

The importance of size for the maintenance of
ecological functions
of the parrotfish *Scarus niger*
on three reefs outside Zanzibar, Tanzania

Charlotte Johansson

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Supervisors:
Magnus Nyström, Jerker Lokrantz, Narriman Jiddawi

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Department of Systems Ecology
Natural Resource Management
Stockholm University
106 91 Stockholm, Sweden

In memoriam of my grandfather and grandmother

*“A butterfly on tender wings crosses the vast ocean
A bird sings at dawn”*

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1. Abstract

Parrotfish are important key-players in maintaining the balance between corals and algae and preparing substrate for coral larval settlement. Parrotfish have long only been targets of a small-scale artisanal fishery but as other fish-populations are rapidly decreasing parrotfish have become prime targets. The increased pressure on large individuals has reduced parrotfish abundance and the fishery now target individuals of smaller sizes as well. By looking at different parameters related to function and behaviour this study estimates how a reduction in average size in individual fish within the *Scarus niger* population may result in loss of ecological function.

The scraping rate, bioerosion rate and food preference within different sizes of *S. niger* were investigated on three coral reefs: Bawe, Chumbe (a reef sanctuary) and Nyange, exposed to different levels of fishing pressure along the west coast of Zanzibar, Tanzania. The results show that fish must reach a critical size before they start to contribute to the investigated functions. Differences between the reefs were discovered and the result points out a dispersed pattern where fish on Bawe never displayed a change in scraping rate and bioerosion rate within the critical sizes. Chumbe and Nyange both showed changes in scraping rate and bioerosion rate within the critical sizes. The results also show that the scraping rate and bioerosion rate were higher on Chumbe and that fish had higher abundance of large individuals performing bigger bites compared to the other sites. For all sites matrix and dead coral were the substratums on which most turf algae were found and constituted the substrates most frequently fed on. These substrates were dominated by massive or branching growth form. At Bawe and Nyange sparse turf algae were most commonly fed on while sedimented turf algae dominated the bites on Chumbe.

This study suggests that size is an important factor estimating the consequences of over-fishing and that protected marine environments allow large sized individuals of *Scarus niger* to have a possibility to perform a maximum function.

2. Introduction

Grazing on coral reefs is a vital function for maintaining coral dominated reefs by keeping the algae population down (Bellwood, 1996; McClanahan et al. 2003). There exist a large number of different algae in the marine environment ranging from fleshy macro algae, filamentous turfs to crustose corallines. These algae are regulated by herbivory, light and salinity (Oliviera et al. 2005). If the algae population becomes too abundant it can have devastating impacts on the coral community by overgrowing and shading the corals and occupy surface and thereby prevent the coral larvae settlement.

Herbivores are a diverse group with a variety of functions on coral reefs. Micro-herbivores, such as amphipods, gastropods and herbivorous polychaetes, are less mobile organisms and act on small scales (square centimeters). The impacts from these organisms are therefore intensive grazing on small temporal and spatial scales. The intensity of grazing is decreasing when the scale is getting bigger. Species foraging on intermediate scales (e.g. sea urchins (Echinoderms) and blennies (Blenniidae)) act on scales ranging from one meter for tens of meters while species with larger mouthparts such as parrotfish (Scaridae), surgeonfish (Acanthuridae) and turtles graze on the largest scales (from meters up to several kilometers)

(Elmqvist et al. 2003; Nyström, 2006). Increases in population abundance, intensifies the herbivorous function and increases the effects on the algal population (Carpenter, 1986) and studies, testing the effect of herbivory exclusion on algal communities, have demonstrated increased algal growth (Lewis, 1986).

As herbivory exists on different scales, each herbivorous group have the ability to specialize their feeding mode and therefore minimize the rate of competition. Although herbivores act on various scales and have different impacts, they all contribute to the same function (Elmqvist et al. 2003). Since different herbivores target different algae, spatial heterogeneity plays an important role for regional coral reef diversity (Lewis, 1986). Parrotfish (Scaridae) is an herbivorous family with species present in all feeding modes. With beak-like jaws and a pharyngeal mill in the oral cavity they are one of the main essential families in the marine environment in terms of bioerosion on coral reef. With the hard beak they graze, scrape or bioerode the substratum and grind the algae and substrate with the pharyngeal mill to assimilate the nutrients (Bellwood & Choat, 1990; Bellwood et al. 2003; Bellwood et al. 2004). Grazing species conduct close cropping of algae without scaring the substratum and therefore maintain the algae in an adequate height, preventing them from growing large enough to shadow corals. Scraping species opens up bare space by scraping the substratum and contribute to the settlement of coral larvae. Erosion of dead and fragile substrate is the third function performed by parrotfish species. The bioeroders help preserving a stable three-dimensional structure on the reef along with the function of removing algae (Bellwood et al. 2004). The main inorganic material ingested is calcium carbonate derived from corals, which is returned to the reef in terms of sediment (Horn, 1989), parrotfish are therefore important agents in the transformation of reef material.

Fishing is one of the main threats to coral reefs (Bellwood et al. 2004). Fish stocks are being depleted at an accelerating rate and the average size of fish within stocks have been reduced and catches have undergone serious declines since the 1980's (Jennings & Polunin, 1997; Pauly et al. 1998; Tupper & Rudd, 2002; Myers & Worm, 2003). The pressure has intensified and the effects are shown as changes in ecosystem dynamics. According to Jackson et al. (2001) the effects of over-fishing are strikingly similar across ecosystems and always precede other human impacts by making ecosystems more sensitive to disturbances i.e. reduced resilience (Nyström et al. 2000), leading to synergistic effects in the face of change. Various studies indicate that over-fishing of herbivores is one of the major disturbances affecting coral reefs and can result in cascading effect (Smith et al. 2001; Boyer et al. 2004; Hughes et al. 2005). Absence of the top trophic levels has shown to have negative impacts on ecosystems where the systems more easily can shift into completely different ecosystems dominated by fleshy macro algae (Hughes, 1994; Hughes et al. 2005).

Hawkins and Roberts (2003) have shown that the distribution of size within a species has changed. As larger fish are targeted the pressure on younger individuals are increasing. In sex-changing species, like parrotfish, over-fishing can prevent individuals from growing large enough to undergo sex-change. The rate of smaller individuals that will turn into adults earlier to maintain the reproductive success among the population will increase. When the average size is reduced the reproductive output will decrease since larger fish produce more eggs than smaller ones (Bohnsack, 1990 in Hawkins & Roberts, 2003). Also absence of one sex can result in a non-reproductive population unless there is an external source of recruitment. Over generations the fish will decrease in size and grow slower (Hawkins & Roberts, 2003). Studies have shown that the ability to remove algae and erode material increases with size

(Bruggemann et al. 1994; Bruggemann et al. 1996) but fishing can reduce the population function by removing the large individuals whose performance are the greatest.

Studies have shown that absence of herbivorous fish can result in algae overgrowing corals (Carpenter, 1986; Hughes, 1994). Considering global over-fishing, it is imperative to investigate what effects fishing have on ecological functions. Reduced size of individuals within a population could affect the capacity of the fish to fulfil ecological functions and the resilience. Few studies have looked at parrotfish function in relation to size in a continuous manner, they have instead referred to size in terms of size-classes. This reduces the possibility to discern if and where the increase in function occurs. The aim with this study is to investigate the relationship between body size and function in the parrotfish *Scarus niger* at three reefs on the west coast of Zanzibar. The study further considers if there is a size-related threshold at which the function starts to increase. Furthermore, this study investigates if general food and substratum preferences between sizes are present.

3. Methods

3.1 Study Area

Zanzibar is located in the Tanzanian archipelago, north of the country's capital Dar es Salaam, on the east coast of Africa. Two islands, Pemba and Unguja, covering 900 km² and 1500 km² respectively, make up Zanzibar. The study took place on Unguja (hereafter Zanzibar) (fig. 1), situated between 6°08'S and 39°20'E (Mbije et al. 2002).

The Eastern African continental shelf stretches about 4 kilometers offshore, where it drops off to depths of 2000 meters. At the Mafia and Zanzibar Channels, the continental shelf is 60 km wide. The seawater temperatures along the Tanzanian coast average 27° C, fluctuating between 25° C to 29° C due to climatic variations and changes of the water masses in the Indian Ocean (UNEP, 2001). The coast of Tanzania experiences two main climatic features, the North East Monsoon (November to February) and the South East Monsoon (April to September). The former is marked by higher temperatures and weaker winds, the opposite to the latter (UNEP, 2001; Jiddawi & Öhman, 2002). Two main currents are active along the east African coast. Flowing westwards and bringing waters of relatively low temperatures is the South Equatorial Current (SEC). SEC divides and flows northwards as the East African Coastal Current (EACC) or Somali current passing between the west coast of Zanzibar and the mainland (UNEP, 2001; Mbije et al. 2002).

