition, thereby the decision to treat them as two separate sites. Since they are both small in comparison to Kisite and Watamu, only 4 fish and benthic transects were conducted at each site.

**Mombasa 1**

Mombasa 1 (locally known as Sea Star) was chosen due to its high cover of macroalgae compared to the other sites. It is an area of 0.1km² with fragmented coral structures (primarily *Porites* bommies) surrounded by areas of turf- and sediment-laden coral rock. Macroalgal genera such as *Sargassum* and *Turbinaria* are common across the site. Sand and seagrass areas mark the borders of the study site. The area is located within the lagoon, with a maximum depth of ~4m at high tide. The distance to the closest opening to the outer reef is ~570m and distance to shore is ~920m. This site is regularly visited by tourists, however, not as frequently as Mombasa 2.

**Mombasa 2**

Mombasa 2 (locally known as Coral Gardens) represents a reef with high turf cover. The study area is roughly 0.06m² and encompasses a 5-8m (high tide) deep sand channel that connects to the outer reef. Pockets of coral (primarily *Porites* and *Acropora*) and turf-laden coral rock can be found on each side of the channel, at a depth of ~3m during high tide. Similarly to Mombasa 1 areas of seagrass mark the boundary of the Mombasa 2 study site. Currents can be strong in
the channel, especially on an outgoing spring tide. The influx of water from the outer reef is likely greater at Mombasa 2 than at the other lagoon sites. The distance to the outer reef is ~350m and to shore ~1020m. The channel also harbours a variety of large fish species, many of which were only encountered occasionally. For example, a school of 20-30 large (>25cm TL) *Scarus ghobban* was sometimes observed to enter the study area during low tide. The site is heavily visited by tourists during peak season (Nov-Feb).

**Watamu**

Watamu was primarily chosen due to its large cover of *Halimeda* since this genus was rarely found at the other sites. The study site is located within the Watamu Marine National Park, which is a 10km² no-take area surrounded by a 32km² reserve. It was one of the first marine parks in Kenya, established in 1968 together with Malindi Marine National Park but focus on enforcement of Watamu only commenced in 1972 (McClanahan and Graham 2005). It is located outside the fishing and tourist town of Watamu, 21km south of the city Malindi.

The study site is an area of roughly 0.2km² with large structures of coral rock (2-3m height at 5m depth) inside the lagoon, with a benthos of live hard coral, *Halimeda* and macroalgae. In between these structures there are areas of sand and turf- and sediment-covered coral rubble. The site is located ~500m from the shore and ~1000m from the outer reef. Furthermore, this site is in close proximity of the Mida creek which runoff can give the water a greenish tint. It is a popular spot for snorkelers and is visited by numerous tour boats during peak season. The area closest to the mooring site has been severely damaged by tourists stepping on coral and the fish are used to being fed. As such, this part of the park was not included in the study.
Appendix B. Limitations with the methodology

The limitations associated with this study can be summarised, but are not limited to, the following key points:

1. **Small scope:** The main limitation of this study is its small size, with only four sites, and limited sample size. Seasonal changes are also not considered due to the limited time of research. As such, the study provides a snapshot of the relationship between benthos, herbivore biomass and parrotfish functional role on Kenyan reefs, which makes it difficult to draw general conclusions beyond the scope of the four sites without corroborating the results with previous studies.

2. **Limited fish assemblage:** The assessment of the feeding function at community level does not consider the whole parrotfish assemblage. The focal species comprise more than 50 percent of the assemblage, which will give a good indication as to what level of feeding impact can be found at each reef. Moreover, not the whole herbivore community is considered in the biomass assessment. Parrot- and surgeonfish are the most common roving herbivores on Kenyan reefs (McClanahan 2011), yet, the results should have been more robust had the whole assemblage been considered.

3. **Unexperienced observer:** Due the data being collected by an unexperienced observer there is a potential for non-exact recording of fish sizes, feeding rates and bite sizes, even though measures were taken to prevent this (e.g. in the beginning of each dive visually estimating objects of known size underwater).

4. **Data transformations and nonparametric tests:** A large part of the data set was heteroscedastic and not normally distributed. Hence, for the parametric test ANOVA and mixed effect modelling the data had to be transformed, which can result in loss of information in the data (Zuur et al. 2009).
Appendix C. Benthic cover and urchin abundance

A.C.1 Mean benthic cover at transect level, i.e. per 250m². The different colour represent the different categories.

A.C.2 Mean urchin density per site, given as an average per 10m quadrate.
Appendix D. Species biomass and abundance

Kisite

A.D.A. Mean a) biomass and b) abundance of each species per transect at Kisite. Green bars indicate surgeonfish and blue bars indicate parrotfish. Functional groups are given in brackets after the species name (bio – bioeroder; br – browser; gr – grazer; pl – planktivore; detr – detritivore).
**Mombasa 1**

![Biomass Chart](chart1.png)

**A.D.B.** Mean a) biomass and b) abundance of each species per transect at Mombasa 1. Green bars indicate surgeonfish and blue bars indicate parrotfish. Functional groups are given in brackets after the species name (bio – bioeroder; br – browser; gr – grazer; pl – planktivore; detr – detritivore).
A.D.C. Mean a) biomass and b) abundance of each species per transect at Mombasa 2. Green bars indicate surgeonfish and blue bars indicate parrotfish. Functional groups are given in brackets after the species name (bio – bioeroder; br – browser; gr – grazer; pl – planktivore; detr – detritivore).
Watamu

A.D.D. Mean a) biomass and b) abundance of each species per transect at Watamu. Green bars indicate surgeonfish and blue bars indicate parrotfish. Functional groups are given in brackets after the species name (bio – bioeroder; br – browser; gr – grazer; pl – planktivore; detr – detritivore).