The coast is one of Tanzania's most valuable natural resources and the coastal region contributes to the country's gross domestic product (GDP) by one-third. Due to an increasing population, the pressure on marine resources is escalating and has become a major social, economical and environmental concern (UNEP, 2001). This has lead to degradation caused by natural and anthropogenic factors acting in synergy. Coral reefs are declining on a local and regional scale caused by pollution from industrial wastes and sewage, destructive fishing methods and increasing seawater temperatures (Mbije et al. 2002). The artisanal fishery employ over 50,000 fishermen along the coast of Tanzania and virtually all operate on the coral reefs. Most of the fishery on Zanzibar is artisanal and small-scale (about 95% of the total catches) in which simple and passive fishing gear are being used (Jiddawi & Öhman, 2002). Since fish is a 'common-pool-resource', anyone can participate in fishing and efforts of fishing-regulations have proven to be problematic in terms of satisfying all parts. Increases

in the number of local fishermen have resulted in that most of the reefs around Zanzibar are showing signs of over-fishing. Sizes of fish are decreasing and catches are dropping. Meanwhile, an intensified demand for sea-products has increased the pressure even more (UNEP, 2001; Jiddawi & Öhman, 2002).



Figure 1. Map of Zanzibar showing Zanzibar Town and the three sites (from Muhando, 2006)

3.2 Study Sites

Three reefs outside the main capital of Unguja, Zanzibar Town, were investigated, Bawe, Chumbe Island Coral Park (CHICOP) and Nyange (fig. 1). These fringing reefs are similar in structure and coral cover (UNEP, 2001; Lokrantz, unpublished). Two of the sites are unprotected (Bawe and Nyange), of which one is frequently fished and visited by tourists (Bawe). The third site (Chumbe) is protected from fishing but put up tourists daily on controlled guided tours on the house reef.

3.2.1 Bawe

Of the three islands investigated, Bawe is located closest (~5.5 km) to Zanzibar Town, at 6°08'S; 39°08'E (Mohammed and Mgaya, 2001). The reef stretches from the northern tip of



Figure 2. *Scarus niger*. A terminal phase male is feeding on sedimented turfs (Photo by J. Lokrantz).

the island along the east side and continues south of the island and is formed by reef flats and slopes. Due to easy access, the reef is frequently visited by tourist, dive operators and local fishermen.

3.2.2 Chumbe (CHICOP)

Chumbe Island Coral Park (hereafter Chumbe) is located approximately 12 km south southwest of Zanzibar Town and 6 km from the closest point on the mainland at 6°16'S; 39°10'E. Chumbe Island became a protected area in 1994 and included a reef sanctuary along its

western side (Castle and Mileto, 1995). The reef extends from the northern tip of the island along the west side and continues south. The area investigated was outside the settlement where all activity takes place. On Chumbe there are daily snorkelling tours offered for the tourists on the reef under supervision of a ranger. No diving or fishing is allowed and the island has patrolling policemen to avoid confrontations with fishermen.

3.2.3 Nyange

Nyange, a sandbank located at 6°14'S; 39°08'E approximately 8.5 km south of Zanzibar Town, is not as visited as other reefs due to its distance from land. The fishing pressure is less compared to the islands closer to Zanzibar Town and the fishing methods used differ to some extent and net fishing is more common than the traditional hook and line fishing. The reef lines the border between a shallow and a deeper sand plateau and is constituted of reef flats, slopes, ridges and small underwater coral islands.

3.3 Study Species

Parrotfish (Scaridae) are a diverse family of coral reef herbivores (Bellwood & Choat, 1990). The family holds 83 species distributed over 9 genera (Randall et al. 1990) with marked ecological, reproductive and behavioural differences within each family. The majority of taxa are confined to the Indo Pacific (Streelman et al. 2002). Parrotfish are diurnal, implying activity only during the day (Frydl & Stearn, 1978). During their life time parrotfish undergo sex-change and experiences three distinct life phases that all have a specific colour phase. The most common feature among parrotfish is protogynous (female first) sex-reversal (Streelman et al. 2002). The life phases are as follows, juvenile, initial phase and terminal phase. There are also occurrences of individuals in in-between phases.

3.3.1 *Scarus niger*

Scarus niger is a scraping species and distinguished by its dark reddish to purple blue coloration pattern and rounder shape (fig. 2). It inhabits coral reefs but has been observed feeding in sea grass beds. According to Smith (2003) and Choat et al. (1996), *S. niger* appears to be monandric where initial phase fish are females and the terminal fish are all secondary males (former females). There is an asymptotic relationship between size and age, indicating a growth maximum age, at which the fish stops growing. The growth is rapid through out the first years and starts to diminish when the fish is 5-8 years and ranges approximately from 20

to 25 cm in standard length (Choat et al. 1996). Choat et al (1996) further show that the distribution of males is concentrated to the larger sizes and that male and females are equally long-lived and that some females maintain their sex throughout life. *S. niger* has previously not been commercially fished. However, as stocks are being over-exploited *S. niger* has become increasingly targeted by artisanal fishery (Jiddawi & Öhman, 2002).

3.4 Study Design

3.4.1 Field study

The data collection was conducted between December 2005 and February 2006. SCUBA equipment was used during the survey and data was recorded on underwater slates. To minimize possible errors due to observer effects, the observers performed the same tasks throughout the study. Before each observation started the fish was given some time to get acclimatized to avoid the possibility of the observers affecting the behaviour. Normally two dives a day were performed between 07:30 am and 17:30 pm. All dives ranged from 0-14 meters of depth and were located on the reef flats and the reef slopes. No general consideration regarding tides was taken at Bawe and Nyange. At Chumbe the access to the reef was restricted during low tide resulting in that most of the dives were made during high tide or outgoing tide. No considerations were taken regarding air- and water temperature since no abrupt differences in climate occurred during the time of study. The sampling method was randomly stratified.

The study was divided into two separate smaller studies 1) Behaviour and 2) Scar, to be performable under water. Data from both studies has been combined in the analyses.

Table 1. Definitions for the substrate and algae categories used (adapted from Bruggemann et al., 1994 and Bellwood, 1995).

Substratum	Definition
Dead coral	Fish feed on dead part of coral, live or dead (species known).
Matrix	Fish feed on dead coral (species unknown).
Stump	Fish feed on remnants of dead coral, probably massive (species known or unknown).
Rubble	Fish feed on dead detached fragments of coral probably branching (species known or unknown).
Live coral	Fish feed on live part of coral (species known).
Sand	Fish feed on sand or sediment on sand.
Others	Fish feed on other substratum then the above mentioned.
Algae	
Macro algae	>15 cm.
Large turf	3,5-15 cm.
Sparse turf	0-3,5 cm.
Sedimented turf	Any of the above mentioned but sedimented.
Crustose coralline	Fish feeding on crustose coralline growing on substratum.

3.4.2 Study 1) Behaviour

To calculate feeding rate the total amount of bites during a known time period was needed. An individual fish was randomly chosen and the number of forays and bites were counted. A foray is a continuous feeding event without any discernible interval other than the time taken to reapply the jaws to the substratum (Bellwood and Choat, 1990). The time was set to a minimum observation time of 3 minutes, this to register at least 20 forays per individual (Bellwood and Choat, 1990), and a maximum of 10 minutes. If the individual was lost before the three minutes were reached, the fish was not included in the data. The observation stopped when 20 forays reached and three minutes past. If ten minutes past and 20 forays not accomplished the observation was stopped and the data used. During the observation, size (total fish length in cm), life phase, start and stop depth for the observation, number of

defecations and number of times the fish was seen feeding in a damselfish territory were noted.

3.4.3 Study 2) Scar

To get estimations of erosion and bite rate, a fish was chosen randomly and time for one foray was taken with a stopwatch. The number of bites within that foray was counted and the size of one of the bites measured. Greatest width, length and depth were estimated using a sliding calliper (Bruggemann et al. 1994). The drawback of taking the maximum measure is that it will give an overestimation of the bite. The lowest value observed was set to 0.1 cm if a scar was visible but too small to give a correct estimate. If the observed fish was seen making two scars in one bite (upper respectively lower jaw) the scars were measured individually and the result added (Bellwood, 1995). When observing the bite, other factors were also recorded. Substrate (matrix, dead coral etc), coral family and algae (macro algae, large turf etc) were noted (table 1). Moreover, presence of crustose coralline algae, coral growth form (massive, branching, columnar etc) and how many percents of the substratum that appeared to be dead was also recorded. The amount of bare substratum in percents in the bite and if the feeding sequence occurred in a damselfish territory was also noted. Size estimations, life phase, start and finish depth of the bite was documented.

3.5 Statistics

Data were divided into two groups, Fish Function (bite volume, scraping rate, bioerosion rate and feeding rate) and Feeding Behaviour (life phase, substrate, coral growth form, algae, dive start and fish bite observation depth), on which different statistical methods were applied. Where life phase, substrate, growth form, algae, dive start and fish bite observation depth were investigated, the analyses were based on all observations. When estimating scraping and bioerosion rate the mean values were used to get an estimate of the mean effect on the reef. Data was transformed to get exponential relationships.

3.5.1 Fish Function

The volume (cm^3) and feeding rate (bites/min) data are based on all observations. When combining the volume data with other variables, a mean value per size has been used. Due to no correlation relationship between size and feeding rate a mean has been estimated and used in the calculations. Scraping rate was estimated by multiplying the mean values of the surface of the bite (cm^2) and feeding rate (bites/min) with the amount of bare substratum in the bite (%) for each size. Bioerosion rate was the result after multiplying volume (cm^3) and feeding rate (bites/min).

3.5.2 Feeding Behaviour

Life phase, substrate, coral growth form, algae, dive start and fish bite observation depth analyses are based on all values observed. The fish bite observation depth refer to the depth on the reef the bite was made. Percentages of food preferences on substratums, coral growth forms and algae are based on the number of bites performed on each specific substrate, coral growth form and algae.

4. Results

4.1 Fish Function

4.1.1 Volume

The results of the volume calculations are based on all observations and demonstrate that the sizes of the bites are increasing with increasing fish size (fig. 3). The data display exponential relationships with R^2 -values of 0.505 (Bawe), 0.5658 (Chumbe) and 0.6043 (Nyange). The highest volumes eroded occurred on Chumbe and ranged up to 0.27 cm^3 , while on Bawe and Nyange the maximum bite volumes detected were 0.08 cm^3 and 0.07 cm^3 . At Chumbe and Nyange the largest individuals observed were responsible for the largest volumes eroded on the reef (fig. 3B and C), while at Bawe individuals of a medium size had the highest values of volume eroded (see fig. 3A).

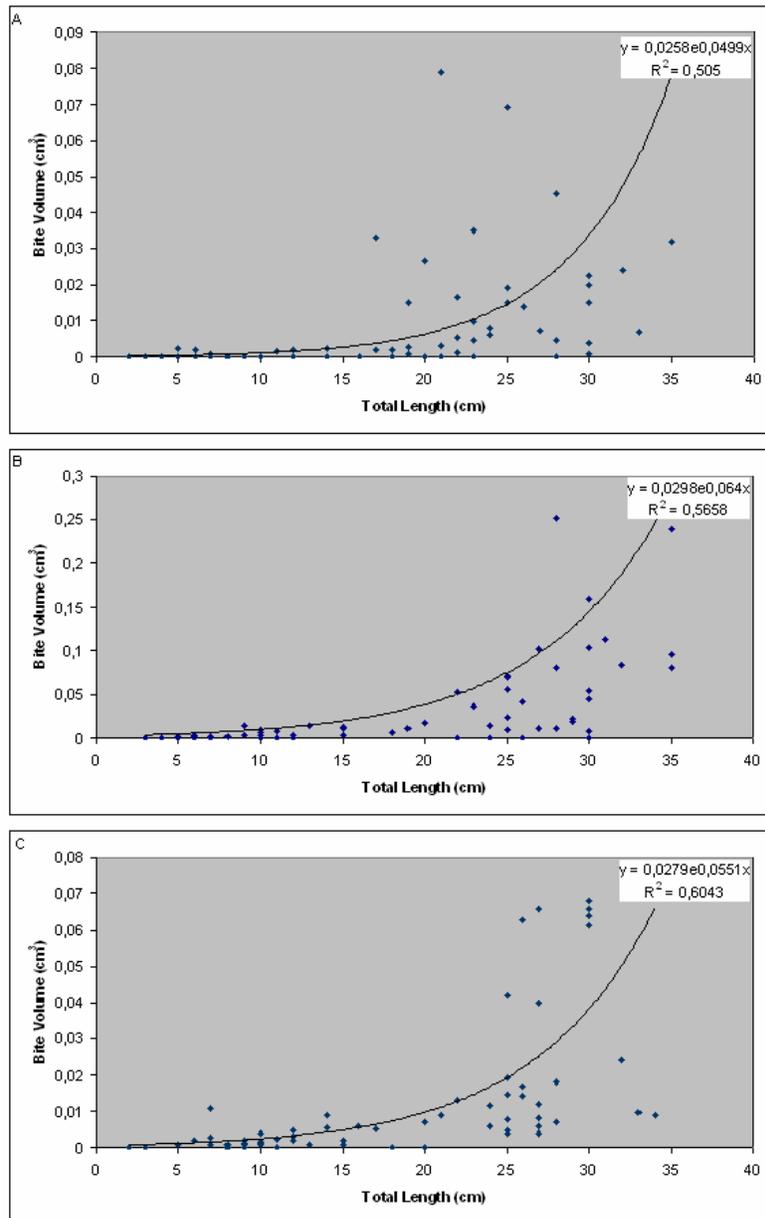


Figure 3. Bite Volume (cm^3) for the three sites A) Bawe ($R^2 = 0.505$), B) Chumbe ($R^2 = 0.5658$) and C) Nyange ($R^2 = 0.6043$).

The data further display a critical threshold where the bite volume starts to increase exponentially. For Bawe and Nyange the increase starts at 17 cm and 20-25 cm respectively. When the increase in volume is visible on Chumbe (20-25 cm), the values equals the highest values encountered on Bawe and Nyange, and therefore illustrate the difference in volume eroded between the three sites. The data further indicate a potential increase in algal removal efficiency with respect to life phase development (fig. 4).

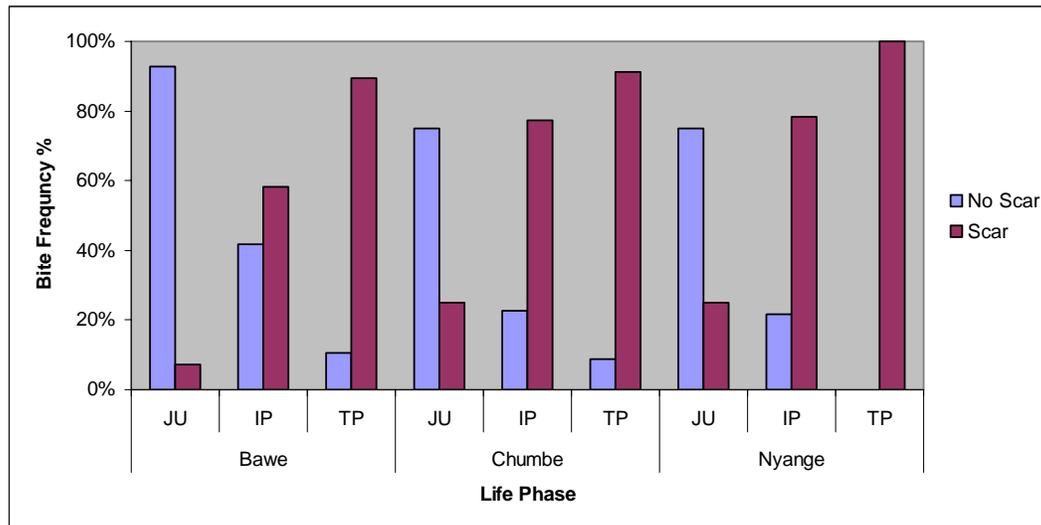


Figure 4. Frequency of bites that left a scar or no scar within life phase (juvenile (JU), initial phase (IP) and terminal phase (TP)) and site.

4.1.2 Feeding Rate

No regression relationships were observed due to great variations between observations at all three sites (fig. 5), confirmed by correlation tests showing R-values of -0.46 (Bawe), 0.08 (Chumbe) and - 0.48 (Nyange). Mean values (9.55 bites per minute for Bawe, 20.63 for Chumbe and 16.96 for Nyange) have therefore been used in the calculations. At Bawe and Nyange the feeding rates display a negative pattern where individuals smaller than 15 cm total length presents higher feeding rates than larger fish.

4.1.3 Scraping Rate

For all three sites the scraping rate increases with increasing size (fig. 6). The results display that Chumbe is the site where the scraping rates are highest followed by Nyange and Bawe. The increase in scraping rate is minor at Bawe but holds the strongest exponential relationship with an R^2 value of 0.73 compared to Nyange ($R^2 = 0.69$) and Chumbe ($R^2 = 0.66$). Looking at all three reefs together the increase in scraping function occurs between 20-25 cm total lengths. More specifically for the reefs are; a slight increase already at 17 cm on Bawe and a more notable increase at 21-25 cm. For Chumbe the increase was observed at 20-25 cm on Nyange at 21-25 cm. Small individuals appeared to have low scraping rates on all three sites although the scraping rates were higher on Chumbe for individuals larger than 9 cm total length.

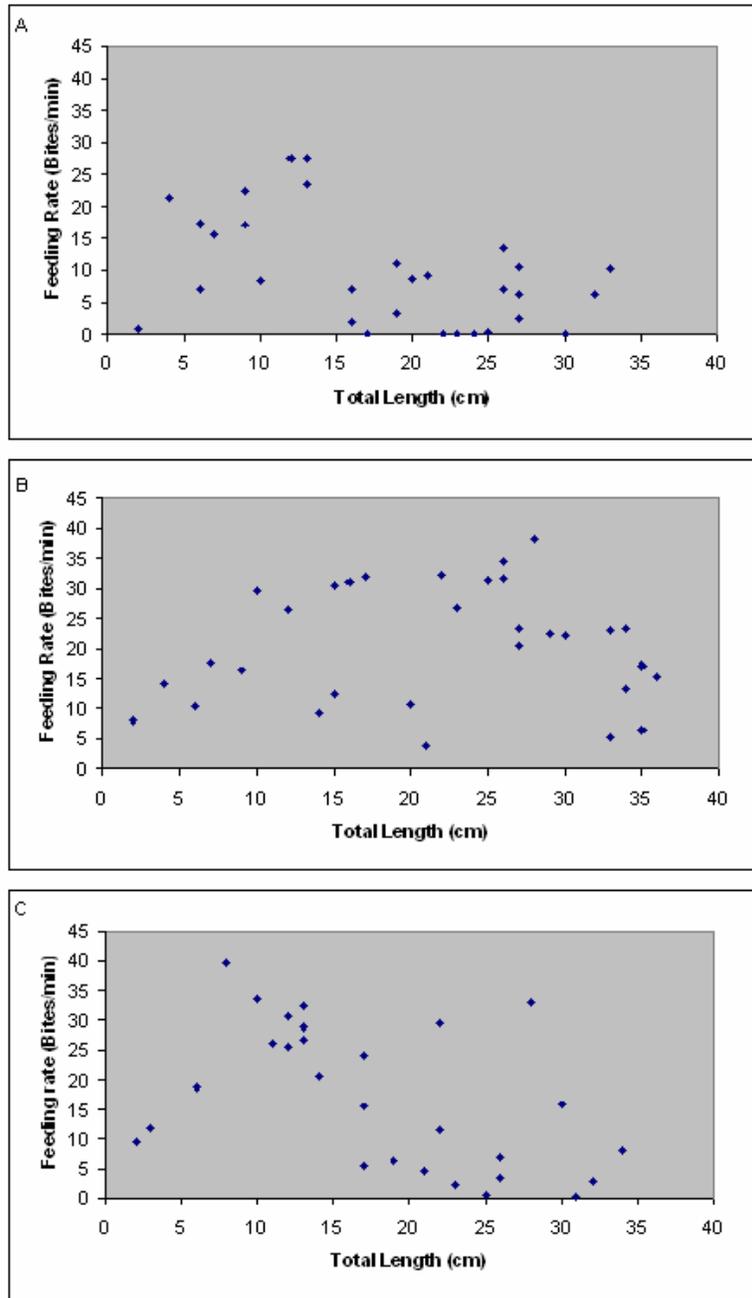


Figure 5. Feeding Rate (bites/min) for all sites A) Bawe, B) Chumbe and C) Nyange. Based on all observations.

4.1.4 Bioerosion Rate

The bioerosion rates demonstrate an exponential relationship between the size of the fish and bioerosion rate (fig. 7) (Bawe, $R^2 = 0.7189$; Chumbe, $R^2 = 0.8136$; Nyange, $R^2 = 0.595$). Chumbe display the highest bioerosion rates of the three sites followed by Nyange and Bawe. The bioerosion rates are similar between the sites up to 20-25 cm after which Chumbe shows a higher increase but differs between the sites and judged from the reefs own maximum bioerosion rate starts at 17 cm (Bawe), 23 cm (Chumbe) and 25 cm (Nyange).

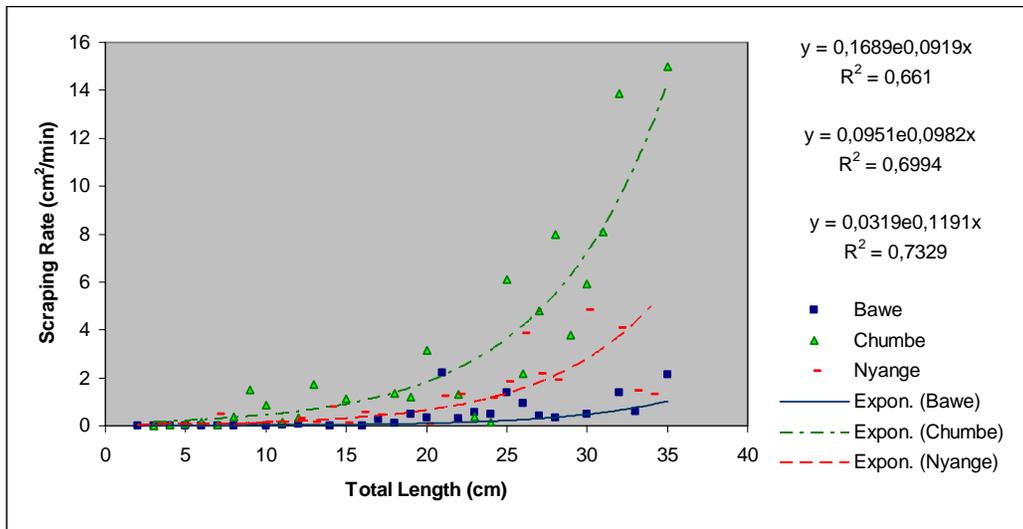


Figure 6. Scraping Rate (cm^2/min) for the three sites.

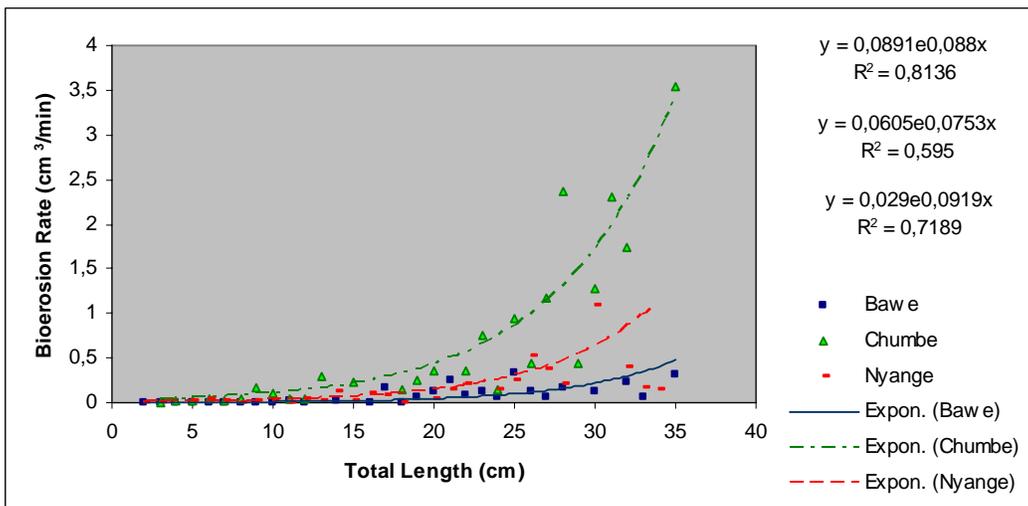


Figure 7. Bioerosion Rate (cm^3/min) for the three sites.

4.2 Feeding Behaviour

4.2.1 Life Phase

From the data it is possible to detect the distributions of life phases and sexes among the observed individuals (fig. 8). For all three sites the overlap between juvenile and initial phase fish is 5 cm and the smallest individual being in initial phase were 4 cm and the largest juvenile 9 cm. The size-distribution among initial phase females and terminal phase males differed between sites. At Bawe, the smallest individual being in the terminal phase was 20 cm. The largest initial phase fish observed was 28 cm. The overlaps of initial and terminal phase and female and male individuals range 8 cm and involved 21 individuals. The smallest individual being in the terminal phase at Chumbe was 24 cm and the largest individual in the initial phase was 27 cm. This overlap ranges 3 cm and involved 10 individuals. On Nyange the overlap between initial and terminal phase was between sizes 24-27 cm and spans 3 cm with 17 individuals encountered.

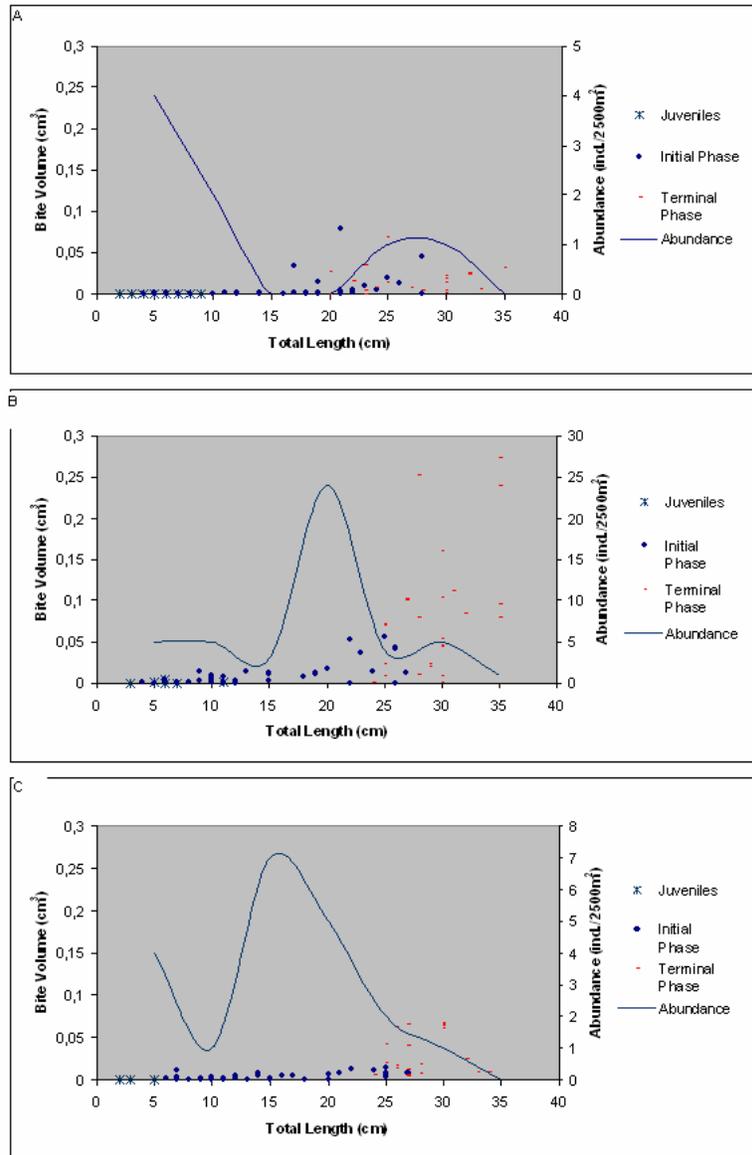


Figure 8. The distribution of Life Phases and the sizes for sex-reversal for the three sites, A) Bawe, B) Chumbe and C) Nyange. Bite Volume (cm^3) and Abundance (ind./2500m^3). (Abundance data borrowed from Lokrantz et al. unpublished).

4.2.2 Substrate

For all three sites matrix and dead coral were the preferred substratums fed on by *Scarus niger* (fig. 9). Matrix dominated the bites on all sites (37% (Bawe), 50% (Chumbe) and 71% (Nyange)) followed by dead coral (32% (Bawe), 32% (Chumbe) and 23% (Nyange)). Few bites were encountered on live corals for all three sites. No general substratum preferences were discovered in relation to size.

4.2.3 Coral Growth Form

Massive and branching were the preferred coral growth forms the fish was observed feeding on (fig. 10). Massive growth forms dominated the bites on Chumbe (60%) and Nyange (69%). On Bawe the fish preferred to feed on branching coral (47%). In 10% of the cases fish at

Bawe was observed feeding on sand. The results are similar for all sites except no individuals larger than 15 cm fed on branching corals at Nyange.

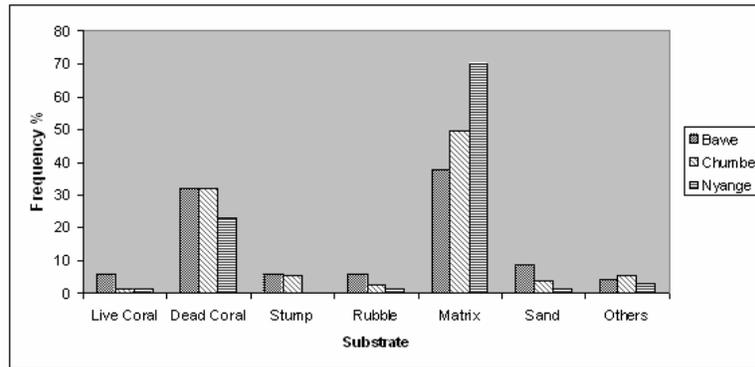


Figure 9. Frequency of bites performed on different substrates for all three sites.

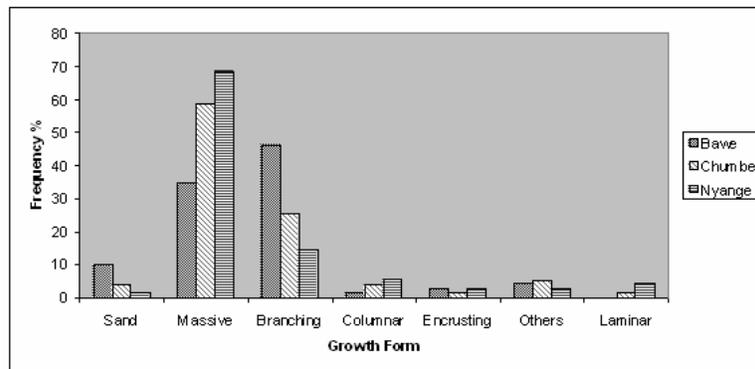


Figure 10. Frequency of bites performed on different growth forms for all three sites.

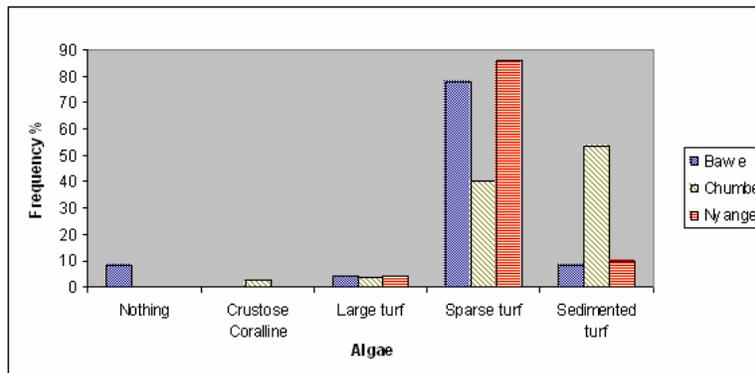


Figure 11. Frequency of bites performed on different algae for all three sites.

4.2.4 Algae

Scarus niger was observed feeding on sparse turfs in 78% (Bawe) and 86% (Nyange) of the feeding events followed by sedimented turfs (fig. 11). On Chumbe most of the bites were performed on sedimented turfs (53%). Large turf algae and crustose coralline algae were not favoured. No size-related preferences were detected.

4.2.5 Start Time and Fish Bite Observation Depth

The dives on the three sites ranged from 08:30 am to 16:00 pm and 0-12 metres of depth (fig. 12 and 13). On Bawe dives ranged between 09:00 am to 14:00 pm with most observations during early dives. At Chumbe most dives were performed early in the morning and late afternoon due to decreased access to the reef during low tide. At Nyange, bite volumes were evenly distributed among the observations but no dive started later than 12:30. The fish bite observation depth refers to the depth on the reef at which the bite was made. At Bawe the largest bites were encountered at low depths and decreased in volume with increasing depth. At Chumbe the bite volumes were evenly distributed between reef depths. The bite volume at Nyange increased with increasing depth but displayed a slight decrease when depths reach over 10 m.

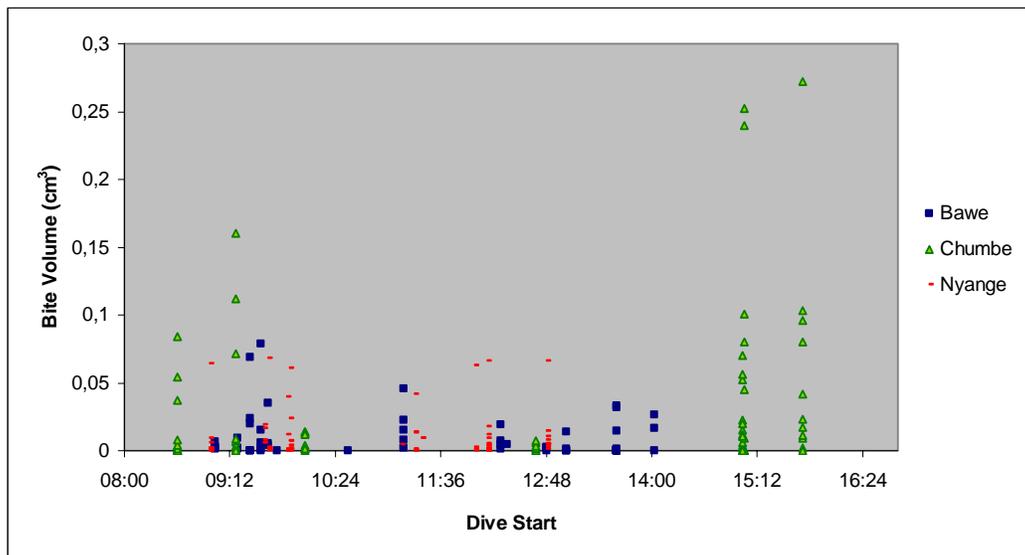


Figure 12. Bite volume (cm³) distributed over the day for the three sites based on all observed individuals. Each dive lasted for approximately 90 minutes.

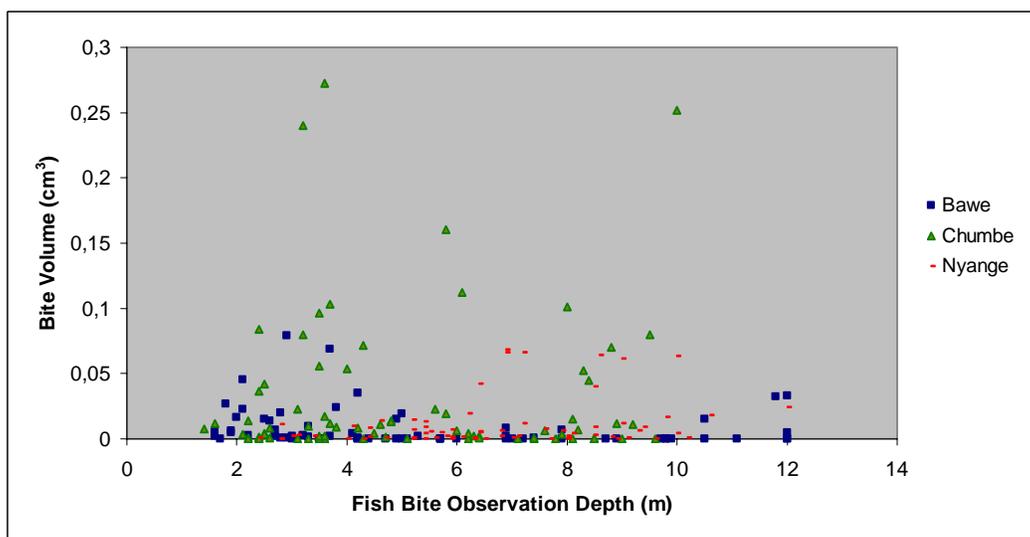


Figure 13. Bite volume (cm³) in relation to fish bite observation depth (m).

5. Discussion

5.1 Fish Function

5.1.1 Volume

The bite volume is a measure of the eroding capability of a fish. The data presented here indicate an exponential relationship between the size of the fish and volume it erodes (fig. 3). The overall volume eroded was higher on Chumbe than on Bawe and Nyange (table 2). A reasonable explanation to this could be the absence of fishing pressure on Chumbe. Fishing pressure could be the reason for less big individuals encountered at Bawe and Nyange compared to at Chumbe. For both Chumbe and Nyange the biggest bites encountered were performed by the largest individuals while on Bawe a different result was discerned. On Bawe, the biggest bites were performed by the medium sized individuals rather than as one might expect by the largest individuals. A possible explanation to this could be that the large individuals on Bawe still have the capability to perform big bites but that they were not encountered in this study. Another explanation could be that the largest fish are put under a more intense pressure and therefore are too stressed to produce bites of large volumes. There result show that increases in bite volume occur at certain sizes, around 17 cm at Bawe and approximately at 20-25 cm on Chumbe and Nyange. The data also display that the number of bites resulting in a scar, increases with life phase for all three sites and that all terminal phase males at Nyange took bites that left a scar (fig. 4), indicating that smaller individuals graze to a higher extent than larger scraping individuals.

Table 2. The table illustrates the total bite volumes (cm^3), scraping rates (cm^2/min) and bioerosion rate (cm^3/min) for the three sites.

	Bawe	Chumbe	Nyange
Bite Volume (cm^3)	0.56	2.30	0.77
Scraping Rate (cm^2/min)	12.58	81.65	28.45
Bioerosion Rate (cm^3/min)	2.34	17.23	4.32

5.1.2 Scraping Rate

The scraping function indicates the ability of a fish to clear an area of algae during a unit time. The results show that the size of fish affects the fish performance (fig. 6). The individuals on Chumbe have higher scraping rate compared to the other reefs (table 2). The total scraping rate decreases

as accessibility increases towards Zanzibar Town and the accessibility can be a reason to the lower numbers of large individuals observed at Bawe and Nyange. Disturbances, like fishing and tourism, can also be a possible explanation to the lower values in feeding rate among terminal phase males at Bawe and Nyange compared to Chumbe, indicating that these individuals might be put under a more extensive stress and therefore lower their feeding rate (table 3). On Chumbe and Nyange, the largest individuals performed the highest scraping rates, giving an exponential relationship. At Bawe, the scraping rate for medium sized individuals is close to that performed by large sized individuals. The fact that the large individuals on Bawe and Nyange have a low scraping rate compared to individuals at Chumbe, could in this small data set be explained by that individuals having high scraping rates were not observed in field. The scraping rate among the smaller individuals is close to zero at Bawe and Nyange and lower compared to Chumbe. These bites on Chumbe are represented by large surface areas, higher values in scraping efficiencies and feeding rates. A possible explanation to the small bites seen in the smaller sizes might be explained by that the fish is mostly capable of grazing and can therefore not scrape to a significantly extent. This pattern was identified by Bernardi et al. (2002) in the Caribbean parrotfish species *Sparisoma*. Furthermore, a grazing mode might be applied by larger individuals, to save energy or

resources when there is a lack of algae to feed on, or simply a result due to the differences in size of the mouth.

5.1.3 Bioerosion Rate

The bite volume eroded per time unit is a measure of the actual bioerosion on the reefs considering the time for feeding events. The results show an exponential relationship between increasing size and bioerosion rate (fig. 7). Individuals on Chumbe display the highest bioerosion rate of the three sites followed by Nyange and Bawe. The bioerosion rate at Bawe display very little increase with size and is similar across sizes. The reason behind the low rate for the large sized individuals on Bawe and Nyange can be caused by a low number of large individuals observed which might not be representative for the population. The bioerosion rate for each individual at Bawe and Nyange is lower than compared to individuals at Chumbe, suggesting that fishing and other disturbances like tourism can be factors preventing large individuals to have a high bioerosion rate. The sites also demonstrate a decrease in total bioerosion rate (table 2) with increased accessibility to Zanzibar Town indicating the effects of disturbances. In general for the three sites, an increase in bioerosion rate with size occurs at 20-25 cm.

5.1.4 Feeding Rate

Bellwood and Choat (1990) showed that on the Great Barrier Reef, *Scarus niger* had a mean feeding rate of 22.9 bites per minute for individuals at a minimum total length of 15 cm. The results from the present study (table 3) show that fish within this size class hold feeding rates on 5.2 bites per minute at Bawe, 22.1 at Chumbe and 10.7 at Nyange. Bruggemann et al. (1996) demonstrated that parrotfish feeding rate are decreasing with increasing fish size as a result of higher energy consumption due to higher growth rates. The present study also presents that individuals smaller than 15 cm have higher feeding rate than individuals larger than 15 cm at Bawe and Nyange (table 3). A possible explanation to this could be, as stated by Bruggemann et al. (1996), that smaller sized individuals have higher energy consumption but also a result due to differences in the size of the mouth which makes the time for reapplying the jaws to the substratum less for smaller sized Scarides. The results are reversed on Chumbe where individuals above 15 cm have a higher feeding rate. A reasonable explanation to this could be that larger sized individuals are not put under the same anthropogenic stress as on Bawe and Nyange and therefore can feed with very little disturbances.

Table 3. The table illustrates the mean feeding rate (bites/min) for individuals smaller and larger than 15 cm total length for the three sites. Total number observed individuals in ().

	Bawe	Chumbe	Nyange
< 14 cm	17.1 (11)	16.5 (8)	25.4 (12)
15 > cm	5.2 (19)	22.1 (23)	10.7 (16)

5.2 Feeding Behaviour

5.2.1 Life Phase

The overlap between initial and terminal and female and male life phases at Bawe span 8 cm and is 5 cm wider compared to the other sites (fig. 8). The span for terminal phase males is ranging 15 cm in total fish length and might indicate external stressors forcing females to undergo sex-reversal at smaller sizes. At Chumbe and Nyange, only terminal phase males are responsible for the largest bites found. At Bawe the largest bites are evenly distributed between initial phase females and terminal phase males. Since Bawe is the most exposed site, this could be a result caused by stressors from tourism, dive operators and fishing. Hawkins

and Roberts (2003) pointed out that frequent disturbances could force an earlier sex-change in the population to sustain reproductive output.

5.2.2 Substrate, Coral Growth Form and Algae

In a study from Boyer et al. (2004) parrotfish tended to favour nutrient-enriched and fast-growing algae instead of untreated algae indicating that they are selective feeders. At Bawe and Nyange the dominating algae fed upon was sparse turf. These algae mainly appeared on dead reef matrix and dead coral. On Chumbe *S. niger* mainly fed on sedimented turf. Due to higher sediment loads in the waters around Chumbe (*pers. obs.*), Chumbe appeared to have a higher abundance of sedimented turf compared to the other sites which could explain these results. Different types of dead substrate dominate the bites on all sites. The main growth forms fed on were massive and branching coral (fig. 9, 10 and 11). No general patterns were discerned in relation to size, regarding substrate, coral growth form or algae except at Nyange where no individuals above 15 cm were encountered feeding on branching coral. Juvenile fish had a greater proportion of bites that did not leave scars compared to initial and terminal phase fish (fig. 4). As argued by Bruggemann (1996), juvenile fish most likely obtain carbonate from feeding exclusively on epilithic algae, while larger individuals show an increased proportion of total ingested sediment from hard substrates.

5.2.3 Dive Start and Fish Bite Observation Depth

Variation in water temperature due to seasonality has been shown, by Hatcher (1981) to affect the feeding rate of grazing fish, where the mean feeding rate decreased with decreasing water temperature. Temporal patterns in feeding rate due to seawater temperature might have been detected if data from the colder season (South East Monsoon) were collected, but since there were no variations in climate at the time for the study, this has most likely had a limited impact on the results in the present study. Observations were only made during the day since *S. niger* is diurnal and bite volumes were higher in the morning and afternoon, but no general patterns could be distinguished with confidence due to differences in observation time (fig. 12). However, as stated by Bellwood (1995), parrotfish tend to be more active and have higher feeding rates in the morning and afternoon than at midday. The depth on the reef for the three sites seemed to have different effects on the bite volumes. At Bawe fish made bites of greater volume at lower depths on the reef, while at Nyange the opposite was observed (fig. 13). For Chumbe the depth did not affect the volume of the bites. A possible explanation to this is probably how the preferred substratums, coral growth forms and algae were distributed on the reef.

5.3 Critical Size

Both the scraping rate and the bioerosion rate starts to increase around 17 to 25 cm and can be referred to as a critical size of functional importance. Individuals within this size range have shown to be important for maintaining the function within the population.

The results show that on Chumbe a high abundance of individuals within the critical sizes may have the same scraping function as few large individuals (fig. 14 and 15). This is not seen at Bawe due to low fish abundance. However, at Bawe, fish around 25 cm holds the highest scraping rate and bioerosion rate. At Nyange the total scraping rate and bioerosion rate for the more abundant medium sized individuals equals that of the less abundant large individuals.

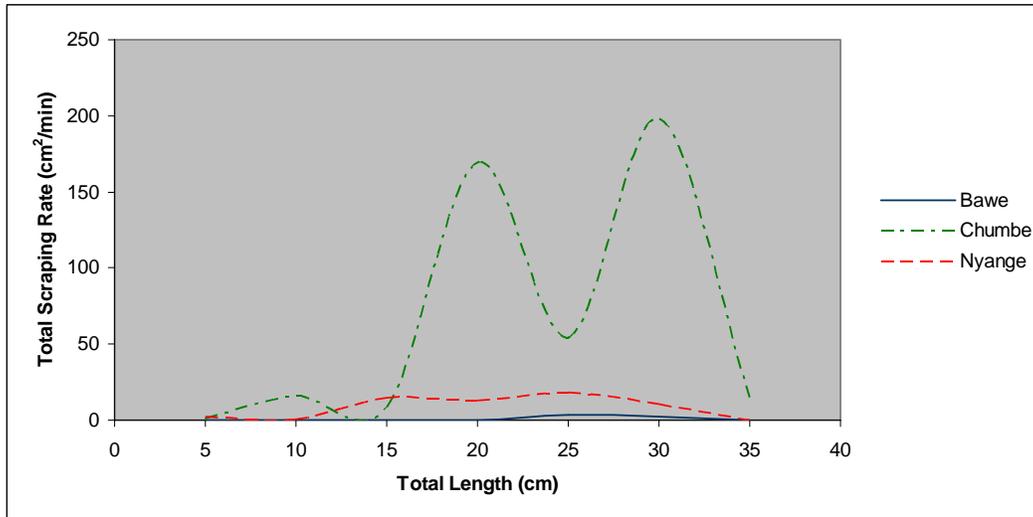


Figure 14. The total scraping rate (cm²/min) for all individuals found in the abundance study. The drops demonstrate sizes with low abundance. Abundance data borrowed from Lokrantz et al. unpublished.

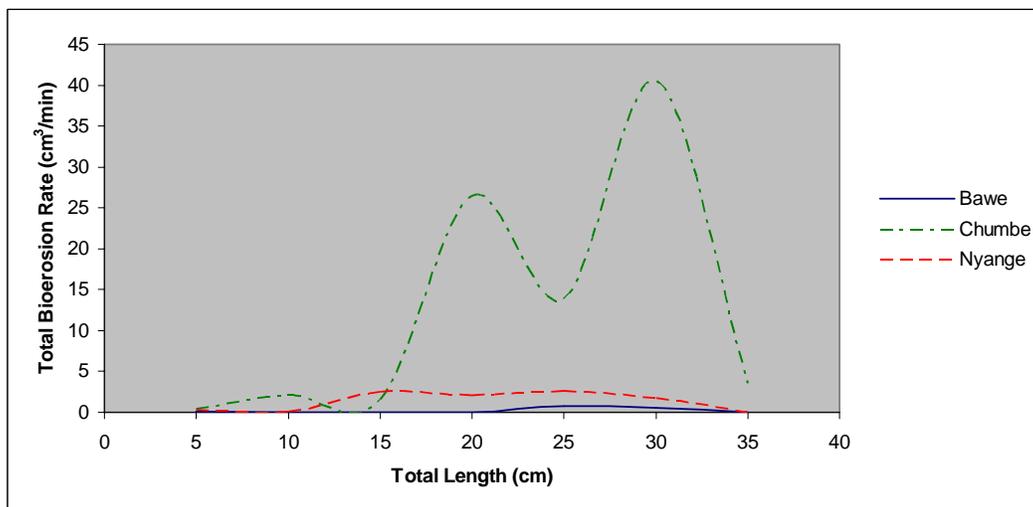


Figure 15. The total bioerosion rate (cm³/min) for all individuals observed in the abundance study. The drops demonstrate sizes with low abundance. Abundance data borrowed from Lokrantz et al. unpublished.

Within the critical size, changes of life phase and sex-reversal are discerned. At Chumbe and Nyange, the terminal phase males have the capability to perform a higher function (fig. 16 and 17). But at Bawe no general change in function was discovered, indicating that initial and terminal phase individuals have the same function. The juvenile function for all three sites was small.

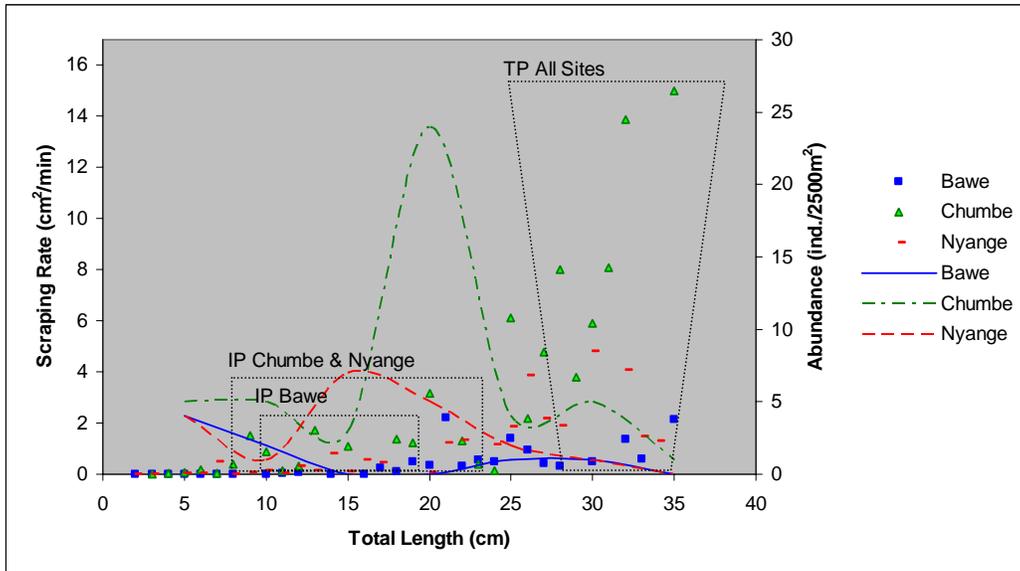


Figure 16. Scraping rate (cm^2/min) at the three sites in relation to abundance ($\text{ind.}/2500\text{m}^2$). Boxes indicate the distribution of life phases (initial phase (IP) and terminal phase (TP)). Values not in the boxes illustrate individuals in phase of life- and sex-change. Abundance data borrowed from Lokrantz et al. unpublished.

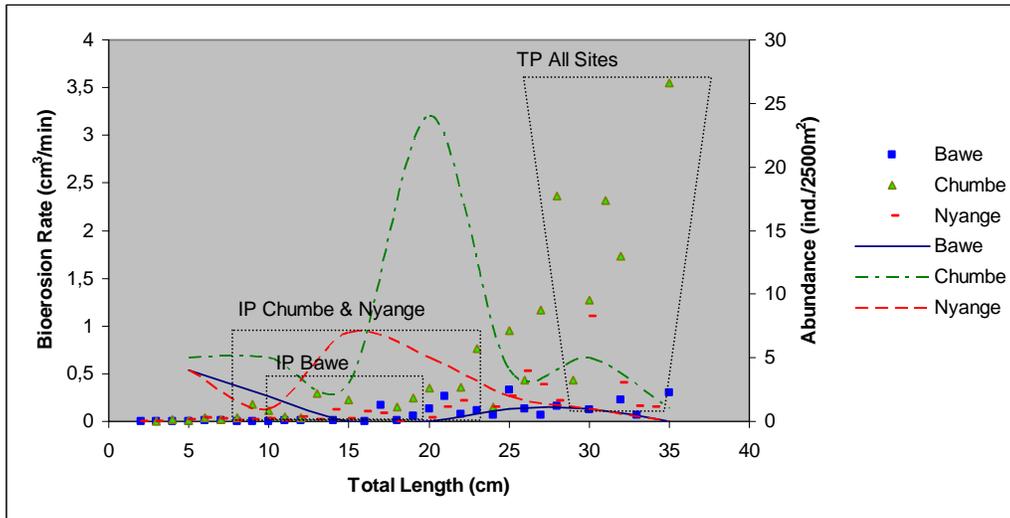


Figure 17. Bioerosion rate (cm^3/min) at the three sites in relation to abundance ($\text{ind.}/2500\text{m}^2$). Boxes indicate the distribution of life phases (initial phase (IP) and terminal phase (TP)). Values not in the boxes illustrate individuals in phase of life- and sex-change. Abundance data borrowed from Lokrantz et al. unpublished.

If the large individuals are being removed, the function will decrease, unless there is a high abundance of medium sized individuals that can compensate for the loss of scraping rate and bioerosion rate. Furthermore, the number of terminal phase males will decrease and reduce the reproductive output. Bawe can be viewed as an example, where a high fishing pressure has reduced the abundance of large individuals. Their scraping rate and bioerosion rate is less compared to other sites and terminal phase males are discovered at smaller sizes, indicating a possible shift in life phase and sex-change to maintain a reproductive output.

5.4 Management

Considering the variety of disturbances from Zanzibar Town, fishing is most likely the reason to the low abundance and the subsequently low scraping rates and bioerosion rates of *Scarus niger* observed at Bawe. Despite the population increase and the increased pressure on natural resources (McClanahan, 2002), regulating the fishery or protecting the reef might be crucial to prevent essential functions from being lost. Regulations of fish size and methods, or temporal or permanent protection of the reef could be part of the solution of maintaining ecological functions in the already heavily affected area. For example, small MPA's has shown higher abundance and biomass of smaller or less migrating species than adjacent fishing areas and are useful tools in management and conservation (Tupper & Rudd, 2002). Thus, they have a potential to act as a seasonal spawning ground and free-zone where fishing is not a disturbing factor. Furthermore the 'catch-per-unit-effort' (CPUE) has proven to be higher close to reserve borders (Tupper & Rudd, 2002) and considering that the other adjacent reefs are not situated far from Bawe a protection might be beneficial to the area. But making directives for management based on a study of one species on one scale could be misleading. Coral reef management must focus on more than one scale and strive towards cross-scale interaction to create an image of the complex dynamics of ecosystems (Nyström & Folke, 2001; Elmqvist et al. 2003).

Loss of critical ecological functions can have severe impacts on coral reefs (Nyström & Folke, 2001). If the herbivorous parrotfish decrease in abundance, changes in the system are likely to be seen (McClanahan et al., 1996). Fishing can control herbivory while herbivory regulate the primary production and algae in the system. Fishing therefore has secondary effects on the ecosystem. Herbivorous populations can be negatively and positively affected by fishing depending on level of intensity in the trophic web (McClanahan & Maina, 2002 c.f. McClanahan, 2002). Although sea urchins have been shown to act as a final 'outpost' for keeping algae populations in control (McClanahan et al. 1996) they may become devastating eroders on the reef if too abundant (McClanahan & Muthiga, 1988). Furthermore, the functions might not be maintained by other herbivores in the system and therefore be lost.

6. Conclusion

This study suggests that there is an exponential relationship between size and function characterized by a threshold. This occurred between 17-25 cm total fish length and has in this study been described as a critical size of functional importance. Chumbe displayed the highest function of the three sites, followed by Nyange and Bawe. The largest individuals were responsible for the highest scraping and bioerosion rates at Chumbe and Nyange. Furthermore, higher abundances of fish within the critical sizes at both sites resulted in a scraping and bioerosion rate close to that of the largest sized individuals. Bawe displayed low scraping and bioerosion rates possibly due to increased accessibility from Zanzibar Town. Within the critical sizes, the change of life phase between initial and terminal phase were detected. At Bawe the terminal phase males were smaller then observed at Chumbe and Nyange and did not display any change in function. The preferred algae the fish were observed feeding on were sparse turfs at Bawe and Nyange and sedimented turfs on Chumbe. These tended to grow on matrix and dead coral which together with massive and branching were encountered being the most common substratums and coral growth forms *Scarus niger* fed on. No food preferences related to size were detected on Bawe and Chumbe, but on Nyange no fish above 15 cm were seen feeding on branching corals.

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